Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2016:23

Drivers of the diversity and distribution of wild bees in a species poor region

Pådriverne bak diversitet og utbredelse av villbier i en artsfattig region

Markus Arne Kjær Sydenham

Drivers of the diversity and distribution of wild bees in a species poor region

Pådriverne bak diversitet og utbredelse av villbier i en artsfattig region

Philosophiae Doctor (PhD) Thesis

Markus Arne Kjær Sydenham

Department of Ecology and Natural Resource Management
Faculty of Environmental Science and Technology
Norwegian University of Life Sciences

Ås 2016

Thesis number 2016:23
ISSN 1894-6402
ISBN 978-82-575-1352-8

Ph.D. supervisors

Professor Stein Ragnar Moe – main supervisor,

Dr. Katrine Eldegard,

Professor Ørjan Totland,

Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
NO-1432 Ås, Norway

PhD evaluation committee

Professor Jens Mogens Olesen,

Department of Bioscience – Genetics, Ecology and Evolution,
Århus University,
DK-8000 Århus, Denmark

Professor John-Arvid Grytnes,

Department of Biology,
University of Bergen,
NO-5020 Bergen, Norway

Committee administrator:

Professor Tone Birkemoe,

Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
NO-1432 Ås, Norway

Acknowledgements

I would like to thank my supervisors for their guidance and mentoring during the past three years. My main supervisor, Prof. Stein R. Moe for giving me the freedom to juggle different research ideas but at the same time being there to show me how to contextualize and develop them into testable hypotheses. Thank you also for always having your door open and so generously revising, discussing and following the production of the manuscripts that have led to this thesis. Prof. Ørjan Totland, I am grateful to you for introducing me to the world of pollinators and that of the people who study them. Thank you also for all your ideas, comments and suggestions that greatly improved the manuscripts in this thesis. Dr. Katrine Eldegard, thank you for being so generous with your time and for guiding and supporting me while developing research ideas. Thank you also for introducing me to the world of statistical modelling and for always being available to provide improvements of manuscripts and ideas as well as a supportive pat on the shoulder. I am grateful to Statnett for funding the fieldwork and species identification that made this thesis possible.

Studying at the Dept. of Ecology and Natural Resource Management (INA) has been a fantastic experience, much thanks to the great working environment there. I would like to thank everyone in the tech-admin group (Annie, Gunnar, Grethe, Kari T., Mette, Ole Wiggo, Stig D. and Ågot) for your patience and for making things run so smoothly. I would especially like to thank Tone G. for making long days in the entomology lab a lot more enjoyable.

I would like to thank the co-authors of the manuscripts that led to this thesis. Collaborating with you has been a great source of motivation. Lise D. Häusler for your hard work in the field and your work in the lab. Diana N. Stanescu-Yadav for your work in the lab. Dr. Stein J. Hegland and Dr. ~~Anders~~ Nielsen for your contributions and thorough revisions of our manuscript and for the great times at SCAPE. Prof. Simon G. Potts, Prof. Michael Kuhlmann and Mr. Stuart P.M. Roberts for generously contributing traits data for the Norwegian bees and for all your constructive revisions and insightful comments on our manuscript. I would like to thank all editors and anonymous reviewers whose strenuous efforts greatly improved this thesis.

Mike and Sue Edwards, Stuart P.M. Roberts, David Baldock and everyone else at the Bees Wasps and Ants Recording Society (BWARS), thank you for providing a welcoming environment for everyone interested in learning about Aculeates. Thank you Mike and Sue for all your hospitality and generosity and for introducing me to bee taxonomy. On that note, I would also like to thank Prof. Emer. Eline and Sigmund Hågvar for talking me into getting started with bees in 2010. I would also like to thank Frode Ødegaard at the Norwegian Institute for Nature Research for taking your time to verify problematic bee specimens and Lars O. Hansen at the Natural History Museum in Oslo for granting me access to the bee collections.

To all my friends, present and former colleagues at INA, you have made long days seem too short. Prof. Kari K. and Prof. Douglas Sheil, working with you to get the Ecology Research Group up and running has been great fun. Prof. Vidar Selås, Dr. Mari H. Lie and Dr. Ronny Steen for the great trips/field courses in Jotunheimen. Prof. Michael Ohlson and Dr. Richard Bischof for taking me on as a teaching assistant, I am grateful for that experience. Mari, thank you for fun trips in the field and to Denmark and Scotland. My good friend and office mate Christian, thank you for your friendship and for reminding me that Kattegat is never far away. Rannveig, John (best-dressed Dane on the slopes), Massimo (for your company in the Oslo ~~café's~~ offices), Hanne, Anne, Carolyn, Walid (for keeping the A-line represented at INA), Sam, Ronny, Jens, Erik, Fredrick and Richard for making the spots in between a lot more fun.

Many people outside my studies have also contributed with their support and friendship. Adrian, thank you for your friendship, assistance in the field and our bee safari to DK. Embret for our skiing trips and nights out in Oslo. Silje, Sigrid, Trygve, Eivor, Harald, Hanna, Håkon, Bull, Helle, Markus, Mari, Brita, Luca, Eirik El Gaucho and Lise Brunbjørn your friendship has been a source of energy during the past three years. Tox, Nikolai, Humle, Troels and André thank you for still reserving a special place in DK for me even after 10 years.

Thank you Mum, Dad, Thomas, David, Rikke, Alma and Otto for always being supportive of my studies (especially Alma) and for all your visits to Norway. Thank you also to everyone in my Norwegian family for all your support and keeping a place for me here in Norway. Finally, I want to thank Celin. You have stood by me in field work; plucking bees out of soup bowls in the middle of the night, installing window traps in two metres of snow and put up with me ranting on about bees 24/7. Most importantly, you have provided a loving home for me to return to late in the evening, I am so grateful for having you by my side.

Markus, Oslo, 2016

Contents

Acknowledgements ... iii
Contents ... v
List of papers ... vii
Summary ... ix
Introduction ... 1
Figure 1. Illustration of differing threatened status for bees in Norway and Europe ... 3
Table 1. Comparison of the European and Norwegian bee fauna ... 4
Objectives ... 6
Figure 2. Illustration of environmental conditions in power line clearings ... 6
Main hypotheses posed in this thesis: ... 7
A: The bee phylogeny predicts community level niche overlap and biogeography (*Paper I*) ... 7
B: Hierarchically structured ecological filters drive bee diversity (*Paper II*) ... 7
C: The diversity of bees depend on non-trophic interactions with non-bee taxa (*Paper III*) ... 7
D: Effects of habitat management on bee diversity depend on ecological filters (*Paper IV*) ... 7
E: Both stochastic and deterministic processes drive community assembly (*Paper V*) ... 7
Materials and methods ... 9
Study system (Paper I) ... 9
Dataset and explanatory variables ... 9
Statistical analyses ... 10
Table 2. Overview of hypotheses and statistical tests applied in Paper I ... 10
Study system (Papers II-V) ... 11
Figure 3. The location of study sites included in Papers II-V ... 12
Functional traits included in Papers II-V ... 13
Table 3. List of the functional traits applied in papers II-V and their description ... 13
Methods specific to Paper II ... 14
Dataset and explanatory variables ... 14
Statistical analyses ... 14
Table 4. Overview of statistical tests applied in Paper II ... 15
Methods specific to Paper III ... 16
Dataset and explanatory variables ... 16
Statistical analyses ... 16
Table 5. Overview of hypotheses and statistical tests applied in Paper III ... 17
Methods specific to Paper IV ... 18

Dataset and explanatory variables 18
Statistical analyses 18
Table 6. Overview of hypotheses and statistical tests applied in Paper IV 19
Methods specific to Paper V 20
Dataset and explanatory variables 20
Statistical analyses 20
Table 7. Overview of hypotheses and statistical tests applied in Paper V 21
Results and discussion 22
Figure 4. Graphical overview of the findings in this thesis 22
Speciation and dispersal limitation (Papers I and V) 23
Figure 5. The short tonged Colletes daviesanus foraging on Leucanthemum vulgare 23
Ecological filtering (Papers I-V) 24
Figure 6. Andrena lapponica an Ericaceae pollen specialist here on Vaccinium myrtilus 26
Ecological drift (Paper V) 27
Figure 7. Illustration of intraspecific variation in functional traits 28
Methodological limitations of the present studies and prospects for future studies 28
Concluding remarks 29
Conferences and outreach contributions 31
References 32

Appendix: Papers I-V

List of papers

Paper I

Sydenham, M.A.K., Eldegard, K., Hegland, S.J., Nielsen, A., Totland, Ø. and Moe, S.R. Community level niche overlap and broad scale biogeographic patterns of bee communities are driven by phylogenetic history. *Invited for resubmission.*

Paper II

Sydenham, M.A.K., Moe, S. R., Totland, Ø. and Eldegard, K. (2015). Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography* **38**: 140-153.

Paper III

Sydenham, M.A.K., Häusler, L.D., Moe, S.R. and Eldegard, K. Inter-assemblage facilitation: The functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees. *Ecology & Evolution (In press).*

Paper IV

Sydenham, M.A.K., Moe, S.R., Stanescu, D.N., Totland, Ø. and Eldegard, K. The effects of habitat management on the species, phylogenetic and functional diversity of bees are modified by the environmental context. *Ecology and Evolution (Uncorrected proof).*

Paper V

Sydenham, M.A.K., Moe, S.R., Kuhlmann, M., Potts, S.G., Roberts, S.P.M., Totland, Ø. and Eldegard, K. Assessing the roles of stochastic and deterministic processes on the assembly of bee communities. *Submitted.*

Papers II-IV are reprinted with the kind permission of the publisher (John Wiley and Sons)

Summary

Bee diversity is declining globally. On a European scale, roughly 10% of the species are considered threatened, but the number may be even higher. The threatened status of bees depends on both the taxonomic and spatial scale. For instance, a relatively high proportion of species within the cold adapted *Bombus* are expected to decline due to global warning. Moreover, numbers may differ among regions and about 25% of the bee species in Norway are considered threatened. Halting or reversing this decline requires that we understand the main drivers of bee diversity within regions. Species-poor regions where the autecology of species are relatively well known may provide valuable model systems for studying the processes behind community assembly. Indeed, due to the low numbers of species and steep environmental gradients one may expect a relatively rapid species turnover over short geographic distances in Norway.

The aim of this thesis was to identify important drivers of bee diversity in Norway. Bee-flower networks from different regions of the world were used to test for the influence of global scaled processes on community assembly **(Paper I)**. We tested if the phylogenetic turnover among Bee-flower networks (i.e. bee communities) increased with geographic distances, thus indicating an influence of speciation and migration, and with dissimilarities in climatic conditions, thus indicating global ecological filtering. We also tested if the niche overlap, in terms of visitations to plant species, was determined by the bee phylogeny, thus indicating within community ecological filtering. We used bee communities sampled in power line clearings surrounded by boreal forests as model systems for studying the influence of dispersal limitation, ecological filtering and ecological drift on the distribution of species within the metacommunity (**Papers II-V**). We established an experiment within this system to test how, and under which conditions, different management practices could improve power line clearings for wild bees (**Paper IV**).

Global scaled processes acting through speciation, migration and ecological filtering explained differences in the phylogenetic diversity of bees among regions. These results imply that the diversity within biogeographic regions is dominated by specific phylogenetic lineages. This dominance may have implications for how the regional biota is able to respond to global environmental change. Within the metacomunity, local bee diversity decreased with elevation and increased along a gradient of floral diversity, from ericaceous shrub dominated to floristically diverse and forb dominated. Clearing power line strips in forb-dominated sites

revealed that bees show strong behavioral responses to changes in local habitat quality. Moreover, the foraging niche overlap between species is related to their phylogeny. Maintaining a high floral diversity is therefore required to sustain a phylogenetically diverse bee species assemblage. In addition to trophic interactions with plants, we also found that non-trophic interactions with cavity producing beetles play important roles in organizing bee communities. Through their production of suitable nesting sites, the diversity of these beetles likely facilitate the diversity of cavity nesting bees.

Management implications: The findings in this thesis illustrate the importance of considering the environmental context prior to implementing cost-intensive habitat management plans. Moreover, since communities are dispersal limited managers should consider local habitats as parts of an interconnected metacommunity by developing management plans that allow species to recolonize restored habitats. For predictive outcomes of habitat management one should consider the role of ecological drift. Random extinctions may lead to the monodominance of one species (i.e. ecological drift). We found that high elevation sites show a greater tendency for monodominance of the regionally most common species. The diversity in low elevation sites therefore seem less susceptible to ecological drift and is more predictable indicating that conservation measures may be more successful at these sites.

Introduction

The bees (Hymenoptera: Apiformes) form a highly diverse taxon with approximately 20,000 species existing today. Nearly all bees are phytophagous and collect pollen for their progeny (Michener 2007). Due to their foraging behavior, many bee species are important pollinators of wild (Ollerton et al. 2011) and domesticated plants (Gallai et al. 2009, Garibaldi et al. 2013) making declines in wild bee diversity (Potts et al. 2010, Ollerton et al. 2014) a matter of public concern. However, the vast majority of bee species, including the ones most negatively affected by agricultural expansion, are not efficient pollinators of crops (Kleijn et al. 2015). The conservation of bee diversity can therefore not be motivated solely by aims of preserving crop pollination in agricultural landscapes, but should also aim to preserve diverse bee species assemblages for their inherent value and the socio-cultural benefits of biodiversity (Senapathi et al. 2015).

In order of promoting diverse wild bee communities one must understand their drivers. The theory of community assembly has undertaken a rapid conceptual development during the past two decades spurred partly by a critique of community ecology for being too case specific to produce general scientific laws, or theorems (Lawton 1999). This critique has increased the focus on how functional traits (Weiher and Keddy 1995, McGill et al. 2006, Weiher et al. 2011) of species and their phylogenies (Webb et al. 2002, Cavender-Bares et al. 2009) may predict how species respond to environmental conditions. There has also been an increased focus on incorporating the dependency of local scale processes on those related to dispersal and speciation (Ricklefs 2008, Vellend 2010) and thus synthesizing across the fields of ecology (Jenkins and Ricklefs 2011). Understanding the drivers of local bee diversity is therefore not only required for a successful conservation of wild bee communities but may also inform community ecology more generally.

Evolutionary history and biogeography is essential to understanding the global distribution of species (Warren et al. 2014). The bees form a monophyletic group that evolved from a clade of predatory wasps (Spheciformes) *c.* 123 million years ago (Cardinal and Danforth 2013). Molecular phylogenies suggest that the oldest extant bee family is Melittidae (Danforth et al. 2013) and that it evolved in what is now Africa (Hedtke et al. 2013). Bees are typically thermophilic and the greatest diversity is found in xeric regions such as in the Mediterranean basin and it declines towards higher latitudes (Michener 2007). Long distance dispersals have allowed some bee taxa to expand their ranges across continents (Kayaalp et al.

2013) whereas others are still endemic to certain continents. For instance, the Stenotridae, a sister family to the Colletidae, evolved after Australia was separated from Gondwanaland and is endemic to Australia (Danforth et al. 2013). The timing of their origin has seemingly limited the emigration of the Stenotrids from Australia. In contrast, the *Bombus* genus which evolved on the Tibetan plateau *c.* 35 million years ago under a global cooling period (Hines 2008) has extended its range to the new world and all the way to southern Chile. Throughout their range, *Bombus* species are mainly confined to Temperate or Alpine areas (Michener 2007). The global distribution of *Bombus* thereby seems limited by an adaptation to cool climates.

Within regions the distribution and diversity of bees depends on environmental conditions and the availability of nesting and foraging resources. Changes in human land use patterns during the past century has had detrimental consequences on the regional bee fauna (Biesmeijer et al. 2006, Potts et al. 2010) and is related to the regional extinction of some species (Ollerton et al. 2014). A recent assessment of the status for the 1,965 European bee species suggests that *c.* 15% of the continental fauna is threatened or near threatened, but this number may be higher as the status for roughly half of the fauna could not be assessed due to the lack of species distributions data (Nieto et al. 2014). The greatest threats to wild bees are related to the loss of and reduction in quality of habitats, resulting from the expansion of agricultural and urban areas, with particularly negative effects on habitat specialists (Nieto et al. 2014). However, the main threats vary among taxonomic groups and as many as 36% of the world's *Bombus* species are expected to experience a contraction of over 80% of their home ranges due to climate change (Rasmont et al. 2015). Indeed, *Bombus* species have in general moved to higher latitudes and elevations during the past century (Kerr et al. 2015). In addition to taxon or trait-specific responses of bees to environmental change (Williams et al. 2010), there are considerable variations in the status of wild bees among regions within Europe. For instance, of the 203 species considered in the Norwegian red list *c.* 25% are considered near threatened or threatened and as many as 6% are expected to have gone regionally extinct (Henriksen and Hilmo 2015).

That such a high proportion of the bee species in northern latitudes are threatened does not necessarily reflect their global status, but rather that these areas lie on the northern distributional limit of species (Nieto et al. 2014). These species would be expected to be confined to the southern-most parts of northern countries (e.g. *Dasypoda hirtipes*, Fig. 1).

Moreover, being on the distributional range limit also means that the regional extinction rates of bees may be partly offset by recolonizations of regionally extinct species and the colonization of new species (Ollerton et al. 2014).

Figure 1. Illustration of differing threatened status for bees in Norway and Europe**.** The solitary bee *Dasypoda hirtipes* is considered vulnerable (VU) in Norway due to a reduction in its sandy habitats (Henriksen and Hilmo 2015) which are confined to the country's southern coasts. In contrast, these habitats are not as limiting a factor on a European (Nieto et al. 2014) or even Swedish (ArtDatabanken 2015) scale where the species is considered of least concern (LC). Photo: Sydenham, M.A.K.

That Norway lies on the distributional range limits of many species means that the influence of environmental gradients, such as elevation, on habitat quality should be greater than in Southern regions. Moreover, although Norway has a relatively low diversity of wild bees (*c.* 205 species), even compared to that of Sweden (*c.* 284 species (Michener 2007)), the proportion of species within families is similar to that of Europe (Table 1). One might therefore expect that taxon specific responses of bees to environmental gradients in Norway are generally scalable to the situation in more specious areas. Furthermore, the low diversity of bees means that regional identification keys (Schmid-Egger and Scheuchl 1997, Amiet et al. 1999, Amiet et al. 2001, 2004, Amiet 2007, Amiet et al. 2010) and detailed information on the life histories (Westrich 1990) are available for most species. The steep gradients in environmental conditions and species turnover combined with the availability of detailed knowledge on the autecology of the regional fauna make species poor regions, such as Norway, ideal 'field laboratories' for studying the processes driving the assembly of bee communities.

Four processes govern the assembly of communities: speciation; migration; ecological filtering; and ecological drift (Vellend 2010). In this context, competition can be viewed as an ecological filter that favors the strongest competitor (Lawton 1999). Speciation generates species diversity. Although the geographic location of speciation events clearly have a large influence on where species, and clades, occur (e.g. Stenotridae (Danforth et al. 2013)), speciation events occur on a timescale that is often not directly relevant to studies on the drivers of community assembly within regions. However, if life history traits are conserved within lineages and these are confined within geographic regions, biogeographic processes may still impose limitations on the ability of the regional fauna to respond to environmental change.

On a regional scale, the migration rates of species determine their relative spatiotemporal distribution among communities (MacArthur and Wilson 1967, Leibold et al. 2004). However, ecological filtering may hinder species from establishing populations within communities if their life history traits do not match those required by the environment (Keddy 1992). Bees are central place foragers and must find: nest sites; nest building materials; nectar; and pollen resources within their foraging range, but often at different habitats (Michener 2007). Because of their dependence on each of these ‘partial habitats’ (Matheson et al. 1996), habitat disturbances can introduce ecological filters if resources available in pristine areas are lacking in disturbed areas. For instance, the availability of nesting sites for below ground nesting bees may be reduced in areas where intensive tilling occurs and thereby lead to an increased proportion of above ground nesting bees in local communities (Williams et al. 2010). Ecological filtering may also occur over elevational gradients as these select for species adapted to cooler climates (Hoiss et al. 2012). Moreover, within communities the diversity and type, of floral resources acts as an ecological filter on bees, due to different floral preferences

Table 1. Comparison of the European and Norwegian bee fauna. The number and proportion (prop.) of species found within the six bee families present in Europe and Norway (source: (Nieto et al. 2014, Henriksen and Hilmo 2015)). A χ^2 test (df = 5, $\chi^2 = 0.01$, p = 1) on the proportion of species found within families shows that the representation of species from different families does not differ substantially between the Norwegian and European fauna.

	European fauna		Norwegian fauna		χ^2-test
Family	Species	Prop. of fauna	Species	Prop. of fauna	Exp. Prop. of fauna
Andrenidae	465	0.24	42	0.20	0.22
Apidae	561	0.29	65	0.32	0.31
Colletidae	146	0.07	19	0.09	0.08
Halictidae	314	0.16	36	0.18	0.17
Megachilidae	442	0.22	39	0.19	0.21
Melittidae	37	0.02	4	0.02	0.02

among species (Potts et al. 2003). Later successional vegetation stages for instance, tend to select for large bodied, long tonged bees (Moretti et al. 2009).

Whereas the process of ecological filtering is deterministic, in that it is related to differences in niches among species, the influence of ecological drift is neutral (Vellend 2010). Ecological drift is the change in the relative frequency of species due to random extinction events (Hubbell 2001). If there is no limitation to the migration among communities then the relative frequency of a species within local communities should mirror that of its regional abundance. In contrast, if the rate of migration is exceeded by that of random extinctions then species will eventually drift to extinction and one species will obtain monodominance (Rosindell et al. 2011). Thus for interconnected communities the probability of a species occurring locally should be proportionate to, and predictable from its regional abundance. In contrast, in isolated communities the probability of relatively uncommon species occurring should be disproportionately low, compared to that of common species. The influence of ecological drift on bee communities has not previously been studied. The reason for this may be the need for studies that can inform habitat management to promote bee diversity (Matheson et al. 1996). However, in order obtain predictable outcomes of habitat management one needs to account for the influence of stochastic processes to minimize the influence of factors we are not able to control.

Objectives

The objective of this thesis was to study the processes that drive the diversity of bees in Norway. We used power line clearings that transect forests as a model system. Power line clearings are standardized in terms of: area as the width of the cleared areas are *c*. 40m per mast (i.e. *c*. 80 metres for double masts); have clearly defined edges; and a flora not found in the neighbouring forests (Eldegard et al. 2015). Moreover, power line clearings are found throughout Norway and the total area cleared in forests alone account for roughly 200 km^2 ensuring long gradients in elevation, site productivity and landscape context (Fig. 2). The standardized size of these areas together with the gradients in environmental conditions make them ideal for studying community assembly. Secondly, power line clearings have previously been shown to host diverse bee communities (Russell et al. 2005). However, unlike other introduced landscape elements, such as road sides (Hopwood 2008, Noordijk et al. 2009), field margins (Scheper et al. 2013) and hedgerows (Morandin and Kremen 2013), no habitat management practice that might improve these areas for wild bees has yet been suggested. Studying community assembly in power line clearings thereby also has the potential to provide bearings for management practices in these introduced landscape elements.

Figure 2. Illustration of environmental conditions in power line clearings. Note the variation in site productivity, forb diversity, landscape complexity and elevation. The lower portion is more productive, has a higher forb diversity and landscape complexity and a lower elevation than the upper part of the picture. Photo: Sydenham, M.A.K.

Main hypotheses posed in this thesis:

A: The bee phylogeny predicts community level niche overlap and biogeography (*Paper **I***)

Both local ecological filtering as well as broad-scaled biogeographic processes determine local bee diversity. We tested if community phylogenetics provides a means to studying patterns of bee diversity, resulting from both within community ecological filtering as well as global distributional patterns stemming from speciation and long distance dispersal events.

B: Hierarchically structured ecological filters drive bee diversity (*Paper **II***)

The influence of ecological filters should be predictable from their place in the hierarchical order of filters (Region > Landscape > Local). Specifically, higher order ecological filters should be more important than lower level filters (Keddy 1992, Lawton 1999).

C: The diversity of bees depend on non-trophic interactions with non-bee taxa (*Paper **III***)

In addition to trophic interactions with plants, some species of bees may depend on cavity producing non-bee taxa for the provisioning of nesting sites. We tested if the diversity of nest site producing, wood boring beetles was related to the diversity of wood nesting bees. This would imply that a lack of wood boring beetles could act as an ecological filter.

D: Effects of habitat management on bee diversity depend on ecological filters (*Paper **IV***)

The effect of habitat management for bees in agricultural landscapes depends on the environmental context, such as availability of source habitats (Scheper et al. 2013). We established an experiment to test how differently managed parts of the power line clearing differed in their attraction of bees from the local community in addition, if the degree of attraction depended on elevation and the species richness of forbs.

E: Both stochastic and deterministic processes drive community assembly (*Paper **V***)

The aim of this study was to propose a novel framework allowing for a joint analysis of the influence of stochastic and deterministic processes on community assembly. We tested if bee communities in power line corridors are dispersal limited and if they are susceptible to ecological drift in addition to being determined by ecological filtering.

Materials and methods

Study system (Paper **I**)

In **Paper I**, we tested if the floral visitation patterns of bees was related to the bee phylogeny, as would be expected if flower type acts as an ecological filter. We also tested if the distribution of bees over large geographic distances and among different climatic regions was related to the bee phylogeny.

We selected three sampling plots near Skedsmokorset in SE Norway. All sampling plots were within 1,000 metres of each other and thereby within the maximum foraging range of most bee species (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). We walked random transect walks within each sampling plot and collected all bees foraging on flowers. On each day of sampling, one hour was spent, per sampling plot, collecting bees and noting the flower on which they were sampled, discounting handling time. Sampling was only conducted on sunny days with little or no wind and always between 11:30 and 18:00. A total of 39 days of sampling was conducted within each sampling plot during the flowering season of 2013 (May-September). Observations of the flower visitations of bees were pooled across the three sampling plots to create one bee-flower network. In addition to the bee-flower network collected for this study, we also extracted the bee-flower networks included in previously published insect-flower networks (Rezende et al. 2007, Hegland et al. 2010, Nielsen and Totland 2014).

Dataset and explanatory variables

We removed species that had not been identified to the species level and updated the species names so that recently synonymized pairs of species were given their correct species name. This resulted in a total of 26 bee flower networks and 592 species. We clustered species according to published phylogenies to create a proxy of a phylogenetic tree that encompassed all 592 species. Only the 18 bee-flower networks with ≥ 10 species were included in subsequent analyses. We used non-metric multidimensional scaling (NMDS) to separate the bees in each bee-flower network according to their floral visitation patterns. For each bee-flower network, all species were assigned the scores corresponding to their loadings on the different axes in the multidimensional floral visitation space. We calculated the geographic distances and the dissimilarity in climatic conditions (following Kottek et al. (2006)) between the locations where the 18 bee flower networks had been sampled.

Statistical analyses

We tested if the position of bees in the floral visitation space (NMDS) was related to the phylogeny of bees. This was done to test if niche-overlap is phylogenetically conserved so that the distribution of species among resource types (flowers) within the community can be explained by the evolutionary history of species. We also tested if the fraction of the phylogeny shared between bee-flower networks was related to the geographic distance and dissimilarity in climatic conditions between them. See Table 2 for an overview of statistical tests applied in **Paper I**.

Table 2. Overview of hypotheses and statistical tests applied in Paper **I**.

Response variable	Model	Note
Hypothesis 1: The niche overlap between bee species is determined by their phylogeny		
Position of species in the multivariate floral visitation space.	Blombergs *K* statistic (Blomberg et al. 2003)	The tests were run separately for each NMDS axis and for each bee-flower network. Only networks with at least 10 species were included in the analyses.
Hypothesis 2: geographic distances and climatic conditions determine the phylogenetic distinctiveness of community members at a global scale.		
Phylogenetic beta diversity	Mantel tests	The phylogenetic turnover among sites was correlated against geographic distances and dissimilarities in climatic conditions. *A. melifera* was excluded as its global distribution reflects beekeeping and not natural dispersals.

Study system (Papers **II-V**)

The last four papers in this thesis are based on bee species assemblages sampled in 46 power line clearings (sites) in SE Norway (Fig. 3). Bees were sampled using windows traps installed following snowmelt, emptied once per month and removed in September at the end of the flowering season, totaling four sampling periods. Data from the power line clearings were used to test the multi-level filter hypothesis (**Paper II**), if wood boring beetle diversity facilitates bee diversity (**Paper III**), if management can increase preferred habitats for bees (**Paper IV**) and to characterize the influence of stochastic processes on bee diversity (**Paper V)**. Two different sampling protocols were used across the 46 sites.

In ‘dataset 1’ (n = 27) bees were sampled using four window traps installed along the centre of the power line clearings (sites are marked with blue, orange and green in Fig. 3). We randomly removed one trap from the first and fourth sampling period in all sites since the material in two sites had been lost during these sampling periods. This ensured an equal sampling intensity across all sites *i.e.* 3, 4, 4 and 3 traps in the first, second, third and fourth sampling period, respectively.

The sites sampled in 2009 and 2010 (n = 17) were used in **Paper II**. We sampled an additional ten sites in 2013 and identified all beetles sampled across all sites to test the hypotheses in **Paper III** (n = 27). In ‘dataset 2’ (n = 19), three window traps were installed in each of three experimental treatment plots (sites are marked in black in Fig. 3); Uncut; the treatment plot was left uncleared, Cut; trees in the treatment plots were cleared and left on the ground and Cut+Remove; trees in the treatment plots were cleared and removed from the plot. The treatment plots, measured 30 m × the width of the power line clearing and were separated by at least 20 metres.

The 19 sites in ‘dataset 2’ were used for the study in **Paper IV** and combined with the 27 sites in ‘dataset 1’ for the study in **Paper V**. The elevation (m. a.s.l.) was recorded at all sites and plant surveys were conducted by visually estimating the percentage cover of plant species in 1m^2 subplots placed within the power line clearings. However, the arrangement of subplots differed between ‘dataset 1’ and ‘dataset 2’ (Fig. 3).

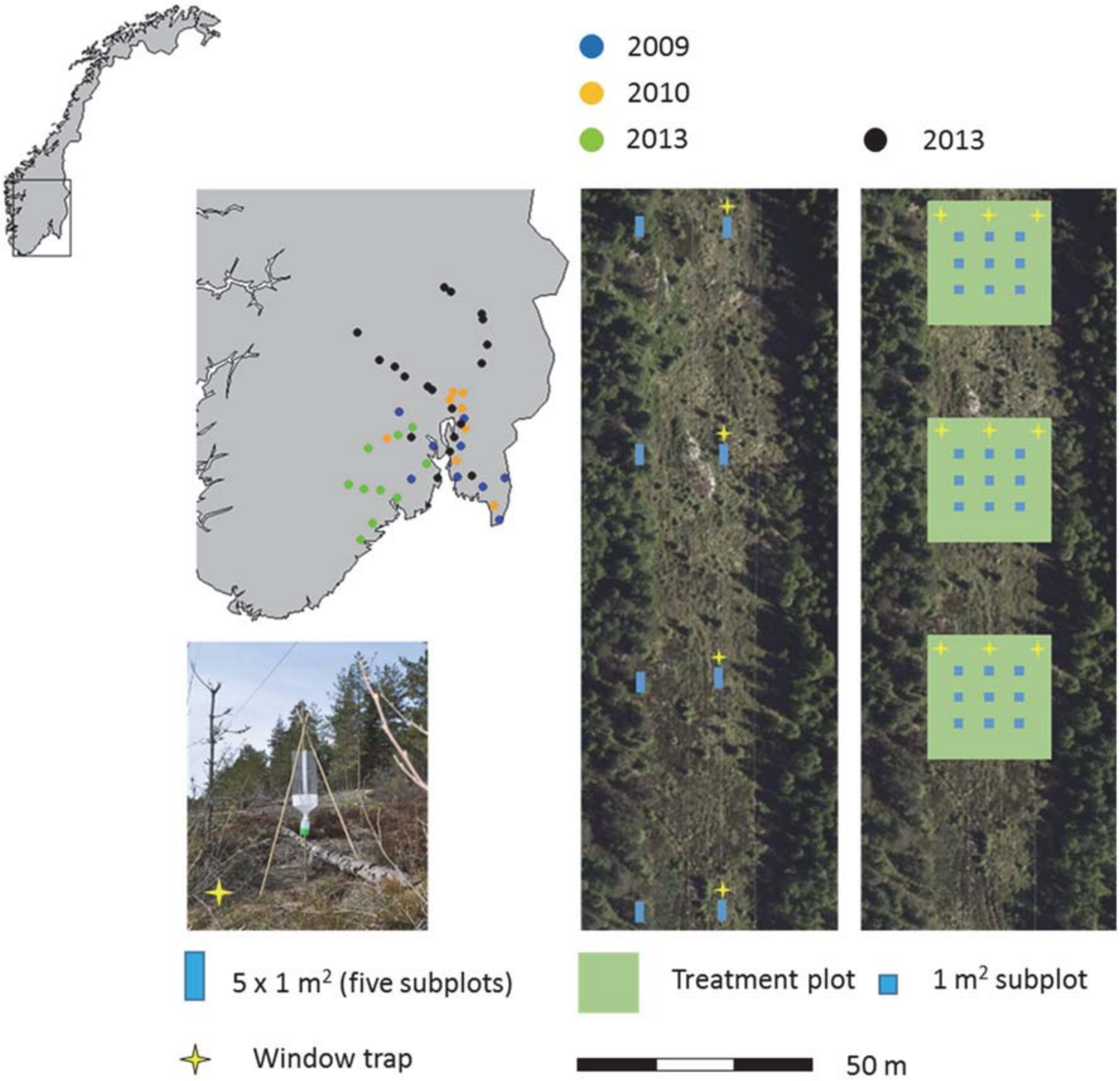


Figure 3. The location of study sites included in Papers **II-V**. The sampling year and study design applied are shown for each site. Sites marked with blue and orange were included in **Paper II** (n = 17). Sites marked in blue, orange and green were included in **Paper III** (n = 27). Sites marked in black were included in **Paper IV** (n = 19) and all sites were included in **Paper V** (n = 46). Plant surveys were conducted within 1 m^2 subplots in all sites, but the arrangement of subplots differed. In sites marked with black circles, each treatment plot was randomly allocated one of three experimental treatments; Uncut, Cut and Cut+Removal of debris. See text for details.

Functional traits included in Papers **II-V**

We included analyses on species-specific functional traits within bee species assemblages. This allowed us to identity potentially mechanistic relationships between specific traits and ecological filters (Weiher and Keddy 1995, McGill et al. 2006). The traits included (Table 3) were chosen as they have previously been shown to determine the responses of bees to landscape disturbance (Williams et al. 2010, Ricotta and Moretti 2011) and ecological filtering (Hoiss et al. 2012). Body size measurements (ITD) were taken from female bees sampled during this study. Other life history traits such as nesting behavior, sociality and lecty status were obtained through the literature (Westrich 1990). M.K., S.G.P. and S.P.M.R. provided traits data used for **Paper V**.

Table 3. List of the functional traits applied in papers **II-V** and their description. See the appendices of each paper for the assignment of traits to individual species.

Functional trait	Description	Paper
Intertegulae distance (ITD)	The width of the thorax in mm. The ITD is correlated with the maximum foraging distance (Greenleaf et al. 2007) and the minimum size of nesting holes a species can utilize.	II-V
Foraging range	Estimated from the ITD following (Greenleaf et al. 2007)	V
Nesting behaviour	Categorical for above vs. below ground nester.	II-V
Sociality	Categorical for social vs. solitary	II
Phenology	Numeric for the emergence month of a species	II, IV
Activity period	Numeric for the number of months a species is active	II
Lecty status	Categorical for if a species is a pollen specialist (Oligolectic) or generalist (Polylectic).	II, IV-V
Host plant taxa	Categorical variable used to differentiate among oligolectics based on the plants they collect pollen. Polylectics were assigned the value FALSE. In **papers I and IV** Ericaceae specialists were treated separately.	II, IV, V
Clepto parasitic	Categorical for cleptoparasitic vs. non-cleptoparasitic	IV
Host genus	Categorical, used to differentiate among cleptoparasites based on the genera of their hosts. Non-cleptoparasites were assigned the value FALSE	IV

Methods specific to Paper **II**

Dataset and explanatory variables

We tested the influence on bee diversity of ecological filters operating at one of three hierarchical levels: regional; landscape; and local. We used elevation as a regional ecological filter and the landscape diversity surrounding each site as a landscape-level filter. As local ecological filters, we used the species composition and the total cover of flowering plants. The plant species composition was related to a gradient in forb diversity, from species poor and dominated by shrubs too species rich and dominated by forbs. Total plant cover was related to the cover of ericaceous shrubs. Cleptoparasites were excluded from this study as they only indirectly rely on the resources sought by their hosts.

Statistical analyses

We tested the influence of ecological filters on the species richness and abundance of bees and on the phylogenetic and functional diversity in bee species assemblages. This was done since closely related species are expected to be more functionally similar, making the phylogeny a proxy for ecological similarity (Webb et al. 2002, Weiher et al. 2011). We followed Hoiss et al. (2012) and constructed a polytomous proxy for a phylogenetic tree by clustering species according to their subgenera (Michener 2007). The phylogeny was built using the R library APE (Paradis et al. 2004) with the p-parameter (Grafen 1989) set to one. We calculated the net relatedness index (NRI) and the nearest taxon index (NTI) for all sites. In addition to these tests, we also tested if the species, phylogenetic and functional dissimilarity among sites varied according to inter-site distances or if northern sites were more dissimilar than southern sites. See Table 4 for an overview of statistical tests applied in **Paper II**.

Table 4. Overview of statistical tests applied in Paper **II**. All models were fitted using forward selection of variables corresponding to the expected hierarchy of the ecological filters. We first entered Elevation, then Landscape diversity followed by plant species composition and Plant cover.

Response variable	Model	Note
Species diversity		
Species richness	Poisson GLM	*Bombus* included
Bee abundance	Negative binomial GLM	*Bombus* included
Phylogenetic diversity		
NRI$_{\text{species weighted}}$, NRI$_{\text{abundance weighted}}$	Linear regression	The NRI and NTI were standardized according to a null distribution allowing comparisons of values among sites with different species richness
NTI$_{\text{species weighted}}$, NTI$_{\text{abundance weighted}}$	Linear regression	
Functional composition		
CWM ITD; CWM activity period; the number of social; spring-active; summer-active; aboveground-nesting; belowground-nesting; oligolectic; and polylectic species.	Multivariate variation partitioning using redunancy Analysis (RDA). Responses scaled to zero-one.	The analyses were run both as species and abundance weighted and including/excluding *Bombus* species.
Dominant trait values		
Average ITD	Linear regression	Models were run as both abundance and species weighted, including and excluding species from the *Bombus* genus.
Average activity period	Linear regression	
Proportion of aboveground-nesters	Linear regression	
Proportion of oligolectics	Linear regression	
Proportion of spring emergers	Linear regression	
Proportion of social bees	Linear regression	

Methods specific to Paper **III**

Dataset and explanatory variables

We tested if the diversity of wood boring beetles was related to the diversity of cavity nesting bees within the 27 sites (Fig. 3). All beetles were identified and categorized as either wood boring or non-wood boring. We assigned all wood boring beetles a trait value corresponding to the diameter of the exit holes they excavate when leaving their nest chamber (Ehnström and Axelsson 2002). We considered beetles that produced cavities above ground with diameters ≥ 3 mm able to produce potential nesting sites for cavity nesting bees. For each site, we calculated a tree regrowth index. The regrowth index was included as an ecological filter on belowground nesting bees as we expected densely vegetated sites to contain fewer nest sites for these species.

Statistical analyses

We calculated three site-specific functional diversity indices based on the cavity diameter produced by large wood boring beetles and the body size of cavity nesting bees. The indices were: the functionally singular species richness (FSSR); the functional dispersion (FDis); and the community weighted mean (CWM). The indices were calculated for both beetle cavities and bee body sizes using the FD library in R (Laliberté and Legendre 2010). These indices allowed us to test if the functional diversity of beetles was related to the diversity of cavity nesting bees. See Table 5 for an overview of hypotheses and statistical tests applied in **Paper III**.

Table 5. Overview of hypotheses and statistical tests applied in Paper **III**. Abreviations are used for: species richness (SR); abundance (Ab); functionally singular species richness (FSSR); community weighted mean (CWM); functional dispersion (FDis); large wood boring beetle (LWBB); small wood boring beetle (SWBB); and non-wood boring beetle (NWBB). Sampling years were: 2009; 2010; and 2013.

Response variable	Explanatory variables	Model	Note
Hypothesis 1: The species diversity of cavity nesting bees increases with the diversity of large wood boring beetles			
Cavity nesting bee SR	LWBB SR; LWBB Ab; SWBB SR; SWBB Ab; NWBB SR; NWBB Ab; Elevation; Sampling year; and Corridor width.	Poisson GLM	
Cavity nesting bee Ab		Negative binomial GLM	
Hypothesis 2: Cavity nesting bees show guild specific relationships to the diversity of large wood boring beetles			
Proportion cavity nesting bee SR	LWBB SR; LWBB Ab; Sampling year; Shading; and Site productivity.	Binomial GLM	Calculated both including and excluding Ericaceae specialists.
Proportion cavity nesting bee Ab		Binomial GLM	
Hypothesis 3: The size diversity of cavity nesting bees increases with the functional diversity of large wood boring beetles			
$\text{FSSR}_{\text{bees}}$	LWBB SR; LWBB Ab; NWBB SR; NWBB Ab; $\text{CWM}_{\text{LWBB}}+\text{CWM}_{\text{LWBB}}^2$; $\text{FDis}_{\text{LWBB}}$; Elevation; and Sampling year.	Poisson GLM	Two sites were omitted as they had < 1 bee species present
CWM_{bees}		Quasipoisson GLM	
$\text{FDis}_{\text{bees}}$		Quasipoisson GLM	

Methods specific to Paper **IV**

Dataset and explanatory variables

Three treatment plots were placed in the 19 power line clearings sampled in 2013 (Fig. 3). Each treatment plot was randomly allocated one of three treatment types. In the Cut treatment, all woody vegetation was cleared and left on the ground. In the Cut+Remove treatment, all woody vegetation was cut and subsequently removed from the plot. The Uncut treatment was left untouched. We used the species richness of forbs within treatment plots as an explanatory variable. Elevation was also included as an explanatory variable as sites were distributed along an elevational gradient. We tested if the attraction of bees differed among treatment types and if this effect was modulated by the environmental context (i.e. forb species richness and elevation).

Statistical analyses

We tested the effect of treatment type and its interaction with the environmental context on both species, phylogenetic and functional bee diversity. This allowed us to test if the outcome of the treatments showed any bias towards specific phylogenetic or functional groups of bees. We clustered bees according to a recently published phylogeny of bees (Schmidt et al. 2015) which included all but two of the species in our survey. We calculated the: phylogenetic species richness (PSR); phylogenetic species variability (PSV); phylogenetic species evenness (PSE); and phylogenetic species clustering (PSC). This allowed us to test if specific treatment types mainly attracted a subgroup of closely related bee taxa resulting in a change in PSV and PSE or if clearing treatment plots attracted species from different taxa, resulting in an increased PSC. We also tested the outcomes of treatment types on the functional diversity of bees. This allowed us to assess if bees were attracted to certain treatment types based on their life history traits. See Table 6 for an overview of hypotheses and statistical tests applied in **Paper IV**

Table 6. Overview of hypotheses and statistical tests applied in Paper **IV**. Explanatory variables were: treatment × forb species richness; treatment × elevation; forb species richness × elevation; and their main effect terms. The sampling intensity was included as an offset variable to account for differences among treatment plots in the number of traps successfully sampled. Site identity was included as a random effect to account for site-specific differences in community size and its effects on the response variable. We performed a backward elimination of variables using likelihood ratio tests. Abbreviations used are: functionally singular species richness (FSSR); functional dispersion (FDis); community weighted mean (CWM); intertegulae distances (ITD); and negative binomial (Neg.Bin.). All models were fitted using generalized linear mixed effect models (GLMMs).

Response variable	Model	Note
Hypothesis 1: Management of power line clearings alters the species richness and abundance of bees		
Species richness	Poisson GLMM	Analyses were also run with cleptoparasites excluded from the data.
Bee abundance	Poisson GLMM	
Hypothesis 2: Management of power line clearings alters the phylogenetic diversity of bees		
Phylogenetic species richness (PSR)	Gamma GLMM	Analyses were run without cleptoparasites as the habitat affiliation of these species is tied to their host and not their phylogeny.
Phylogenetic species variability (PSR), evenness (PSE) and clustering (PSC)	Gaussian GLMM	
Hypothesis 3: Management of power line clearings alters the functional diversity of bees		
FSSR	Neg.Bin. GLMM	Cleptoparasites were excluded from analyses on the proportion of below ground nesters and oligolectics as these only indirectly depend on the resources sought by their hosts.
FDis, CWM ITD and CWM emergence	Gaussian GLMM	
Proportion of below ground nesters and oligolectics	Binomial GLMM	

Methods specific to Paper **V**

Dataset and explanatory variables

We included all 46 datasets on solitary bees sampled in power line clearings (Fig. 3). We derived a univariate variable allowing us to test the influence of dispersal limitation in a univariate framework. The variable ‘distance to source habitat’ was calculated by first calculating the Euclidean distance between all sites. For each site × species combination, we then calculated the distance to the nearest site in which that species had been found. We also calculated the number of each species sampled across all sites, i.e. the metacommunity abundance. By subtracting the abundance of a species within a given site from the metacommunity abundance, we calculated the number of individuals of each species found outside the focal community, i.e. the regional abundance. The distance to source habitat and regional abundance were included to test the influence of stochastic processes on community assembly. We also included elevation and forb species richness as these variables had previously been shown to be important determinants of bee diversity within our system (e.g. **Paper II** and **Paper IV**) to illustrate how the influence of ecological filtering (e.g. deterministic processes) could be included in our suggested framework.

Statistical analyses

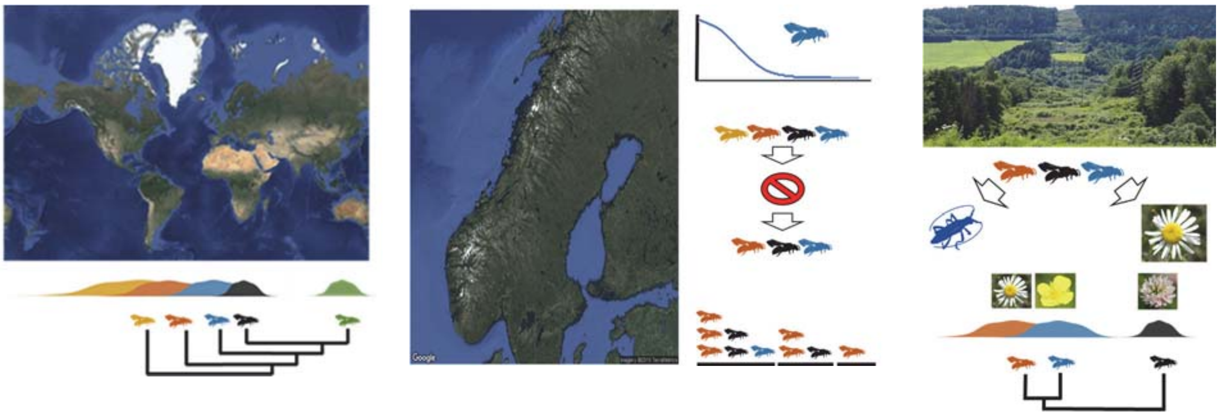
We used Binomial GLMMs to test the influence of stochastic and deterministic processes on the assembly of bee communities. We included random effect terms to account for pseudoreplication of sites and species and to account for differences in bee and plant survey protocols used in the two different datasets (i.e. the 19 experimental, and the 27 non-experimental sites). See Table 7 for an overview of hypotheses and statistical tests applied in **Paper V**.

Table 7. Overview of hypotheses and statistical tests applied in Paper **V**. Explanatory variables were: ericaceae affiliation × forb species richness; distance to source habitat × foraging range; distance to source habitat × nesting behavior; elevation × regional abundance; and their main effect terms. Site identity and species identity were included as random effects to account for multiple testing on the same sites and species. Study design was included as a random effect term to account for the differences between 'Dataset 1' and 'Dataset 2' in the number of traps per site. We also included forb species richness × ericaceae affiliation as a random slope to account for the differences in plant survey protocols between study designs (Fig. 3). The model was fitted with a Binomial GLMM and a cloglog link to account for the high proportion of zeros in the response variable.

Response variable	Model	Note
Hypothesis 1: Stochastic and deterministic processes drive the assembly of bee communities		
Presence of species	Binomial GLMM	Cleptoparasites were excluded from the data. We first conducted a backward elimination of random effect terms using the Bayesian Information Criterion (BIC). We then used likelihood ratio tests (LRTs) to conduct a backward elimination of fixed effect terms by sequentially dropping the least significant term, until all variables were significant ($p < 0.05$). Species occurring in < 2 sites were excluded from the analyses.
Hypothesis 2: The rarest species in the metacommunity mainly occur at low elevations.		
Presence of species	Binomial GLMM	We ran a separate analysis with the presence of single site inhabitants as a response variable and elevation as the explanatory variable. This was done since these species were excluded from the main analysis but accounted for as much as 31% of all species sampled (14/44).

Results and discussion

The following discussion of the results from this thesis is structured according to Vellend's (2010) conceptual syntheses of the four processes behind community assembly. Bee communities are assembled through the dispersal histories of species and speciation events, which determine the global distribution of phylogenetic lineages. Within a region, migration limitation, ecological filtering and ecological drift determine the species composition of communities. At the community scale, the distribution of species is determined through non-trophic interactions and behavioral responses of individuals to the quality of resource patches and phylogenetically conserved floral preferences (Fig. 4).



The global distribution of species and lineages is determined by their phylogeny (**Paper I**). This relationship indicates that speciation, migration and climatic conditions (an ecological filter) drive bee diversity on a global scale.

The regional distribution of species is driven by dispersal limitation among habitats (**Paper V**). Hierarchically structured ecological filters determine which species establish within habitats (**Paper II**). The relative probability of a species occurring locally is related to its regional abundance (**Paper V**) suggesting an influence of ecological drift.

The local diversity of bees is driven by non-trophic interactions with cavity producing beetles (**Paper III**). Species aggregate at high quality habitats (**Paper IV**) and forage niche overlap is phylogenetically conserved (**Paper I)**

Figure 4. Graphical overview of the findings in this thesis. Maps produced from Google satellite imagery ©NASA 2016.

Speciation and dispersal limitation (Papers **I and V**)

Communities are not enclosed entities (Ricklefs 2008) but are embedded in a regional network of communities (i.e. the metacommunity (Leibold et al. 2004)), connected through the dispersal of individuals. That the phylogenetic turnover among bee communities increases with geographic distance and with dissimilarity in climatic conditions at a global scale (**Paper I**) shows that regional species pools are also systematically connected through the biogeography of clades. This may have important implications for how well the species within a region adapt to environmental change if the adaptability of species varies among clades of bees. This has been shown for long tonged bees (i.e. Apidae and Megachilidae) which have generally been more adversely affected by land use change than short tonged bees (i.e. Andrenidae, Colletidae and Halictidae, Fig. 5) during the past century (Biesmeijer et al. 2006). Moreover, since *Bombus* species are adapted to cool climates (Hines 2008) they are particularly susceptible to global warming (Bartomeus et al. 2013, Rasmont et al. 2015). Indeed, northwards range shifts of *Bombus* (i.e. Apidae) species, in the northern hemisphere, expected to result from global warming occur across continents (Kerr et al. 2015). The proportion of *Bombus* species increases with elevation and latitude (**Paper II**, Hoiss et al. (2012) and of Norway's 205 bee species as many as 17% belong to this genus. Communities situated in areas with cool climates may therefore experience a relatively larger species and phylogenetic turnover due to global warming than communities situated in warmer climates. Importantly the results in **Paper I** underline the importance of establishing a syntheses among hierarchies (e.g. community ecology and biogeography) in the organization of biodiversity (Jenkins and Ricklefs 2011).

Figure 5. The short tonged *Colletes daviesanus* foraging on *Leucanthemum vulgare*. Short tonged and long tonged bees have responded differently to changes in land use during the past century (Biesmeijer et al. 2006). Long tonged bees in particular have declined, together with the plants on which they forage. Thus understanding what determines the floral associations of bees is important for the management of species rich communities. Photo: Sydenham, M.A.K.

Within the metacommunity, communities are connected through the dispersal of individuals (Leibold et al. 2004, Logue et al. 2011). Bees are central place foragers with foraging ranges typically restricted to about 1,000 m, albeit this depends on their body size (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). Indeed, the abundance of bees show a pronounced decrease as the distance to source habitats increases, contrasting that of the more ephemerally distributed hoverflies (Syrphidae) (Jauker et al. 2009). Bees may therefore be particularly vulnerable to habitat fragmentation. In **Paper V**, we show that the probability of a species occurring within a local community decreases with the distance to the nearest community harbouring that species. These results show that species are not randomly distributed across the landscape and suggest the bee communities in our study system are dispersal limited. Similar patterns have been found for protected areas in Ireland where the species turnover between communities increases with geographic distance (Murray et al. 2012).

The vulnerability to habitat isolation, e.g. the dispersal ability, seems to vary among species and in bees depend on their life history traits (Williams et al. 2010). We found no such influence of the nesting biology of bees nor of their maximum foraging range on their degree of dispersal limitation (**Paper V**). This may have been because the distances among our study sites were too large to allow the detection of trait specific differences in dispersal capabilities. For instance, although the spatial scales at which bees respond to landscape change varies with the size of bees (Steffan-Dewenter et al. 2002), all respond to differences in landscape composition well within 5,000 metres (the minimum distance among sites in this study, i.e. Fig. 3). Nonetheless, the results presented in **Paper V** demonstrate the importance of accounting for the connectivity among communities for accurate predictions of the local species pool.

Ecological filtering (Papers **I-V**)

In **Paper II,** we show that the influence of regional filters on bee diversity within communities is more pronounced than that of local filters. Specifically, as bee diversity declines with elevation communities become increasingly dominated by *Bombus* species. Indeed, elevation was also found to be a more important driver of bee diversity in grasslands than floral diversity and habitat management (Hoiss et al. 2012). This supports the hypothesis that the assembly of communities is governed by a hierarchy of ecological filters as also found in plant communities (de Bello et al. 2013). Within bees, the abundance and species richness of cold adapted taxa, such as *Bombus*, would be expected to show a less steep decrease with elevation, relative to that of taxa not adapted to cool climates. Indeed, we only found elevation to be related to changes in the dominant functional trait values when *Bombus* species were included in the analyses (**Paper II**). This suggests that among non-*Bombus* species, elevation did not select for species based on their functional traits. Instead, the influence asserted by elevation on non-*Bombus* species in our system was a general reduction in bee species richness and abundance. In contrast, when excluding *Bombus* species, Hoiss et al. (2012) found an increased proportion of non-cleptoparasitic species and individuals, as well as an increased proportion of social species of taxa. We did not include clepto-parasites in **Paper II**. However, it would have been interesting to test if the findings of Hoiss et al. (2012) also applies to our system. A decreased proportion of cleptoparasitic bees with elevation could result from lower densities of potential hosts at high elevations and lead to a reduced parasitism rate. When *Bombus* species were excluded, the only remaining facultative social species in the 17 sites included in **Paper II** were *Lasioglossum calceatum* and *Halictus rubicundus*. The low number of social non-*Bombus* species in our system may explain why we did not find that the proportion of social species increased with elevation when *Bombus* species were removed.

Landscape level ecological filters also influenced the functional diversity within bee communities in our system (**Paper II**). However, this influence was confounded by that of elevation. In our study system (Fig. 3), power line clearings situated at intermediate to high elevations tended to be surrounded by a more homogeneously forested landscape whereas low elevation landscapes contained more farmland and open semi-natural grasslands. We may therefore not have been able to disentangle the direct influence of landscape composition on the diversity of bees within power line clearings. Moreover, bee diversity increases with landscape disturbance in forested landscapes (Winfree et al. 2007) but decreases in agricultural landscapes (Steffan-Dewenter et al. 2002, Williams et al. 2010). There may therefore have been contrasting effects on bee diversity of landscape diversity in different portions of the study area in **Paper II**. For instance, in a study conducted within an agricultural landscape in South East Norway, Sydenham et al. (2014) found that areas with a high proportion of semi natural landscape elements contained more phenologically diverse bee communities. This may suggests that the influence of landscape diversity is more context dependent within our region than elevation.

At the local level, we found a strong sorting mechanism of forb diversity on the functional diversity of solitary bees (**Paper II, IV-V**). Specifically, sites dominated by Ericaceous shrubs had a poorer solitary bee fauna containing mainly the Ericaceae specialists: *Andrena fuscipes*, *A. lapponica* (Fig. 6) and *Colletes succinctus* together with a high proportion of *Bombus* species.

As the forb diversity increases, at the expense of shrubs, so does the solitary bee diversity. The gradient from forb poor and dominated by shrubs to forb species rich has also been found to explain gradients in bee diversity in forested ecosystems in the south eastern USA (Hanula et al. 2015). This gradient is likely related to the floral preferences and phenology of bees. Indeed, bees show distinct floral affiliations which are often related to their taxonomy and describe their spatial (Potts et al. 2003) and successional distribution (Moretti et al. 2009, Ricotta and Moretti 2011). In **Paper I**, we found that closely related species tend to have a larger niche overlap than distantly related species. This may explain why we found a packing of closely related species in cleared treatment plots with a high diversity of forbs (**Paper IV**), if these plots were able to cater for a wide array of taxa, due to taxon-specific floral preferences. Importantly, the solitary bee faunas in areas with a high diversity of forbs were also the most responsive to habitat management (**Paper IV**). This suggests that improving the habitat quality for bees in power line clearings will be most cost efficient if management schemes are implemented in areas with a relatively high diversity of forbs. That the outcome of management schemes depends on the environmental context has also been found for agri-environmental schemes that have been adopted over large areas (Scheper et al. 2013). Managers should therefore account for the influence of local ecological filters during the planning phase and aim to identify areas in which the outcome of habitat improvement schemes will be greatest.

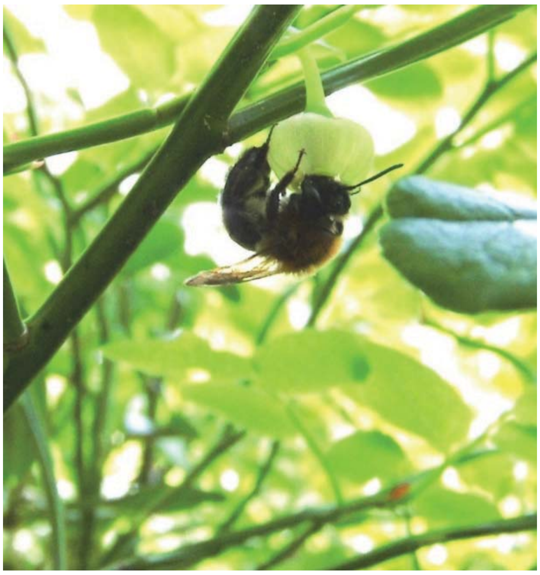


Figure 6. *Andrena lapponica* an Ericaceae pollen specialist here on *Vaccinium myrtilus***.** *A. lapponica* is one of the most common solitary bee species in Norway and one of the dominant species in Ericaceous shrub dominated power line clearings. Photo: Sydenham, M.A.K.

In addition to floral diversity being an important ecological filter, the availability and diversity of nest sites also drive local bee diversity (Potts et al. 2005, Murray et al. 2012). Bees display a dazzling variety of nesting habits ranging from below ground nesting species that excavate their nests in soils to bees that excavate their own cavities in suitable nesting substrates above ground (Michener 2007). The nesting habits of bees are related to how they respond to landscape disturbance (Williams et al. 2010). Many bee species depend on pre-existing cavities such as abandoned beetle burrows in dead wood (Westerfelt et al. 2015). However, modern silviculture has reduced the amount of large woody debris in the forested landscape with detrimental effects on wood boring beetle diversity (Grove 2002). This may have indirectly affected the diversity of cavity nesting bees as it increases with the diversity of cavity producing beetles (**Paper III**). Wood boring beetles thereby function as allogenic ecosystem engineers (Lawton 1994) by producing cavities in dead wood so this nesting substrate becomes available for secondary cavity nesting bees. Managing forests to sustain these ecosystem engineers may benefit the diversity of bees since the availability of nest sites limits the population size of cavity nesting bees (Steffan-Dewenter and Schiele 2008). Moreover, that the a greater functional diversity of wood boring beetles is related to an increased size diversity of cavity nesting bees (**Paper III**), suggest that forest managers should aim to preserve enough large woody substrates for a variety of beetles to occupy. Importantly, these findings illustrate that management of bee habitats requires a community wide approach that also includes the management of habitats for non-bee taxa.

Ecological drift (Paper V)

While the influence on bee diversity of local ecological filters such as floral diversity can be managed by mowing and sowing wild flower mixes (Hopwood 2008, Noordijk et al. 2009) the influence of stochastic processes cannot. However, by limiting the establishment of costly management regimes to areas where the outcome is predictable it should be possible to increase their cost-efficiency. We found that the diversity within bee communities was generally less predictable at high latitudes than at low latitudes (**Paper II**). This was further elaborated on in **Paper V** where we found that while the probability of a solitary bee species occurring within a community on average decreased with elevation, the rate of decrease depended on the regional abundance and was most pronounced for regionally rare species. These results suggests that ecological drift plays an increasingly important role at marginal (high elevation) habitats. The increased role of ecological drift at high elevations would be expected if high elevation sites are more isolated (Rosindell et al. 2011) for instance by foraging resources being more sparsely distributed and less abundant (Hoiss et al. 2013). Indeed, a decreasing degree of connectivity has been found to be related to a decrease in the evenness of species abundance distributions (Marini et al. 2014) suggesting that as habitats become more isolated the species composition tends towards monodominance of regionally abundant species. These results suggest that habitat management aimed at promoting solitary bee diversity should generally produce the most predictable outcomes in areas at low elevations.

Methodological limitations of the present studies and prospects for future studies

A notable omission of the approaches used in this thesis is the influence that competition between species may have one local species diversity. Although the outcomes of competitive interactions may be unpredictable when evaluating entire species assemblages (Lawton 1999) it has been shown that high densities of *A. melifera* can suppress the development of *Bombus* colonies (Elbgami et al. 2014) and are related to a decrease in floral visitation by wild bees (Torné-Noguera et al. *In Press*). Species may co-exist within communities if differences in competitive abilities among species are counterweighted by density dependent, stabilizing mechanisms such as resource portioning and predation (Chesson 2000, HilleRisLambers et al. 2012). Within bees, nest sites may be more limiting than foraging resources (Steffan-Dewenter and Schiele 2008). Therefore, although we found that closely related bee species tend to have a larger niche overlap in terms of floral visitation patterns than distantly related species (**Paper I)** a low availability of nest sites may hinder a depletion of foraging resources. If bee species are more specialized in terms of their nesting-habitats than their foraging-habits this may prevent competitive exclusion from occurring. However, I am unaware of any studies documenting how bee species differentiate along different behavioral niche axes. Such studies might allow a more direct inference of the effect of competition on bee community assembly

Trait diversity is measured at the species level in most studies on the drivers of the functional diversity in bee communities (Greenleaf et al. 2007, Williams et al. 2010, Kremen and M'Gonigle 2015 and **Papers II-V**). However, there may be considerable intraspecific trait variation (Fig. 7). Future studies should aim to include the intraspecific trait variation in studies of the assembly of bee communities. Indeed, it has been suggested that this may also more generally allow for more accurate predictions in community ecology (Violle et al. 2012). A potential solution would be to use the approach we propose in **Paper V** but with the presence of

Figure 7. Illustration of intraspecific variation in functional traits**.** The body size of the cavity nesting bee *Chelostoma florisomne* varies considerably among individuals. It is unknown how this may affect the foraging range and preferred nest site diameters of individuals. Photo: Sydenham, M.A.K.

individuals, instead of species, as the response variable. Doing so would allow the inclusion of intra-specific trait variation and testing if this converges across taxa due to ecological filtering, or dispersal abilities due to dispersal limitation.

A limitation for the interpretation of the results in papers that included phylogenies (**Papers I, II, IV and V**) is that the phylogenies were not produced directly from molecular data. Instead, we clustered species according to recently published phylogenies introducing the need to use arbitrary branch lengths and not ones based on relative differences in the molecular markers. All phylogenetic diversity indices used in this thesis assume that ecological dissimilarly between species increases monotonically, following a Brownian motion, over evolutionary time. The phylogenetic tree used in such analyses should therefore ideally be based on neutral markers. However, the motivation for including phylogenetic diversity indices in community ecological studies is based on the assumption that closely related species are more ecologically similar than distantly related species (Webb et al. 2002, Vamosi et al. 2009). If the evolution of a certain niche has evolved at different rates in different lineages, a phylogeny based on neutral markers may not accurately account for this. An example could be sociality which is predominant in the *Bombus* genera but has evolved several times in *Halictus* and *Lasioglossum* (Danforth 2002). The evolution of certain traits may even change the evolutionary rate and both eusociality and cleptoparasitism are related to an increased pace of molecular changes in the Hymenoptera (Bromham and Leys 2005). Using neutral molecular markers and assuming a Brownian motion mode of trait evolution does therefore not seem like an optimal choice for community phylogenetics if the aim is to relate patterns in phylogenetic diversity to the timing of trait divergence. However, using phylogenies based on such markers, or with arbitrary branch lengths (as done in this thesis) may still provide important information on whether or not the topology of the tree changes according over ecological gradients or if members of different clusters on the tree differ in their niches. The low resolution of the phylogenies and arbitrary branch lengths meant that the results should be interpreted with some caution. We were for instance unable to determine if speciation events or historical migrations drove the increased phylogenetic beta-diversity with geographic distance (**Paper I**).

Concluding remarks

The diversity and spatio-temporal distribution of biodiversity is determined by four processes (Vellend 2010) that create variation (e.g. speciation); translocate and reorganize variation (e.g. dispersal); decrease variation (e.g. ecological filtering); and purely stochastic events (e.g. ecological drift). The bees are an enormously specious and functionally diverse taxon. As central-place foragers, with relatively short home ranges bees are ample model organisms for community ecology. In this thesis, it has been shown that the distribution of bee species in Norway is predictable from how their life history traits determine their responses to ecological filters but that stochastic processes, related to dispersal and ecological drift, need to be accounted for in order to form accurate predictions of species distributions and the outcome of habitat management.

Ecological filters operate at the individual or population level meaning that inferring their influence based on properties of diversity indices that aggregate information from species or individuals may not be problem free (e.g. Leinster and Cobbold 2012, Warren et al. 2014, Warton et al. 2015). In **Paper V**, we expanded on previous univariate approaches (Leinster and Cobbold 2012, Kremen and M'Gonigle 2015) and developed a novel framework for testing the influence of dispersal limitation, ecological filtering and ecological drift on the probability of a species occurring within a site. An important aspect of this approach is that because it is based on the occurrence of species and can be adapted to the occurrence of individuals it is scalable to population level processes. Moreover, applying the approach to sets of communities sampled at varying spatial scales should allow the incorporation of biogeographic and metacommunity ecological processes into the same analytical framework.

Conferences and outreach contributions

Sydenham, M.A.K., Totland, Ø. 2012. *Phenologically restricted responses of solitary bees to habitat and landscape context.* Poster at the Scandinavian Association for Pollination Ecologists (SCAPE) conference, Kirkøy, Norway.

Sydenham, M.A.K., Eldegard, K., Heggland, S.J., Nielsen, A, Totland, Ø. and Moe, S.R. 2015. *Community phylogenetics provide a common currency for the processes involved in community assembly: Exemplified using bee species assemblages.* Talk at the Norwegian Ecological Society (NØF) conference, Bergen, Norway.

Sydenham, M.A.K., Moe, S.R., Stanescu, D.N., Totland, Ø. and Eldegard, K. 2015. *Wild bees in artificial landscapes - Drivers of bee diversity in power line clearings*. Invited talk at the Bees Wasps and Ants Recording Society (BWARS) annual general meeting, Oxford, United Kingdom.

Sydenham, M.A.K., Moe, S.R., Stanescu, D.N., Totland, Ø. and Eldegard, K. 2015. *Does habitat management increase the species richness, phylogenetic and functional diversity of bees in power line clearings?* Talk at the Scandinavian Association for Pollination Ecologists (SCAPE) conference, Silkeborg, Denmark.

Sydenham, M.A.K., Moe, S.R., Stanescu, D.N., Totland, Ø. and Eldegard, K. 2015. *Using species, phylogenetic and functional diversity metrics to test the outcome of an experimental management of wild bee habitats.* Poster at the British Ecological Society (BES) conference, Edinburgh, United Kingdom.

References

Amiet, F. 2007. Fauna Helvetica 20. Apidae 5 : Ammobates, Ammobatoides, Anthophora, Blastes, Ceratina, Da Objectives sypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa. Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., M. Herrmann, A. Müller, and R. Neumeyer. 2001. Fauna Helvetica 6. Apidae 3: Halictus, Lasioglossum. Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., M. Herrmann, A. Müller, and R. Neumeyer. 2004. Fauna Helvetica 9. Apidae 4: Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis. Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., M. Herrmann, A. Müller, and R. Neumeyer. 2010. Fauna Helvetica 26. Apidae 6: Andrena, Melitturga, Panurginus, Panurgus. Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., A. Müller, and R. Neumeyer. 1999. Fauna Helvetica 4. Apidae 2: Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha. Centre Suisse de Cartographie de la Faune (CSCF).

ArtDatabanken. 2015. Rödlistade arter i Sverige 2015. ArtDatabanken SLU, Uppsala.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. Proceedings of the National Academy of Sciences **110**:4656-4660.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313**:351-354.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution **57**:717-745.

Bromham, L., and R. Leys. 2005. Sociality and the rate of molecular evolution. Molecular biology and evolution **22**:1393-1402.

Cardinal, S., and B. N. Danforth. 2013. Bees diversified in the age of eudicots. Proc R Soc B **280**: 20122686 http://dx.doi.org/10.1098/rspb.2012.2686.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters **12**:693-715.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Danforth, B. N. 2002. Evolution of sociality in a primitively eusocial lineage of bees. Proceedings of the National Academy of Sciences **99**:286-290.

Danforth, B. N., S. Cardinal, C. Praz, E. A. B. Almeida, and D. Michez. 2013. The impact of molecular data on our understanding of bee phylogeny and evolution. Annual Review of Entomology **58**:57-78.

de Bello, F., S. Lavorel, S. Lavergne, C. H. Albert, I. Boulangeat, F. Mazel, and W. Thuiller. 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography **36**:393-402.

Ehnström, B., and R. Axelsson. 2002. Insektsgnag i bark och ved. Artdatabanken, SLU, Uppsala.

Elbgami, T., W. E. Kunin, W. O. Hughes, and J. C. Biesmeijer. 2014. The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. Apidologie **45**:504-513.

Eldegard, K., Ø. Totland, and S. R. Moe. 2015. Edge effects on plant communities along power line clearings. Journal of Applied Ecology **52**: 871-880.

Gallai, N., J.-M. Salles, J. Settele, and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics **68**:810-821.

Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, and O. Afik. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science **339**:1608-1611.

Gathmann, A., and T. Tscharntke. 2002. Foraging ranges of solitary bees. Journal of Animal Ecology **71**:757-764.

Grafen, A. 1989. The phylogenetic regression. Philos Trans R Soc Lond B Biol Sci **326**:119-157.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia **153**:589-596.

Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics **33**:1-23.

Hanula, J. L., S. Horn, and J. J. O'Brien. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? Forest Ecology and Management **348**:142-152.

Hedtke, S., S. Patiny, and B. Danforth. 2013. The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. BMC Evolutionary Biology **13**:138.

Hegland, S. J., J. Dunne, A. Nielsen, and J. Memmott. 2010. How to monitor ecological communities cost-efficiently: The example of plant-pollinator networks. Biological Conservation **143**:2092-2101.

Henriksen, S., and O. e. Hilmo. 2015. Norsk rødliste for arter 2015. Artsdatabanken, Norge.

HilleRisLambers, J., P. Adler, W. Harpole, J. Levine, and M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics **43**:227-248.

Hines, H. M. 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera : Apidae : Bombus). Systematic Biology **57**:58-75.

Hoiss, B., J. Gaviria, A. Leingärtner, J. Krauss, and I. Steffan-Dewenter. 2013. Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. Diversity and Distributions **19**:386-395.

Hoiss, B., J. Krauss, S. G. Potts, S. Roberts, and I. Steffan-Dewenter. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proceedings of the Royal Society B-Biological Sciences **279**:4447-4456.

Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation **141**:2632-2640.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). Princeton University Press.

Jauker, F., T. Diekoetter, F. Schwarzbach, and V. Wolters. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology **24**:547-555.

Jenkins, D. G., and R. E. Ricklefs. 2011. Biogeography and ecology: two views of one world. Philosophical transactions of the Royal Society B: Biological sciences **366**:2331-2335.

Kayaalp, P., M. P. Schwarz, and M. I. Stevens. 2013. Rapid diversification in Australia and two dispersals out of Australia in the globally distributed bee genus, Hylaeus (Colletidae: Hylaeinae). Molecular Phylogenetics and Evolution **66**:668-678.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science **3**:157-164.

Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, and L. L. Richardson. 2015. Climate change impacts on bumblebees converge across continents. Science **349**:177-180.

Kleijn, D., R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, A.-M. Klein, C. Kremen, L. K. M'Gonigle, and R. Rader. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature communications **6**: DOI; 10.1038/ncomms8414

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Koppen-Geiger climate classification updated. Meteorologische Zeitschrift **15**:259-263.

Kremen, C., and L. K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. Journal of Applied Ecology **52**:602-610.

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology **91**:299-305.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos **3**:367-374.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos **84**:177-192.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law, and D. Tilman. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters **7**:601-613.

Leinster, T., and C. A. Cobbold. 2012. Measuring diversity: the importance of species similarity. Ecology **93**:477-489.

Logue, J. B., N. Mouquet, H. Peter, H. Hillebrand, and M. W. Group. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology & Evolution **26**:482-491.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press.

Marini, L., E. Öckinger, K. O. Bergman, B. Jauker, J. Krauss, M. Kuussaari, J. Pöyry, H. G. Smith, I. Steffan-Dewenter, and R. Bommarco. 2014. Contrasting effects of habitat area and connectivity on evenness of pollinator communities. Ecography **37**:544-551.

Matheson, A., S. Buchmann, C. O'toole, P. Westrich, and I. Williams. 1996. The conservation of bees. Academic Press for the Linnean Society of London and the International Bee Research Association.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution **21**:178-185.

Michener, C. D. 2007. The bees of the world. 2nd edition. Johns Hopkins University Press, Baltimore.

Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications **23**:829-839.

Moretti, M., F. De Bello, S. P. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. Journal of Animal Ecology **78**:98-108.

Murray, T. E., U. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown, and R. J. Paxton. 2012. Local-scale factors structure wild bee communities in protected areas. Journal of Applied Ecology **49**:998-1008.

Nielsen, A., and Ø. Totland. 2014. Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. Oikos **123**:323-333.

Nieto, A., S. P. M. Roberts, J. Kemp, P. Rasmont, M. Kuhlmann, M. García Criado, J. C. Biesmeijer, P. Bogusch, H. H. Dathe, P. De la Rúa, T. De Meulemeester, M. Dehon, A. Dewulf, F. J. Ortiz-Sánchez, P. Lhomme, A. Pauly, S. G. Potts, C. Praz, M. Quaranta, V. G. Radchenko, E. Scheuchl, J. Smit, J. Straka, M. Terzo, B. Tomozii, J. Window, and D. Michez. 2014. European Red List of bees. Publication Office of the European Union, Luxembourg.

Noordijk, J., K. Delille, A. P. Schaffers, and K. V. Sýkora. 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biological Conservation **142**:2097-2103.

Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. Science **346**:1360-1362.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos **120**:321-326.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics **20**:289-290.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25**:345-353.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? Ecology **84**:2628-2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology **30**:78-85.

Rasmont, P., M. Franzén, T. Lecocq, A. Harpke, S. Roberts, J. C. Biesmeijer, L. Castro, B. Cederberg, L. Dvorak, and Ú. Fitzpatrick. 2015. Climatic risk and distribution atlas of European bumblebees. BioRisk **10**:1-236.

Rezende, E. L., J. E. Lavabre, P. R. Guimaraes, P. Jordano, and J. Bascompte. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature **448**:925-928.

Ricklefs, R. E. 2008. Disintegration of the ecological community. The American Naturalist **172**:741-750.

Ricotta, C., and M. Moretti. 2011. CMW and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia **167**:181-188.

Rosindell, J., S. P. Hubbell, and R. S. Etienne. 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology & Evolution **26**:340-348.

Russell, K., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. Biological Conservation **124**:133-148.

Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, and D. Kleijn. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss–a meta-analysis. Ecology Letters **16**:912-920.

Schmid-Egger, C., and E. Scheuchl. 1997. Illustrierte bestimmungstabellen der wildbienen Deutschlands und Österreichs, Band 3: Schlüssel der arten der familie Andrenidae. Velden, Germany: Eigenverlag.

Schmidt, S., C. Schmid-Egger, J. Morinière, G. Haszprunar, and P. D. Hebert. 2015. DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources.

Senapathi, D., J. C. Biesmeijer, T. D. Breeze, D. Kleijn, S. G. Potts, and L. G. Carvalheiro. 2015. Pollinator conservation — the difference between managing for pollination services and preserving pollinator diversity. Current Opinion in Insect Science **12**:93-101.

Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421-1432.

Steffan-Dewenter, I., and S. Schiele. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats. Ecology **89**:1375-1387.

Sydenham, M., K. Eldegard, and Ø. Totland. 2014. Spatio-temporal variation in species assemblages in field edges: seasonally distinct responses of solitary bees to local habitat characteristics and landscape conditions. Biodiversity and Conservation **23**:2393-2414.

Torné-Noguera, A., A. Rodrigo, S. Osorio, and J. Bosch. Collateral effects of beekeeping: Impacts on pollen-nectar resources and wild bee communities. Basic and Applied Ecology. *In Press* doi:10.1016/j.baae.2015.11.004

Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Molecular Ecology **18**:572-592.

Vellend, M. 2010. Conceptual synthesis in community ecology. The Quarterly Reviews of Biology **85**:183-206.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution **27**:244-252.

Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking geography for biology: inferring processes from species distributions. Trends in Ecology & Evolution **29**:572-580.

Warton, D. I., B. Shipley, and T. Hastie. 2015. CATS regression – a model-based approach to studying trait-based community assembly. Methods in Ecology and Evolution **6**:389-398.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics **33**:475-505.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Phil. Trans. R. Soc. B **366**:2403-2413.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos **74**:159-164.

Westerfelt, P., O. Widenfalk, Å. Lindelöw, L. Gustafsson, and J. Weslien. 2015. Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. Insect Conservation and Diversity **8**:493-504.

Westrich, P. 1990. Die Wildbienen Baden-Württembergs. 2 Bände, 972 S., 496 Farbfotos. Stuttgart (E. Ulmer).[2., verb. Auflage].

Williams, N. M., E. E. Crone, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation **143**:2280-2291.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of Human Disturbance on Bee Communities in a Forested Ecosystem. Conservation Biology **21**:213-223.

Paper I

Community level niche overlap and broad scale biogeographic patterns of bee communities are driven by phylogenetic history

Markus Arne Kjær Sydenham[1], Katrine Eldegard[1], Stein Joar Hegland[2], Anders Nielsen[3], Ørjan Totland[1] and Stein R. Moe[1].

[1]*M.A.K. Sydenham (markus.sydenham@nmbu.no), K. Eldegard (katrine.eldegard@nmbu.no), Ø. Totland (orjan.totland@nmbu.no) and S. R. Moe (stein.moe@nmbu.no) Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.B. 5003, NO-1432 Ås, Norway.*

[2]*S. J. Hegland (Stein.Joar.Hegland@hisf.no) University College of Sogn and Fjordane, Faculty of Engineering and Science, P.O. Box 133, N-6851 Sogndal, Norway.*

[3]*A. Nielsen (anders.nielsen@ibv.uio.no) Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066, NO-0316 Blindern, Oslo Norway*

Keywords: Beta diversity, Biogeography, Community ecology, Phylogenetic signal, Plant-pollinator networks, Wild bees

ABSTRACT

Aim To test if phylogenies provide a common currency for the processes involved in community assembly, i.e. niche overlap, environmental filtering, speciation and migration.

Location Global

Methods We clustered 592 bee species that occurred within 26 bee-flower networks according to their phylogenetic relationships. Each network consisted of a matrix of bee and plant species and information on whether or not a bee species had been observed visiting flowers of a given plant species. We used Bloomberg’s K-value to examine whether the floral associations (niche overlap) of bees within networks displayed a significant phylogenetic signal and, whether the phylogenetic beta-diversity increased with geographic distance and dissimilarity in climatic conditions between networks. We focused on bees because they are monophyletic, central place foragers with limited foraging ranges, which make them good model organisms for community ecology.

Results We found a phylogenetic signal (Blomberg’s K-value close to or larger than 1) for niche overlap in 15 of the 18 bee-flower networks. Randomization tests showed that the phylogenetic signal was statistically significant for all eight of the bee-flower networks that had > 20 species, which is the minimum number of species required to obtain a sufficiently high statistical power for such tests. On a global scale, the phylogenetic beta-diversity increased with geographic distances up to approximately 5,000 km and with climatic dissimilarity between sites.

Main conclusions Our findings show that local bee communities are structured by ecological filtering processes operating at the floral resource and global scales, through floral visitation and climatic conditions, respectively. The influence of geographic distances suggest that regional speciation events and subsequent migrations are important determinants of local bee

diversity. Our findings suggest that difficulties related to the interpretation of community phylogenetic patterns – resulting from either community level or biogeographical processes – may be overcome by including explanatory variables describing processes operating on both local and global scales.

INTRODUCTION

By studying the role of functional traits in organizing species assemblages community ecologists have become increasingly reductionistic in the search for general assembly rules (Keddy 1992, McGill et al. 2006, Williams et al. 2010). Hypotheses about the ecological processes that influence the dispersion of functional traits (Weiher and Keddy 1995, de Bello et al. 2013) and the phylogenetic relatedness among community members (Webb 2000, Webb et al. 2002, Hoiss et al. 2012), have brought severalt important conceptual syntheses to community ecology (Cavender-Bares et al. 2009, Vamosi et al. 2009, Weiher et al. 2011), leading to a new mechanistic theoretical framework. The suggested theory of community ecology states that the species composition of local communities is the product of speciation, migration, ecological filtering and ecological drift (Vellend 2010). By focusing on the phylogenetic composition of communities, it is possible to use the same 'currency' to measure the influence of each of the four processes, although they may operate on different spatial and temporal scales.

The use of phylogenies in community ecology has a long history (Elton 1946) and can be traced back to Darwin. Darwin (1859) stated that since closely related species generally are more functionally similar than distantly related species, they should compete more intensively. Competition should therefore result in communities in which species are less closely related than expected by chance (Webb 2000). However, interpreting the phylogenetic dispersion observed within communities (Webb et al. 2002) solely as a result of either competition (leading to over-dispersion) or environmental filtering (leading to under-dispersion) is problematic since these patterns may also arise due to regional speciation and dispersal processes (Warren et al. 2014). Moreover, in contrast to sessile organisms that rely on spatially fixed resources, the observed patterns of co-occurrence of mobile species within an area need not be inherently linked to shared resources (Weiher et al. 2011). These issues may be overcome by sampling species on a resource scale, thereby linking the phylogenetic signal to actual resource use, or on a biogeographic scale, thereby linking the phylogenetic signal to migration, and by selecting suitable model organisms.

Wild bees are well-suited model organisms for community ecology since they form a monophyletic group and belong to the same trophic level (i.e. all bees visit flowers for nectar and females often also for pollen) (Michener 2007). Moreover as bees are central place foragers with typical foraging ranges within a 1 km radius from the nest (Darvill et al. 2004, Gathmann and Tscharntke 2002) their presence within an area suggests that suitable nest locations occur nearby. The ecology of wild bees has received increasing attention during the past two decades due to documented declines in population sizes and diversity (Biesmeijer et al. 2006, Potts et al. 2010, Winfree et al. 2011). It is well documented that filtering processes operating at the habitat level through gradients in floral (Potts et al. 2003) and nest site (Potts et al. 2005, Murray et al. 2012) availability and variety are important determinants of the diversity of local bee species assemblages. The availability of these resources at the landscape scale is also an important driver of local bee diversity (Steffan-Dewenter et al. 2002, Williams et al. 2010). Finally, differences in climatic conditions within a region, for example along gradients in elevation or latitude (Hoiss et al. 2012, Sydenham et al. 2015), act as important environmental filters on local bee diversity. To our knowledge, less is known about the drivers of resource partitioning within bee species assemblages and thereby ultimately the relationship between bee and floral diversity (but see, Potts et al. (2003)). The roles of migration history or environmental filtering at large spatial scales and their roles in shaping local bee species assemblages have also received limited attention (but see Hedtke et al. (2013)), although these processes are important precursors for the regional and thereby local species diversity (Vellend 2010). We addressed these questions by hypothesizing that (1) the similarity in the floral associations of bee species is determined by their phylogenetic history. We therefore expected to find that the relative position of species in a multidimensional niche space should reveal a phylogenetic signal. Secondly, we hypothesized that (2) the phylogenetic turnover among bee species assemblages is driven by speciation and migration history as well as climate conditions (environmental filtering) at a global scale. We therefore expected that the degree of phylogenetic dissimilarity among bee species assemblages would increase with geographic distance as well as differences in climatic conditions.

METHODS

We downloaded data on bee species and their floral associations from 26 previously published plant-pollinator networks (Appendix S1). Bees that had not been designated species epithets were removed from the datasets, and we thereafter updated the nomenclature of the species within each network according to the Integrated Taxonomic Information System (ITIS 2014) and Ascher and Pickering (2014). Following the update, networks with fewer than 10 bee species were only included to supply species for the construction of the phylogeny, but otherwise excluded from the analyses. We added one unpublished bee-flower network from Norway (Appendix S2) to the collection, resulting in a total of 18 bee-flower networks with at least 10 bee species, covering climatic zones from the tropics to the boreal zone (Fig. 1). The networks consisted of binary information on the plant species each bee species visited (Qualitative networks).

To quantify the relatedness among the 592 bee species included in our study, we constructed a polytomous, ultra-metric phylogenetic tree (Fig. 2) using the R package Picante (Kembel et al. 2010). The tree was structured by clustering species and higher level taxa according to published molecular and morphological phylogenies of bees (Danforth et al. 2006, Larkin et al. 2006, Cameron et al. 2007, Praz et al. 2008, Almeida and Danforth 2009, Kuhlmann et al. 2009, Gonzalez et al. 2012, Danforth et al. 2013, Hedtke et al. 2013, Kayaalp et al. 2013, Sedivy et al. 2013a). Branch lengths were calculated in the Picante package (Kembel et al. 2010) in R following Grafen (1989) with the p-parameter set to 0.25. This relatively low p-parameter was chosen to account for the rapid diversification of bee families early in the evolutionary history of bees (Cardinal and Danforth 2013).

Niche overlap vs. phylogenetic distance

We tested if the degree of niche overlap between bee species displayed a phylogenetic signal by calculating and testing the significance of Blomberg's K-value (Blomberg et al. 2003) with the floral associations of bees as 'functional traits'. The floral associations of bees were calculated by placing all species in a non-metric multidimensional (NMDS) trait space defined by their Jaccard's dissimilarities in resource use. This approach allowed us to quantify the dissimilarities among species on several uncorrelated gradients of resource use. We applied the NMDS analysis since it is suitable when the underlying data are binary (occurrence), in contrast to weighted average based approaches, such as correspondence analysis (CA) and detrended correspondence analysis (DCA). Species with proximate scores on a NMDS axes were interpreted to have overlapping niches in that niche-dimension. Prior to the NMDS analyses we removed disconnected species (i.e. bee species sampled on flowers that no other species were sampled on) from each network as these did not provide any information on dissimilarities in patterns of floral associations compared to other species. At the most two species had to be removed from a network to ensure connectedness among network members and thus it is unlikely that this influenced the results (network abbreviation = removed species/species in full network; M2 = 1/11, HN = 1/12, PA = 1/13, HR = 1/47, KT = 1/57, CO = 2/83, PD = 2/238). Each resulting bee-flower network was combined with a pruned phylogeny to ensure that the order of the taxa were consistent for both the network of connected species and the phylogeny. The NMDS ordinations were run using the step-across function to account for 100%

dissimilarities within pairs of species. We set the maximum number of random starting points and iterations to 1000, which ensured that the final NMDS reached a convergent solution. For each bee-flower network, we initially ran the NMDS with three dimensions. If no solution was reached with a three dimensional NMDS we reduced the number of dimensions to two, and finally one if necessary. For the largest bee-flower network (236 species) a convergent solution could only be reached when the NMDS was conducted on four dimensions. Each NMDS gradient thus reflected a unique part of the niche-space covered by the bees in the bee-flower network.

The species-specific scores on each NMDS axis were mapped onto the phylogeny for the species present in the bee-flower network. Subsequently we used the function phylosig in the R package Phytools (Revell 2012) to calculate the Blombergs K-value of each NMDS axis, which reflects if the position of traits on a phylogeny follows a Brownian motion mode of evolution. The K-value is scaled according to the underlying phylogeny, making comparisons of the phylogenetic signal of traits possible across phylogenies of different sizes (Blomberg et al. 2003). K-values close to zero are indicative of no phylogenetic signal, whereas values close to one are indicative of traits following a Brownian motion mode of evolution. K-values above one indicate that traits show a phylogenetic clustering stronger than that expected under a Brownian mode of evolution (Blomberg et al. 2003, Swenson 2014). The observed K-values were tested against a null-distribution based on 10,000 randomizations of the locations of traits on the phylogeny. Randomization tests have low power and increased risk of type-II errors when fewer than 20 species are present in the phylogeny (Blomberg et al. 2003). For the networks with fewer than 20 species we therefore interpreted non-significant K-values that were close to, or larger than, 1 as evidence of a weak phylogenetic signal. We calculated the standard deviation of the significant K-values. Non-significant K-values that were larger than one minus the standard deviation were considered to be close to (or larger than) one.

To remove the influence of the most generalist species we repeated the analyses on a subset of the data consisting of the most dissimilar species, in terms of floral associations. Only species belonging to one of two clusters i.e. with scores along the first, second and third NMDS axes with either lower than the 25% or higher than the 75% quartiles were included in these analyses. This approach removed species that did not strongly diverge from either of the two clusters. Networks with less than ten species, following the sub-setting, were excluded from the analyses. The observed K-values were tested against a null-distribution based on 10,000 randomizations of the locations of NMDS axis scores on the phylogeny.

Geographic and climatic influences on biogeography

We analysed how the phylogenetic beta-diversity was related to both geographic distance (a proxy for migration distance) and dissimilarities in climatic conditions (an environmental filter). We used the function 'unifrac' in the Picante library in R to calculate the fractions of unshared branch-lengths between bee-flower networks as a measure of phylogenetic turn-over (beta-diversity) between networks (Lozupone et al. 2006, Kembel et al. 2010). We included the 17 networks with at least ten species, excluding *Apis mellifera* (L.), and used only the ten most widely sampled species in each network (i.e. with the highest rank-abundance, in terms of number of plants visites). This was done since the relative occurrences and niche-width of flower visiting species, in terms of the number of plant species visited, tends to be relatively stable, irrespective of sampling intensity (Hegland et al. 2010). In five cases, the number of ties in frequency-classes prevented us to rank the ten most common species. In these cases we included all species with the same frequency as the species ranked as number 10, assuming their detectability was qualitatively similar. Although this selection criterion may have removed some common, but highly specialized (monolectic) species, we deemed it as appropriate since specialization on a single plant species rarely occurs. Indeed, specialization is generally confined to the family or generic level (oligolectics) of plants (Michener, 2007). The final dataset consisted of 17 networks and 165 bee species.

The geographic distance between each network-pair within the 17 networks was calculated based on their GPS locations (WGS 84) using the fossil package in R (Vavrek 2011). In cases where the exact GPS-locations of the study sites were unavailable we used the coordinates of the nearest known location obtained from the site-descriptions in the studies. Information on climatic conditions at each location, based on a 0.5 degree grid system, was extracted from Kottek et al. (2006). The climatic conditions at each site were defined according to the three categories; 'main climate' with factor levels; *Snow*, *Warm temperate* and *Arid*, 'precipitation' with factor levels; *Summer dry, Steppe* and *Fully humid* and 'temperature' with factor levels; *Cold arid, Hot summers, Warm summers* and *Cool summers* (Kottek et al. 2006). We calculated the Gower distances (Gower 1971) between pairs of sites according to the climatic conditions using the cluster package in R (Maechler et al. 2014) and used the distances between pairs of sites as a proxy for dissimilarities in climatic conditions.

We tested if the phylogenetic beta-diversity increased with the geographical distance between bee-flower networks and dissimilarity in the climatic conditions where the bee-flower networks had been sampled. The relationships between phylogenetic beta-diversity and geographic distance and climatic conditions were tested using Mantel tests with Spearman's correlation coefficient and 10,000 permutations. The analyses were done with the R package Vegan (Oksanen et al. 2013). In addition to the Mantel tests, we conducted a multiple regression on distance matrices (MRM) with rank correlations, allowing us to estimate the explanatory power of the geographic distance and climatic conditions. The MRM was conducted using the R package Ecodist (Goslee and Urban 2007). Finally, an average based hierarchical clustering method was used to visualize how the phylogenetic beta-diversity related to the geographical locations – in terms of countries – of the bee-flower networks. All statistical analyses were done with R version 3.1.1 (R development core team 2014).

RESULTS

Nice overlap vs. phylogenetic distance

The niche overlap, in terms of floral associations among bee species, was related to the phylogenetic distance among them (Fig. 3, Table 1). This relationship was most prevalent for the first niche dimension (NMDS1) and 10 of the 18 networks showed statistically significant K-values (Fig. 3A). In contrast, when evaluating the niche overlap among bees on the second (Fig. 3B) and third (Fig. 3C) niche dimensions (NMDS axes 2 and 3) a significant phylogenetic signal was only found in four of 17 and five of 12 networks, respectively.

The proportion of bee-flower networks displaying a significant phylogenetic signal depended on the dimensionality of the underlying dissimilarity matrix. When only networks with at least three niche dimensions (NMDS axes) were evaluated, the NMDS1 displayed a significant phylogenetic signal in 75% (i.e.12) of the networks, compared to 61% (i.e. 18) of the networks, when all networks were included (Table 1). In addition to the dependence on the niche dimension, the significance of the phylogenetic signal in the floral associations of bees also depended on the number of bee species sampled. We found a significant phylogenetic signal in niche overlap among bees in only two of the ten bee-flower networks with fewer than twenty species and only on the first NMDS axis (Fig. 3A). In contrast, the niche overlap displayed a significant phylogenetic signal on at least one of the NMDS axes in all networks with more than 20 bee species. However, the K-values in six of the eight networks with non-significant K-values on the first NMDS axis were larger than 0.78 (e.g. one minus the standard deviation of the significant K-values) and had a p-value ≤ 0.1, suggesting the presence of a phylogenetic signal also in these networks. These findings therefore suggest the presence of a phylogenetic signal in niche-overlap in 15 of the 18 examined networks.

Among the networks with > 20 species, the K-values were consistently slightly lower than one, indicating a slightly weaker phylogenetic signal than that expected under a Brownian motion mode of evolution. However, when only the most dissimilar bee species in terms of floral associations (i.e. NMDS scores < 25th or >75th quantiles) were included in the analysis, all the six significant K-values from NMDS1 were ≥ 1 (Fig. 4A). For NMDS2 and NMDS3 the results were more varied (Fig. 4 B-C).

Geographic and climatic influences on biogeography

The biogeographical analyses based on the ten most generalist bee species in each network showed that geographic distance and climatic conditions influenced the global distribution of bee taxa. The phylogenetic beta-diversity between bee-flower networks increased with geographic distance, but this increase was only present at distances up to about 5,000 km (Mantel *rho* = 0.43, p = 0.001, Fig. 5). The phylogenetic beta-diversity also increased with the dissimilarity in climatic conditions (*rho* = 0.42, p < 0.001, Fig. 5). The multiple regression on distance matrices (MRM) revealed that the geographic distance and the dissimilarity in climatic conditions together explained 35 % of the variation in phylogenetic beta-diversity among bee-flower networks (MRM, $\beta_{\text{geographic distance}} = 0.42$, p < 0.001, $\beta_{\text{dissimilarity in climatic conditions}} = 0.43$, p < 0.001, $R^2 = 0.35$, p-model < 0.001). The geographic distance among bee-flower networks and their dissimilarity in climatic conditions were not correlated (Mantel *rho* = 0.02, p = 0.38). The hierarchical clustering of the average pairwise phylogenetic beta-diversity between bee-flower networks revealed a weak split between northerly located networks and networks from the Canary Islands, Spain, Greece and South-America (Fig. 6). The northern group was further divided into a North American and a Eurasian group, which did not include the Mediterranean but did include New Zealand. The southern group was divided into a South-American and a Mediteranean/east Atlantic group.

DISCUSSION

The resource use by bees within species assemblages (bee-flower networks) displayed a phylogenetic signal, which was significant for all networks with > 20 species. Moreover, in six of the eight networks with < 20 species the phylogenetic signal tended towards a Brownian motion mode of evolution (i.e. K-values were close to, or larger than, one). The biogeographic analyses showed that the presence of taxa within species assemblages was partly determined by speciation events and the migration history of species and climatic conditions. Our findings suggest that Vellend's (2010) theory of community ecology provides a useful conceptual framework. Moreover, we show how phylogenies can provide a common currency for at least three of the four processes involved in community assembly (i.e. speciation, migration, ecological filtering).

Nice-overlap vs. phylogenetic distance

We found that the niche overlap among bee species – in terms of floral associations within species assemblages (bee-flower networks) – displayed a phylogenetic signal (Table 1, Fig. 5A-C). Our findings are in accordance with Darwin's (1859) hypothesis that ecological similarity is related to the evolutionary history of the species. Following this hypothesis, it is predicted that competitive exclusion should prevent the co-occurrence of closely related species within species assemblages, unless other environmental filters select for ecologically similar species (Webb 2000). However, this is contingent on resource limitation. Since bees depend on both nesting (Potts et al. 2005) and foraging resources, which may be further subdivided into nectar and pollen resources, it is possible that competitive exclusion only occurs between species that share resources on several niche dimensions. Additionally, the tendency for closely related species to utilize the same resource may be due to filtering processes operating on resource acquisition, as found for mammalian ecto-parasites (Krasnov et al. 2014) and flower-visitor networks spanning across several taxonomic orders (Rezende et al. 2007). In this case, one would expect bee species ensembles (*sensu* Fauth et al. (1996)) to be phylogenetically under-dispersed. Our results suggest that phylogenetically conserved traits govern the partitioning of foraging resources within bee communities. Such traits include tongue-length, which determine whether bees can access the nectar from concealed flowers, such as legumes (Michener 2007); phenology, which determines if the bees are active during the flowering of particular plant species (Oertli et al. 2005); foraging preferences related to floral rewards (Potts et al. 2003), and the capability of digesting pollen toxins (Sedivy et al. 2013b).

The tendency for floral associations to be phylogenetically confined within taxa offers a mechanistic explanation for the frequent finding that the diversity in bee species assemblages is associated with different aspects of floral diversity (Potts et al. 2003, Roulston and Goodell 2011, Winfree et al. 2011). Importantly, our results suggest that entire clades of bees may be negatively affected if the predicted impact of land-use and climate change on plant diversity (Pompe et al. 2008) shifts the floral composition towards plants not accessible to those bee taxa. Such changes have historically included the introduction of soil fertilizers and industrial fixation of atmospheric nitrogen, which both reduced legume rotations in agriculture. These changes coincided with an increased rate of bee extinctions in both Britain (Ollerton et al. 2014) and the Netherlands, where long-tongued bees have declined more than short-tongued bees during the past century (Biesmeijer et al. 2006).

We found that the statistical significance of the phylogenetic signal depended on niche dimension (Fig. 3A-C), the dimensionality of the underlying data, and on the number of bee species recorded (Table 1). Network size has previously been found to influence the probability of observing significant relationships between phylogenetic distance and ecological similarity

(Rezende et al. 2007, Slingsby and Verboom 2006). Moreover, Blomberg et al. (2003) showed that the statistical power of phylogenetic randomization tests is most robust in networks with > 20 species. Indeed, all except two networks with < 20 species showed K-values that were close to (> 0.78), or larger than, one, suggesting that a phylogenetic signal in floral visitation equivalent to that expected under a Brownian motion mode of evolution was present. However, the lack of statistical significance from the randomization tests may also reflect the nature of the ecological patterns in the data. For instance, small networks tend to be dominated by relatively common and highly inter-connected species, while larger networks include a higher proportion of rare and less-connected species (Hegland et al. 2010). It is therefore possible that functionally or behaviourally different groups of bees are underrepresented in the smaller networks, as well as in the networks in which the niche width of species has been underestimated (i.e. displays a low dimensionality) and do not fully account for the niche differentiation among species. Indeed, among the bee-flower networks with at least three niche dimensions, 75% showed a significant phylogenetic signal on the first NMDS axis. Moreover, the strength of the phylogenetic signal (K-value) increased when only the two clusters of bees with the most dissimilar niches were included in the analyses (Fig. 4A). These results suggest that species within bee species assemblages can be grouped into three categories, depending on their floral associations and phylogenetic relatedness to the other group members. Two of the groups consist of closely related species for which niche overlap is confined within each group (i.e. species ensembles *sensu* Fauth et al. (1996)). The third group consists of a cluster of bee species with varying degrees of relatedness and where resource use is not phylogenetically constrained.

Geographic and climatic influences on biogeography

The phylogenetic beta-diversity among bee species assemblages increased with geographic distance up to ca. 5,000 km (Fig. 5). The increase in phylogenetic beta-diversity with distance likely reflects the migration history (Cavender-Bares et al. 2009) and regional radiations of bee taxa. Although the low resolution of our phylogeny did not allow us to distinguish between these two processes (e.g. speciation and migration) these results do suggest a high degree of regional endemism that ultimately creates the foundation for speciation as well as dispersal events within this functionally important group of taxa. However, some of the observed relationships between phylogenetic beta-diversity and distance were caused by the presence of introduced taxa in non-native regions. For instance, whereas the presence of *Hylaeinae* species in networks in New Zealand and Japan (Appendix S1 T1) can partly be explained by natural dispersal events from Australia (Kayaalp et al. 2013) the presence of *Bombus* in New Zealand is due to anthropogenic introductions in the 20th century (Michener 2007). The clustering of individual pairs of sites according to their phylogenetic beta-diversity should therefore be interpreted with some caution. Despite this potential limitation we view the split between the two northern groups and the southern group as robust since the two northern regions (North-America and North-Eurasia) do share many Holarctic taxa from the genera *Hylaeus* (Kayaalp et al. 2013), *Andrena* (Michener 2007) and *Bombus* (Hines 2008), due to past speciation and migration events.

We also found a significant increase in phylogenetic beta-diversity with dissimilarity in present day climatic conditions (Fig. 5), suggesting that environmental filtering pose barriers to the global distribution of bee taxa. The increase in phylogenetic beta-diversity with dissimilarities in climatic conditions may reflect past migrations of bee taxa into areas of favourable climates. For instance, the predominantly northerly-distributed genus *Bombus* originated at high altitudes and migration events between and across continents coincide with global cooling periods and subsequent habitat expansions (Hines 2008). Moreover, *Bombus* species seem less affected by climatic filters associated with altitude and latitude than other bees within the regional species pool (Hoiss et al. 2012, Sydenham et al. 2015). However, it is possible that the climatic gradient used in this study was too coarse to capture climatic differences at intra-continental spatial scales < 5,000 km. Indeed, environmental filters, such as elevation (Hoiss et al. 2012) and latitude (Sydenham et al. 2015), are important determinants of the composition of local bee species assemblages. Environmental filters operating at a regional scale may therefore have selected for some closely related species partly resulting in the observed positive relationship between phylogenetic beta-diversity and distance.

CONCLUDING REMARKS

The inclusion of community phylogenetics into the theory of community ecology allows for a predictive community ecology that is theoretically reducible to mechanisms operating at the population level. This study demonstrates that the degree of niche overlap between species-pairs within species assemblages depends on the phylogenetic distance between them (hypothesis 1) and that speciation and migration history, as well as ecological filtering (hypothesis 2 and 3), are important determinants of community composition at the global scale. A further understanding of such distributional patterns will aid the conservation of phylogenetically diverse species assemblages of bees. Specifically, we suggest that future studies on bees on the local scale aim at investigating whether niche overlap in terms of other local resources, such as nesting substrates, are phylogenetically conserved. We also recommend more detailed community level approaches in order to separate the phylogenetic signals in the nectar and pollen preferences of bees. At the global scale, it will be important to separate the influence of speciation and migration events and their interaction on the phylogenetic turnover among bee species assemblages. This will help identify areas that act as global sources of bee diversity where speciation occurs at relatively high rates and from which species migrate to neighbouring regions.

ACKNOWLEDGEMENTS

We wish express our gratitude to the community of ecologists working on plant-pollinator networks for making their data easily accessible. A. N. and S. J. H. were supported by The Research Council of Norway through the Norwegian environmental research towards 2015 program (MILJØ2015: project 230279 / E50 awarded A. N. and project 204403 awarded S. J. H.).

REFERENCES

Almeida, E. A. B. & Danforth, B. N. (2009) Phylogeny of colletid bees (Hymenoptera: Colletidae) inferred from four nuclear genes. *Molecular Phylogenetics and Evolution,* **50**, 290-309.

Ascher, J. S. & Pickering, J. (2015) *Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila).* url: http://www.discoverlife.org/mp/20q?guide=Apoidea_species.

Biesmeijer, J. C. et al. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* **313**, 351-354.

Blomberg, S. P. et al. (2003) Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* **57**, 717-745.

Cameron, S. A. et al. (2007) A comprehensive phylogeny of the bumble bees (Bombus). *Biological Journal of the Linnean Society* **91**, 161-188.

Cardinal, S. & Danforth, B. N. (2013) Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20122686.

Cavender-Bares, J. et al. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693-715.

Danforth, B. N. et al. (2013) The Impact of Molecular Data on Our Understanding of Bee Phylogeny and Evolution. *Annual Reviews of Entomology* **58**, 57-78.

Danforth, B. N. et al. (2006) Analysis of family-level relationships in bees (Hymenoptera : Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. *Molecular Phylogenetics and Evolution* **39**, 358-372.

Darvill, B. et al. (2004) Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* **107**, 471-478.

Darwin, C. (1859) *On the origin of species or the preservation of favoured races in the struggle for life*. John Murray.

de Bello, F. et al. (2013) Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* **36**, 393-402.

Elton, C. (1946) Competition and the structure of ecological communities. *Journal of Animal Ecology* **15**, 54-68.

Fauth, J. et al. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The American Naturalist* **147**, 282-286.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology* **71**, 757-764.

Gonzalez, V. H. et al. (2012) Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. *Systematic Entomology* **37**, 261-286.

Goslee, S. C. & Urban, D. L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* **22**, 1-19.

Gower, J. C. (1971) A General Coefficient of Similarity and Some of Its Properties. *Biometrics* **27**, 857-871.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences* **326**, 119-57.

Hedtke, S. et al. (2013) The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evolutionary Biology* **13**, 138.

Hegland, S. J. et al. (2010) How to monitor ecological communities cost-efficiently: The example of plant-pollinator networks. *Biological Conservation* **143**, 2092-2101.

Hines, H. M. (2008) Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera : Apidae : Bombus). *Systematic Biology* **57**, 58-75.

Hoiss, B. et al. (2012) Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B-Biological Sciences* **279**, 4447-4456.

ITIS (2014) *The Integrated Taxonomic Information System on-line database*. url: http://www.itis.gov/.

Kayaalp, P. et al. (2013) Rapid diversification in Australia and two dispersals out of Australia in the globally distributed bee genus, Hylaeus (Colletidae: Hylaeinae). *Molecular Phylogenetics and Evolution* **66**, 668-678.

Keddy, P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**, 157-164.

Kembel, S. W. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463-1464.

Kottek, M. et al. (2006) World map of the Koppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**, 259-263.

Krasnov, B. R. et al. (2014) Co-occurrence and phylogenetic distance in communities of mammalian ectoparasites: limiting similarity versus environmental filtering. *Oikos* **123**, 63-70.

Kuhlmann, M. et al. (2009) Molecular phylogeny and historical biogeography of the bee genus Colletes Latreille, 1802 (Hymenoptera: Apiformes: Colletidae), based on mitochondrial COI and nuclear 28S sequence data. *Insect Systematics & Evolution* **40**, 291-318.

Larkin, L. L. et al. (2006) Phylogeny of the Callandrena subgenus of Andrena (Hymenoptera : Andrenidae) based on mitochondrial and nuclear DNA data: Polyphyly and convergent evolution. *Molecular Phylogenetics and Evolution* **38**, 330-343.

Lozupone, C. et al. (2006) UniFrac – An online tool for comparing microbial community diversity in a phylogenetic context. *BMC Bioinformatics* **7**, 1-14.

Maechler, M. et al. (2014). *cluster: Cluster Analysis Basics and Extensions. R package version 1.15.3,* http://CRAN.R-project.org/package=cluster.

McGill, B. J. et al. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**, 178-185.

Michener, C. D. (2007) *The bees of the world*. Johns Hopkins University Press.

Murray, T. E. et al. (2012) Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology* **49**, 998-1008.

Oertli, S. et al. (2005) Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). *European Journal of Entomology* **102**, 53-63.

Oksanen, J. et al. (2013) *vegan: Community Ecology Package. R package version 2.3-0,* http://CRAN.R-project.org/package=vegan.

Ollerton, J. et al. (2014) Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* **346**, 1360-1362.

Pompe, S. et al. (2008) Climate and land use change impacts on plant distributions in Germany. *Biology Letters* **4**, 564-567.

Potts, S. G. et al. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**, 345-353.

Potts, S. G. et al. (2003) Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* **84**, 2628-2642.

Potts, S. G. et al. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* **30**, 78-85.

Praz, C. J. et al. (2008) Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). *Molecular Phylogenetics and Evolution* **49**, 185-197.

R development core team 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Revell, L. J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217-223.

Rezende, E. L. et al. (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925-928.

Roulston, T. H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* **56**, 293-312.

Sedivy, C. et al. (2013a) Molecular phylogeny of the bee genus Hoplitis (Megachilidae: Osmiini) - how does nesting biology affect biogeography? *Zoological Journal of the Linnean Society* **167**: 28-42.

Sedivy, C. et al. (2013b) Host range evolution in a selected group of osmiine bees (Hymenoptera: Megachilidae): the Boraginaceae-Fabaceae paradox. *Biological journal of the Linnean Society* **108**, 35-54.

Slingsby, J. A. & Verboom, G. A. (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenoid sedges (Cyperaceae : Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist* **168**, 14-27.

Steffan-Dewenter, I. et al. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421-1432.

Swenson, N. G. (2014) *Functional and Phylogenetic Ecology in R,* Springer New York.

Sydenham, M. A. K. et al. (2015) Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography* **38**, 140-153.

Vamosi, S. M. et al. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* **18**, 572-592.

Vavrek, M. J. (2011) fossil: Palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica* **14**, 1T. http://palaeo-electronica.org/2011_1/238/index.html

Vellend, M. (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology* **85**, 183-206.

Warren, D. L. et al. (2014) Mistaking geography for biology: inferring processes from species distributions. Trends in Ecology and Evolution **29**, 572-580.

Webb, C. O. (2000) Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist* **156**, 145-155.

Webb, C. O. et al. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics* **33**, 475-505.

Weiher, E. et al. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2403-2413.

Weiher, E. & Keddy, P. A. (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* **74**, 159-164.

Williams, N. M. et al. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* **143**, 2280-2291.

Winfree, R. et al. (2011) Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics* **42**, 1-22.

Tables and Figures

Table 1 Phylogenetic signal in the floral associations of bees along each NMDS axis in bee-flower networks with ≥ 10 species. K-values close to or equal to one indicate that the floral associations of bees follow a Brownian motion mode of evolution. K-values below and above one indicate that the phylogenetic signal was weaker or stronger than expected under a Brownian motion mode of evolution, respectively. The statistical significance ($p < 0.05$) of the phylogenetic signal was tested by comparing the observed K-value to a distribution of K-values obtained from a one-sided randomization test. Significant values are marked in bold.

			Blomsberg's K-value on individual NMDS axes							
			NMDS1		NMDS2		NMDS3		NMDS4	
Network	Sp	Stress	K	P	K	P	K	P	K	P
M2	10	0.017	**1.38**	**0.003**	0.62	0.302	-	-	-	-
NN	10	0.023	1.17	0.051	0.57	0.992	0.87	0.476	-	-
DH	11	0.039	0.95	0.102	0.85	0.226	-	-	-	-
HN	11	0.011	0.72	0.812	0.78	0.593	0.99	0.154	-	-
SA	11	0.001	0.38	0.899	0.41	0.754	-	-	-	-
DI	12	<0.001	1.03	0.060	0.81	0.316	-	-	-	-
DO	12	0.052	**1.20**	**0.010**	0.70	0.910	0.99	0.118		
PA	12	0.014	0.50	0.579	0.45	0.742	-	-	-	-
SL	15	0.081	0.81	0.091	0.75	0.152	0.64	0.379	-	-
SM	16	0.064	0.89	0.074	-	-	-	-	-	-
A1	25	0.090	**0.89**	**0.004**	0.50	0.416	0.56	0.232	-	-
BE	28	0.042	**0.78**	**0.048**	0.75	0.078	0.65	0.298	-	-
MT	31	0.067	**0.80**	**0.035**	0.72	0.131	**0.78**	**0.049**	-	-
SH	35	0.105	**0.93**	**0.002**	**0.76**	**0.036**	**0.82**	**0.009**	-	-
HR	46	0.126	**0.77**	**0.008**	**0.76**	**0.008**	0.54	0.537	-	-
KT	56	0.148	**0.69**	**0.014**	**0.72**	**0.006**	**0.75**	**0.004**	-	-
CO	81	0.151	**0.77**	**<0.001**	0.54	0.282	**0.65**	**0.004**	-	-
PD	236	0.165	**0.86**	**<0.001**	**0.63**	**0.000**	**0.54**	**0.000**	0.47	0.117

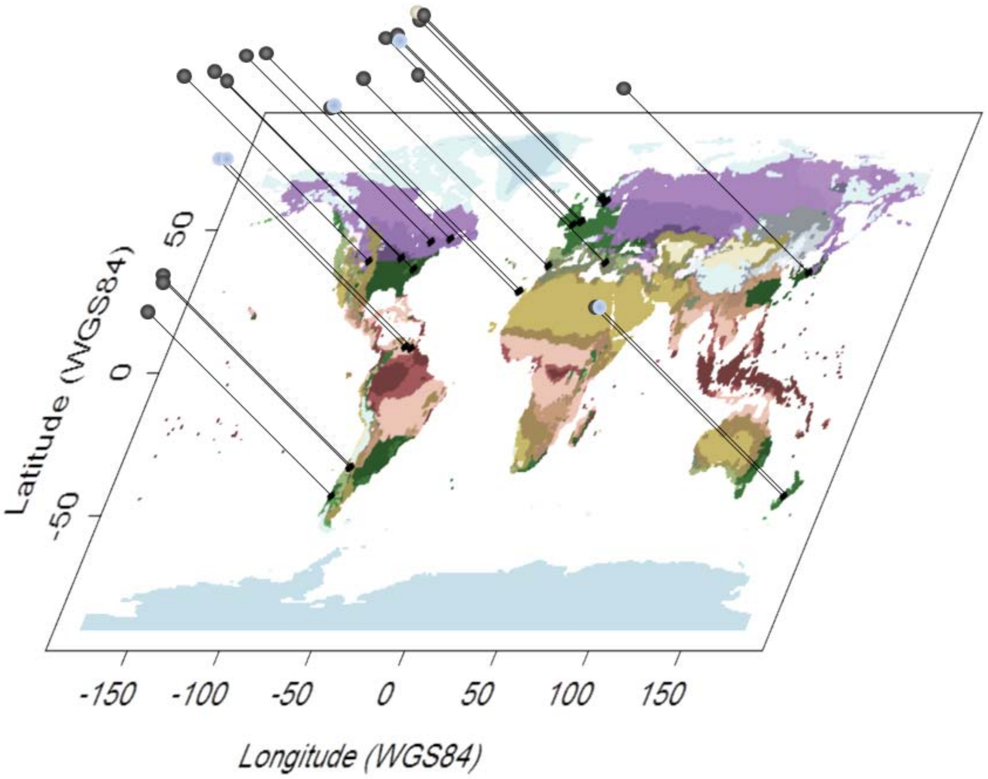


Figure 1 World map coloured according to climatic conditions (after Kottek, M. et al. (2006)) and the geographic locations of the bee-flower networks included in this study. Dark pins show the locations of the networks used for both the global and community scale analyses, two networks are in the same location on the map but at different elevations. Bright pins show the locations of the networks that were used exclusively in the community scale analysis (i.e. the species richness was ≥ 10), including *Apis mellifera*. Blue pins show the locations of the five networks with <10 species that were only included in the construction of the phylogeny. See Appendix S1 for details.

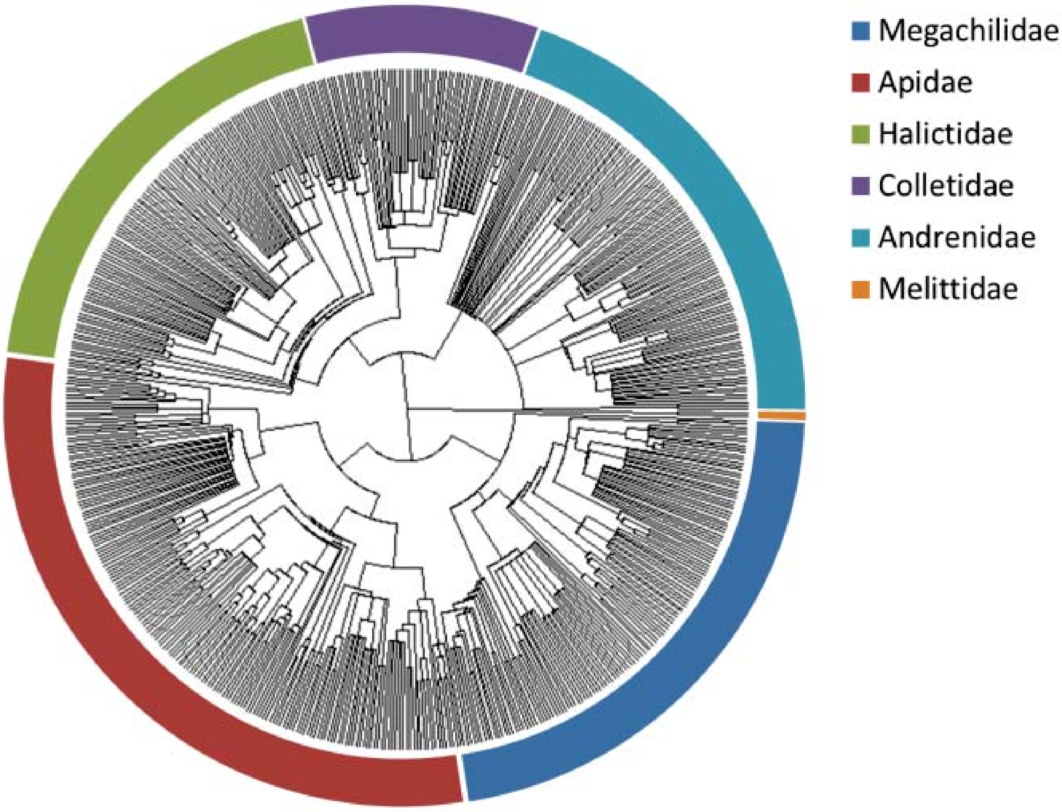


Figure 2 The hypothesized phylogenetic relationships between the 592 species of bees sampled in 26 bee-flower networks. Two species belonged to the Melittidae. The long tongued bees included 130 and 175 species within the Megachilidae and Apidae families, respectively. Within the short tongued bees, 112 species belonged to Halictidae, 56 species to Colletidae and 117 to Andrenidae.

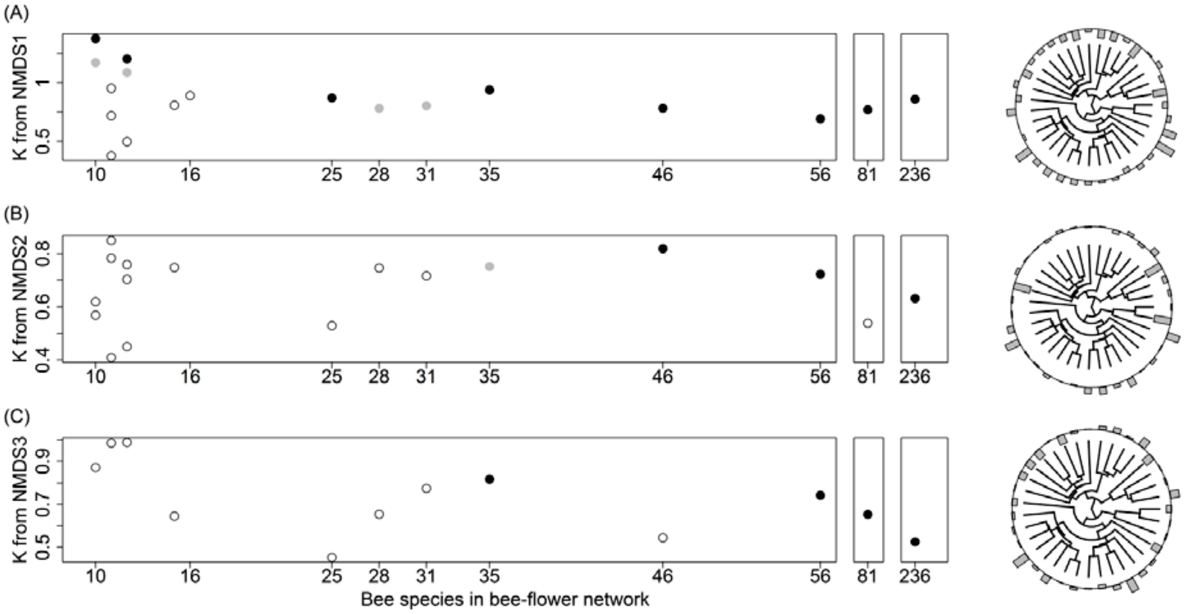


Figure 3 Phylogenetic signal of the similarity in floral associations of bees when including all species in bee-flower networks (≥10 bee species). The phylogenetic signal within each network was quantified by means of Blomberg's K-value and tested against a null distribution of K-values obtained by shuffling the species scores on the first (A), second (B) and third (C) NMDS axis. The statistical significance of the K-values are indicated by open ($p > 0.05$), grey ($0.025 < p < 0.05$) and black ($p < 0.025$) circles. The phylogenies on the right show the scores on the first, second and third NMDS axes for the bee-flower network SH with 35 bee species. Positive and negative scores on the NMDS axes are shown as outward and inward pointing bars, respectively. The heights of the bars indicate the numeric value of the scores on the NMDS axes.

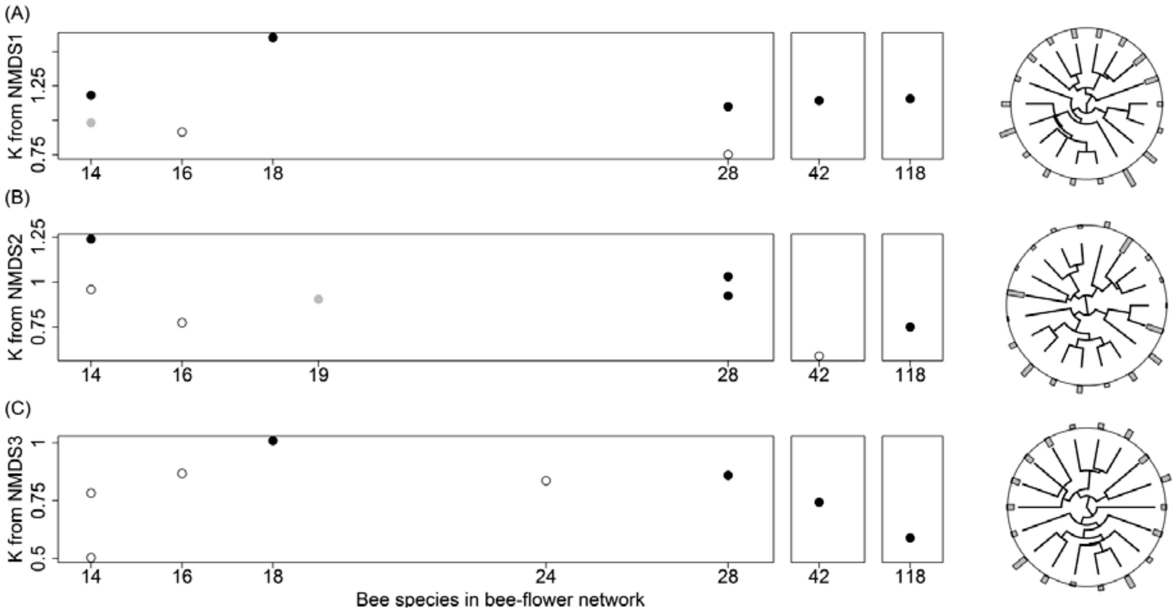


Figure 4 Phylogenetic signal of the similarity in floral associations of bees in bee-flower networks followed the Brownian motion mode of evolution when considering only species with scores outside the 25th or 75th quantiles on the first (A), second (B) and third (C) NMDS axes . The statistical significance of the K-values are indicated by open ($p > 0.05$), grey ($0.025 < p < 0.05$) and black ($p < 0.025$) circles. The phylogenies on the right show the species scores on the first (18 species), second (19 species) and third (18 species) NMDS axes for the bee-flower network SH. Positive and negative scores on the NMDS axes are shown as outward and inward pointing bars, respectively. The heights of the bars indicate the numeric value of the scores on the NMDS axes.

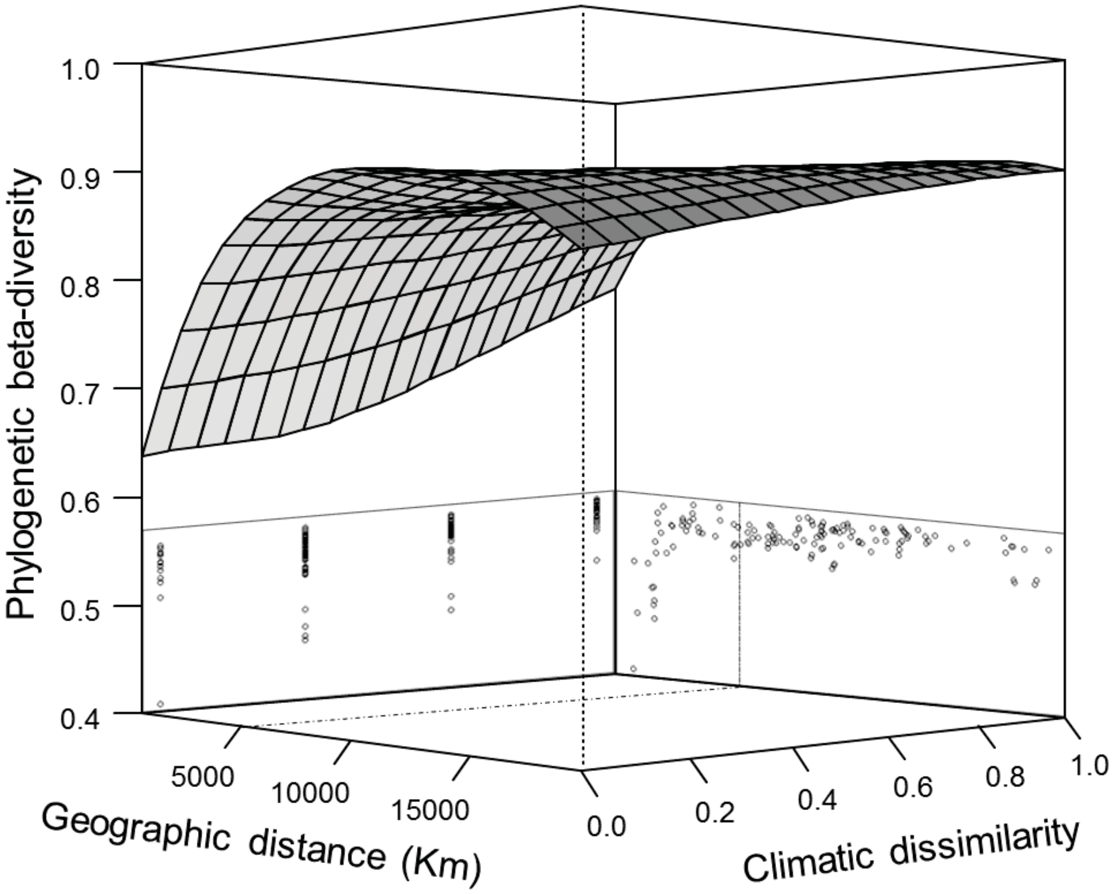


Figure 5 Phylogenetic beta-diversity among bee-flower network pairs increased with both geographic distance and dissimilarity in climatic conditions. The two scatterplots inside the three dimensional box show the relationships between the phylogenetic beta-diversity (y-axis range: 0.4-1) and geographic distance and climatic dissimilarity. The dotted reference line shows how the increase in phylogenetic beta-diversity with geographic distance seemed to saturate at ca 5,000 km.

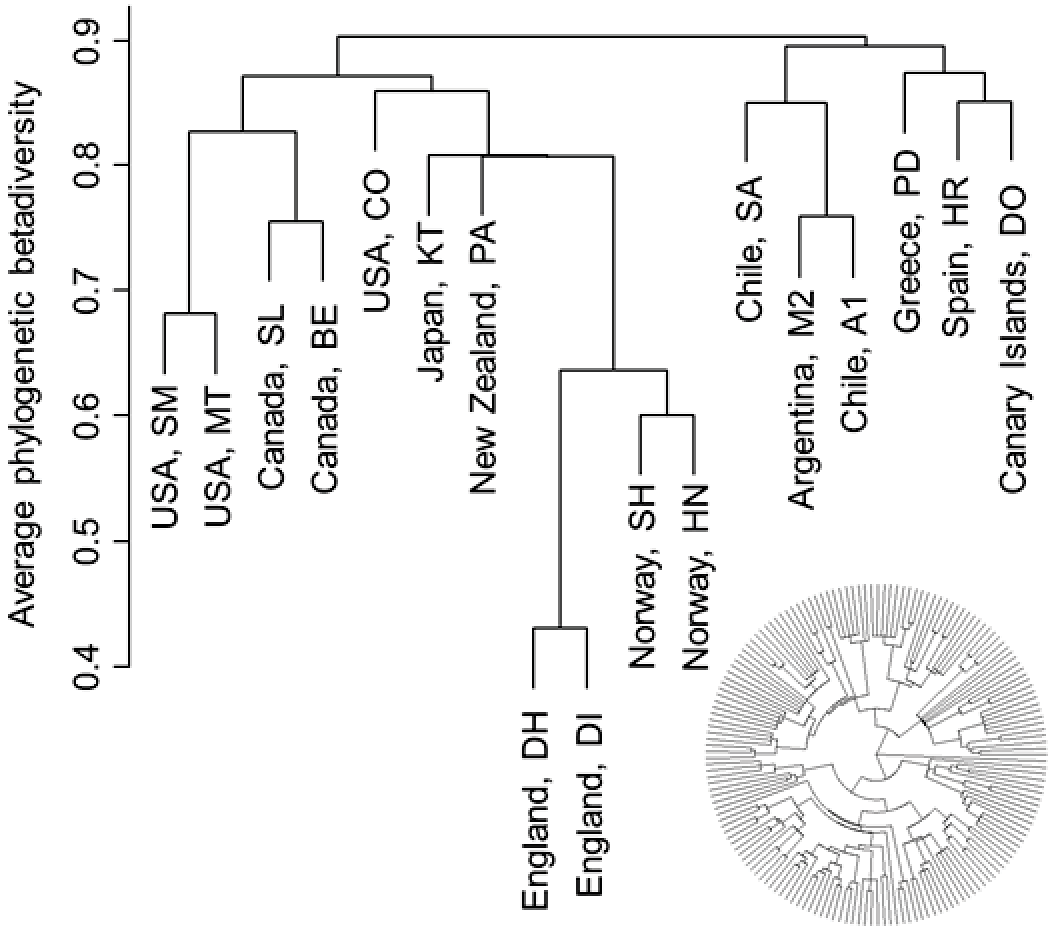


Figure 6 Average pair-wise phylogenetic beta-diversity between clusters of the 17 bee-flower networks with ≥ 10 species, excluding *Apis mellifera*. The country of origin is displayed together with the abbreviation used for each network (Table A1). The hypothesized phylogeny for the 165 species included in the analysis is shown in the figure's bottom right corner.

Supplementary material for paper I

Appendix S1 Summary statistics of the 26 networks included in the analyses. The majority of the networks were obtained from Rezende et al. (2007). The table shows the quantile distribution of the number of plant species different bee species were observed to visit (degrees). The total number of interactions between bees and plants are noted as the ∑ of all degrees in each network.

	Taxa in network		Quantile distribution of degrees					
Network	Bees*	Plants	0 %	50 %	100 %	∑ degrees	Country	Reference
M1	3	4	1	1	3	5	Argentina	Medan et al. (2002)**
A3	3	5	2	2	3	7	Chile	Arroyo et al. (1982)**
OU	5	20	3	3	14	31	Spain	Olesen unpubl**
MM	5	7	1	2	5	14	England	Memmott (1999)**
RR	6	11	1	1.5	8	16	Venezuela	Ramirez and Brito (1992)**
RZ	7	27	1	7	17	55	Venezuela	Ramirez (1989)**
A2	7	13	1	3	8	22	Chile	Arroyo et al. (1982)**
PG	9	15	1	1	9	20	New Zealand	Primack (1983)**
NN	10	16	1	4.5	12	51	Norway	Nielsen and Totland (2014)
SA	11	23	1	4	21	77	Chile	Smith-Ramirez et al. (2005)
M2	11	9	1	2	4	20	Argentina	Medan et al. (2002)
DH	11	16	1	1	10	30	England	Dicks et al. (2002)
DO	12	10	1	3.5	6	41	Canary Islands	Dupont et al. (2003)
DI	12	17	1	2.5	10	43	England	Dicks et al. (2002)

HN	12	39	1	5	25	104	Norway	Hegland et al. (2010)
PA	13	25	1	2	10	37	New Zealand	Primack (1983)
SL	15	13	3	5	11	88	Canada	Small (1976)
SM	16	7	1	1	6	30	USA	Schemske et al. (1978)
A1	25	28	1	2	13	75	Chile	Arroyo et al. (1982)
BE	28	12	1	1	8	53	Canada	Barrett and Helenurm (1987)
MT	31	13	1	3	7	99	USA	Motten (1986)
SH	35	41	1	4	23	205	Norway	Appendix S2 Table 1
HR	47	24	1	2	14	134	Spain	Herrera (1988)
KT	58	75	1	2	25	253	Japan	Kato et al. (1990)
CO	84	82	1	3	37	510	USA	Clements and Long (1923)
PD	240	131	1	3	104	1325	Greece	Petanidou (1991)

* Only bees that were identified to species were included in each network. ** Networks < 10 species only used to supply species for constructing the phylogeny.

References

Arroyo, M. T. K. et al. (1982) Community Studies in Pollination Ecology in the High Temperate Andes of Central Chile .1. Pollination Mechanisms and Altitudinal Variation. *American Journal of Botany* **69**, 82-97.

Barrett, S. C. H. and Helenurm, K. (1987) The Reproductive-Biology of Boreal Forest Herbs .1. Breeding Systems and Pollination. *Canadian Journal of Botany* **65**, 2036-2046.

Clements, F. E. and Long, F. L. (1923) *Experimental pollination; an outline of the ecology of flowers and insects*. Carnegie Institution of Washington.

Dicks, L. V. et al. (2002) Compartmentalization in plant-insect flower visitor webs. *Journal of Animal Ecology* **71**, 32-43.

Dupont, Y. L. et al. (2003) Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* **26**, 301-310.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1-10.

Hegland, S. J. et al. (2010) How to monitor ecological communities cost-efficiently: The example of plant-pollinator networks. *Biological Conservation* **143**, 2092-2101.

Herrera, J. (1988) Pollination Relationships in Southern Spanish Mediterranean Shrublands. *Journal of Ecology* **76**, 274-287.

Kato, M. et al. (1990). *Insect-flower relationship in the primary beech forest of Ashu, Kyoto: an overview of the flowering phenology and the seasonal pattern of insect visits*. Contributions from the Biological Laboratory, Kyoto University 309-375.

Medan, D. et al. (2002) Plant-pollinator relationships at two altitudes in the Andes of Mendoza, Argentina. *Arctic Antarctic and Alpine Research* **34**, 233-241.

Memmott, J. (1999) The structure of a plant-pollinator food web. *Ecology Letters* **2**, 276-280.

Motten, A. F. (1986) Pollination Ecology of the Spring Wildflower Community of a Temperate Deciduous Forest. *Ecological Monographs* **56**, 21-42.

Nielsen, A. and Totland, Ø. (2014). Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos* **123**, 323-333.

Petanidou, T. (1991) *Pollination ecology in a phryganic ecosystem.* Unp. Aristotelian University.

Primack, R. B. (1983) Insect Pollination in the New-Zealand Mountain Flora. *New Zealand Journal of Botany* **21**, 317-333.

Ramirez, N. (1989). Biología de polinización en una comunidad arbustiva

tropical de la alta Guyana Venezolana. *Biotropica* **21**, 319-330.

Ramirez, N. and Brito, Y. (1992) Pollination Biology in a Palm Swamp Community in the Venezuelan Central Plains. *Botanical Journal of The Linnean Sociecty* **110**, 277-302.

Rezende, E. L. et al. (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925-928.

Schemske, D. W. et al. (1978) Flowering Ecology of Some Spring Woodland Herbs. *Ecology* **59**, 351-366.

Small, E. (1976) Insect pollinators of the Mer Bleue peat bog of Ottawa. *Canadian Field Naturalist* **90**, 22-28.

Smith-Ramirez, C. et al. (2005) Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloe Island, Chile. *Botanical Journal of The Linnean Society* **147**, 399-416.

Appendix S2 Bee-flower network provided by Sydenham, M.A.K., Moe, S.R., Eldegard, K. and Totland, Ø. Bees were collected on flowers on 39 days from 25.05.13 to 04.09.2013 at three different localities by the main author. All three localities were within 1 km of each other so that all bees could be assumed to be part of the same community (World Geodetic System 84; **locality 1:** lat = 59˚59’57.099, lon = 10˚57’29.779 **locality 2:** lat = 59˚59’48.235, lon = 10˚57’24.372 **locality 3:** lat = 60˚00’10.965, lon = 10˚58’17.789). Sampling took place between 12 PM and 6 PM on sunny days with little wind and temperatures above 15˚C. During each sampling event random transect walks were conducted for one hour in each locality, discounting time spent on handling bees. We used random transect walks since flowers showed a spatio-temporal variation in distribution. This method allowed us to avoid spending time on flower-free patches. All bees that were observed visiting flowers within 1.5 meters from the observer were collected, the plant species noted, and brought back to the entomological laboratory at the Norwegian University of Life Sciences for pinning, labeling and Identification. All specimens are stored in the entomology collection at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences.

	Andrena bicolor	Andrena fucata	Andrena semilaevis	Andrena subopaca	Bombus bohemicus	Bombus campestris	Bombus hortorum	Bombus humilis	Bombus hypnorum	Bombus lapidarius	Bombus lucorum aggr	Bombus pascuorum	Bombus pratorum	Bombus ruderarius	Bombus soroeensis	Bombus sporadicus	Bombus sylvarum	Bombus sylvestris	Chelostoma campanularum	Chelostoma florisomne	Dufourea dentriventris	Eucera longicornis	Halictus tumulorum	Hylaeus angustatus	Hylaeus communis	Hylaeus confusus	Hylaeus rinki	Lasioglossum albipes	Lasioglossum fratellum	Lasioglossum fulvicorne	Lasioglossum leucopus	Lasioglossum rufitarse	Megachile alpicola	Nomada flavoguttata	sphecodes geofrellus
Vicia sepium	0	0	0	0	0	0	9	2	0	2	0	16	0	12	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus pratensis	0	0	0	0	0	0	3	0	0	0	0	12	0	3	0	0	14	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Raununculus acris	0	0	0	18	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	63	0	0	6	0	1	0	1	9	1	1	1	1	0	1	1

Silene dioica	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	2	0	1	1	0	1	0	1	0	0	1	3	0	2	0	1	0	0	3	0	0	1	0	0	0	0	3	1	1	0	0	0	2	0
Glechoma hederacea	0	0	0	0	0	0	0	0	0	0	0	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium sylvaticum	0	2	0	0	0	0	0	0	4	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus idaeus	0	1	0	0	0	0	0	0	0	0	7	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raununculus repens	0	0	0	4	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	14	0	0	2	0	0	0	0	3	0	0	0	0	0	2	0
Hieracium sp	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	3	0	0	2	0	2	0	0	0	0	0	2	0
Trifolium medium	0	0	0	0	0	0	21	4	0	1	0	10	0	18	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium hybridum	0	0	0	0	0	0	1	0	0	13	4	17	1	1	2	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cirsium vulgare	0	0	0	0	1	0	0	2	1	32	2	22	4	9	13	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stellaria nemorum	0	0	0	5	0	0	0	0	0	3	0	2	0	2	1	0	2	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0
Solidago virgaurea	0	0	0	0	12	0	0	0	3	11	5	22	13	5	3	0	15	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Trifolium pratense	0	0	0	0	0	0	9	0	0	1	1	21	0	1	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium murorum	0	0	0	0	0	0	0	1	0	43	16	7	1	0	7	0	10	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
Filipendula ulmaria	0	1	0	1	0	0	0	0	1	0	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Vicia cracca	0	0	0	0	0	0	0	0	0	0	0	8	0	6	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium repens	0	0	0	0	0	0	0	0	0	1	1	4	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geum urbanum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypericum maculatum	0	0	0	6	0	0	0	0	0	2	2	4	0	0	0	0	1	0	0	0	0	0	0	0	1	1	12	1	0	0	1	0	0	0	0
Galeopsis tetrahit	0	0	0	0	0	0	6	0	0	0	0	19	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angelica sylvestris	0	0	0	0	1	0	0	0	0	1	16	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
Lotus corniculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stachys palustris	0	0	0	0	0	0	1	0	0	0	0	6	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	6	2	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	2	0	0	0	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Chamerion angustifolium	0	0	0	0	0	0	0	0	0	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium umbellata	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Centaurea jacea	0	0	0	0	0	1	0	0	0	0	0	14	0	8	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lapsana communis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aegopodium podagraria	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium montanum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla tormentilla	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	6	1	0	0	0	0	0	0	0
Achillea millefolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Veronica chamaedrys	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthriscus sylvestris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium foliosa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbarea vulgaris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Paper II

Ecography 38: 140–153, 2015
doi: 10.1111/ecog.00938
© 2014 The Authors. Ecography © 2014 Nordic Society Oikos
Subject Editor: Ken Kozak. Accepted 2 June 2014

Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages?

Markus Arne Kjær Sydenham, Stein R. Moe, Ørjan Totland and Katrine Eldegard

M. A. K. Sydenham (markus.sydenham@nmbu.no), S. R. Moe, Ø. Totland and K. Eldegard, Dept of Ecology and Natural Resource Management, Norwegian Univ. of Life Sciences, POB 5003, NO-1432 Ås, Norway.

A central goal in ecology is to develop theories that explain the diversity and distribution of species. The evolutionary history of species and their functional traits may provide mechanistic links between community assembly and the environment. Such links may be hierarchically structured such that the strength of environmental filtering decreases in a step-wise manner from regional conditions through landscape heterogeneity to local habitat conditions. We sampled the wild bee species assemblages in power-line strips transecting forests in south-eastern Norway. We used altitude, landscape diversity surrounding sites and plant species composition, together with total plant cover as proxies for regional, landscape and local environmental filters, respectively. The species richness and abundance of wild bees decreased with altitude. The reduction in species richness and abundance was accompanied by a phylogenetic clustering of wild bee individuals. Furthermore, regional filters followed by local filters best explained the structure of the functional species composition. Sites at high altitudes and sites with Ericaceae-dominated plant communities tended to have larger bees and a higher proportion of social and spring-emerging bees. When *Bombus* species were excluded from the analysis, the proportion of pollen specialists increased with the dominance of Ericaceae. Furthermore, we also found that the taxonomic, phylogenetic and functional compositional turnover between sites was higher in the northern region than in the southern part of the study region. Altogether, these results suggest that regional filters drive the species richness and abundance in trait-groups whereas local filters have more descrete sorting effects.

We conclude that the model of multi-level environmental filters provides a good conceptual model for community ecology. We suggest that future studies should focus on the relationship between the biogeographical history of species and their current distribution, and on the assumption that closely related species do indeed compete more intensely than distantly related species.

A main goal in ecology is to develop general theories that explain how and why biodiversity varies among regions, landscapes and communities. For instance, communities always consist of a few abundant and many rare species (McGill et al. 2007). However, despite being an area of intensive research for at least three decades, attempts to determine the factors driving the structure of communities has yielded few general rules, partly due to the frequent focus on only a few species (Lawton 1999). A community is defined as a group of species found within a geographic boundary. Within the community, monophyletic groups of species, such as bees, are referred to as species assemblages. Further, a group of community members that share resources are defined as a local guild when composed of a polyphyletic group and a species ensemble if members have a common ancestor (Fauth et al. 1996).

Both environmental constraints and species interactions structure communities (Cornell and Lawton 1992, Keddy 1992). For instance, species belonging to the same local guild or species ensemble may compete for resources. Assuming that differences in the resource requirements of individuals are the result of a Brownian-motion mode of evolution, the strength of interactions between community-members should decrease as the phylogenetic distance between them increases (Webb 2000, Blomberg and Garland 2002). Following this rationale, Elton (1946) concluded that competitive exclusion shapes local communities causing the relatively low species-to-genus ratio observed in local species assemblages, compared to that of the regional species pools. However, if strong competitive interactions between species drive the process of species assembly, one should expect the species richness of local communities to saturate along a gradient of regional species richness. This is rarely the case because local richness tends to increase proportionately with regional species richness, suggesting that environmental and biogeographic factors, rather than species interactions, structures community composition (Cornell and Lawton 1992, Lawton 1999, Gaston 2000).

One potential explanation for the seemingly weak link between species interactions and community assembly may be that other processes have a stronger effect (Lawton 1999). Keddy (1992) suggested that communities consist of a subset of species from the regional species pool that have successfully passed through a series of environmental filters acting at different spatial scales. Furthermore, he suggested that species interactions could be integrated into the model by viewing competition as a local filter that favoured strong competitors. Following the concept of multi-level filters, Lawton (1999) suggested that species interactions may be of lower importance in the structuring of species assemblages, and that attention should be on higher level filters. Although they did not include competition as a local variable, the claims of Lawton were partly supported by de Bello et al. (2013). They found that large-scale filters, such as altitude, were related to differences in the central tendency of functional traits between plant assemblages. In contrast, local filters, such as soil conditions, were primarily related to the functional dispersion between species assemblages.

The most commonly used measures in assessing community changes along environmental gradients are species richness and abundance, although these metrics do not provide complete ecological information (Cadotte et al. 2011). Therefore, different measures of functional diversity have been proposed to improve the theory of community assembly (McGill et al. 2006, Petchey and Gaston 2006). Since functional traits provide more mechanistic links between species and their environment (Cadotte et al. 2011), they may improve our understanding of general patterns in community ecology (McGill et al. 2006).

The development of the ‘net relatedness index’ and the ‘nearest taxon index’ allow the degree of phylogenetic relationship between species within communities to be incorporated into community ecology, as opposed to the relatively coarse species-to-genus ratio (Webb 2000). Webb et al. (2002) suggested that four possible scenarios of phylogenetic structure could be defined, based on the phylogenetic history of traits and species. Each scenario reveals whether the community is structured by competition or environmental filters, assuming that ecologically similar species compete more intensely than ecologically different species. 1) If traits are conserved within sister clades, a clustered phylogenetic structure within communities suggests that environmental filters ‘force’ closely related species together. Conversely, 2) if the phylogenetic distance between community-members is large, interspecific competition limits the coexistence of ecologically similar species. 3) If the same traits are not evolutionarily fixed within clades, but appear frequently in sister clades; large phylogenetic distances between community members suggest that environmental filters remove ecologically different species from the community. 4) Following the same reasoning as in 3), phylogenetic clustering would be expected if competition, rather than environmental filters, shapes the community composition (Webb et al. 2002).

Successful integration of phylogenetic relationships, life-history traits and environmental filters in community ecology requires a well-described species pool. In addition, the communities should consist of species that are relatively sedentary, to minimize the probability of migration masking links between life-history traits and environmental conditions. As such, bees (Hymenoptera: Apiformes) provide good model organisms. Their phylogeny is relatively well resolved (Michener 2007), they are central place foragers and have relatively small home ranges (typically within 1 km) (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). Moreover, the life-history and ecology of northern Europe’s bee species have been described in detail (Westrich 1989). Furthermore, the factors affecting species richness, abundance and diversity of bees has received increasing attention during the past decade (reviewed by Winfree et al. 2011). Finally, recent studies have linked the life-history traits of bees to environmental perturbations (Williams et al. 2010, Ricotta and Moretti 2011) and altitudinal gradients (Hoiss et al. 2012).

The main aim of this study was to create a conceptual model of bee species assemblages based on the phylogeny and life-history traits of bees. Our hypothesized model (Fig. 1) conceptualizes the multi-level filters suggested by Keddy (1992) and others (Poff 1997, Webb et al. 2002, de Bello et al. 2013). The model suggests that any observed species assemblage is the outcome of hierarchically structured environmental filters. The regional filters sort the entire regional species pool. Regional filters include broad scale constraints, such as climatic conditions (Hoiss et al. 2012). Landscape filters may include the spatial configuration of the landscape (Westrich 1996, Steffan-Dewenter et al. 2002, Williams et al. 2010) and landscape diversity (Murray et al. 2012). An important filter at the local level may be the availability of foraging resources (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Müller et al. 2006). In all cases, we expected the effect of the regional filter to be more pronounced than the landscape filter, which we expected to have a larger effect than the local filter.

In contrast to being a product of environmental filters, dissimilarities in species composition between species assemblages may be a result of the geographic distance between them. Certainly, on a global scale there are strong spatial

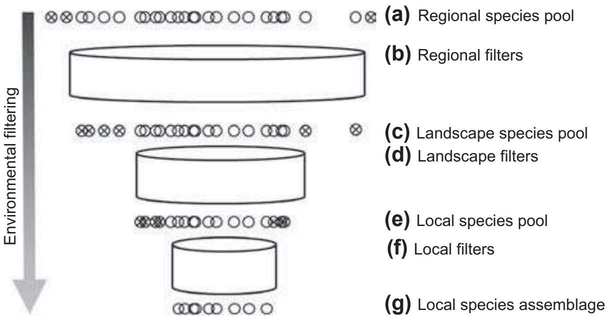


Figure 1. The hierarchy of environmental filters. The distance between species (circles) represents phylogenetic and/or ecological distance. Similar species are hypothesized to respond similarly to any given filter. Following the model a subset of the species (open circles) present in the regional species pool (a) are able to pass through the broad regional filters, such as altitude (b). Species that pass through (c) are subsequently subjected to filtering at the landscape level (d). Species that passed through (b) and (d) are then subjected to filtering processes at the local level (f). The hierarchical filtering process results in a predictable species assemblage (g) where species interactions may further determine the final species composition e.g. by strong competitors excluding weak competitors. Following each filter, species (crossed circles) that are not adapted to the present environmental conditions fail to establish populations within the species assemblage, and hence reduce the overall variability between species assemblages.

patterns in the distribution of lineages. For instance, within the bees the species richness within clades is often highest at the location of their origination as found for both the genus *Hylaues* (Kayaalp et al. 2013) and *Bombus* (Hines 2008). Furthermore, despite habitat type being the most important factor, a substantial amount of the species species richness in Ireland could be attributed to species turnover between regions (Murray et al. 2012). A secondary goal of our study was therefore to assess if species assemblages of bees located in the same climatic region were more similar than sites located in different climatic regions and if the similarity between species assemblages differed between climatic regions, as would be expected following the filtering model.

Firstly, we assessed the strength of each filter by predicting that; 1) the strength of environmental drivers on bee species richness and abundance decreases from the regional to the landscape and the local level filters, 2) the phylogenetic structure of species assemblages becomes increasingly clustered following an environmental filter, 3) the strength of the environmental drivers on the distribution of life-history traits within species assemblages decreases from the regional to the local level. Secondly, we investigated if 4) the taxonomic, phylogenetic and functional β-diversity differed between spatial scales and climatic regions.

Methods

Site selection

We sampled bees and conducted vegetation surveys in 20 sites in south-eastern Norway. Ten sites were sampled in 2009 and ten in 2010. The 20 sites were haphazardly chosen within the extensive network of power-line strips in Norway (the regional and distribution grids stretch over a total of 310 000 km). The sites were separated by at least 9 km, which is further than the foraging range of most bees (Gathmann and Tscharntke 2002) and were between 25 and 73 m wide.

We used power-line strips because they are valuable habitats for bees that provide abundant nesting substrates and foraging resources (Russell et al. 2005) and because their borders are clearly defined by adjacent forest edges. Power-line strips transect a wide variety of landscapes, both in terms of productivity (e.g. soil nutrient levels associated with distinct plant species assemblages) and landscape complexity (e.g. the spatial configuration of landscape types adjacent to power-line strips). Thus, sampling bees across a large spatial area within power-line strips enabled us to capture a variation in environmental conditions of potential importance for environmental filtering on large and small spatial scales.

Bee sampling

We sampled the bee species assemblages in each power-line strip with four flight interception-traps placed 50 m apart along the power-line. The traps were placed 1 m above ground in the center of the power-line strip. Traps were emptied four times during the activity period of bees (April–September). The traps consisted of two transparent plexiglas screens, measuring 370 × 210 mm, and assembled so that they formed a cross with a white funnel underneath. Flying insects are intercepted by the screen and collected in a bottle attached to the bottom of the funnel. The bottles were filled with green propylene glycol with a drop of detergent (Zalo Ultra, Lilleborg, Norway). Pan-traps are the most commonly used passive method for sampling bees, although flight interception-traps have also been used in previous studies (Moretti et al. 2009, Ulyshen et al. 2010). We regard flight interception-traps a better method for our study since it allowed us to sample communities over an extensive area at the same time. In addition, since pan-traps attract foraging bees, their efficiency may decrease as the floral community becomes more complex during the season if the combined visual and chemical cues of true flowers out-compete the visual cues of pan-traps. In contrast, flight intersection-traps do not actively attract bees, and their efficiency may therefore be more consistent across spatial and temporal gradients of floral complexity.

We removed three sites before data processing since they had lost > 1 trap during one of the four sampling periods. Two of the remaining sites had lost one trap during sampling period 1 and 4. To ensure equal sampling effort from each site, we randomly selected and removed the data collected from one trap during the 1st and 4th sampling period from all other sites. After these corrections, our dataset consisted of 17 power-line strips sampled four times during the season with a sampling intensity of 3, 4, 4 and 3 traps.

All individuals of non-*Bombus* bees were identified to species using regional identification keys (Schmid-Egger and Scheuchl 1997, Amiet et al. 1999, Scheuchl 2000, 2006, Amiet 2001, 2004). *Bombus* species were identified by a national expert. We grouped *Bombus cryptarum*, *B. terrestris* and *B. lucorum* into one morpho-species; '*B. lucorum* aggr.', due to the unreliability of morphological identification within this cryptic group (Wolf et al. 2010, Carolan et al. 2012, Williams et al. 2012). All clepto-parasites and social-parasites were removed from all analyses since we assumed their presence depends on their hosts rather than the environment per se.

Functional traits

All species were assigned six functional traits (Supplementary material Appendix 1, Table A1) that are often included in studies of wild bees (Moretti et al. 2009, Williams et al. 2010, Hoiss et al. 2012): body size, nesting behaviour (below- or above-ground nesters), sociality (social or solitary), phenology (spring or summer active), floral specialization (specialists or generalists), and activity period (number of months the species is foraging). We used the intertegulae distance (ITD) as a measure of body size for each species since it correlates with foraging range (Greenleaf et al. 2007). Values of intertegulae distance were based on the average measurements taken from 2–10 individuals (depending on the number of available individuals of each species). Since female bees found and provide for the nests, we assumed that any environmental filtering acting on foraging range would affect the female rather than male individuals of a population. We therefore only used ITD values for females.

Specimens for these measurements were obtained from the bee collection at the Natural History Museum at the Univ. of Oslo, Norway. We were unable to obtain measures of the body size of *Bombus ruderarius* and *B. soroeensis* and the sociality for *Lasioglossum albipes*, *L. fratellum* and *L. punctatissimum* these species was excluded from analyses on those traits (Supplementary material Appendix 1, Table A1). Information on each species was compiled from Westrich (1989).

Data preparation and statistical analyses

Environmental filters

We defined three levels at which environmental conditions might determine the structure of species assemblages; 'regional' reflecting a gradient in climatic conditions, 'landscape' reflecting a gradient in the presence of source habitat types in the surrounding landscape, and 'local', reflecting a gradient in local habitat conditions and potential forage resources in the power-line strip.

We used altitude (m a.s.l.) and latitude (UTM32 coordinates) as measures of regional climatic conditions. The altitudinal gradient ranged from 31 to 380 m a.s.l. The average monthly temperature decreases by 0.7°C for every 100 m from March–August (Supplementary material Appendix 2, Fig. A2). The distance between the northernmost and the southernmost localities was 131 km.

We used digital maps (AR5$^{\text{©geovekst}}$) provided by the Norwegian Forest and Landscape Inst. (Bjørdal and Bjørkelo 2006) to extract GIS information on landscape context within a 2000 m radius of each site. The digital maps were the most accurate maps available in Norway at the time the study was conducted. We used ArcGIS (ESRI, CA, USA) to extract the percentage cover of arable land, non-tilled arable land, pastures, roads (i.e. road sides), urban fabric, semi natural areas, mires, water bodies, rocky surfaces and forests. We used the Shannon diversity (H′) index as an estimate of landscape heterogeneity (Nagendra 2002 and references therein). The index was calculated as;

$$H' = -\sum p_{ij} \times ln(p_{ij})$$

Where p_i is the proportion of the landscape occupied by landscape type i at the jth site. All values of H′ were within the range of 0.24 and 1.04. The most dominant landscape type was forests, which covered between 30 and 96% of the landscape at the 2000 m radius.

We used the natural variation in the flowering plant species composition among power-line strips to obtain proxies for local environmental filters. We placed eight main plots of 4×5 m within each site. The eight main plots were arranged so that four sets, consisting of two parallel plots, followed the direction of the power-line. The distance between the two nearest sets of plots was 50 m. The two parallel plots where placed so that one was in the center of the power-line and one was placed in the corridor along the forest edge. We placed five 1 m^2 quadrats along the centre line of each of the eight main 4×5 m plots, and estimated the percentage cover of dwarf shrubs and herbaceous plant species within each quadrat by visual estimation.

We used the R-package vegan (Oksanen et al. 2013) to conduct a principal components analysis (PCA) where we collapsed the variation in plant species composition between sites onto two principle component axes. In order to remove the effect of rare plant species, we only included species occurring at two or more sites. The remaining species abundances were scaled to a 0–1 range to allow equal treatment of all plant species according to their natural occurrences in our system. Axis 1 and 2 accounted for 28.5 and 13.7% of the total inertia, respectively. We only included axis 1 in the following analysis (herafter reffered to as plant axis one).

We used the average percentage flowering plant-cover, pooled across all sub-plots, as plant cover correlates with bee abundance (Steffan-Dewenter and Tscharntke 2001). We only included plants occurring at more than two sites. In our system, plants cover was correlated to the cover of Ericaceae ($r = 0.78$) and specifically the cover of *Vaccinium vitis-idaea* ($r = 0.59$) and *Calluna vulgaris* ($r = 0.44$). However, plant cover was only weakly correlated to plant axis one ($r = 0.27$). We therefore interpreted plant cover as being related to plants visited mainly by *Bombus* species and some pollen specialist Andrenids and Colletids. The plant species richness ranged from 6 to 19 per site, and the average cover ranged from 15 to 46% per square metre.

We used a Pearson's correlation matrix to evaluate the relationship between all explanatory variables. In order to avoid collinearity between explanatory variables within each filter we removed one variable from variable pairs that were highly correlated (Pearson's $r > 0.5$). Altitude increased with latitude ($r = 0.73$) and therefore we retained only altitude in the analysis since this variable has been used in a previous study on wild bees (Hoiss et al. 2012). Landscape diversity tended to decrease with altitude ($r = -0.48$). Moreover, landscape diversity was positively associated with the amount of semi-natural areas ($r = 0.75$), road sides ($r = 0.61$), pastures ($r = 0.62$), arable land ($r = 0.55$), urban fabric ($r = 0.46$), and negatively with forest cover ($r = -0.79$). We therefore only included landscape diversity as a filter at the landscape level. At the local level, plant axis one was negatively related with both total ($r = -0.72$) and herbaceous species richness ($r = -0.82$) and abundance ($r = -0.88$), and positively related to Ericaceae species richness ($r = 0.82$) and abundance ($r = 0.67$). We therefore only included plant axis one, and total plant cover as filters at the local level.

All environmental variables (altitude, landscape diversity, plant axis one and plant cover) were zero-skewness standardized (Økland et al. 2001) before analyses and scaled to a 0–1 range to enhance comparability of effect sizes for variables measured on different units.

Species richness and abundance

We used R (R Development Core Team) to conduct a multiple regression analysis to test if the species richness and abundance of bee communities were related to the environmental filters. Response variables were bee species richness (number of species) and bee abundance (number of individuals). We fitted generalised linear models (GLMs) with log-link function, assuming a Poisson error distribution. Evironmental variables were selected by conducting a manual forward selection of environmental variables, including all variables where $p < 0.1$. We entered the variables in the following order; altitude, landscape diversity, plant axis one and plant cover to account for the assumed hierachical structure of the filters (region–landscape–local). Since the model with bee abundance as a response was over-dispersed we instead fitted a negative binomial GLM with a log-link function.

Phylogenetic analysis

All bees were classified to family following Danforth et al. (2006). From family to subgenus we followed Michener (2007). We used the R-package APE (Paradis et al. 2004) to build a polytomous, ultra-metric tree (Supplementary material Appendix 3, Fig. A3). Branch lengths were calculated by setting the p-parameter to 1 following Hoiss et al. (2012).

We used the R-package Picante (Kembel et al. 2010) to calculate the phylogenetic structure as both the net relatedness index (NRI) and nearest taxon index (NTI) for each site (Webb et al. 2002). We calculated the NRI and NTI as species and abundance-weighted to account for inter-specific and inter-individual changes in phylogenetic composition (Kembel et al. 2010). We generated 10 000 null species assemblages for each site by randomly selecting species from the entire species pool, until the species richness of the null species assemblage matched the species richness at the target site. The use of this null-model removed the effect of species richness on the phylogenetic signal. We calculated the average and standard deviation from the null distribution of phylogenetic distances obtained for each site. The observed NRI and NTI values were compared to their corresponding null-distributions to test if individual species assemblages showed significant phylogenetic over or under-dispersion.

We calculated the phylogenetic independent contrast (PIC) for each of the functional traits included in the study to test if the functional traits displayed significant phylogenetic signals. The observed PIC value was compared to a null distribution generated by randomly shuffling the taxa names across the phylogeny, while leaving the functional traits in place. We ran a total of 10 000 reiterations to ensure that the null-distribution of PIC values reached a stable state. If the observed PIC value for a trait was lower than 95% of the permuted PIC-values, we interpreted it as displaying a non-random phylogenetic signal.

We conducted one-sample t-tests on the NRI and NTI to tests if the average phylogenetic structure deviated significantly from zero. We tested for effects on both species and abundance weighted NTI and NRI and set the alpha value to 0.05.

We used a linear multiple regression analysis to test if the phylogenetic structure of bee communities was related to environmental filters. We selected variables by conducting a manual forward selection of environmental variables and included all variables with $p < 0.1$. In order to account for the assumed hierachical structure of the filters (region–landscape–local), we entered the variables in the following order: altitude, landscape diversity, plant axis one and plant cover. Responses were; $\mathrm{NRI}_{\text{species-weighted}}$, $\mathrm{NTI}_{\text{species-weighted}}$, $\mathrm{NRI}_{\text{abundance-weighted}}$ and $\mathrm{NTI}_{\text{abundance-weighted}}$.

Drivers of the functional composition of bee species assemblages

We used a multivariate variation partitioning analysis to determine which environmental filters were most important in sorting bee species assemblages in a multidimensional trait-space. Response variables were average body size (ITD), average activity period, the number of social species, solitary species, spring active species, summer active species, aboveground nesting species, belowground nesting species, floral specialists and floral generalists. The analysis was conducted on both species richness and abundance within each trait group and both with and without *Bombus* species. We rescaled all the responses to a 0–1 range to ensure that all traits were on the same scale and received equal weights in the analysis. We used a redundancy analysis (RDA) with manual forward selection to screen the environmental variables and select those to be included in the variation partitioning analysis. The variables were entered following the expected hierarchical order of the environmental filters, i.e. altitude, landscape diversity, plant axis one and plant cover. All variables with $p < 0.1$ were kept in the models.

We used the varpart function available in the vegan package (Oksanen et al. 2013) to partition the variation accounted for by each environmental filter after removing the effect of the other filters in the model (Peres-Neto et al. 2006). After variation partitioning, the significance of each fraction was tested individually with a permutation test of the conditional RDA models, using 1000 permutations.

Proportionate shifts in trait-specific functional species richness and abundance

We ran a series of linear regression analysis with manual forward selection to test if the proportionate contribution of individual traits changed following the environmental filters. Reponses were the proportion of aboveground nesters, floral specialists, spring-emerging and social bees. The average body size (average ITD) and average activity period (months) for species or individuals in the species assemblage were not proportions. Because the proportion based response variables were limited between 0 and 1, we initially fitted models with a binomial distribution and logit link to these responses. Variables were entered into the model following the order described in the previous section. However, graphical diagnostics and the the generalised Pearson statistic, $gPs = \chi^2/(N-p)$, where N = number of observations and p = number of parameters (Crawley 2013) showed that the final logistic regression models were under-dispersed, i.e. had gPs values substantially smaller than 1. Therefore, we re-specified the model using quasi-binomial rather than binomial errors, and this substantially improved the model fit. However, since the results from these GLMs were qualitatively very similar to results obtained from standard linear regression models (assuming Gaussian distributions), we present results from the latter since this enabled calculations of true R^2-values. All analyses were conducted with responses as both species richness and abundance within each trait category. We fitted models with and without *Bombus* species since the measured life-history traits are highly conserved within this genus.

Does the compositional turn-over between species assemblages vary across spatial scales?

We used the function Rao provided by de Bello et al. (2010) in R to calculate the unweighted, Jost-adjusted Rao's index of β-diversity for all site-pairs, since this index allows direct comparison of taxonomic, phylogenetic and functional β-diversities. Trait-based distances between species were calculated using the Gower distance since this allowed inclusion of both continuous and categorical traits (Gower 1971). The proportionate contribution of β-diversity between sites was calculated on both the abundance and on the occurrence of species within bee species assemblages, since the occurrence-based index is less influenced by the most abundant species (de Bello et al. 2007).

We calculated a matrix containing the Euclidian distance between all pairs of the 17 sites, based on their geographical eastern and northern-coordinates. We used the R-package cluster (Maechler et al. 2013) to cluster sites according to their Euclidian distances. The clustering followed the average-based clustering method since this method produced inter-cluster distances that were highly correlated with the original spatial structure in the data ($r = 0.77$). There were six clusters with an average inter-cluster distance shorter than 20 km. We used this scale as our smallest spatial scale and compared it to a second scale with inter-site distances greater than a 100 km (large scale). The small scale consisted of 12 site pairs, and the large scale of 26 site pairs. Sites within pairs at the small scale were on average more similar in terms of altitude than sites within pairs at the large scale (Supplementary material Appendix 4, Fig. A4). We also selected the five northernmost and five southernmost clusters of sites to assess if the degree of compositional similarity between site pairs differed between climatic regions rather than spatial scale per se. For this we calculated new β-diversity indexes for each cluster of five sites an extracted the β-diversity for each site-pair within each cluster. This was done since we were interested in the difference between the two groups of sites, disregarding all other sites.

We ran two separate analyses. First, we tested if the average β-diversity between site-pairs differed between sites grouped according to their geographical distance (small vs large scale). Second, we ran the same analysis but with site-pairs grouped according to their regional location (northern vs southern). For each analysis the observed difference was compared against null-models. We used the R-package permute (Simpson 2012) to randomly allocate the β-diversities within and among the two groups and calculate 10 000 new average differences for the analysis on spatial scales, and 1000 new average differences for the analysis on interregional. This method broke any link between group affiliation and the observed difference in average β-diversity between groups. We rejected the null hypothesis when the observed absolute differences between groups fell out-side the 95% quartile distributions of the null-model distributions (i.e. $p < 0.025$). However, this method randomly allocated the potentially group-specific variation in β-diversity between the two groups. We therefore also used the R-package boot (Canty and Ripley 2013) to boot-strap the distributions of β-diversities within each group. We retained the number of site-pairs within each group but randomly selected site-pairs, with replacement, and calculated a new average β-diversity for each. In total we calculated 10 000 group-dependent average β-diversities for each group in the analysis on geographic distances, and 1000 group-dependent averages for the analysis on differences between the northern and southern region. We accepted differences between groups if the two distributions had non-overlapping 95% quartile distributions.

Results

Species richness and abundance

The removal of sites and traps, to standarzise the sampling intensity, reduced the total sample of wild bees from 2272 to 1914 individuals and from 56 to 52 species. The most abundant genus was *Bombus*, accounting for 87.7% of all wild bee individuals. The most abundant genera of non-*Bombus* species were *Hylaeus* and *Andrena* with a total of 89 and 87 individuals, respectively (Table 1). The species richness and abundance of wild bees showed a pronounced decrease with altitude (Fig. 2a–b).

Phylogenetic structure

Most of the traits showed a significant phylogenetic signal (Table 2). The largest bees were found within the genus *Bombus*. Aboveground nesting was exclusive to the Megachilid genera *Megachile*, *Osmia* and *Hoplitis*, *Bombus* species belonging to the subgenera *pyrobombus*, and the Colletid genus *Hylaeus*. Pollen specialization did not display a strong phylogenetic signal. Sociality was largely confined to *Bombus* species. However, some Halictid species also displayed sociality. The month of emergence was in general latest for Megachilids, Halictids and Colletids. However, the latest species-specific phenology seemed to be for *Andrena fuscipes* and *Colletes succinctus*, which are both specialized on late-blooming Ericaceae plants. Species within the genera *Bombus*, *Halictus* and *Lasioglossum* had the longest activity periods.

Table 1. Species richness and number of individuals of wild bees within genera in 17 power-line strips in southern Norway. Also the number of individuals belonging to the most abundant species within each genus is shown. Clepto- and social parasites included 4 species of *Bombus*, 2 species of *Nomada* and 2 species of *Sphecodes*. These were excluded from all analyses.

Genus	Species	Individuals	Most abundant species	Individuals
Andrena	12	87	*A. lapponica*	41
Anthidium	1	1	*A. punctatum*	1
Bombus	13	1680	*B. lucorum* aggr.	895
Colletes	2	3	*C. daviesanus*	2
Halictus	1	4	*H. rubicundus*	4
Hoplitis	1	1	*H. tuberculata*	1
Hylaeus	5	89	*H. confuses*	48
Lasioglossum	6	26	*L. fratellum*	13
Megachile	2	2	*M. nigriventris*	1
Nomada	2	2	*N. flavoguttata*	1
Osmia	5	15	*O. nigriventris*	8
Sphechodes	2	4	*S. hyalinathus*	3

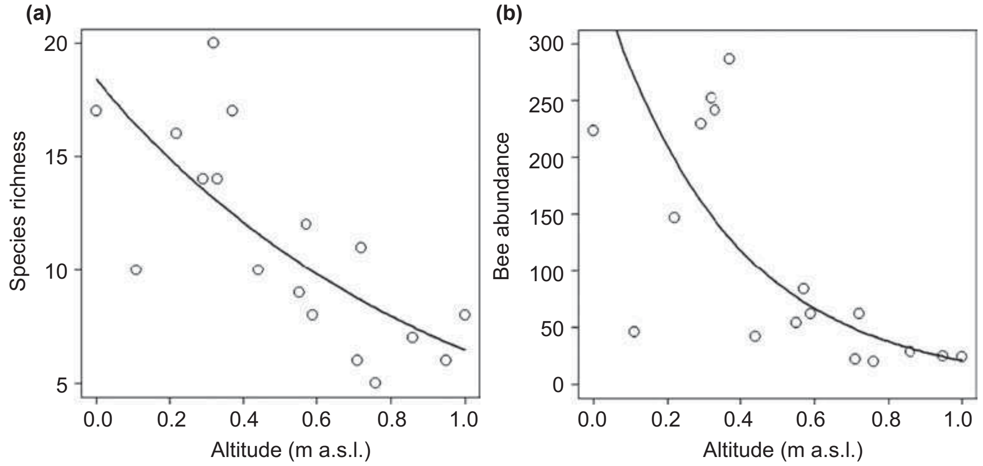


Figure 2. Species richness and abundance of wild bees decreased with altitude. (a) A generalized linear model (GLM) with Poisson distribution of errors showed that wild bee species richness decreased with altitude ($p < 0.001$). (b) A GLM with negative binomial errors revealed that bee abundance decreased with altitude ($p < 0.001$). The explanatory variable (Altitude) was transformed to achieve zero scewness before scaling to a zero to one scale. Altitude ranged from 30 to 380 m a.s.l.

The bee species assemblages in power-line strips varied in terms of phylogenetic clustering (Table 3). Although there was a large variation between species assemblages in terms of the strength of the phylogenetic structure, individuals within 8 sites displayed significant phylogenetic clustering in terms of NRI. On average there was a weak tendency for phylogenetic clustering. Although the average species-weighted net relatedness index (NRI) did not differ significantly from zero, the nearest taxon index (NTI), the abundance weighted NRI, and the NTI did.

We found no relationships between the species weighted NRI or the NTI and the environmental filter variables. However, the abundance-based NRI and NTI had contrasting relationships with the measured environmental conditions. The NRI between individuals in power-line strips decreased with altitude ($p = 0.11$) and increased with plant cover ($p = 0.1$). However, although the p-value of the model was low it was not statistically significant ($R^2 = 0.33$, $p = 0.063$). In contrast, the mean nearest taxon index between individuals and their closest hetero-specific relative increased with altitude, but had no relationship with the other environmental filters (Fig. 3).

Drivers of the functional composition of bee species assemblages

The functional composition, in terms of the species richness in each trait, was best explained by altitude and landscape diversity (Fig. 4a). Variance partitioning revealed that 14% of the variance explained by landscape diversity was shared with altitude, and that the individual contribution of landscape diversity was negligible. In contrast, the individual contribution of altitude was significant. The functional composition in terms of species abundance within each trait was best explained by altitude, followed by plant cover (Fig. 4b). Variance partitioning revealed that the two predictors shared only 2% of the total explained variation, and that the individual contributions of plant cover and altitude were significant.

Analyses without *Bombus* showed that altitude and landscape diversity together explained 28% of the variation in the functional composition of species assemblages, in terms of species richness (Fig. 4c). However, 10% of the explained variation was shared between the two variables, and only altitude significantly contributed to explain variation

Table 2. The phylogenetic signal in the life-history traits of wild bees. The traits included in the analysis were; body size (inter tegulae distance, ITD), above ground nesting, pollen specialists (Oligoletic), social nesting behavior (Social), time of emergence (Spring active) and the duration of flight activity in months (Activity length). Each trait was analyzed separately to account for the varying number of missing information on species. Note that the Blomberg K statistic should be interpreted only for ITD and Activity length as they were the only traits not coded as factors. The test of the significance of the phylogenetic independent contrasts (PIC) were based on the comparison between the variance of the observed contrasts (PIC.var.obs) and the mean variance in contrasts obtained by randomizing the relationship between the trait and the phylogeny (PIC.var.rnd.mean). The relationship between the two provided a z-value (PIC.var.Z). The significance test was based on the quartile of the null distribution. Thus if the PIC.var.obs for a trait was smaller than the 0.05 quartile of the PIC.var.rnd distribution we concluded that the trait displayed significant phylogenetic signal.

	Bloomberg K	PIC.var.obs	PIC.var.rnd.mean	PIC.var.P	PIC.var.Z
ITD	1.04475	3.052119	25.80521	<0.001	–4.34601
Above gr. nesting	–	0.62378	3.157584	<0.001	–4.8469
Oligolectic	–	1.143914	1.741085	0.057	–1.58268
Social	–	0.241383	2.450231	<0.001	–4.52819
Spring active	–	1.224459	2.952992	<0.001	–3.58726
Activity length	0.290396	12.95246	30.30397	<0.001	–3.14616

Table 3. The phylogenetic structures of the bee species assemblages. The average phylogenetic relatedness between species and individuals in each site was estimated as the net relatedness index (NRI) and the nearest taxon index (NTI). The analysis was run with species abundances (ab) and occurences (sp) so that the indexes could be interpreted as measurements of either the average phylogenetic distance between individuals or between species in the community, respectively. The corresponding p-value for each comparison is listed to the right of the phylogenetic index. Indexes revealing significant ($p < 0.05$) phylogenetic clustering are marked in bold letters. The observed values were tested against null models produced by 10 000 permutations. At the bottom of the table a 95% confidence interval and the corresponding p-value shows the general tendency for each index obtained through a one-sample t-test.

Site id	NRI_{sp}	p	NRI_{ab}	p	NTI_{sp}	p	NTI_{ab}	p
1	–0.515	0.640	**1.971**	**0.050**	1.494	0.066	–0.153	0.573
2	0.270	0.284	**2.486**	**0.008**	0.788	0.215	0.138	0.476
3	–0.516	0.644	**2.091**	**0.013**	1.286	0.099	0.287	0.419
4	–0.384	0.562	**2.360**	**0.015**	0.089	0.477	–0.415	0.650
5	0.149	0.316	1.345	0.123	0.232	0.382	0.214	0.441
6	1.622	0.065	**2.272**	**0.029**	0.294	0.392	0.235	0.447
7	0.750	0.148	0.979	0.175	**1.811**	**0.032**	–0.197	0.575
8	–0.333	0.500	–1.234	0.918	0.405	0.316	0.383	0.389
9	–0.333	0.550	1.244	0.126	–0.310	0.557	0.566	0.310
10	**4.334**	**0.008**	**2.761**	**0.002**	–1.444	0.933	0.405	0.361
11	–0.474	0.595	1.744	0.061	0.842	0.193	0.439	0.359
12	0.242	0.242	**1.938**	**0.049**	–0.902	0.826	–0.014	0.524
13	–0.491	0.605	0.356	0.328	0.745	0.228	0.469	0.337
14	–0.201	0.429	1.950	**0.031**	0.989	0.157	0.191	0.460
15	–0.263	0.458	0.158	0.323	0.318	0.371	0.614	0.277
16	1.703	0.056	**2.533**	**0.013**	**2.082**	**0.021**	0.722	0.253
17	–0.008	0.346	0.967	0.175	0.903	0.186	0.726	0.231
95% CI	–0.31; 0.97	0.294	**0.99; 2.06**	**<0.001**	**0.10; 1.03**	**0.02**	**0.10; 0.44**	**0.003**

in the model. Moreover, the functional composition in terms of species abundance within each trait was significantly explained by altitude, landscape diversity and plant axis one (Fig. 4d). Altitude and landscape diversity shared a large part of their explanatory power and their unique contributions were not significant. The unique contribution of plant axis one was significant.

Proportionate shifts in trait-specific functional species richness and abundance

The environmental filters changed the proportionate distribution of individual traits (Table 4). The average body size (ITD) of species and the average foraging period increased with altitude. The average body size (ITD) of individuals decreased with landscape heterogeneity and increased with plant cover within power-line strips. The decrease in average activity period of individuals was not significantly related to altitude, although the p-value was low. The proportion of social species in the assemblage increased with altitude and plant axis one, whereas the proportion of social individuals increased with plant cover. Moreover, the proportion of spring emerging bee individuals also increased with plant cover.

Analyses without *Bombus* showed no relationships between the individual functional traits and altitude (Table 4). However, the average activity period of species decreased with plant cover. Moreover, the average body size of individuals increased with plant axis one and plant cover, whereas the average activity period of bee individuals decreased with plant axis one and plant cover. Furthermore, the proportion of specialized individuals increased along plant axis one.

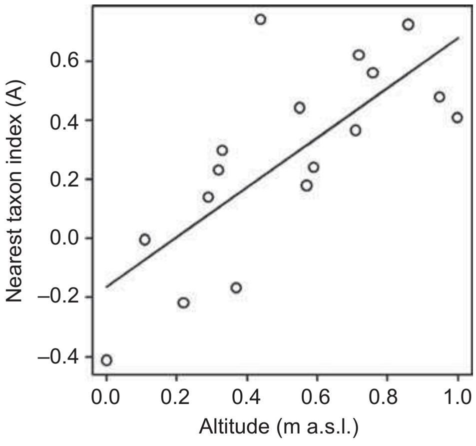


Figure 3. The phylogenetic relatedness between wild bee indivdiuals and their closest hetero-specific relatives increased with altitude ($R^2 = 0.55$, $p < 0.001$). The explanatory variable (Altitude) was transformed to achieve zero scewness before scaling to a zero to one scale. Altitude ranged from 30 to 380 m a.s.l.

Does the compositional turn-over between species assemblages vary across spatial scales?

Sites located within 20 km of each other did not differ significantly from sites located more than 100 km from another in terms of the average taxonomic, phylogenetic or functional β-diversity between site pairs within each cluster. (Supplementary material Appendix 5, Fig. A5). However, species assemblages located in the northern part of the study-region were on average less similar than species assemblages located in the southern part (Fig. 5). This was true for the taxonomic, phylogenetic and functional measure of β-diversity and for both abundance and occurrence-based calculations. However, the differences were more pronounced when information on species abundances was used.

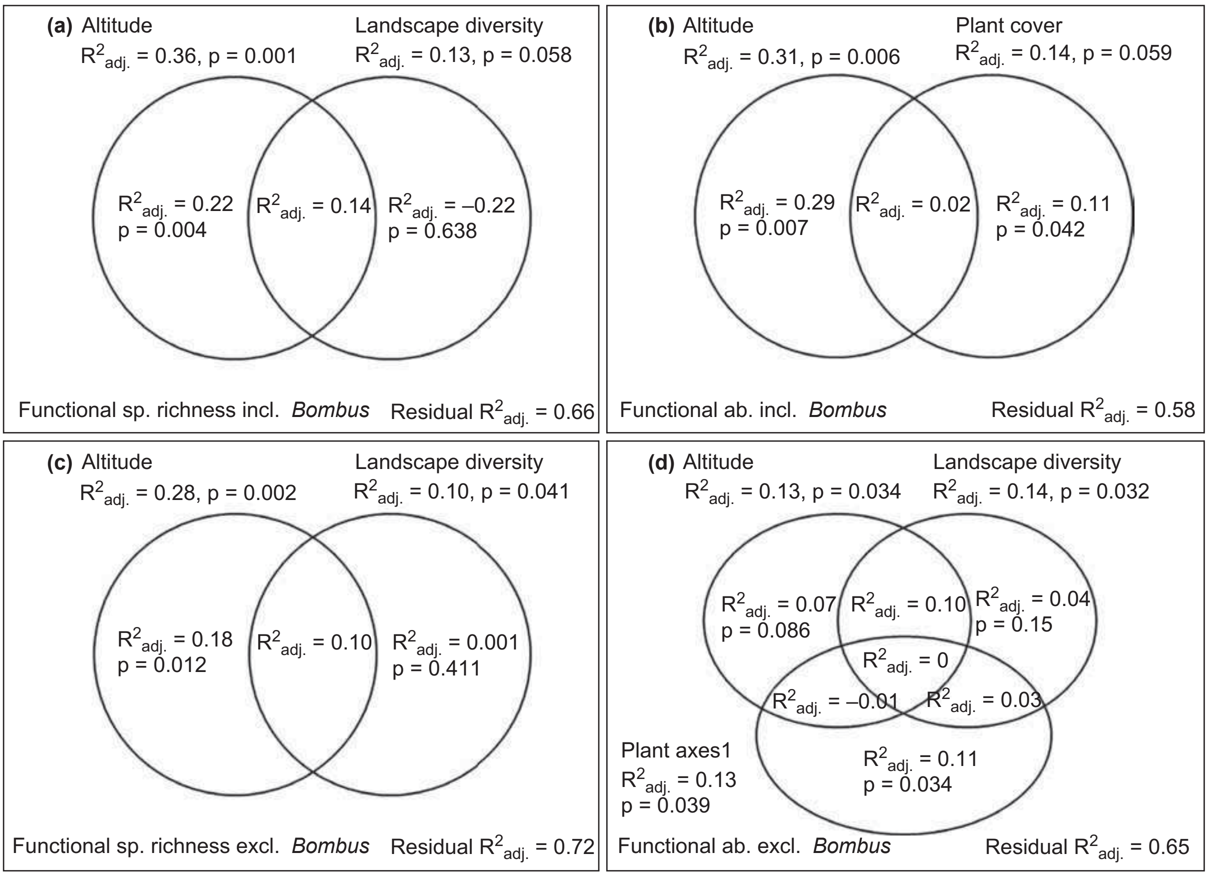


Figure 4. Influence of environmental filters on trait-composition of bee species assemblages. Bee species were categorized according to nesting behavior, floral specialization, sociality, body size, spring or summer active and the duration of their flight period. When all wild bees were included (a, b) the species richness in trait groups (a) was best explained by altitude (m a.s.l) and landscape diversity (Shannon's index). The bee abundance in trait groups (b) was best explained by with altitude and plant cover. When *Bombus* species were excluded from the analysis (c, d) the species richness in trait groups (c) was best explained by altitude and landscape diversity. In terms of bee abundance in trait groups (d), the composition was best explained by with altitude, landscape diversity and plant axis one. All p-values were obtained through individual permutation tests of the RDA analyses.

Table 4. Results from the multiple linear regression analysis showing how the inter-site variation in life-history traits in bee communities relate to environmental filters. The analyses were run on both richness (number of species) and abundance (number of individuals) within trait-categories as response variables, and both including and excluding the *Bombus* species. Only significant responses are shown. Responses were average body size measured as the intertegulae distance per species (ITD$_r$) and individual (ITD$_a$) in mm, the average number of active months per species (Months$_r$) and individual (Months$_a$), the proportion of social species (Sociality$_r$) and individuals (Sociality$_a$), the proportion of spring active individuals (Spring$_a$) and the proportion of pollen specialized individuals (Oligo$_a$). The analyses were run using manual forward selection following the hypothesized hierarchy of the explanatory variables, i.e. in the order; m a.s.l., landscape diversity, plant axis one and finally plant cover. Only variables were the p-value was < 0.1 prior to inclusion into the model are shown. All explanatory variables were zero-skewness standardized before analyses and ranged to a common 0–1 scale (Økland et al. 2001).

		Regional filter: m a.s.l.			Landscape filter: landscape diversity			Local filter: plant axis one			Local filter: plant cover			Model fit:	
Response:	DF	β	SE	p	β	SE	P	β	SE	p	β	SE	p	R²	p
Richness weighted incl. *Bombus*															
ITD$_r$	15	0.85	0.40	0.05										0.23	0.049
Months$_r$	15	0.74	0.25	0.01										0.375	0.009
Sociality$_r$	14	0.19	0.10	0.08				0.17	0.09	0.07				0.35	0.047
Abundance weighted incl. *Bombus*															
ITD$_a$	14				–0.36	0.35	0.33				0.84	0.42	0.06	0.41	0.026
Months$_a$	15	–0.37	0.19	0.07										0.20	0.071
Sociality$_a$	15										0.26	0.09	0.01	0.36	0.010
Spring$_a$	15										0.13	0.05	0.02	0.33	0.015
Richness weighted excl. *Bombus*															
Months$_r$	15										–0.86	0.27	<0.01	0.42	0.005
Abundance weighted excl. *Bombus*															
ITD$_a$	14							0.35	0.12	0.01	0.43	0.17	0.02	0.61	0.001
Months$_a$	14							–0.40	0.22	0.09	–1.05	0.32	<0.01	0.58	0.002
Oligo$_a$	15							0.32	0.11	0.01				0.37	0.009

The boot-strapped distribution of averages revealed that the northern sites, in addition to being more dissimilar on average, also had a higher variation in inter-site β-diversity. Although this difference in variation was also present when the analysis was run on occurrence data, it was not as pronounced.

Discussion

Species richness and abundance

The species richness and abundance of wild bees declined along the altitudinal gradient, whereas there were no significant relationships with landscape diversity, plant cover and plant composition. These findings suggest that broad level filters may be the most important in determining the overall structure of bee assemblages in our study system. A similar response to altitude was also found by Hoiss et al. (2012), who used a gradient ranging from 600 to 2000 m a.s.l., whereas our gradient was only 30 to 380 m a.s.l. However, the dominance of *Bombus* and *Andrena lapponica* in our study region correspond to the bee assemblages at high altitudes in the study by Hoiss et al. (2012), suggesting that the more northern positions of our study sites may have increased the effect of our relatively short altitudinal gradient.

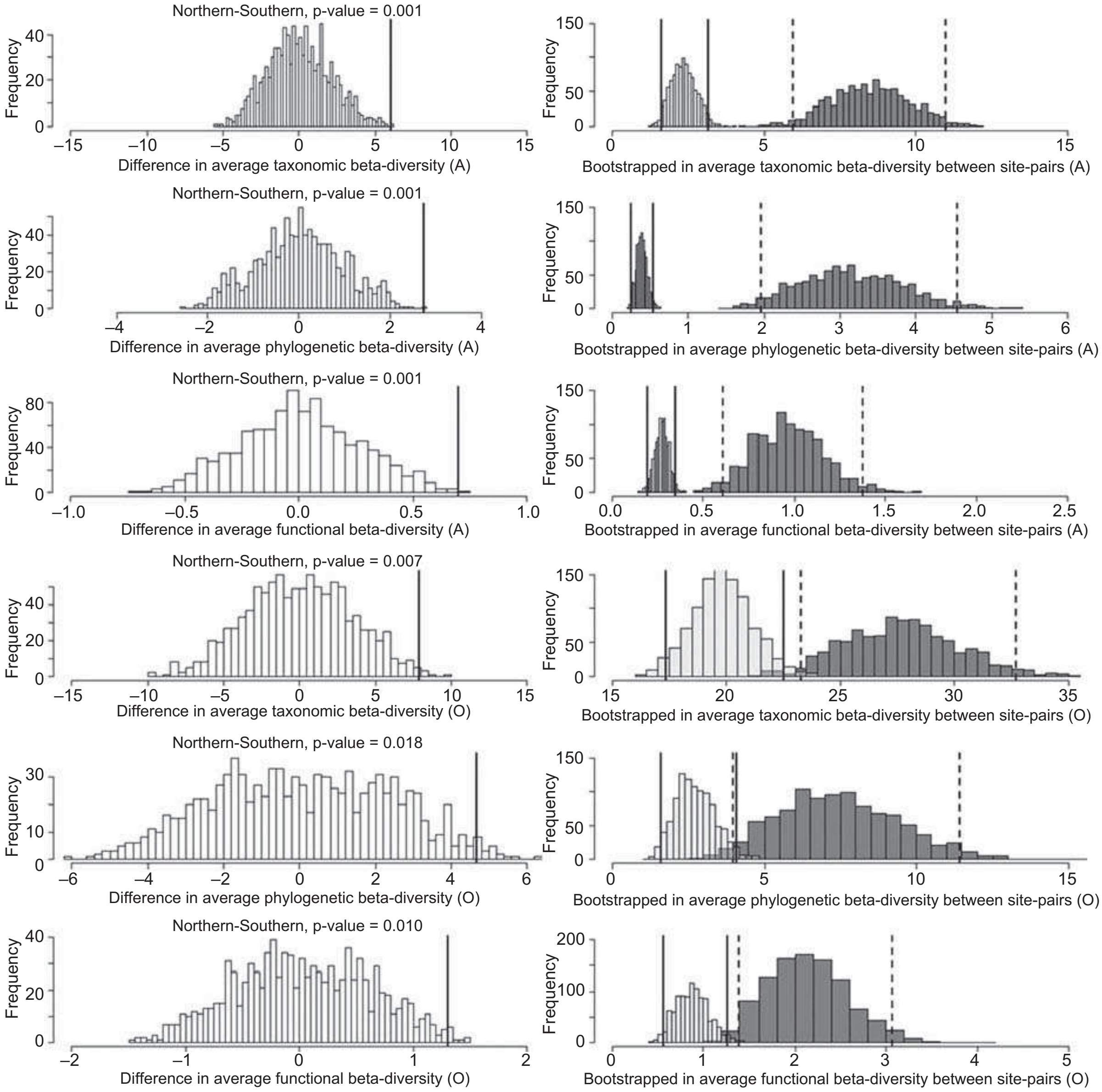


Figure 5. Showing the differences in average inter-site β-diversity between the five northern and five southern species assemblages. The differences were calculated for both abundance based and occurrence based β-diversity indexes marked with (A) and (O) respectively. The left column displays the observed differences in the average β-diversity between the northern and southern species assemblages (dashed line). The p-values specify the proportion of differences from the null distribution that are higher than the absolute difference in the observed values. The right column displays the 95% quartile intervals calculated from the bootstrapped distribution of the average β-diversity between species assemblage-pairs in the southern region (filled lines) and the northern region (dashed lines).

Disentangling the direct effect of altitude is problematic since it is often correlated with several abiotic and biotic environmental variables (Körner 2007). Indeed, landscape diversity decreased with the altitude, presumably due to less favorable agricultural conditions even at moderate altitudes in our study region. Moreover, a post hoc linear regression (not shown in result section) revealed that when landscape diversity was tested separately it explained 26% of the variation in log(species richness) ($p = 0.04$) but very little, if any, of the variation in log(bee abundance) ($R^2 = 0.13$, $p = 0.16$).

Landscape composition and diversity are important predictors of wild bee species richness (Steffan-Dewenter et al. 2002, Williams et al. 2010, Murray et al. 2012). However, the influences of landscape composition and diversity are highly context- and species-dependent (Winfree et al. 2007). It is therefore likely that altitude influences wild bee species richness both directly through climate conditions, and indirectly through its effects on land-use. However, the effect of land-use may be negligible in our system if power-line strips provide ample forage and nesting sites, and thereby meet the complex habitat requirements of bees (Westrich 1996).

Phylogenetic structure

The majority of the functional traits for species included in this study displayed significant phylogenetic signals but were often conserved within distantly related genera. In contrast the continuous trait Body size (ITD) seemed to follow a Brownian mode of evolution (K equal to or greater than 1). Thus, whether phylogenetic over or underdispersion reflects environmental filtering may be trait dependent. For instance if ecologically similar species from distantly related taxa (e.g. the late emerging, solitary and Ericaceae specialized *Colletes succinctus* and *Andrena fuscipes*) are present in species poor sites it may down-weigh phylogenetic signals in the species assemblages caused by the presence of closely related and ecologically similar species that are also present.

Some species assemblages were subjected to environmental filtering, but the degree of this varied within our study region. Analysis of how the phylogenetic structure changed according to environmental filters showed that only the abundance weighted NTI had a significant positive relationship to altitude while the NRI tended to decrease. High NTI values and low NRI value may reflect a clustering of closely related species within clades of distantly related species (Webb et al. 2002).

Contrary to our results, Hoiss et al. (2012) found that both species and individual weighted NTI and NRI increased with altitude, suggesting a phylogenetic packing at low and high taxonomic levels. There are several possible explanations for the contradictory findings between their and our study. The differences may result from the higher bee diversity in their study region, which could yield a parallel response in NTI and NRI if higher bee diversity is followed by a more even distribution of taxa across clades. This would suggest that in diverse ecosystems, a gradual phylogenetic clustering will occur at multiple taxonomic scales whereas in simple ecosystems a parallel phylogenetic clustering between clades is less frequent, with only few species of any given clade present. In the latter case, strong phylogenetic clustering should be observed only at the tip of the phylogenetic tree. This pattern might also be expected if the tree includes several distantly related taxonomic orders (Kraft et al. 2007, Silver et al. 2012). Another explanation may be that since all the species assemblages in all our study sites showed at least a weak phylogenetic structure, the potential effect of altitude on broad taxonomic scales (NRI) may be weaker than otherwise expected. This might be the case if one clade dominates, as in our study region where *Bombus* was the most abundant and the second most species rich genus (Table 1). The phylogenetic structuring of bees following the broad level filter (altitude), and the presence of only weak patterns when using lower level environmental filters, may suggest that environmental filtering can only explain phylogenetic patterns when filters encapsulate extreme environmental gradients at the local level.

Drivers of the functional composition of bee species assemblages

Environmental filters produce differences in the composition of life-history traits in the bee species assemblages (Fig. 4), in accordance with the hypothesized multi-level filtering model proposed by Keddy (1992) and others (Poff 1997, Diaz et al. 1998). The effects of individual filters seem to work hierarchically, with the broad-level filter having a larger effect than the local filters.

Altitude and landscape diversity were related to compositional changes in functional trait richness in the species assemblages. However, the variation accounted for by landscape diversity was shared with that of altitude. The same pattern was detected in analyses without *Bombus*. These patterns would be expected since species richness in general declined with altitude in our study. Since complex landscapes do not naturally occur in our study system but are found in agricultural landscapes at low altitudes, some correlation occurred between landscape diversity and altitude. Nonetheless, the proportion explained by altitude exceeded that explained by landscape diversity, suggesting that filtering effects in terms of species richness within functional groups are strongest at broad-level filters.

Compositional differences in functional trait abundance between species assemblages were related to altitude and plant cover. The effects of the two filters were largely unique. Analyses without *Bombus* showed that altitude, landscape diversity and plant axis one were important drivers of the composition of functional traits within sites. Murray et al. (2012) also found non-*Bombus* species to be more sensitive to landscape diversity than *Bombus* and attributed that to their shorter foraging ranges. Moreover, in this case, the largest unique fraction of variation was explained by plant axis one, while landscape diversity and altitude shared a large fraction of their contribution to the model.

These results suggest that the effect of environmental filtering decreased from regional to the local level and that life-history traits determine which species pass through the environmental filters. However, they also suggest that the responses to filters may be taxon specific in that the abundance non-*Bombus* individuals within trait-groups were strongly affected by local filters. Moreover, it should be noted that the effect of the local filter may have been underestimated as we did not study the effect of nest site availability which has been shown to be an important determinant of species assembly within bees (Murray et al 2012). However, the gradient in plant community composition is likely to be related to environmental factors such as soil depth; e.g. dwarf-shrub dominated areas being situated in areas with a thinner soil-cover and hence reduced nesting sites for below-ground nesting bees, in contrast to the diverse plant communities located on deeper soils.

Proportional shifts in functional species richness and abundance

The analysis on individual traits revealed that altitude, high plant cover and low plant diversity favoured species and individuals with large body size, long activity periods, social behavior and early emergence time. These patterns point to the prevalence of *Bombus* species and individuals in cool regions dominated by Ericaceae species, as in our system. This pattern was also found by Hoiss et al. (2012) and would be expected since the genus *Bombus* evolved in alpine areas of China (Hines 2008). Moreover, we did not find any changes in the proportion of life history traits with altitude in analyses without *Bombus*. This suggests that all non-*Bombus* species responded similarly to altitude in our system. However, non-*Bombus* species responded differently to local filters depending on their traits. Localities dominated by Ericaceae favored large bees with short activity periods and pollen specialization. These findings reflect the dominance of *Andrena lapponica*, a large spring-active *Vaccinium*-specialist in *Ericaceae* dominated plant communities. Indeed, a post hoc simple linear regression analysis (not shown in Results) revealed that the proportion of *Andrena lapponica* increased with *Ericaceae*-cover ($R^2 = 0.41$, p-value = 0.006).

Unlike Hoiss et al. (2012), we did not find that altitude filtered against above-ground nesting bees. There are several possible explanations for this. Power-line strips provide more potential nesting resources for above-ground nesting bees than grasslands (Russell et al. 2005). The ratio of above- to below-ground nesting species and individuals may therefore be higher in our system than in the grasslands studied in southern Germany by Hoiss et al. (2012). This might require a more extreme climatic gradient before any filtering on this trait occurs. Moreover, since our altitudinal gradient was shorter than that of Hoiss et al. (2012), we may not have been able to capture any threshold values where filtering on nesting behavior occurs. Another explanation may be that nest site location is not a trait affected by altitude per se. For instance, Sedivy et al. (2013) found that below-ground-nesting behavior in *Hoplitis* is most common in southern species, whereas northern species mainly nest above ground. Furthermore, in analyses without the predominately below-ground-nesting *Bombus*, Hoiss et al. (2012) found no relationship between altitude and nesting behavior suggesting that it may have been other traits inherent to *Bombus* species that selected for them in high altitude areas. It might be expected that they aquired such traits as they evolved in a cool climate (Hines 2008).

Does the compositional turn-over between species assemblages vary across spatial scales?

The average taxonomic, phylogenetic and functional β-diversity between species assemblages did not differ between the two spatial scales. Our results suggest that geographic distance per se does not influence the species assembly process in power-line strips, at least within the scale of our study. However, Murray et al. (2012) found that the compositional similarity, in terms of species, decreased with geographic distance in some habitat types, but not in others, suggesting that different habitat types may differ in terms of harbouring an equilibrium-type community. If habitats, such as power-line strips, contain mainly broadly distributed species, we may expect the species turnover between sites to be lower along a spatial gradient, than if habitats harbour mainly locally distributed species unable to disperse over even short distances.

In contrast, the northern-most sites had a higher average taxonomic, phylogenetic and functional β-diversity and displayed a higher variation between site-pairs, than the southern-most sites. This pattern may have been caused by differences in the climatic conditions affecting the species assemblages located in each of the two clusters. For instance, latitude was strongly correlated with altitude in our study region ($r = 0.73$). This could increase the relative importance of local factors in affecting the species composition in the northern-most localities, leading to a higher degree of patchiness, which in turn increases the species and functional turnover between sites, even across relatively small geographical distances. This might explain why we found a negative relationship between NRI_{ab} and altitude but a positive relationship with plant cover. In contrast, the southern-most species assemblages had a lower beta-diversity and also smaller variation between site-pairs, suggesting that these were more homogenous, as would be expected if resource levels and climatic conditions are similar across the landscape.

Conclusions and suggestions for future research

Our results suggest that local bee species assemblages are composed of species filtered from a regional species pool. The filters work hierarchically, where regional filters affect species stronger than the landscape and local filters, which mainly have a sorting mechanism. The environmental filters select species based on their phylogeny and their functional traits, and hence the composition of local species assemblages should be predictable if the regional species pool is known, and specific filters can be determined a priori.

Together with the findings of others (Keddy 1992, Poff 1997, de Bello et al. 2013), our results suggest that the multi-scale model of environmental filtering provides a good conceptual model for community ecology. It provides a logical framework for integrating biogeography, landscape ecology, community ecology and population ecology into a general theory of species assembly. Furthermore, the conceptual model provides guidelines for future studies on the distribution of biodiversity.

We suggest a need for model improvements on the above-regional and the below-local level to elucidate the effects on species assembly of migration history and competition, respectively. As illustrated in our example with species from the genus *Bombus*, it is likely that an improved knowledge on ecological links between major biogeographic distributional patterns and evolutionary history will increase our understanding of why and how species respond to regional, landscape and local filters. Moreover, at the local level it will be important to find suitable signals for locating species ensembles within the species assemblage (Fauth et al. 1996). One possible trajectory would be to examine whether the degree of competition for important resources and niche overlap increases with phylogenetic similarity, by testing the 'competition-relatedness hypothesis' (Cahill et al. 2008).

Acknowledgements – We wish to thank Dag Slettebø, Are Endal Rognes, Adrian Rasmussen, Håkon Celius, Lisbeth Nordtiller, Torbjørn Kornstad, Morten Meland, Marte Lilleeng, Ronny Steen and John Gunnar Dokk for field and laboratory assistance. Agnes Kammerhofer prepared the GIS maps. Kjell Magne Olsen identified all *Bombus* species. Data collection and species identification was funded by STATNETT.

References

Amiet, F. 2001. Apidae. 3, *Halictus*, *Lasioglossum*. – Schweizerische Entomologische Gesellschaft.

Amiet, F. 2004. Apidae. 4, *Anthidium*, *Chelostoma*, *Coelioxys*, *Dioxys*, *Heriades*, *Lithurgus*, *Megachile*, *Osmia*, *Stelis*. – Schweizerische Entomologische Gesellschaft.

Amiet, F. et al. 1999. Apidae. 2, *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. – Schweizerische Entomologische Gesellschaft.

de Bello, F. et al. 2007. Importance of species abundance for assessment of trait composition: an example based on pollinator communities. – Community Ecol. 8: 163–170.

de Bello, F. et al. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. – J. Veg. Sci. 21: 992–1000.

de Bello, F. et al. 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. – Ecography 36: 393–402.

Bjørdal, I. and Bjørkelo, K. 2006. AR5 klassifikasjonssystem: klassifikasjon av arealressurser. – Norsk institutt for skog og landskap.

Blomberg, S. P. and Garland, T. Jr 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. – J. Evol. Biol. 15: 899–910.

Cadotte, M. W. et al. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. – J. Appl. Ecol. 48: 1079–1087.

Cahill, J. F. et al. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? – Perspect. Plant Ecol. Evol. Syst. 10: 41–50.

Canty, A. and Ripley, B. 2013. boot: Bootstrap R (S-Plus) functions. – R package ver. 1.3-9.

Carolan, J. C. et al. 2012. Colour patterns do not diagnose species: quantitative evaluation of a DNA barcoded cryptic bumblebee complex. – PLoS One 7: e29251.

Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities – a theoretical perspective. – J. Anim. Ecol. 61: 1–12.

Crawley, M. J. 2013. The R book, 2nd ed. – Wiley.

Danforth, B. N. et al. 2006. Analysis of family-level relationships in bees (Hymenoptera : Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. – Mol. Phylogenet. Evol. 39: 358–372.

Diaz, S. et al. 1998. Plant functional traits and environmental filters at a regional scale. – J. Veg. Sci. 9: 113–122.

Elton, C. 1946. Competition and the structure of ecological communities. – J. Anim. Ecol. 15: 54–68.

Fauth, J. E. et al. 1996. Simplifying the jargon of community ecology: a conceptual approach. – Am. Nat. 147: 282–286.

Gaston, K. J. 2000. Global patterns in biodiversity. – Nature 405: 220–227.

Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. – J. Anim. Ecol. 71: 757–764.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. – Biometrics 27: 857–871.

Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. – Oecologia 153: 589–596.

Hines, H. M. 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). – Syst. Biol. 57: 58–75.

Hoiss, B. et al. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. – Proc. R. Soc. B 279: 4447–4456.

Kayaalp, P. et al. 2013. Rapid diversification in Australia and two dispersals out of Australia in the globally distributed bee genus, *Hylaeus* (Colletidae: Hylaeinae). – Mol. Phylogenet. Evol. 66: 668–678.

Keddy, P. A. 1992. Assembly and response rules – 2 goals for predictive community ecology. – J. Veg. Sci. 3: 157–164.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. – Bioinformatics 26: 1463–1464.

Körner, C. 2007. The use of 'altitude' in ecological research. – Trends Ecol. Evol. 22: 569–574.

Kraft, N. J. B. et al. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. – Am. Nat. 170: 271–283.

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

Maechler, M. et al. 2013. Cluster: cluster analysis basics and extensions. – R package ver. 1.14.4.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – Trends Ecol. Evol. 21: 178–185.

McGill, B. J. et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. – Ecol. Lett. 10: 995–1015.

Michener, C. D. 2007. The bees of the world. – Johns Hopkins Univ. Press.

Moretti, M. et al. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. – J. Anim. Ecol. 78: 98–108.

Müller, A. et al. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. – Biol. Conserv. 130: 604–615.

Murray, T. E. et al. 2012. Local-scale factors structure wild bee communities in protected areas. – J. Appl. Ecol. 49: 998–1008.

Nagendra, H. 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. – Appl. Geogr. 22: 175–186.

Økland, R. H. et al. 2001. Vegetation–environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. – Sommerfeltia 29: 1–190.

Oksanen, J. et al. 2013. vegan: community ecology package. – R package ver. 2.0-9.

Paradis, E. et al. 2004. APE: analyses of phylogenetics and evolution in R language. – Bioinformatics 20: 289–290.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. – Ecology 87: 2614–2625.

Petchey, O. L. and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. – Ecol. Lett. 9: 741–758.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – J. N. Am. Benthol. Soc. 16: 391–409.

Potts, S. G. et al. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? – Ecology 84: 2628–2642.

Ricotta, C. and Moretti, M. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. – Oecologia 167: 181–188.

Russell, K. N. et al. 2005. The potential conservation value of unmowed powerline strips for native bees. – Biol. Conserv. 124: 133–148.

Scheuchl, E. 2000. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs Band I Anthophoridae. – Eigenverlag.

Scheuchl, E. 2006. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs Band II Megachilidae – Melittidae. – Eigenverlag.

Schmid-Egger, C. and Scheuchl, E. 1997. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs Band III Andrenidae. – Eigenverlag.

Sedivy, C. et al. 2013. Molecular phylogeny of the bee genus *Hoplitis* (Megachilidae: Osmiini) – how does nesting biology affect biogeography? – Zool. J. Linn. Soc. 167: 28–42.

Silver, C. A. et al. 2012. Temporary and permanent wetland macroinvertebrate communities: phylogenetic structure through time. – Acta Oecol. 39: 1–10.

Simpson, G. L. 2012. permute: functions for generating restricted permutations of data. – R package ver. 0.7-0.

Steffan-Dewenter, I. and Tscharntke, T. 2001. Succession of bee communities on fallows. – Ecography 24: 83–93.

Steffan-Dewenter, I. et al. 2002. Scale-dependent effects of landscape context on three pollinator guilds. – Ecology 83: 1421–1432.

Ulyshen, M. D. et al. 2010. On the vertical distribution of bees in a temperate deciduous forest. – Insect Conserv. Divers. 3: 222–228.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – Am. Nat. 156: 145–155.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Westrich, P. 1989. Die Wildbienen Baden-Württembergs. – E. Ulmer.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partialhabitats. – In: Matheson, A. et al. (eds), The conservation of bees. Academic Press, pp. 1–16.

Williams, N. M. et al. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. – Biol. Conserv. 143: 2280–2291.

Williams, P. H. et al. 2012. Unveiling cryptic species of the bumblebee subgenus *Bombus s. str.* worldwide with COI barcodes (Hymenoptera: Apidae). – Syst. Biodivers. 10: 21–56.

Winfree, R. et al. 2007. Effect of human disturbance on bee communities in a forested ecosystem. – Conserv. Biol. 21: 213–223.

Winfree, R. et al. 2011. Native pollinators in anthropogenic habitats. – Annu. Rev. Ecol. Evol. Syst. 42: 1–22.

Wolf, S. et al. 2010. The reliability of morphological traits in the differentiation of *Bombus terrestris* and *B. lucorum* (Hymenoptera: Apidae). – Apidologie 41: 45–53.

Supplementary material (Appendix ECOG-00938 at <www.ecography.org/readers/appendix>). Appendix 1–5.

Ecography

ECOG-00938
Sydenham, M. A. K., Moe, S. R., Totland, Ø. and Eldegard, K. 2014. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? – Ecography doi: 10.1111/ecog.00938

Supplementary material

Supplementary material Appendix 1, Table A1 The life-history traits attributed to bee species sampled in power-line strips in southeast Norway. Traits were; body size (average intertegulae distance in millimeters, ITD) measured on the available nest founding females (Ind) at the Natural History Museum in Oslo, belowground nesters (End), aboveground nesters (Hyp), pollen specialists (Olig), pollen generalists (Poly), solitary (Soli), social (Soci), species emerging from march through April (Spri) and the duration the flight period lasts in months (Acti). For some species trait values were unattainable (n.a.). Only non-parasitic bees were included in the analysis throughout the paper. Traits were compiled following Westrich (1989). The nomenclature follows Michener (2007).

Species	ITD	Ind	End	Hyp	Olig	Poly	Soli	Soci	Spri	Acti
Andrena										
A. bicolor	2.1	10	X			X	X		X	5
A. carantonica	3.0	10	X			X	X		X	5
A. cineraria	2.9	10	X			X	X		X	2
A. clarkella	3.2	10	X		X		X		X	3
A. fucata	2.2	10	X			X	X		X	4
A. fulvida	2.3	4	X			X				2
A. fuscipes	2.2	10	X		X		X			3
A. haemorrhoa	2.6	10	X			X	X		X	4
A. helvola	2.4	10	X			X	X		X	4
A. lapponica	2.5	10	X		X		X		X	3
A. subopaca	1.4	10	X			X	X		X	6
A. wilkella	2.5	10	X		X		X			3
Anthidium										
A. punctatum	3.0	10		X		X	X			4
Bombus										
B. hortorum	6.0	10	X			X		X	X	7
B. hypnorum	5.7	2		X		X		X	X	6
B. jonellus	4.7	2		X		X		X	X	7
B. lucorum aggr	6.1	10	X			X		X	X	6
B. pascuorum	5.4	10	X			X		X	X	8
B. pratorum	5.2	10		X		X		X	X	7
B. ruderarius	n.a.	n.a.		X		X		X		5

B. soroeensis	n.a.	n.a.	X			X		X		5
B. sylvarum	5.4	2	X			X		X	X	7
Colletes										
C. daviesanus	2.6	10	X		X		X			4
C. succinctus	3.1	10	X		X		X			4
Halictus										
H. rubicundus	2.1	10	X			X		X	X	6
Hoplitis										
H. tuberculata	2.2	10		X		X	X			3
Hylaeus										
H. angustatus	0.9	5		X		X	X			5
H. annulatus	1.5	10		X		X	X			6
H. communis	1.4	10		X		X	X			5
H. confusus	1.5	10		X		X	X			5
H. hyalinatus	1.2	10		X		X	X			5
Lasioglossum										
L. albipes	1.5	10	X			X	n.a.	n.a.	X	7
L. calceatum	2.0	10	X			X		X	X	7
L. fratellum	1.5	10	X			X	n.a.	n.a.	X	6
L. leucopus	1.1	10	X			X	X		X	6
L. punctatissimum	1.3	10	X			X	n.a.	n.a.	X	7
L. rufitarse	1.4	10	X			X	X		X	6
Megachile										
M. nigriventris	4.3	3		X	X		X			2
M. versicolor	3.3	10		X		X	X			5

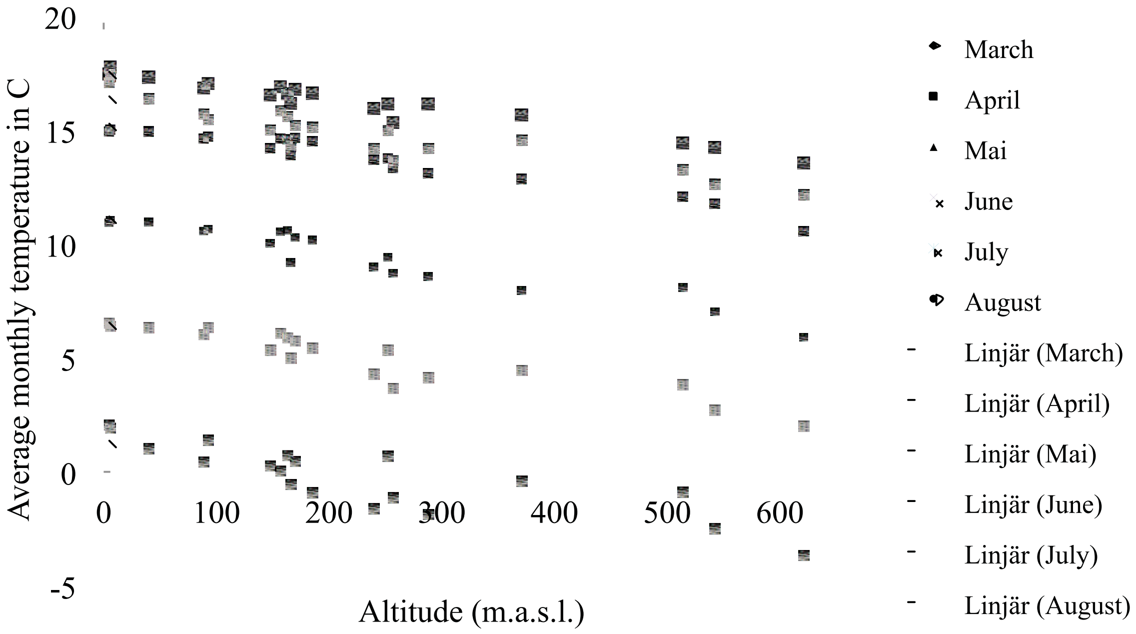
Osmia										
O. bicornis	3.1	10		X		X	X		X	5
O. caerulescens	2.5	8		X		X	X		X	5
O. nigriventris	3.3	8		X		X	X		X	3
O. parietina	2.1	9		X		X	X			3
O. uncinata	2.5	3		X		X	X			2

References

Michener, C. D. 2007. The bees of the world. — Johns Hopkins University Press.

Westrich, P. 1989. Die Wildbienen Baden-Württembergs. — E. Ulmer.

Supplementary material Appendix 2, Fig. A2.

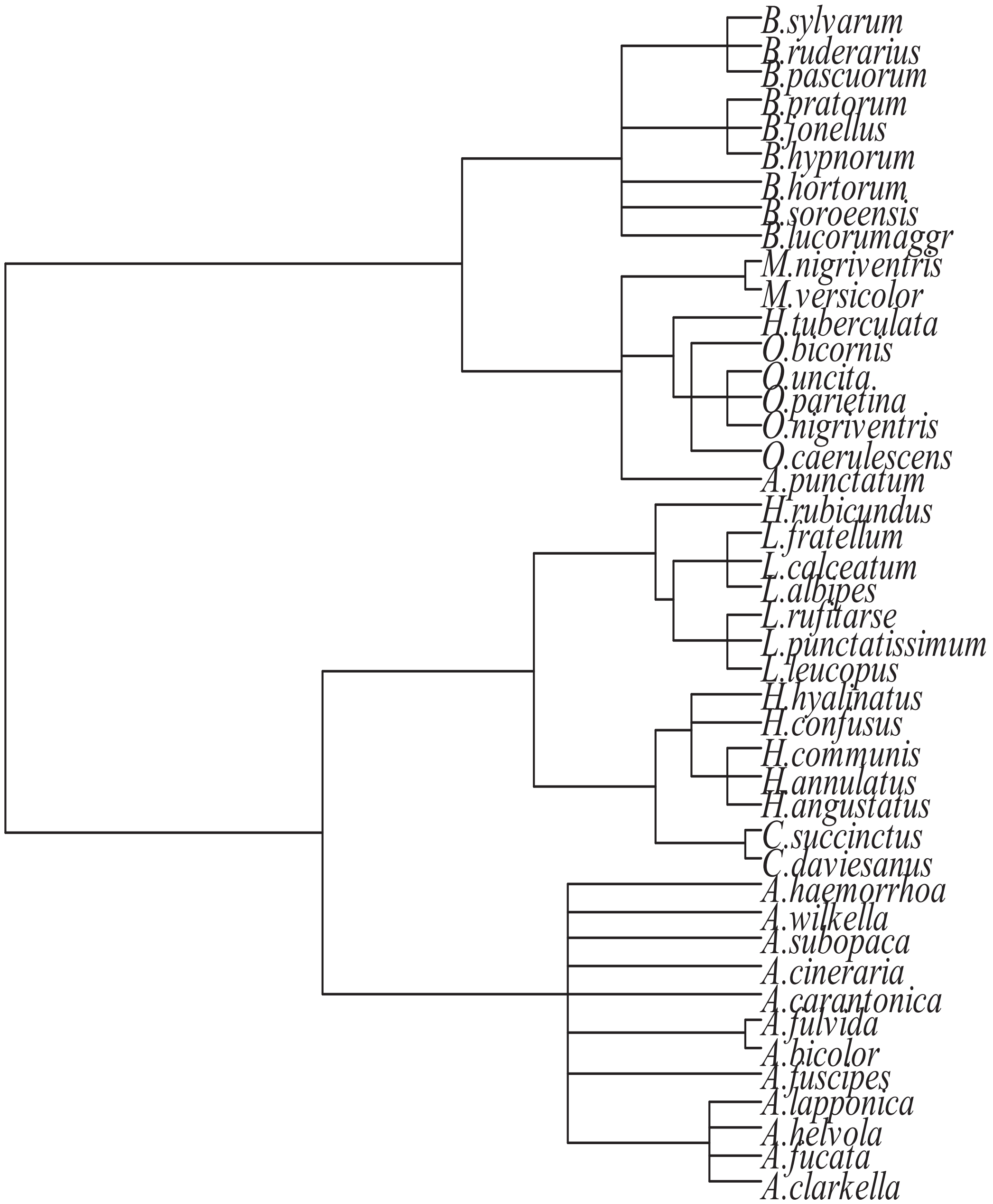


Supplementary material Appendix 2, Fig. A2 the linear relationship between altitude (m.a.s.l.) and the average temperature for March, April, Mai, June, July and August based on 20 meteorological climate stations within the study region. The temperature dropped by 0.69 C on average, as the altitude increased by 100 meters. Measurements at each altitudinal point were based on averages taken from the average monthly temperature during the time period 2003-2012. There were two climate stations situated at 240 m.a.s.l. providing the annual monthly average temperature at that altitude with two measurements. The included stations were, station number; 34130, 27500, 17150, 17850, 32060, 5590, 1130, 19710, 24890, 28380, 6020, 7010, 12680, 37230, 8140, 28800, 14600, 18950, 21680 and 61770.

References

The Norwegian meteorological institute: www.eklima.no.

Supplementary material Appendix 3, Fig. A3.



Supplementary material Appendix 3, Fig. A3 the hypothesized taxonomic relationship between the non-cleptoparasitic bees sampled in power-line strips in 2009 and 2010 in southeast Norway. The phylogeny was based on the taxonomy of Dansforth et al. (2006) and Michener (2007). The tree included: tongue length, family, sub family, tribe, genus, sub genus and species. The polytumous ultrametric tree was constructed using the r-package APE with the power-value set to 1 (Paradis et al. 2004)

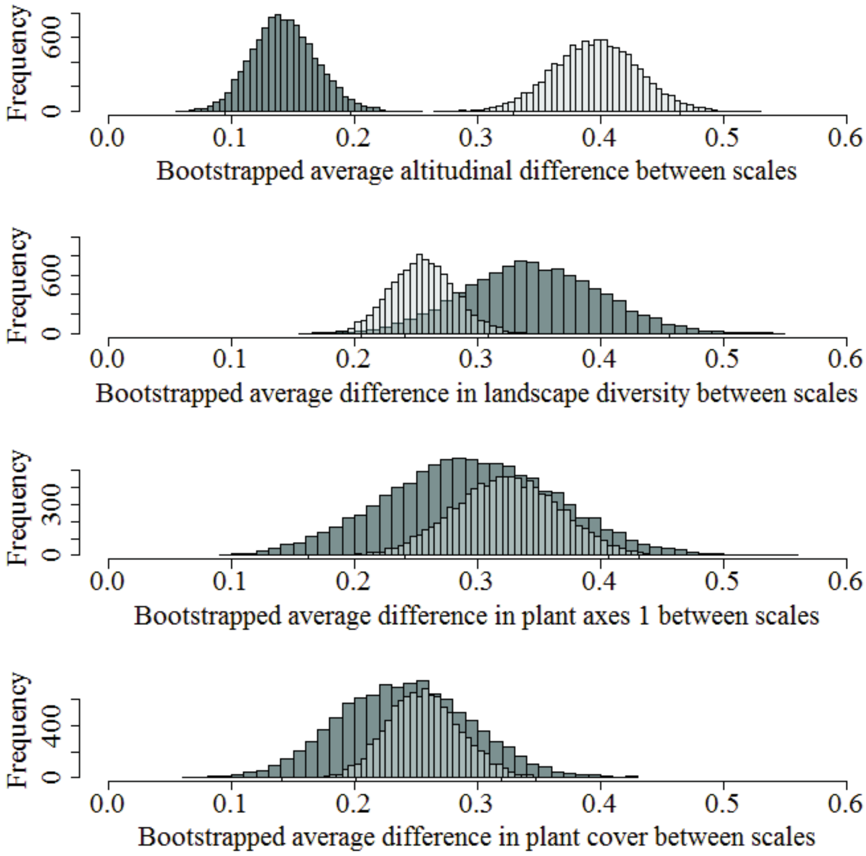
References

Danforth, B. N. et al. 2006. Analysis of family-level relationships in bees (Hymenoptera : Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. — Mol Phylogenet Evol 39: 358-372.

Michener, C. D. 2007. The bees of the world. — Johns Hopkins University Press.

Paradis, E. et al. 2004. APE: Analyses of Phylogenetics and Evolution in R language. — Bioinformatics 20: 289-290.

Supplementary material Appendix 4, Fig. A4.



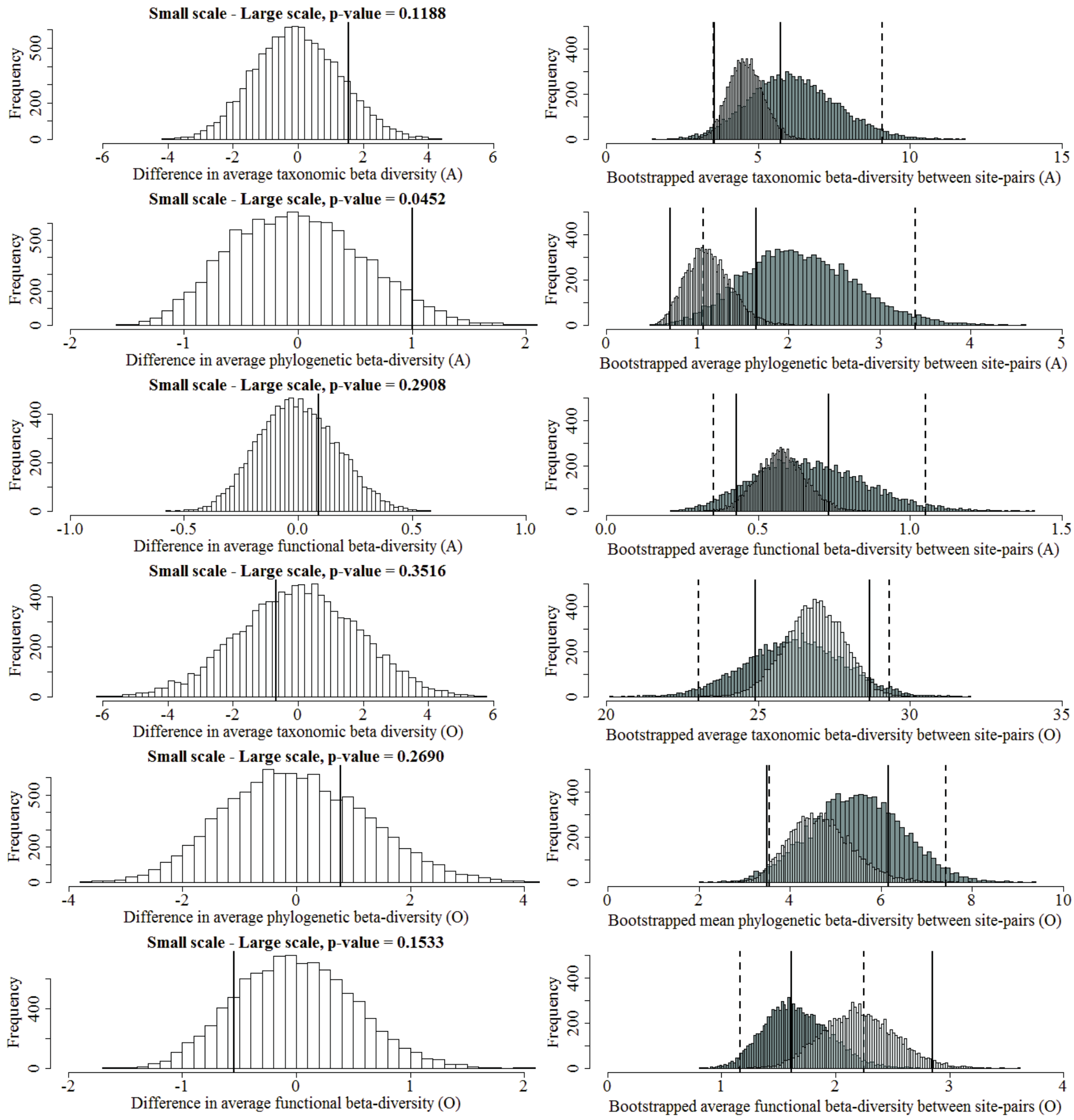
Supplementary material Appendix 4, Fig. A4 showing the distribution of average dissimilarity in environmental conditions between site-pairs located closer to each other than 20 km (small scale; dark grey) and site-pairs located farther from each other than 100 km (large scale; light grey).

The average dissimilarity in altitude between sites was smaller at the small scale than at the large scale (panel 1).The distributions of the two scales overlapped in terms of similarity in landscape diversity, plant axis one and plant cover (panels 2-4). The distributions were calculated by calculating the euclidian distance between all site-pairs in terms of each environmental variable. Variable pairs were then grouped according to the geographic distances between pair-members. We then used the R-package *boot* (Canty and Ripley 2013) to calculate a boot-strapped distribution of averages within each scale through 10,000 permutations, with replacement. The line below each distribution, attaching it to the x-axis, shows the 95% quantile of the distribution.

Refferences

Canty, A. and Ripley, B. 2013. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-9.

Supplementary material Appendix 5, Fig. A5.



Supplementary material Appendix 5, Fig. A5 showing the differences in average inter-site β-diversity between pairs of species assemblages located within 20 km of each other (small scale), and those located further than 100 km from each other (large scale). The differences were calculated for both abundance based and occurrence based β-diversity indexes marked with (A) and (O) respectively. The left column displays the observed differences in the average β-diversity between species assemblages in the small and in the large scale (dashed line). The p-values specify the proportion of differences from the null distribution that are higher than the absolute difference in the observed values. The right column displays the 95% confidence intervals calculated from the bootstrapped distribution of the average β-diversity between species assemblage-pairs in the small scale (filled lines) and the large scale (dashed lines).

Paper III

Ecology and Evolution

Open Access

Inter-assemblage facilitation: the functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees

Markus A. K. Sydenham, Lise D. Häusler, Stein R. Moe & Katrine Eldegard

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P. O. B. 5003, Ås NO-1432, Norway

Keywords
Cavity nesting bees, community assembly, community ecology, facilitation, functional diversity, functional traits, pollinators, wild bees, wood boring beetles.

Correspondence
Markus A. K. Sydenham, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P. O. B. 5003, NO-1432 Ås, Norway.
Tel: 0047 67231657
E-mail: markus.sydenham@nmbu.no

Funding Information
Field work and species identifications for this study were funded by STATNETT.

Received: 2 July 2015; Revised: 10 November 2015; Accepted: 19 November 2015

doi: 10.1002/ece3.1871

Abstract

Inter-specific interactions are important drivers and maintainers of biodiversity. Compared to trophic and competitive interactions, the role of non-trophic facilitation among species has received less attention. Cavity-nesting bees nest in old beetle borings in dead wood, with restricted diameters corresponding to the body size of the bee species. The aim of this study was to test the hypothesis that the functional diversity of cavity-producing wood boring beetles - in terms of cavity diameters - drives the size diversity of cavity-nesting bees. The invertebrate communities were sampled in 30 sites, located in forested landscapes along an elevational gradient. We regressed the species richness and abundance of cavity nesting bees against the species richness and abundance of wood boring beetles, non-wood boring beetles and elevation. The proportion of cavity nesting bees in bee species assemblage was regressed against the species richness and abundance of wood boring beetles. We also tested the relationships between the size diversity of cavity nesting bees and wood boring beetles. The species richness and abundance of cavity nesting bees increased with the species richness and abundance of wood boring beetles. No such relationship was found for non-wood boring beetles. The abundance of wood boring beetles was also related to an increased proportion of cavity nesting bee individuals. Moreover, the size diversity of cavity-nesting bees increased with the functional diversity of wood boring beetles. Specifically, the mean and dispersion of bee body sizes increased with the functional dispersion of large wood boring beetles. The positive relationships between cavity producing bees and cavity nesting bees suggest that non-trophic facilitative interactions between species assemblages play important roles in organizing bee species assemblages. Considering a community-wide approach may therefore be required if we are to successfully understand and conserve wild bee species assemblages in forested landscapes.

Introduction

In community ecology we tend to study the processes related to the diversity within a single species assemblage (Fauth et al. 1996; Lawton 1999) such as competition and trophic interactions (Potts et al. 2003) or the impact of environmental filters on the functional and phylogenetic diversity of bee species assemblages (Hoiss et al. 2012). A species assemblage is here defined following Fauth et al. (1996) as those species found within a community that belong to the same taxa. However, the diversity within species assemblages may also depend on non-trophic facilitative interactions with other species assemblages in the same community through processes of ecosystem engineering, whereby some species alter the environment in ways that opens niches for other species to occupy (Jones et al. 1994; Lawton 1994; Bruno et al. 2003). Improving our understanding of the influence of such interactions may have considerable bearing on the successful management of habitats that host species assemblages of conservation priority.

Wild bees have received increased attention over the last two decades due to declines in pollinator diversity worldwide (Potts et al. 2010) and their expected impact on seed production in domesticated (Klein et al. 2007) and wild plants (Fründ et al. 2013), where an estimated

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

87.5% of wild angiosperms are pollinated by animals (Ollerton et al. 2011). Indeed, the influences of many important drivers on the diversity of wild bees in anthropogenic landscapes are well documented (Winfree et al. 2011). Bees rely on forage resources, nest sites and nest building materials, each of which are sometimes found in separate habitats (Westrich 1996). The diversity of both foraging (Potts et al. 2003; Müller et al. 2006) and nesting resources (Potts et al. 2005; McFrederick and LeBuhn 2006a,b; Murray et al. 2012) contribute to structuring wild bee species assemblages at the local scale. At the landscape scale a shortage of habitat types providing these resources partly explains the variation in diversity between bee species assemblages (Steffan-Dewenter et al. 2002; Hopfenmüller et al. 2014). In addition to resource-related habitat conditions, large-scale environmental filters such as differing climatic and nesting conditions along elevational gradients also play an important role in structuring wild bee species assemblages (Hoiss et al. 2012; Sydenham et al. 2015).

In the course of the past decade, there has been an increased focus on the role functional traits play in organizing species assemblages (Weiher et al. 2011). Functional diversity indices may reveal mechanistic links between biodiversity and ecological processes (Petchey and Gaston 2006; Laliberté and Legendre 2010; Ricotta and Moretti 2011) which may not be found if one relies solely on indices based on the species richness and abundances of individuals (Cadotte et al. 2011). Indeed, the consequences of land-use change for wild bee species assemblages depend on the functional traits of bee species such as nesting habits (Williams et al. 2010; Hopfenmüller et al. 2014). One functional trait-group is the cavity-nesting bees, here defined as solitary bees that nest in pithy stems as well as abandoned beetle burrows in dead wood. In meadows, the diversity of cavity-nesting bee species assemblages is higher in sites containing old fruit trees compared to sites lacking of old trees (Tscharntke et al. 1998), suggesting that nesting substrates may be a limiting factor for these bees (Steffan-Dewenter and Schiele 2008).

During the past century, silviculture has reduced the amount of dead wood in forests by as much as 90–98% in some areas (Siitonen 2001), leading to the regional extinctions of several species of wood boring beetles (Grove 2002). In Norway, 40% of the red listed beetle species depend on forest habitats and dead wood (Kålås et al. 2010). Wood boring beetles play an important function in forested landscapes by excavating cavities in dead wood, which - once abandoned - go on to be occupied by other species of cavity-nesting insects such as bees (Ehnström and Axelsson 2002; Stokland et al. 2012). Although many species of Hylaeine and Megachiline bees (hereafter referred to as cavity-nesting bees) nest in abandoned beetle nests in dead wood (Westrich 1989), and that some bee species are directly associated with forests (Winfree et al. 2007), the influence of the diversity of wood boring beetles on the diversity of cavity-nesting bees has received little attention (but see Westerfelt et al. 2015). For instance, as cavity-nesting bee species vary in body-size and prefer different diameters of potential nest-sites (Gathmann et al. 1994; Tscharntke et al. 1998), they are likely to nest in holes produced by different species of beetles. Understanding the properties of such relationships may be of high importance for the conservation of bees if historical reductions of dead wood have had cascading effects on cavity-nesting bees by initially reducing the diversity of wood boring beetles. Moreover, compared to artificial nests, only a small proportion of natural beetle borings are occupied by bees and other Aculeates (Westerfelt et al. 2015), suggesting that the quality of the nesting substrate is of high importance when bees evaluate the suitability of a nesting site. It is therefore possible that the functional diversity of freshly emerged wood boring beetles provides an informative surrogate for the availability and diversity of recently excavated, i.e. high quality, cavities in an area. We formulated three hypotheses allowing us to infer if the diversity of wood boring beetles is an important determinant of cavity nesting bee diversity.

Hypothesis 1: The species richness and abundance of cavity nesting bees show a significant increase with the species richness and abundance of wood boring beetles. A similar relationship is not expected for the species richness and abundance of non-wood boring beetles or wood boring beetles that produce cavities that are too small for bees to occupy. Additionally, the influence of the species richness and abundance of cavity producing beetles is not driven by a co-variation with other environmental filters, such as elevation or the area of similar habitat (i.e. width of the power line clearing).

Hypothesis 2: The positive associations between cavity nesting bees and cavity producing beetles are driven by nest-site facilitation and not by shared positive responses to underlying foraging resources, such as floral diversity, which should also favour non-cavity nesting bees. An increased cavity-producing beetle species richness and abundance should therefore lead to an increased proportion of cavity nesting bees in local bee species assemblages. This relationship should be significant even when the nesting conditions for ground nesting bees are accounted for (i.e. the degree of shading due to regrowth).

Hypothesis 3: The occupation of beetle borings by cavity nesting bees depends on the diameter of the boring,

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

and the size of the bee. An increased species richness, abundance and functional diversity (in terms of boring diameters) of wood boring beetles in the forested landscape should provide a higher diversity of nesting spaces and lead to a high size diversity (in terms of body sizes) of cavity-nesting bees.

Materials and Methods

Study system and sampling

The study was conducted in 30 power line clearings (mean width = 42 m, SD = 18 m) along an elevational gradient (36–568 m a.s.l.) in a landscape dominated by boreal forests with varying proportions of the main tree species: Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and birch *Betula* spp. (Fig. S1, Supporting information). Power line clearings are typically situated in areas of low to intermediate productivity and cleared every 5–10 years to prevent trees from encroaching on the aerial lines. Establishing and maintaining power line clearings creates "through corridors" of earlier successional vegetation and long, often sharply defined, permanent edges on either side of the clearing (Eldegard et al. 2015). Edge creation and selective felling of tall trees leads to increased tree mortality and a greater abundance of snags and logs at edges (Harper et al. 2005, pers. obs.). It is therefore likely that dead wood is less of a limiting factor for wood boring beetles in these habitats than in the intensively managed forests although dead wood is also found in these habitats (e.g. in the form of stumps in recently cleared forests). The system thereby creates a good model-system for evaluating the role of wood boring beetles as facilitators for cavity-nesting bees.

Sampling was conducted at 30 different sites in, respectively, 2009 (10 sites), 2010 (10) and 2013 (10). Inter-site distances (mean = 83 km, min = 9 km, max = 187 km) were greater than the foraging range of the bees (Gathmann and Tscharntke 2002; Greenleaf et al. 2007) ensuring independency among bee species assemblages. Beetles and bees were sampled using flight-interception traps, which allowed for a standardized sampling at several sites covering a large geographic area. Flight interception traps are commonly used to sample beetles (Økland 1996) and have been especially recommended for the collection of wood-nesting bees (Rubne et al. 2015). Each trap consisted of two Plexiglas screens (370 × 210 mm) assembled to form a cross attached to a white funnel with a collecting bottle attached to it. The bottle was filled with a 50:50 mixture of green propylene glycol and water plus a few drops of detergent to break the surface tension. Four traps were deployed along the centre of the power line clearings in each of the 10 sites sampled in 2009 and 2010. Since some traps were destroyed during the sampling periods in 2009 and 2010 the number of traps per site was increased to five in 2013. The traps were installed following snow-melt (April/May) and removed in the early autumn (August/September). The traps were emptied four times during the trapping season and the collected material stored in 80% ethanol before pinning and identification.

We placed four 4 × 5 m plots along the centre of the power line clearing, following the direction of the corridor. The distance between the two nearest plots was 50 m. Within each of the four plots, we recorded the total number of tree species, the tree height and the crown of all species taller than one metre. In addition to the measures of tree numbers and sizes, we also recorded the basal area (relascope sum) and site productivity (see Eldegard et al. (2015)). For each site, we calculated the following variables: The total number of coniferous, Norway spruce, Scots pine and deciduous trees as well as the total number of trees. We also calculated the average height and crown width of trees within the sites as well as the maximum tree height, crown width and productivity recorded in any one of the four plots. Together these variables described the amount of regrowth and productivity and hence shading within the site. To deal with collinearity among these variables, we condensed them into two principal components. The variables were scaled to zero mean and unit deviance. Thereafter, the scaled variables were run through a Principal Components Analysis (PCA) using the "vegan" library in R (Oksanen et al. 2013) whereby we extracted the two-first axes. The Eigenvalues and proportion variation explained were 5.54 and 50.4% and 2.45 and 22.5% for PCA axis one and two, respectively. PCA axis one was positively related to all the variables and thereby indicated a gradient in regrowth (i.e. shading). PCA axis two was positively related to the total number of trees, number of deciduous trees, number of spruce trees as well as the site productivity and weakly related to the maximum crown width, and negatively related to the number of coniferous trees, pine trees, average and maximum tree height, basal area and crown cover. It thereby separated sites according to productivity and along a successional gradient being positively related to regrowth of trees in the clearings (Table S1, Supporting information). We extracted the site scores on the first two PCA axes and used these as variables to explain the effect of shading.

Statistical analyses

In order to compensate for traps lost during the sampling periods, a subset of traps were randomly selected and removed from each sampling period so that the sampling intensity within sites was equal across all sites and years. Three sites had lost more than one trap during a sampling period and were removed from the final dataset. The final dataset consisted of 27 sites each sampled with three traps during the first sampling period, four traps during the second and third and three traps during the final sampling period. All specimens collected in a site were pooled and sites were used as sampling units in the analyses. Cleptoparasitic bees were excluded from the analyses as they only indirectly depend on the nesting and foraging resources sought by their hosts.

The beetles were categorized into four groups. The first group consisted of "all beetles" sampled in the study. The second group consisted of all non-wood boring beetles. The third group consisted of small wood boring beetles that excavate cavities in dead wood with a diameter smaller than 3 mm or in the roots of plants. The fourth group consisted of large wood boring beetles that are known to excavate cavities with a diameter >3 mm in wood (Ehnström and Axelsson 2002). The distinction between the small and the large wood boring beetles was made because only beetles making holes, above ground, with diameters ≥3 mm are producers of possible nesting holes for the cavity nesting bees in our region (Budrienė et al. 2004; Westerfelt et al. 2015). All large wood boring beetle species were assigned to a diameter class equal to the diameter of the exit holes produced by the emerging adults (Ehnström and Axelsson 2002). Cavity nesting bees were grouped according to their thorax width (Table S2, Supporting information), since body size determines the minimum diameter of cavities in which they nest.

Three metrics that together account for the size diversity within bee and the functional diversity within beetle species assemblages were used in order to assess whether an increased functional diversity of wood boring beetles leads to a high size diversity of cavity-nesting bees. The functionally singular species richness (FSSR) is the number of unique size types found within the assemblage. As such it is the functional equivalent of nomenclatural species richness. The community weighted mean trait value (CWM) is a measure of the dominant trait value within a species assemblage. The functional dispersion (FDis) is a measure of the variation in trait values within a species assemblage (Laliberté and Legendre 2010). When the FDis is based on a single, numerical trait, it equals the mean absolute Euclidean distance of trait values found within the species assemblage to the CWM. These metrics were chosen since changes in both the dispersion of trait values and the CWM have been shown to be informative metrics for studies on functional bee ecology (Ricotta and Moretti 2011). Since an increase in the functional diversity of wood boring beetles should lead to an increased diversity and accessibility of nesting niches for bees, it should be expected that an increase in the FSSR, FDis and CWM of wood boring beetles would lead to an increase in FSSR, FDis and CWM of cavity nesting bees. The R (R development core team 2014) library "FD" (Laliberté and Legendre 2010) was used to calculate the size class richness ($\mathrm{FSSR}_{\mathrm{bees}}$), the community-weighted mean size ($\mathrm{CWM}_{\mathrm{bees}}$) and the dispersion of size classes ($\mathrm{FDis}_{\mathrm{bees}}$) for the cavity nesting bees. For the large wood boring beetles the CWM and the FDis were weighted according to the abundance of each species. The measures for bees were not abundance-weighted as doing so might decrease the influence of the relatively large Megachilids. Although species within this family were relatively rare, compared to the most abundant *Hylaeus* species, their presence within species assemblages provide important information about the niche-space occupied by bees in the species assemblage. However, the non-abundance weighted measures of both the $\mathrm{FDis}_{\mathrm{bees}}$ and the $\mathrm{CWM}_{\mathrm{bees}}$ were highly correlated with their abundance weighted counterparts (rho = 0.96, $P < 0.001$ and rho = 0.97, $P < 0.001$, respectively) suggesting only a small influence of abundance weighting the indices.

Due to the presence of multicolinearity among the explanatory variables (Table S3, Supporting information), the influence on response variables of each of the explanatory variables were analysed individually and the strengths of significant relationships assessed based on the Nagelkerke R^2, standardized effect sizes and P-values. This approach allowed an evaluation of the direct influence of each explanatory variable separately, in contrast to solely evaluating its influence based on the marginal effect as would be the case were it tested simultaneous with other variables. Variables with P-values ≤0.10 were then included in a full model which was subjected to a stepwise backward elimination based on likelihood ratio tests (LRTs) by dropping variables one at a time until all the remaining variables were significant ($P \leq 0.05$).

The species richness and abundance of cavity nesting bees increase with the species richness and abundance of large wood boring beetles (Hypothesis 1)

The association between cavity nesting bees and large wood boring beetles was compared to the association with small wood boring beetles, non-wood boring beetles and elevation. The individual influences of the explanatory variables on cavity nesting bee species richness were tested using generalized linear models (GLMs) with Poisson distributed errors. For the abundance of cavity nesting bees over-dispersion was accounted for by using negative binomial regressions in the "MASS" library (Venables and Ripley 2002) in R. Sampling year was included as a categorical variable with three levels (2009, 2010 and 2013) to account for potential among-year differences in cavity nesting bee species richness and abundance due to inter-annual climatic variations. Model fit was assessed from Nagelkerke R^2 values. In addition to comparing the influence of the explanatory variables based on their standardized effect sizes (z-values), Nagelkerke R^2 values and P-values a backward elimination of explanatory variables was conducted to allow a formal comparison of variables based on their marginal effects. Candidate models, consisting of all explanatory variables with $P < 0.10$, were subjected to backward elimination of variables. The relative importance of each variable was tested using likelihood ratio tests. One by one the variables with the lowest χ^2 score and highest P-value were removed from the model until all variables in the final model were significant ($P < 0.05$).

We also tested if the species richness and abundance of cavity nesting bees and large wood boring beetles showed significant relationships with the width of the power line clearing. This was done to test the assumption that a positive association among cavity nesting bees and wood boring beetles was not driven by similar species-area relationships. We used the width of the power line clearing as an explanatory variable indicating the area of similar habitat conditions and the species richness and abundance of either cavity nesting bees or large wood boring beetles as response variables. The analyses with species richness response variables were run using GLMs, assuming Poisson distributed errors whereas the analyses with abundances as response variables were run using negative binomial regressions.

The proportion of cavity nesting bees in bee species assemblages increases with the species richness and abundance of large wood boring beetles independent of vegetation shading the ground (Hypothesis 2)

For each site, the proportion of cavity nesting bee species and individuals were calculated relative to the total number of non-cavity nesting bee species and individuals. Since the cavity nesting bees in our study sites mainly forage on forbs rather than dwarf shrubs (Ericaceae), we also calculated the proportion of cavity nesting bee species and individuals for each site when the dwarf shrub (Ericaceae) specialists *Andrena fuscipes, A. lapponica* and *Colletes succinctus* were removed from the data, resulting in a total of four response variables.

The relationships between the proportion of cavity nesting bee species and individuals and the species richness and abundance of large wood boring beetles and sampling year were assessed using binomial generalized linear models (GLMs). We also included the two PCA axes related to shading and site productivity to account for potentially contrasting responses of cavity nesting and ground nesting bees to regrowth, which might prevent ground nesting bees from nesting in the site. The significance of each explanatory variable was tested separately using likelihood ratio tests. All explanatory variables with P-values ≤ 0.10 were included in a full model and subjected to a manual step-wise backward elimination until all variables were statistically significant ($P \leq 0.05$).

The functional diversity within beetle species assemblages drives the size diversity within bee species assemblages (Hypothesis 3)

The relationship between the size diversity of cavity nesting bees and the species richness, abundance and functional diversity of large wood boring beetles was compared to the relationship with the species richness, abundance of non-wood boring beetles, small wood boring beetles and elevation. Response variables were the number of unique bee size classes ($\mathrm{FSSR_{bees}}$), the community-weighted mean ($\mathrm{CWM_{bees}}$) body size and the variation in body sizes ($\mathrm{FDis_{bees}}$) in each site. Explanatory variables were the species richness, abundance, CWM and FDis of large wood boring beetles, the species richness and abundance of non-wood boring beetles and small wood boring beetles and elevation. The sampling year was included as a categorical variable with three levels (2009, 2010 and 2013).

Analyses with the $\mathrm{FSSR_{bees}}$ as response variables were conducted using GLMs with Poisson distributed errors. The analyses with the $\mathrm{CWM_{bees}}$ and the $\mathrm{FDis_{bees}}$ as responses were conducted using quasipoisson GLMs. The models with CWM of large wood boring beetles (L WB B) as explanatory variables were fitted using the second order polynomial to account for the hump-backed relationship with the response variable, which was detected in the exploratory analyses of the data. Since the size diversity could not be calculated for sites where no bees were sampled, two sites were omitted from these analyses. The influence of the explanatory variables was assessed based on to their Nagelkerke R^2, z-values and their P-values ($\alpha = 0.05$).

Results

A total of 621 species and 14,609 individuals of beetles and 47 species and 354 individuals of solitary and primitively eusocial bees were sampled. Sixty-five species and

1974 individuals of the beetles were woodborers. Of the wood boring beetles, 18 species and 791 individuals produced cavities in wood with a diameter ≥3 mm in which bees may nest (Table S2, Supporting information). Of the bees 15 species and 147 individuals were cavity nesters, and 9 species and 20 individuals were clepto-parasites (Table S4, Supporting information).

The species richness and abundance of cavity nesting bees increase with the species richness and abundance of large wood boring beetles (Hypothesis 1)

The species richness of cavity nesting bees increased with the species richness (Fig. 1, df = 1, $\chi^2 = 8.85$, $P = 0.003$) and abundance (Fig. 1, df = 1, $\chi^2 = 12.01$, $P = 0.001$) of large wood boring beetles and decreased with elevation (Fig. 1, df = 1, $\chi^2 = 5.09$, $P = 0.024$). The abundance of large wood boring beetles was the most important variable explaining cavity nesting bee species richness and was the only explanatory variable left in the final model, following backward elimination (Table 1). In contrast the species richness of cavity nesting bees was not influenced by the species richness (df = 1, $\chi^2 = 2.31$, $P = 0.129$) or abundance (df = 1, $\chi^2 = 0.73$, $P = 0.394$) of small wood boring beetles or by the species richness (df = 1, $\chi^2 = 0.52$, $P = 0.470$) or abundance (df = 1, $\chi^2 = 2.39$, $P = 0.123$) of non-wood boring beetles. Nor were there any significant difference in cavity nesting bee species richness among years (df = 2, $\chi^2 = 3.99$, $P = 0.136$).

The abundance of cavity nesting bees increased with the species richness (Fig. 1, df = 1, $\chi^2 = 11.97$, $P = 0.001$) and abundance (Fig. 1, df = 1, $\chi^2 = 35.17$, $P < 0.001$) of large wood boring beetles, and the abundance of non-wood boring beetles (Fig. 1, df = 1, $\chi^2 = 4.33$, $P = 0.037$) when each explanatory variable was tested separately. However, the abundance of large wood boring beetles was the most influential explanatory variable and the only variable remaining in the negative binomial regression model following backward elimination of variables (Table 1). We did not find a significant change in cavity nesting bee abundance with elevation (df = 1, $\chi^2 = 3.10$, $P = 0.079$) or among years (df = 2, $\chi^2 = 4.91$, $P = 0.086$), but the *P*-values were low. We found no effect on cavity nesting bee abundance of small wood boring beetle species richness (df = 1, $\chi^2 = 1.04$, $P = 0.307$) or abundance (df = 1, $\chi^2 = 1.07$, $P = 0.302$) or non-wood boring beetle species richness (df = 1, $\chi^2 = 0.16$, $P = 0.686$). See Table S5 (Supporting information) for test statistics and parameter estimates for the individual explanatory variables and full models.

The significant relationship between cavity nesting bee species richness and abundance and the species richness and abundance of large wood boring beetles was not due to co-variation with habitat area: we found no relationship between the species richness of cavity nesting bees (df = 1, $\chi^2 = 0.09$, $P = 0.762$) or large wood boring beetles (df = 1, $\chi^2 = 1.04$, $P = 0.307$) and the width of the power line clearing. Nor did we find any significant relationship between the abundance of cavity nesting bees (df = 1, $\chi^2 = 0.12$, $P = 0.728$) or large wood boring beetles (df = 1, $\chi^2 = 0.27$, $P = 0.605$) and the width of the power line clearing.

The proportion of cavity nesting bees in bee species assemblages increases with the species richness and abundance of large wood boring beetles independent of vegetation shading the ground (Hypothesis 2)

The proportion of cavity nesting bee species in local bee species assemblages did not change significantly according to the species richness (df = 1, $\chi^2 = 1.19$, $P = 0.28$) or abundance (df = 1, $\chi^2 = 0.02$, $P = 0.89$) of large wood boring beetles. Nor did it vary among sampling years (df = 2, $\chi^2 = 0.45$, $P = 0.80$) or with vegetation shading the ground (PCA axis one; df = 1, $\chi^2 = 1.95$, $P = 0.16$, PCA axis two; df = 1, $\chi^2 = 0.23$, $P = 0.63$). Similarly, when Ericaceae specialists were excluded from the data, the relative proportion of cavity nesting bee species remained stable along the gradients in large wood boring beetle species richness (df = 1, $\chi^2 = 0.86$, $P = 0.35$) and abundance (df = 1, $\chi^2 = 0.01$, $P = 0.93$), among sampling years (df = 2, $\chi^2 = 0.49$, $P = 0.78$), PCA axis one (df = 1, $\chi^2 = 2.80$, $P = 0.09$) and two (df = 1, $\chi^2 < 0.01$, $P = 0.99$).

In contrast, the proportion of cavity nesting bee individuals (abundance) increased with the species richness (Fig. 2, df = 1, $\chi^2 = 5.08$, $P = 0.024$) and abundance (Fig. 2, df = 1, $\chi^2 = 6.29$, $P = 0.012$) of large wood boring beetles. The abundance of large wood boring beetles was the most important variable explaining the proportion of cavity nesting bee individuals (Table 2). There was no significant difference among sampling years (df = 2, $\chi^2 = 2.52$, $P = 0.28$) or along PCA axis one (df = 1, $\chi^2 = 1.52$, $P = 0.22$) and two (df = 1, $\chi^2 = 0.83$, $P = 0.36$). The results were qualitatively similar when Ericaceae specialists were removed from the data, except from that the degree of tree regrowth and site productivity (PCA axes one and two) had a significant influence. The proportion of cavity nesting bee individuals increased with the species richness (Fig. 2, df = 1, $\chi^2 = 5.25$, $P = 0.022$) and abundance (Fig. 2, df = 1, $\chi^2 = 7.94$, $P = 0.005$) of large wood boring beetles and decreased with PCA axis one (Fig. 2, df = 1, $\chi^2 = 4.17$, $P = 0.041$) but was not influenced by PCA axis two (df = 1, $\chi^2 = 0.11$, $P = 0.74$) and did not differ among sampling years (df = 2, $\chi^2 = 1.67$, $P = 0.44$). When included as

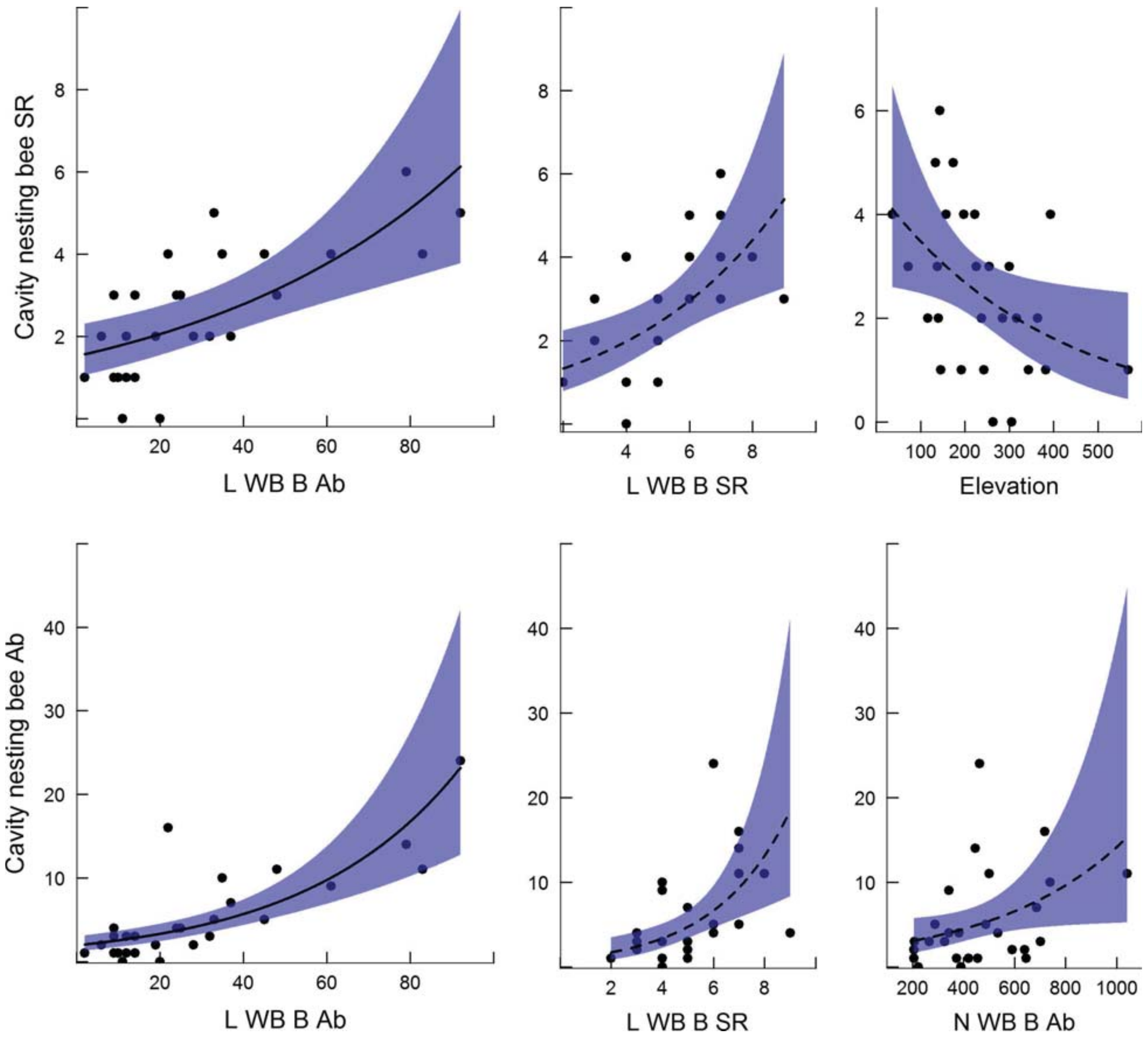


Figure 1. The species richness (SR) of cavity nesting bees (top panel) was influenced by the abundance (Ab) and species richness (SR) of large wood boring beetles (L WB B) which excavate cavities with diameters ≥3 mm and elevation (m a.s.l.). Similarly, the abundance of cavity nesting bees (lower panel) was related to the L WB B Ab, L WB B SR but also the abundance of non-wood boring beetles (N WB B Ab). Enlarged plots with solid regression lines show estimated values for the explanatory variables remaining after backward elimination (see text and Table 1 for test statistics).

explanatory variables in the same model the abundance of large wood boring beetles (df = 1, $\chi^2 = 13.07$, $P < 0.001$) and PCA axis one (df = 1, $\chi^2 = 14.85$, $P < 0.001$) remained statistically significant whereas the species richness of large wood boring beetles did not (df = 1, $\chi^2 = 0.23$, $P = 0.64$). However, if the abundance of large wood boring beetles was not included in the model, both the species richness of large wood boring beetles (df = 1, $\chi^2 = 6.68$, $P = 0.010$) and PCA axis one (df = 1, $\chi^2 = 5.60$, $P = 0.020$) were significant. Thus, the most important predictors of change in the proportionate abundance of cavity nesting bees, when Ericaceae specialists were excluded, were the abundance of large wood boring beetles and PCA axis one (Fig. 2).

The functional diversity within beetle species assemblages drives the size diversity within bee species assemblages (Hypothesis 3)

The size diversity of cavity-nesting bees increased with species richness (SR), abundance (Ab) and functional

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Table 1. Final models for cavity nesting bee species richness and abundance following backward elimination of the explanatory variables with a *P*-value <0.10 (Table S5, Supporting information). The model for bee species richness was fitted using GLMs with Poisson distributed errors, while the influence of explanatory variables on bee abundance was modelled using negative binomial regressions to account for overdispersion. Large wood boring beetles excavate cavities with diameters ≥3 mm suitable for cavity nesting bees. Nagelkerke R^2 values are shown.

	df	β	SE	*z* value	R^2	*P*-value
Cavity nesting bee species richness						
Intercept	25	0.417	0.206	2.03		0.043
Large wood boring beetles abundance		0.015	0.004	3.65	0.54	<0.001
Cavity nesting bee abundance						
Intercept	25	0.658	0.216	3.04		0.002
Large wood boring beetles abundance		0.027	0.005	5.73	0.80	<0.001

diversity of wood boring beetles in the community (Table 3, Fig. 3). Specifically, the number of unique size clases (FSSR) of cavity-nesting bees increased with the abundance of large wood boring beetles (df = 1, χ^2 = 5.40, *P* = 0.020). We found no significant influence of the large wood boring beetle (L WB B) species richness (df = 1, χ^2 = 3.37, *P* = 0.066), FDis (df = 1, χ^2 = 2.68, *P* = 0.101) and elevation (df = 1, χ^2 = 2.73, *P* = 0.098), although the p-values were low. The $\text{FSSR}_{\text{bees}}$ was not influenced by non-wood boring beetles (SR; df = 1, χ^2 = 0.09, *P* = 0.759, Ab; df = 1, χ^2 = 0.56, *P* = 0.456), small wood boring beetles (SR; df = 1, χ^2 = 0.07, *P* = 0.798, Ab; df = 1, χ^2 = 0.01, *P* = 0.927), $\text{FSSR}_{\text{L WB B}}$ (df = 1, χ^2 = 0.33, *P* = 0.566), $\text{CWM}_{\text{L WB B}}$ (df = 2, χ^2 = 3.90, *P* = 0.142) or sampling year (df = 2, χ^2 = 2.53, *P* = 0.282). The strongest relationship was found between the functionally singular species richness of cavity nesting bees and the abundance of large wood boring beetles, and the latter was the only explanatory variable included in the final model following backward elimination (Fig. 3, Table 3).

The community-weighted mean body-size of bees (CWM_{bees}) increased with the abundance (Fig. 3, df = 1, scaled deviance (D) = 4.91, *P* = 0.027) and FDis (Fig. 3, df = 1, D = 5.78, *P* = 0.016) of large wood boring beetles. Although not statistically significant the results for the influence of the $\text{CWM}_{\text{L WB B}}$ (df = 2, D = 4.59, *P* = 0.101) and elevation (df = 1, D = 2.71, *P* = 0.100) also suggested a trend. The CWM_{bees} was not influenced by the species richness (df = 1, D = 1.38, *P* = 0.239) or the $\text{FSSR}_{\text{L WB B}}$ (df = 1, D = 0.03, *P* = 0.872) of large wood boring beetles. Nor was there any influence of non-wood boring beetles (SR; df = 1, D = 1.38, *P* = 0.240, Ab; df = 1, D = 0.10, *P* = 0.750), small wood boring beetles (SR; df = 1, D = 1.20, *P* = 0.273, Ab; df = 1, D = 0.358, *P* = 0.550) or among year differences (df = 2, D = 3.63, *P* = 0.163). The $\text{FDis}_{\text{L WB B}}$ was the strongest explanatory variable and the only explanatory variable retained in the model following backward elimination of variables (Fig. 3, Table 3).

The functional dispersion in terms of bee body-sizes ($\text{FDis}_{\text{bees}}$) decreased with elevation (Fig. 3, df = 1, D = 4.08, *P* = 0.044), increased with the abundance of large wood boring beetles (Fig. 3, df = 1, D = 4.14, *P* = 0.042), showed a hump-backed relationship with the community-weighted mean diameter-class (Fig. 3, df = 2, D = 6.41, *P* = 0.041) of large wood boring beetles and increased with the functional dispersion of wood boring beetles (Fig. 3, df = 1, D = 9.58, *P* = 0.002). The $\text{FDis}_{\text{bees}}$ was unaffected by the species richness (df = 1, D = 2.30, *P* = 0.129) and FSSR (df = 1, D = 0.07, *P* = 0.789) of large wood boring beetles. Also, the $\text{FDis}_{\text{bees}}$ was unaffected by the species richness and abundance of non-wood boring beetles (SR; df = 1, D = 0.10, *P* = 0.758, Ab; df = 1, D = 0.16, *P* = 0.69) and small wood boring beetles (SR; df = 1, D = 0.23, *P* = 0.63, Ab; df = 1, D = 0.13, *P* = 0.72). There was no significant change in the FDis between years (df = 2, D = 2.74, *P* = 0.25). The $\text{FDis}_{\text{L WB B}}$ was the only variable included in the final model after backward elimination of variables (Fig. 3, Table 3).

The different measures of the size diversity within cavity-nesting bee species assemblages were highly correlated, showing that the most diverse bee communities, in terms of body sizes, had more large bees (namely Megachilids), while still containing the smaller *Hylaeus* species. Specifically, $\text{FSSR}_{\text{bees}}$ increased with both the $\text{FDis}_{\text{bees}}$ (Spearman's rank correlation; rho = 0.93, *P* < 0.001) and CWM_{bees} (rho = 0.61, *P* = 0.001). Similarly, the $\text{FDis}_{\text{bees}}$ also increased with the CWM_{bees} (rho = 0.70, *P* < 0.001). Moreover, the species richness of cavity nesting bees was also strongly related to $\text{FSSR}_{\text{bees}}$ (rho = 0.90, *P* < 0.001), $\text{FDis}_{\text{bees}}$ (rho = 0.84, *P* < 0.001) and CWM_{bees} (rho = 0.50, *P* < 0.011).

Discussion

Previous studies have identified the importance of nesting substrates (Potts et al. 2005; Murray et al. 2012) in organizing bee species assemblages. Moreover, it has recently been shown that cavities produced by wood boring beetles provide nest sites for secondary nesting Aculeates, including cavity nesting bees, but that the occupation of nest sites depends on substrate characteristics (Westerfelt et al. 2015). The present study shows that the species diversity of cavity-nesting bees is related to the species diversity of cavity-producing beetles and that this rela-

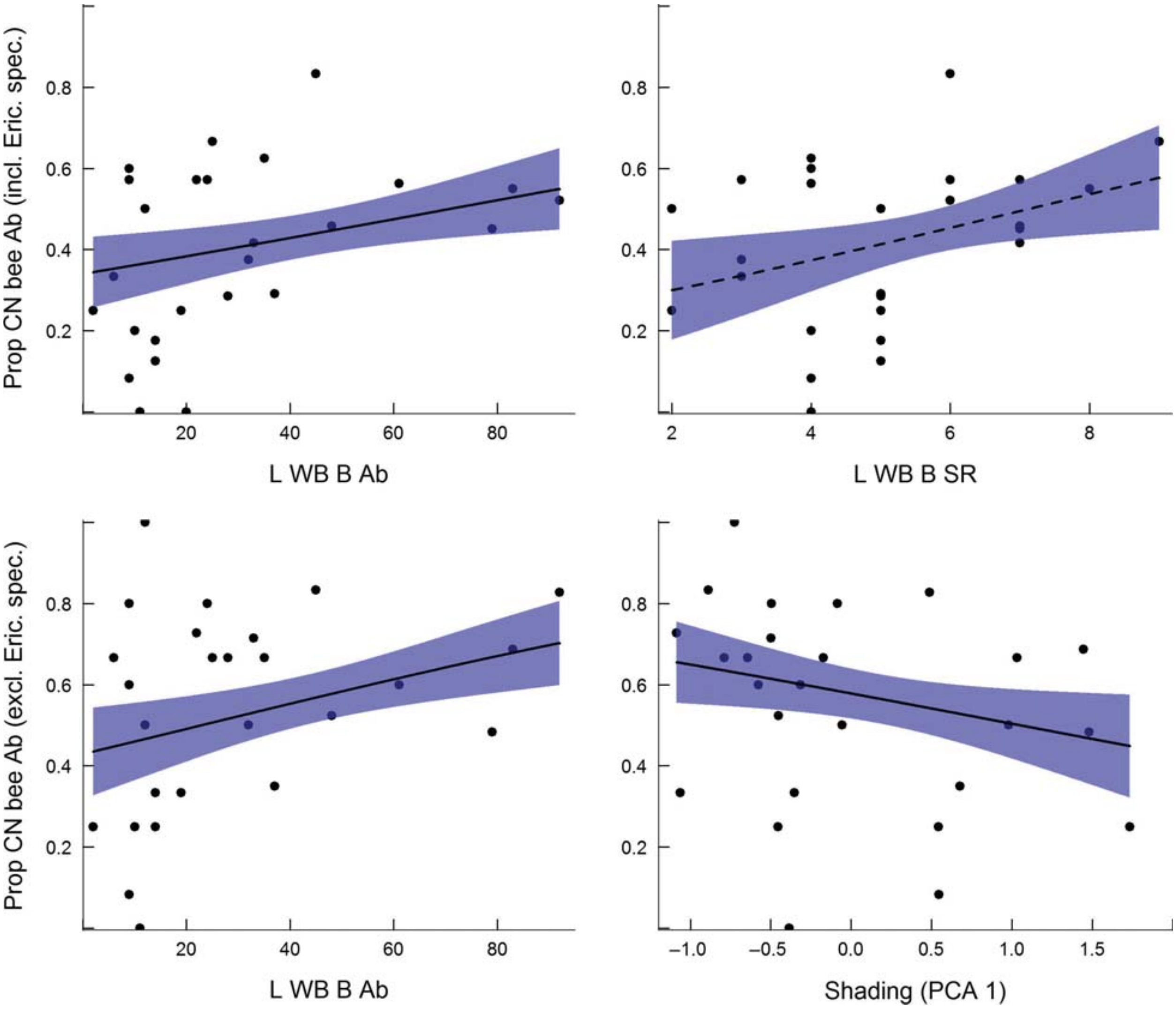


Figure 2. The proportion of cavity nesting (CN) bee species richness (SR) and abundance (Ab) increased with the Ab and SR of large wood boring beetles (L WB B) which excavate cavities with diameters ≥3 mm. The proportion of cavity nesting bees in the bee species assemblage was calculated both with (incl. Eric. spec.) and without (excl. Eric. spec.) Ericaceae specialists. In both cases the L WB B Ab (fitted with solid lines) was the variable, that exerted the stongest influence on the bee response (see text and Table 2 for test statistics). However, the proportion of cavity nesting bee individuals also showed a decrease with the amount of shading (PCA one).

tionship can be explained by the size diversity within both taxa (Tables 1–3, Figs 1–3).

Importantly, the abundance of large wood boring beetles was a more important determinant of cavity nesting bee species richness and abundance than the abiotic filter elevation (Fig. 1, Table S5, Supporting information). This is somewhat surprising, because elevation has been shown to exert a strong influence on bee species assemblages (Hoiss et al. 2012; Sydenham et al. 2015). However, the elevational gradient in the present study may not have been long enough to enforce the strong filtering effect found by Hoiss et al. (2012). Yet the elevational gradient did drive a synchronous decrease in both cavity nesting bee species richness (Fig. 1, Table S5, Supporting information) and large wood boring beetles (species richness vs. elevation; rho = -0.43, $P = 0.001$, abundance vs. elevation; rho = -0.40, $P = 0.003$) suggesting that elevation did pose a filtering effect on the entire, beetle and bee, community. Some of the variation in bee species richness explained by large wood boring beetles may therefore have been driven by a synchronous decline with elevation. Even so, the variance explained by large wood boring beetles was larger than that of elevation suggesting a substantial influence of wood boring beetles per se.

Furthermore, that the cavity nesting bee species richness and abundance were not significantly related to the

Table 2. The proportion of cavity nesting bee individuals in local bee species assemblages increased with the species richness and abundance of large wood boring beetles, which excavate cavities with diameters ≥3 mm. When Ericaceae specialists were excluded the proportion of cavity nesting bees also decreased with the degree of vegetation shading (PCA axis one) the ground. Models were fitted using binomial GLMs, Nagelkerke R^2 values are shown.

	df	β	SE	*z* value	R^2	P-value
Proportion of cavity nesting bee individuals (incl. Ericaceae specialists)						
Intercept	25	−1.179	0.437	−2.70		0.007
Large wood boring beetle species richness		0.166	0.074	2.23	0.22	0.026
Intercept	25	−0.662	0.204	−3.26		0.001
Large wood boring beetle abundance		0.009	0.004	2.49	0.27	0.013
Proportion of cavity nesting bee individuals (excl. Ericaceae specialists)						
Intercept	25	−0.773	0.472	−1.64		0.102
Large wood boring beetle species richness		0.184	0.081	2.27	0.21	0.023
Intercept	25	−0.285	0.232	−1.23		0.219
Large wood boring beetle abundance		0.012	0.005	2.77	0.31	0.006
Intercept	25	0.315	0.129	2.44		0.015
PCA axis one (shade)		−0.301	0.148	−2.03	0.17	0.042

Table 3. Final models for the size diversity of cavity nesting bees following backward elimination of the explanatory variables with a *P*-value <0.10 (Table S6, Supporting information). Models were fitted using Poisson (Functionally singular species richness$_{bees}$) and Quasipoisson (Community weighted mean$_{bees}$ and Functional dispersion$_{bees}$) generalized linear models (GLMs). Large wood boring beetle species excavate cavities with diameters ≥3 mm which may be used as nest sites by cavity nesting bees. Nagelkerke R^2 values are shown.

	df	β	SE	*z* value	R^2	*P*-value
Functionally singular species richness$_{bees}$						
Intercept	23	0.253	0.243	1.04		0.298
Large wood boring beetle abundance		0.012	0.005	2.42	0.48	0.015
Community weighted mean$_{bees}$						
Intercept	23	0.279	0.114	2.44		0.023
Functional dispersion$_{beetles}$		0.389	0.164	2.36	0.21	0.027
Functional dispersion$_{bees}$						
Intercept	23	−3.391	0.948	−3.58		0.002
Functional dispersion$_{beetles}$		3.278	1.199	2.73	0.33	0.012

species richness and abundance of small and non-wood boring beetles and that cavity nesting bees and large wood boring beetles did not co-vary with habitat area also suggests that there was a guild specific link between cavity nesting bees and large wood boring beetles. The hypothesis that the relationship between cavity nesting bees and large wood boring beetles was driven by nest site facilitation rather than by a shared response to the availability of forage resources was supported by an increase in the proportion of cavity nesting bee individuals with the abundance and species richness of large wood boring beetles (Table 2). Indeed, the estimated proportion of cavity nesting bee individuals increased with the abundance of large wood boring beetles (min = 2, max = 92) from 34% to 55% when Ericaceae specialists were included and from 44% to 70% when specialists were excluded (Table 2, Fig. 2). Importantly, this relationship was not an artefact of the productivity and regrowth in the site as the positive relationship between large wood boring beetles and the proportion of cavity nesting bees remained significant when shade (PCA axis one) was included as explanatory variable in the model. That shade was related to a decrease in the proportion of cavity nesting bees may have been due to an increased abundance of ground nesting bees in areas with a high site index. This would be expected if soils deep enough for ground nesting bees to nest in are mainly found in the more productive sites in our region. That secondary cavity-nesters depend on cavity-excavators has previously been shown for other functional groups of bees such as ground nesting bumblebees (*Bombus* sp.) that nest in rodent holes (McFrederick and LeBuhn 2006a,b) as well as for the variety of non-bee taxa dependent on abandoned wood-pecker nests (Martin and Eadie 1999). Although our findings are based on correlative and not experimental evidence, our findings concur with the results of an experiment showing that the availability of nesting resources pose a major limiting factor in the common cavity-nesting bee *Osmia bicornis* (Syn. = *O. rufa*) (Steffan-Dewenter and Schiele 2008) and also that nesting substrates are important drivers of bee diversity (Potts et al. 2005; Murray et al. 2012). Moreover, of the cavity-nesting bee species found in this study only *Megachile nigriventris* is able to excavate their own cavities in dead wood (Westrich 1989). It is therefore unlikely that the observed increase of cavity-nesting bees with large wood boring beetles was caused by both species groups responding in similar ways to the availability of dead wood, an important driver of beetle diversity (Grove 2002; Lachat et al. 2012).

The relationships between the functional diversity of large wood boring beetles and cavity nesting bees suggest a mechanistic link between the two groups (Fig. 3, Table 3). Indeed, Westerfelt et al. (2015) found that the diameter of nest holes was an important determinant of

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

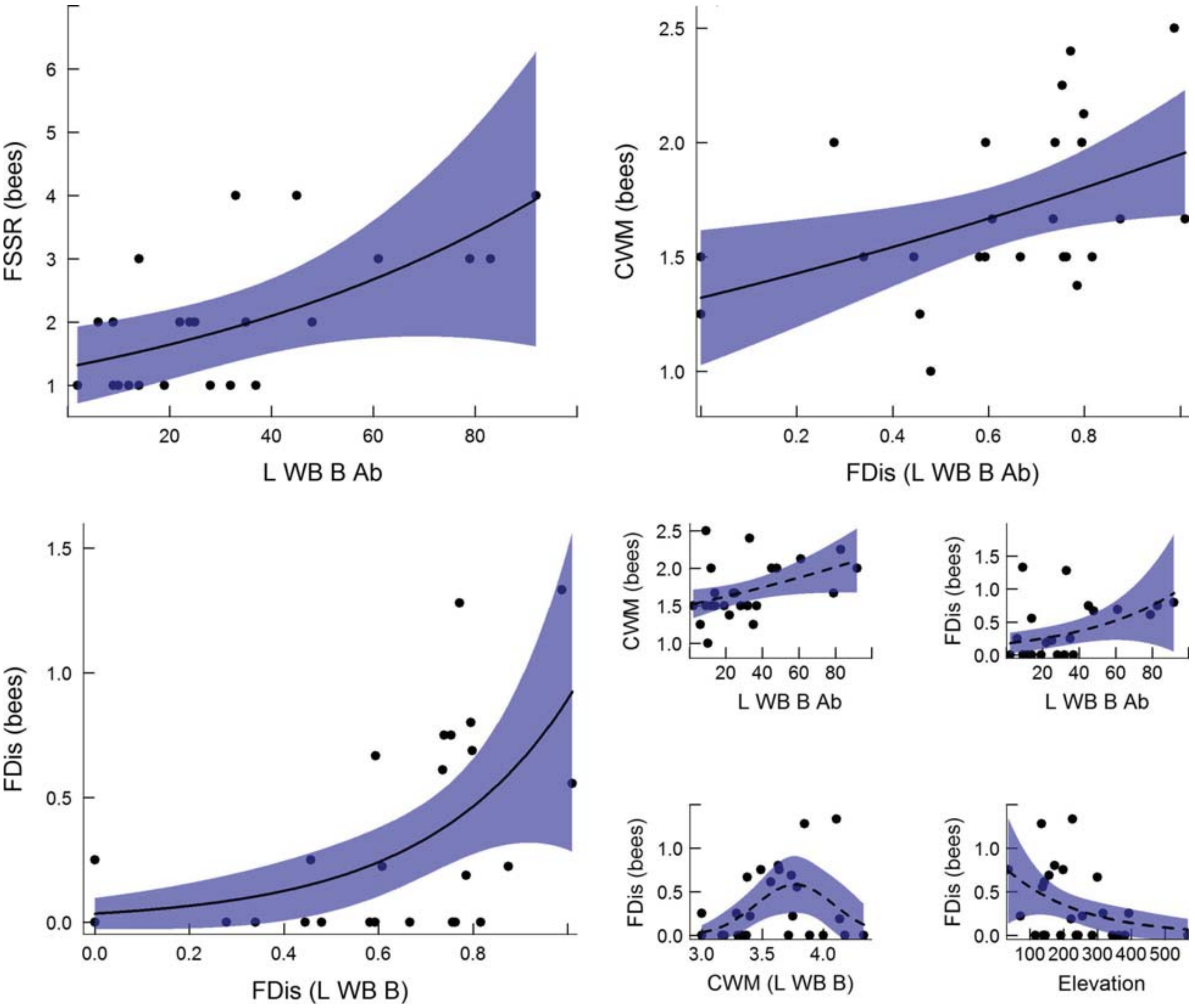


Figure 3. Enlarged plots showing the most important drivers of the functionally singular species richness (FSSR), community weighted mean (CWM) and functional dispersion (FDis) of the body size of cavity nesting bees. Relationships in reduced plots, with dashed regression lines, were significant when tested separately, but were not included following backward elimination of variables. The explanatory variables were the abundance, functional dispersion and community weighted mean of large wood boring beetles (L WB B) which excavate cavities with diameters ≥3 mm and elevation (m a.s.l.).

nest occupancy by cavity nesting Aculeates. That the number of different size classes (FSSR) of cavity-nesting bees increased with the abundance of large wood boring beetles suggests that the density of nest holes is an important driver of the functional composition of cavity nesting bee species assemblages. This was also supported by the finding that the community-weighted mean bee size (CWM) increased with the functional dispersion (FDis) of large wood boring beetles, suggesting that the largest bees were only able to find suitable nesting sites in the most functionally diverse beetle assemblages. Indeed, the functional dispersion (FDis) of cavity nesting bees also increased with the most functionally diverse beetle species assemblage. Interestingly, the $\mathrm{FDis}_{\mathrm{bees}}$ showed a hump-backed relationship to the CWM of large wood boring beetles (Fig. 3, Table S6, Supporting information). This pattern would be expected if intermediate values of $\mathrm{CWM}_{\mathrm{L\ WB\ B}}$ indicated that all functional types of large wood boring beetles were present and equally common within an area, thereby supporting a high diversity of nesting opportunities for cavity nesting bees. In contrast, if low or high values of $\mathrm{CWM}_{\mathrm{L\ WB\ B}}$ indicates the dominance of either, relatively, small or large, large wood boring beetles, it might indicate situations where not all niches are supported for cavity nesting bees. This would be in line with Grime's (1998) "biomass ratio hypothesis" that the impact of species on ecosystem functioning is proportionate to their abundance, so that the most dominant species are the most influential.

Conclusions

The role of facilitation in organizing communities has traditionally received less attention than competitive and trophic interactions (Bruno et al. 2003). This study documents a strong relationship between wood boring beetles and cavity nesting bees suggesting that non-trophic facilitative interactions among species assemblages likely play a significant role in maintaining both size and species diversity within cavity nesting bee species assemblages. Indeed, identifying and managing for such interactions may be of high importance for restoration ecology (Byers et al. 2006) and conservation biology (Martin and Eadie 1999).

Data Accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.5r6pq

Acknowledgments

We wish to thank Sindre Ligaard for beetle identification. Dag Slettebø, Are Endal Rognes, Adrian Rasmussen, Håkon Celius, Lisbeth Nordtiller, Torbjørn Kornstad, Morten Meland, Marte Lilleeng, Ronny Steen and John Gunnar Dokk assisted in field and laboratory work. Jonathan Howard Sydenham at JHS International ApS helped to brush up our English. Two anonymous reviewers and the assisting editor provided a constructive critique that greatly improved the manuscript. This study was funded by STATNETT.

Conflict of Interest

None declared.

References

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18:119–125.

Budrienė, A., E. Budrys, and Ž. Nevronytė. 2004. Solitary Hymenoptera Aculeata inhabiting trap-nests in Lithuania: nesting cavity choice and niche overlap. Latv. Entomol. 41:19–31.

Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. G. Lambrinos, et al. 2006. Using ecosystem engineers to restore ecological systems. Trends Ecol. Evol. 21:493–500.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48:1079–1087.

Ehnström, B., and AxelssonR. 2002. Insektsgnag i bark och ved. Artdatabanken, SLU, Uppsala.

Eldegard, K., Ø. Totland, and S. R. Moe. 2015. Edge effects on plant communities along power line clearings. J. Appl. Ecol. 52:871–880.

Fauth, J. E., J. Bernardo, M. Camara, W. J. Resetarits, J. VanBuskirk, and S. A. McCollum. 1996. Simplifying the jargon of community ecology: a conceptual approach. Am. Nat. 147:282–286.

Fründ, J., C. F. Dormann, A. Holzschuh, and T. Tscharntke. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94:2042–2054.

Gathmann, A., and T. Tscharntke. 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71:757–764.

Gathmann, A., H. J. Greiler, and T. Tscharntke. 1994. Trap-nesting bees and wasps colonizing set- aside fields: succession and body size, management by cutting and sowing. Oecologia 98:8–14.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86:902–910.

Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33:1–23.

Harper, K. A., S. E. Macdonald, P. J. Burton, J. Chen, K. D. Brosofske, E. S. Saunders, et al. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. 19:768–782.

Hoiss, B., J. Krauss, S. G. Potts, S. Roberts, and I. Steffan-Dewenter. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proc. R. Soc. B Biol. Sci. 279:4447–4456.

Hopfenmüller, S., I. Steffan-Dewenter, and A. Holzschuh. 2014. Trait-specific responses of wild bee communities to landscape composition. Configuration and local factors. PLoS One 9:e104439.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Kålås, J., Å. Viken, S. Henriksen, and S. Skjelseth. 2010. Norsk rødliste for arter—Norwegian red list. Artsdatabanken, Trondheim.

Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, et al. 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. 274:303–313.

Lachat, T., B. Wermelinger, M. M. Gossner, H. Bussler, G. Isacsson, and J. Müller. 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecol. Ind. 23:323–331.

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos 71:367–374.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

Martin, K., and J. M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manage. 115:243–257.

McFrederick, Q. S., and G. LeBuhn. 2006a. Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)? Biol. Conserv. 129:372–382.

McFrederick, Q. S., and LeBuhn, G. 2006b. Corrigendum to "Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)?" [Biol. Conserv. 129 (2006) 372–382]. Biol. Conserv., 132, 277.

Müller, A., S. Diener, S. Schnyder, K. Stutz, C. Sedivy, and S. Dorn. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. Biol. Conserv. 130:604–615.

Murray, T. E., U. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown, and R. J. Paxton. 2012. Local-scale factors structure wild bee communities in protected areas. J. Appl. Ecol. 49:998–1008.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. Eur. J. Entomol. 93:195–209.

Oksanen, J., BlanchetF. G. , Kindt, R. , Legendre, P. , Minchin, P. R., O'Hara, R. B. , et al. 2013. vegan: Community Ecology Package. R package version 2.0-10, http://CRAN.R-project.org/package=vegan.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9:741–758.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84:2628–2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, et al. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol. Entomol. 30:78–85.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25:345–353.

R development core team. (2014). R: a language and environment for statistical computing. R foundation for statistical computing. R development core team, Vienna, Austria.

Ricotta, C., and M. Moretti. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167:181–188.

Rubne, D., M. Schroeder, and T. Ranius. 2015. Estimating bee and wasp (Hymenoptera: Acuelata) diversity on clear-cuts in forest landscapes – an evaluation of sampling methods. Insect Conserv. Divers. 8:261–271.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 49:11–41.

Steffan-Dewenter, I., and S. Schiele. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? Ecology 89:1375–1387.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432.

Stokland, J. N., J. Siitonen, and B. G. Jonsson. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge.

Sydenham, M. A. K., S. R. Moe, Ø. Totland, and K. Eldegard. 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? Ecography 38:140–153.

Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. J. Appl. Ecol. 35:708–719.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366:2403–2413.

Westerfelt, P., O. Widenfalk, Å. Lindelöw, L. Gustafsson, and J. Weslien. 2015. Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. Insect Conserv. Divers. 8:493–504.

Westrich, P. 1989. Die Wildbienen Baden-Württembergs. E. Ulmer, Stuttgart.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. Pp. 1–16 *in* A. Matheson, I. H. Williams, S. L. Buchmann, C. O'Toole, P. Westrich, eds. The conservation of bees. Academic Press, London.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol. Conserv. 143:2280–2291.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21:213–223.

Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. Annu. Rev. Ecol. Evol. Syst. 42:1–22.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of study sites in south east Norway.
Table S1. Results from Principal Components Analysis (PCA) on variables related to regrowth and productivity (i.e. shading) within power line clearings.
Table S2. List of the species richness and abundance of large wood boring beetles and cavity nesting bees and the diameter of the exit holes they produce and widths of their thorax (ITD).
Table S3. Spearman's rank correlation among explanatory variables.
Table S4. Solitary bees sampled in power line clearings.
Table S5. Outputs from GLMs on the species richness and abundance of cavity nesting bees and all explanatory variables tested individually as well as the full models.
Table S6. Outputs from GLMs on the size diversity of cavity nesting bees and all explanatory variables tested individually as well as the full models.

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Supplementary material for paper III

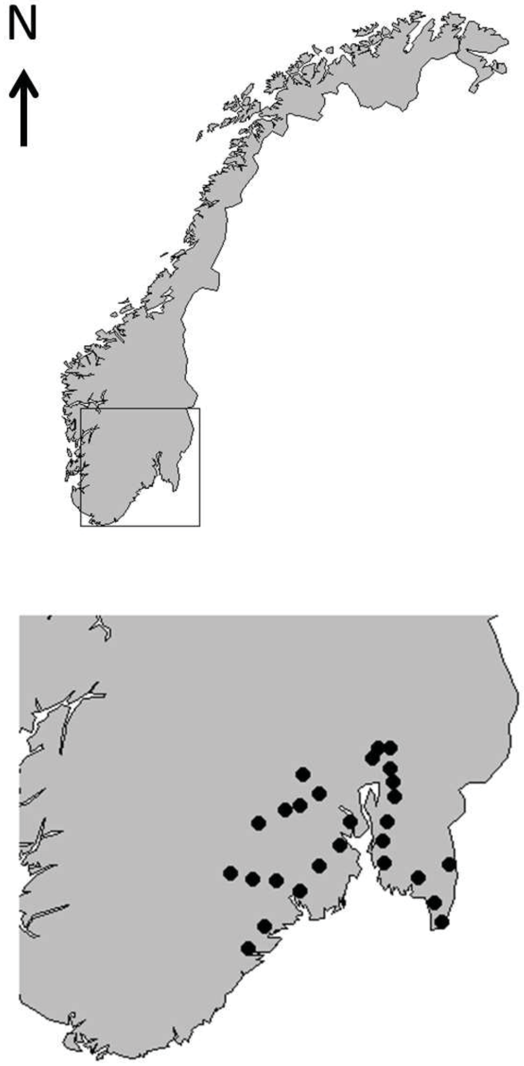


Figure S1. Map of the study area in south east Norway showing the location of the 27 study sites included in the analyses (filled circles). The distance between the southernmost and the northernmost sites was 160 kilometres. The nearest and the most distant site were 9 and 187 km apart, respectively.

Table S1 Results from Principal components analysis (PCA) on the degree of regrowth and productivity (site index) within power line clearings. See Methods and Eldegard et al. (2015) for details.

PCA Gradient characteristics						
	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	5.54	2.47	1.10	0.90	0.46	0.24
Proportion Explained	0.50	0.23	0.10	0.08	0.04	0.02
Cumulative Proportion	0.50	0.73	0.83	0.91	0.95	0.97
Loadings						
	PC1	PC2	PC3	PC4	PC5	PC6
Relascope sum	0.95	-0.52	0.01	0.27	0.36	-0.16
No. trees	1.08	0.43	-0.19	0.18	-0.32	-0.02
No. coniferous trees	0.56	-0.94	-0.56	-0.07	-0.12	0.10
No. deciduous trees	0.96	0.68	-0.05	0.20	-0.30	-0.04
No. Spruce trees	0.54	0.16	-0.72	-0.83	0.05	-0.09
No. Pine trees	0.31	-1.10	-0.22	0.36	-0.16	0.16
Mean tree height	1.09	-0.18	0.45	-0.19	-0.08	0.15
Mean tree crown width	0.87	-0.24	0.64	-0.46	-0.22	0.11
Max tree height	1.05	-0.29	0.30	-0.14	0.38	-0.16
Sum crown width	1.08	0.28	-0.16	0.33	-0.04	-0.24
Site index	0.77	0.73	-0.23	0.16	0.39	0.43

References

Eldegard, K., Totland, Ø. & Moe, S. R. (2015). Edge effects on plant communities along power line clearings. *Journal of Applied Ecology* (in press DOI: 10.1111/1365-2664.12460).

Table S2. The number of individuals and diameter class of large wood boring beetles and the number of individuals of cavity-nesting bees. The number of individuals and diameter class of large wood boring beetles and the number of individuals of cavity-nesting bees. The diameter class shows the diameter, in millimetres, of exit holes produced by adult beetles when leaving their nest chamber and the width of the thorax, inter-tegulae distance (ITD), of the cavity nesting bees in millimetres. ITD n shows the number of individuals used to calculate the average ITD and its standard deviation (ITD SD.)

Order	Family	Species	Individuals	Diameter Class	ITD n	ITD SD.
Coleoptera	Anthribidae	*Platystomus albinus*	3	4		
	Buprestidae	*Anthaxia quadripunctata*	38	3		
		Buprestis octoguttata	19	5		
	Cerambycidae	*Aegomorphus clavipes*	2	6		
		Alosterna tabacicolor	1	3		
		Anoplodera maculicornis	101	4		
		Anoplodera rubra	100	5		
		Anoplodera sanguinolenta	81	3		
		Arhopalus rusticus	1	5		
		Clytus arietis	15	3		
		Leptura maculata	1	5		
		Leptura melanura	351	3		
		Leptura nigra	1	3		
		Leptura quadrifasciata	70	5		
		Pogonocherus fasciculatus	2	3		

		Saperda scalaris	1	5		
		Tetropium castaneum	2	4		
	Curculionidae	*Pissodes pini*	2	5		
Hymenoptera						
	Colletidae	*Hylaeus angustatus*	7	0.9 = 1*	5	0.04
		Hylaeus annulatus	17	1.5 = 1.5*	10	0.10
		Hylaeus brevicornis	2	0.95 = 1*	10	0.04
		Hylaeus communis	24	1.4 = 1.5*	10	0.05
		Hylaeus confusus	69	1.5 = 1.5*	10	0.10
		Hylaeus hyalinatus	7	1.2 = 1*	10	0.13
		Hylaeus rinki	1	1.15 = 1*	2	0.05
	Megachilidae	*Hoplitis tuberculata*	1	2.2 = 2*	10	0.17
		Megachile nigriventris	2	4.3 = 4.5*	3	0.13
		Megachile versicolor	1	3.3 = 3.5*	10	0.16
		Osmia bicornis	1	3.1 = 3*	10	0.13
		Osmia caerulescens	1	2.5 = 2.5*	8	0.22
		Osmia nigriventris	8	3.3 = 3.5*	8	0.16
		Osmia parietina	4	2.1 = 2*	9	0.16
		Osmia uncinata	2	2.5 = 2.5*	3	0.11

* Measurements of thorax width were rounded to the nearest 0.5 mm to account for intra-specific variation and potential measurement errors (ITD SD). The rounded values were used in the analyses of functional bee diversity.

Table S3. Spearman’s rank correlations (rho) among explanatory variables from 27 power line clearings. The non-abbreviated form of the variables; species richness (SR), abundance (Ab) large wood boring beetle (L WB B), functionally singular species richness (FSSR), functional dispersion (FDis), community weighted mean (CWM), non-wood boring beetles (N WB B) and small wood boring beetles (S WB B). Large wood boring beetles excavate cavities with diameters larger than 3 mm, which may be occupied by cavity nesting bees.

	L WB B Ab		L WB B SR		L WB B FGR		L WB B FDis		L WB B CWM	
	rho	p	rho	p	rho	p	rho	p	rho	p
L WB B SR	0.65	<0.01								
L WB B FSSR	0.49	0.01	0.69	<0.01						
L WB B FDis	0.33	0.09	0.41	0.03	0.46	0.02				
L WB B CWM	0.18	0.36	0.39	0.04	0.50	0.01	0.78	<0.01		
N WB B Ab	0.28	0.16	0.35	0.08	0.16	0.41	0.14	0.49	0.09	0.67
N WB B SR	0.06	0.76	0.28	0.15	0.01	0.97	0.10	0.63	-0.06	0.76
S WB B Ab	0.01	0.97	0.09	0.67	0.27	0.18	-0.29	0.14	-0.19	0.34
S WB B SR	0.13	0.53	0.47	0.01	0.62	<0.01	0.03	0.89	0.16	0.42
Elevation	-0.40	0.04	-0.43	0.03	-0.17	0.40	-0.43	0.03	-0.32	0.11

	N WB B Ab		N WB B SR		S WB B Ab		S WB B SR	
	rho	p	rho	p	rho	p	rho	p
N WB B SR	0.74	<0.01						
S WB B Ab	0.21	0.29	0.22	0.28				
S WB B SR	0.22	0.27	0.14	0.48	0.53	0.00		
Elevation	-0.34	0.09	-0.29	0.14	0.42	0.03	-0.12	0.56

Table S4. Solitary bees sampled in 27 sites in power line clearings (Fig. 1). The table shows the number of species and individuals for each genus and the number of individuals of the most abundant species within each genus.

Family	Genus	Species	Individuals	Most abundant species	Individuals
Andrenidae					
	Andrena	13	124	*A. lapponica*	64
Colletidae					
	Colletes	2	2	*C. daviesanus*	1
	Hylaeus	7	124	*H. confusus*	69
Halictidae					
	Halictus	1	4	*H. rubicundus*	4
	Lasioglossum	6	54	*L. leucopus*	24
	Sphecodes	3*	5	*S. hyalinatus*	3
Megachilidae					
	Anthidium	1	1	*A. punctatum*	1
	Hoplitis	1	1	*H. tuberculata*	1
	Megachile	2	3	*M. nigriventris*	2
	Osmia	5	16	*O. nigriventris*	8
	Stelis	1	1	*S. ornatula*	1
Apidae					
	Nomada	5	14	*N. panzeri*	7

* One *Sphecodes* specimen was too damaged for identification and was assigned to a morpho species

Table S5.1. Relationships between the species richness (SR) and abundance (Ab) of cavity nesting bees and the diversity of beetles, elevation and sampling year. Explanatory variables were the species richness and abundance of large wood boring beetles (L WB B), small wood boring beetles (S WB B) and non-wood boring beetles (N WB B) and the elevation of the study site and the year the sampling was conducted at each site. Large wood boring beetles excavate cavities with diameters larger than three mm. Analyses were performed using Poisson generalized linear models (cavity nesting bee SR) and negative binomial regressions (cavity nesting bee Ab). Nagelkerke R^2-values are shown.

	DF	β	SE	z value	R^2	p-value
Cavity nesting bee SR						
Intercept	25	-0.118	0.392	-0.30		0.763
L WB B SR		0.200	0.067	3.01	0.42	0.003
Intercept	25	0.417	0.206	2.03		0.043
L WB B Ab		0.015	0.004	3.65	0.54	<0.001
Intercept	25	0.470	0.331	1.42		0.156
S WB B SR		0.053	0.034	1.57	0.12	0.116
Intercept	25	0.839	0.168	4.99		<0.001
S WB B Ab		0.002	0.002	0.89	0.04	0.373
Intercept	25	0.554	0.548	1.01		0.312
N WB B SR		0.005	0.006	0.73	0.03	0.468
Intercept	25	0.504	0.310	1.62		0.105
N WB B Ab		0.001	0.001	1.58	0.13	0.114
Intercept	25	1.506	0.271	5.55		<0.001
Elevation		-0.003	0.001	-2.18	0.26	0.029
Intercept (2009)	24	1.237	0.180	6.89		<0.001
Year (2010)		-0.483	0.302	-1.60		0.11

Year (2013)		-0.495	0.283	-1.75	0.21	0.08
Cavity nesting bee Ab						
Intercept	25	-0.148	0.520	-0.29		0.776
L WB B SR		0.340	0.094	3.62	0.46	<0.001
Intercept	25	0.658	0.216	3.04		0.002
L WB B Ab		0.027	0.005	5.73	0.80	<0.001
Intercept	25	1.144	0.528	2.17		0.030
S WB B SR		0.063	0.057	1.09	0.06	0.274
Intercept	25	1.462	0.264	5.54		<0.001
S WB B Ab		0.005	0.004	1.19	0.06	0.233
Intercept	25	1.364	0.856	1.60		0.111
N WB B SR		0.004	0.010	0.39	0.01	0.694
Intercept	25	0.729	0.462	1.58		0.114
N WB B Ab		0.002	0.001	2.18	0.21	0.029
Intercept	25	2.355	0.421	5.60		<0.001
Elevation		-0.003	0.002	-1.80	0.16	0.071
Intercept (2009)	24	2.147	0.289	7.43		<0.001
Year (2010)		-0.825	0.443	-1.86		0.062
Year (2013)		-0.760	0.414	-1.84	0.23	0.067

Table S5.2 Full models on the species richness (SR) and abundance (Ab) of cavity nesting bees. Explanatory variables from the single variable models listed Table S6.1 with p-values from likelihood ratio tests ≤ 0.1 were included in the full models. Variables marked in bold were included in the final models following backward elimination of variables.

	DF	β	SE	z value	R^2	p-value
Cavity nesting bee SR	23				0.62	
Intercept		0.144	0.598	0.24		0.810
L WB B AB		**0.011**	**0.005**	**1.95**		**0.051**
L WB B SR		0.106	0.083	1.28		0.201
Elevation		-0.001	0.001	-0.44		0.660
Cavity nesting bee Ab	20				0.90	
Intercept		-0.734	0.665	-1.10		0.270
L WB B AB		**0.029**	**0.007**	**4.34**		**<0.001**
L WB B SR		0.160	0.092	1.73		0.084
N WB B Ab		<0.001	0.001	0.22		0.829
Elevation		0.001	0.001	0.43		0.664
Year (2010)		0.220	0.357	0.62		0.538
Year (2013)		0.600	0.458	1.31		0.190

Table S6.1. Relationships between the size diversity of cavity nesting bees and the nomenclatural and functional diversity of wood boring beetles. Explanatory variables were the functionally singular species richness (FSSR), Community-weighted mean (CWM) diameter class and the functional dispersion of diameter classes of large wood boring beetles (L WB B) and the species richness (SR) and abundance (Ab) of small (S WB B) and non-wood boring (N WB B) beetles. Large wood boring beetles excavate cavities which may be occupied by cavity nesting bees. Variables were tested individually using Poisson generalized linear models (GLMs) for bee FSSR and Quasipoisson GLMs for bee CWM and FDis. Nagelkerke R^2-values are shown.

Response	Explanatory variable	*Df.*	β	SE	z	R^2	P
Bee Functionally singular species richness							
	Intercept	23	0.335	0.621	0.54		0.590
	L WB B FSSR		0.125	0.221	0.57	0.03	0.572
	Intercept	23	0.020	0.457	0.04		0.965
	L WB B FDis		0.997	0.636	1.57	0.25	0.117
	Intercept	22	0.628	0.150	4.18		<0.001
	L WB B $CWM_{\beta1}$		0.282	0.836	0.34		0.736
	L WB B $CWM_{\beta2}$		-1.571	0.863	-1.82	0.35	0.069
	Intercept	23	-0.095	0.457	-0.21		0.838
	L WB B SR		0.145	0.079	1.85	0.31	0.065
	Intercept	23	0.253	0.243	1.04		0.297
	L WB B Ab		0.012	0.005	2.42	0.48	0.015
	Intercept	23	0.573	0.415	1.38		0.167
	S WB B SR		0.011	0.044	0.26	0.01	0.797
	Intercept	23	0.687	0.206	3.34		0.001
	S WB B Ab		-0.0003	0.003	-0.09	<0.01	0.928

	Intercept	23	0.483	0.637	0.76		0.448
	N WB B SR		0.002	0.007	0.31	0.01	0.758
	Intercept	23	0.417	0.375	1.11		0.266
	N WB B Ab		0.001	0.001	0.76	0.05	0.450
	Intercept (2009)	22	0.965	0.218	4.42		<0.001
	Year (2010)		-0.480	0.353	-1.36		0.174
	Year (2013)		-0.454	0.338	-1.34	0.24	0.179
	Intercept	23	1.147	0.314	3.66		<0.001
	Elevation		-0.002	0.001	-1.60	0.25	0.110
Bee CWM ITD							
	Intercept	23	0.497	0.185	2.69		0.013
	L WB B FSSR		0.011	0.067	0.16	<0.01	0.873
	Intercept	23	0.279	0.114	2.44		0.023
	L WB B FDis		0.389	0.164	2.36	0.21	0.027
	Intercept	22	0.522	0.042	12.46		<0.001
	L WB B CWM$_{\beta 1}$		0.266	0.217	1.23		0.231
	L WB B CWM$_{\beta 2}$		-0.381	0.217	-1.76	0.18	0.093
	Intercept	23	0.379	0.134	2.83		0.009
	L WB B SR		0.029	0.025	1.15	0.06	0.251
	Intercept	23	0.413	0.067	6.21		<0.001
	L WB B Ab		0.004	0.002	2.25	0.19	0.034
	Intercept	23	0.659	0.129	5.17		<0.001
	S WB B SR		-0.015	0.014	-1.09	0.05	0.289

	Intercept	23	0.554	0.064	8.63		<0.001
	S WB B Ab		-0.001	0.001	-0.59	0.02	0.561
	Intercept	23	0.747	0.192	3.89		0.001
	N WB B SR		-0.003	0.002	-1.17	0.06	0.254
	Intercept	23	0.561	0.117	4.79		<0.001
	N WB B Ab		-0.0001	0.0002	-0.32	0.01	0.753
	Intercept (2009)	22	0.636	0.072	8.88		<0.001
	Year (2010)		-0.138	0.105	-1.31		0.204
	Year (2013)		-0.191	0.103	-1.85	0.15	0.077
	Intercept	23	0.666	0.094	7.07		<0.001
	Elevation		-0.001	0.0004	-1.63	0.11	0.117
Bee FDis ITD							
	Intercept	23	-1.343	1.064	-1.26		0.220
	L WB B FSSR		0.101	0.380	0.27	<0.01	0.794
	Intercept	23	-3.391	0.948	-3.58		0.002
	L WB B FDis		3.278	1.199	2.73	0.33	0.012
	Intercept	22	-1.308	0.298	-4.39		<0.001
	L WB B $CWM_{\beta1}$		2.233	1.654	1.35		0.191
	L WB B $CWM_{\beta2}$		-3.385	1.725	-1.96	0.27	0.062
	Intercept	23	-2.221	0.844	-2.63		0.015
	L WB B SR		0.214	0.140	1.52	0.12	0.142
	Intercept	23	-1.746	0.458	-3.82		0.001
	L WB B Ab		0.018	0.009	2.13	0.22	0.044

	Intercept	23	-0.748	0.723	-1.04		0.312
	S WB B SR		-0.038	0.082	-0.46	0.01	0.647
	Intercept	23	-0.977	0.356	-2.74		0.012
	S WB B Ab		-0.002	0.006	-0.35	0.01	0.732
	Intercept	23	-0.748	1.075	-0.70		0.494
	N WB B SR		-0.004	0.013	-0.31	0.01	0.762
	Intercept	23	-1.312	0.658	-1.99		0.058
	N WB B Ab		0.001	0.001	0.41	0.01	0.689
	Intercept (2009)	22	-0.609	0.344	-1.77		0.090
	Year (2010)		-0.976	0.657	-1.49		0.152
	Year (2013)		-0.642	0.564	-1.14	0.14	0.267
	Intercept	23	-0.137	0.495	-0.28		0.785
	Elevation		-0.005	0.002	-1.89	0.18	0.072

Table S6.2 Full models on Relationships between the size diversity of cavity nesting bees and the nomenclatural and functional diversity of wood boring beetles. Explanatory variables from the single variable models listed Table S7.1 with p-values from likelihood ratio tests ≤ 0.1 were included in the full models. Variables marked in bold were included in the final models following backward elimination of variables. Nagelkerke R^2 for the full models are shown.

Response	Explanatory variable	*Df.*	β	SE	z	R^2	P
Bee Functionally singular species richness							
	Intercept	20	-0.031	0.810	-0.04	0.58	0.97
	L WB B SR		0.041	0.103	0.40		0.688
	L WB B Ab		**0.008**	**0.006**	**1.32**		**0.187**
	L WB B FDis		0.499	0.771	0.65		0.518
	Elevation		-0.001	0.002	-0.40		0.691
Bee CWM ITD		*Df.*	β	SE	z	R^2	P
	Intercept	19	0.092	0.371	0.25	0.33	0.806
	L WB B Ab		0.002	0.002	1.21		0.243
	L WB B FDis		**0.632**	**0.525**	**1.20**		**0.243**
	L WB B $\text{CWM}_{\beta1}$		-0.398	0.562	-0.71		0.488
	L WB B $\text{CWM}_{\beta2}$		0.268	0.456	0.59		0.564
	Elevation		-0.0002	0.0004	-0.46		0.653
Bee FDis ITD		*Df.*	β	SE	z	R^2	P
	Intercept	19	-5.858	2.553	-2.30	0.51	0.033
	L WB B Ab		0.016	0.011	1.55		0.139
	L WB B FDis		**6.583**	**3.396**	**1.94**		**0.068**
	L WB B $\text{CWM}_{\beta1}$		-4.653	4.180	-1.11		0.280
	L WB B $\text{CWM}_{\beta2}$		3.100	3.576	0.87		0.397
	Elevation		-0.001	0.003	-0.36		0.726

Paper IV

Ecology and Evolution

Open Access

The effects of habitat management on the species, phylogenetic and functional diversity of bees are modified by the environmental context

Markus A. K. Sydenham, Stein R. Moe, Diana N. Stanescu-Yadav, Ørjan Totland & Katrine Eldegard

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.B. 5003, NO-1432 Ås, Norway

Keywords
Bees, biodiversity, functional diversity, habitat management, phylogenetic diversity, pollinators, power line clearings.

Correspondence
Markus A. K. Sydenham, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.B. 5003, NO-1432 Ås, Norway.
Tel: +47 94423661;
E-mail: markus.sydenham@nmbu.no

Funding Information
This study was funded by Statnett.

Received: 8 October 2015; Revised: 9 December 2015; Accepted: 21 December 2015

***Ecology and Evolution* 2016; 6(4): 961–973**

doi: 10.1002/ece3.1963

Abstract

Anthropogenic landscape elements, such as roadsides, hedgerows, field edges, and power line clearings, can be managed to provide important habitats for wild bees. However, the effects of habitat improvement schemes in power line clearings on components of diversity are poorly studied. We conducted a large-scale experiment to test the effects of different management practices on the species, phylogenetic, and functional diversity of wild bees in power line clearings (n = 19 sites across southeastern Norway) and explored whether any treatment effects were modified by the environmental context. At each site, we conducted the following treatments: (1) Cut: all trees cut and left to decay in the clearing; (2) Cut + Remove: all trees cut and removed from the plot; and (3) Uncut: uncleared. The site-specific environmental context (i.e., elevation and floral diversity) influenced the species, phylogenetic, and functional diversity within bee species assemblages. The largest number of species was found in the Cut + Remove treatment in plots with a high forb species richness, indicating that the outcome of management practices depends on the environmental context. Clearing of treatment plots with many forb species also appeared to alter the phylogenetic composition of bee species assemblages, that is, more closely related species were found in the Cut and the Cut + Remove plots than in the Uncut plots. *Synthesis and applications:* Our experimental simulation of management practices in power line clearings influenced the species, phylogenetic, and functional diversity of bee species assemblages. Frequent clearing and removal of the woody debris at low elevations with a high forb species richness can increase the value of power line clearings for solitary bees. It is therefore important for managers to consider the environmental context when designing habitat improvement schemes for solitary bees.

Introduction

Human disturbance is currently reducing biodiversity globally (Dirzo et al. 2014). Declining populations of animal pollinators (Potts et al. 2010) are of particular concern, as they sustain sexual reproduction of an estimated 88% of wild angiosperm species (Ollerton et al. 2011). The bees (Hymenoptera: Apiformes) is an important group of pollinators, and intensified agriculture and other land use changes during the past century have caused increased extinction rates of wild bees (Ollerton et al. 2014) and declines in regional population densities and occurrences (Biesmeijer et al. 2006). Currently, about 9% of the European bee species are threatened (Nieto et al. 2014). The availability of suitable habitats is a limiting factor for bees in modern agricultural landscapes, and a positive relationship between the proportion of semi-natural habitats and bee diversity in these landscapes has been reported in a number of studies (Steffan-Dewenter et al. 2002; Winfree et al. 2011).

Semi-natural grasslands, such as calcareous grasslands, provide important habitats for bees (Murray et al. 2012), but are often lost due to changes in land use, particularly reduced livestock grazing (Stoate et al. 2009). However, other anthropogenic landscape elements, such as power line clearings (Russell et al. 2005), hedgerows (Morandin

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

and Kremen 2013), and agricultural field edges (Sydenham et al. 2014), may also provide important habitats for bees in the agricultural landscape matrix. For example, road verges may mimic semi-natural habitats if re-sown with native plant species (Hopwood 2008) or managed to promote the species richness of forbs (Noordijk et al. 2009). In addition, restoring hedgerows along fields increases the occurrence of specialized bees, which typically decline in richness and density in agricultural landscapes (Kremen and M'Gonigle 2015). Thus, developing ecologically sound management plans for marginal areas is of high importance for bee conservation (Nieto et al. 2014). However, as the response of bees to habitat improvement schemes in agricultural landscapes may depend on the initial quality of the habitat (Scheper et al. 2013), the outcome of management practices should be assessed under different environmental contexts before widely implemented.

In many forested landscapes, the establishment and maintenance of power line clearings have created extensive networks of habitat of early successional vegetation (Wojcik and Buchmann 2012). In Norway, where our study is conducted, the area below the regional power lines that transect forests covers approximately 200 km^2. The woody vegetation in these areas is cut every 5–10 years to prevent trees from encroaching on the power lines. If appropriately managed, these already disturbed areas may benefit pollinators, such as bees (Wojcik and Buchmann 2012) and butterflies (Berg et al. 2013), as they contain a higher floral diversity than the neighboring forests (Eldegard et al. 2015). Indeed, open-canopy areas in forested landscapes increase the species richness and abundance of many bee species (Winfree et al. 2007; Hanula et al. 2015). However, while management strategies that increase the sun exposure in power line clearings may benefit thermophilic organisms, such as bees (Sydenham et al. 2014) and reptiles (Shine et al. 2002), organisms that require humid environments (e.g., gastropods and amphibians) may prefer more shaded habitats in late successional stages of power line clearings. If the aim of management is to improve habitat conditions for a wide variety of organisms, and thus maximize the positive effects on diversity, managers may therefore need to apply a combination of different management strategies to accommodate the habitat requirements of each organism group.

Even among bee species, habitat requirements differ substantially. Evaluating the success of management plans based solely on the effect on bee species richness and abundance is therefore not recommended as these indices may provide limited ecological information. Instead, these indices should be accompanied by measures of the functional diversity within species assemblages (Cadotte et al. 2011) as the functional and species diversity indices may reveal contrasting patterns to habitat conditions (Forrest et al. 2015). Indeed, the response of bee species to land use changes can be explained by functional traits, such as nest-site locations, body size, floral specialization (Williams et al. 2010), and phenology (Sydenham et al. 2014), which, together with the bee phylogeny, provide important information about the distribution of bees along environmental gradients (Hoiss et al. 2012; Sydenham et al. 2015). Thus, an ideal outcome of habitat management aimed at promoting the diversity of bees should be an increased species richness and abundance, accompanied by an increased (or at least an unchanged) phylogenetic and functional diversity. While these outcomes should manifest themselves at the population level, the initial response to altered habitat conditions occurs at the behavioral level of individuals within the community (Wong and Candolin 2015). Differences in the number of species and individuals among treatments likely reflect habitat use by bees from the local species pool. Given that the individuals are free to choose habitat, a higher use of one habitat over another likely reflects that the more used habitat is more preferred and thus profitable. A contrasting attraction or avoidance of species to differently managed habitat patches within the spatial scale of the community can therefore reveal which of the management practices best accommodate the preferred habitat of bees from the local species pool.

We established a large-scale field experiment to test how the species, phylogenetic, and functional diversity of wild bees responded to different management practices in power line clearings in a varying environmental context. At each study site (n = 19), we established three plots and randomly assigned either of three treatments to each plot: (1) Cut: all trees cut and left to decay in the clearing; (2) Cut + Remove: all trees cut and removed from the plot; and (3) Uncut: uncleared. The sites were distributed across a large geographic area covering an elevation gradient and a gradient in floral diversity. This allowed us to study how the environmental context affected the local species pool and thereby whether the outcome of management practices depended on the environmental context.

We sampled the bee community within each treatment plot in each site and hypothesized that:

Cleared plots (i.e., treatments Cut and Cut + Remove) should attract more bee species from the local species pool than uncleared plots (i.e., Uncut) as sun exposure is an important determinant of local bee species richness and abundance in boreal forest ecosystems (Sydenham et al. 2014). We expected to find the highest species richness of bees in plots where the woody debris was removed (Cut + Remove) and, consequently, a larger area of potential nesting sites exposed, as many bee species nest in sun-exposed soils. Moreover, as local bee diversity may be positively related to floral diversity (Potts et al. 2003), we expected that the relative difference in the number of bee species and individuals between cleared and uncleared treatment plots would increase with local floral diversity. In contrast, as bee diversity normally decreases with elevation (Hoiss et al. 2012; Sydenham et al. 2015), we expected that the effect of clearing would decrease with elevation.

As habitat improvement increases the presence of habitat specialists in hedgerows (Kremen and M'Gonigle 2015), we also expected an increase in the number of species and individuals of bees after clearing plots with a high floral diversity to be accompanied by an increased phylogenetic and functional diversity. In contrast, we expected the phylogenetic and functional diversity to decrease with elevation because of reduced bee diversity with increasing elevation (Hoiss et al. 2012; Sydenham et al. 2015).

Methods

Study design and data collection

We identified 19 sites within the main power line grid in southeast Norway, which had a stretch of at least 200 m with substantial regrowth of trees below the power lines. Sites were located between latitudes 59.33°–61.12°N and longitudes 08.95–11.36°E at 48–536 m.a.s.l. The clearings varied in width from c. 40 to c. 80 m. All the sites had been subjected to the same management regime with manual clear-cutting of all woody vegetation every 5–10 years, over large stretches of the corridor, where felled trees were left on site.

At each site, three rectangular plots extending 30 m along the power line clearing and covering the whole width of the clearing were established at least 20 m apart. During the late autumn 2012 (16 sites) and early spring 2013 (3 sites), we randomly allocated one of the plots to three treatments: (1) Cut: all trees were cut and left to decay in the plot; (2) Cut + Remove: all trees were cut and immediately removed from the plot, that is, mimicking harvesting of biomass for, for example, biofuels; and (3) Uncut: the plot was left uncleared (Fig. 1).

In the center of each treatment plot, we placed nine 1-m^2 subplots 5 m apart in a regularly spaced grid pattern. We visually estimated the total cover of all forb species in the nine subplots within each of the three treatment plots at every site. We also estimated the cover of four Ericaceae shrub species (*Calluna vulgaris, Vaccinium myrtillus, V. vitis-idaea,* and *V. uliginosum*), which are visited by the regionally common pollen specialists *Andrena fuscipes, A. lapponica,* and *Colletes succinctus*. We focused on forbs and ericaceous shrubs because the relative dominance of these groups may be an important determinant of bee species composition in forested ecosystems (Hanula et al. 2015; Sydenham et al. 2015). We calculated the species richness of forbs and ericaceous shrubs within each treatment plot by pooling all species occurring in the nine 1-m^2 subplots. The abundance of forbs and ericaceous shrubs was quantified by calculating their average cover per subplot in each treatment plot. The species richness of forbs was strongly positively correlated with the cover of forbs ($\rho = 0.76$) and negatively correlated with both the cover ($\rho = -0.60$) and species richness ($\rho = -0.59$) of Ericaceous shrubs. Thus, the gradient in forb species richness represented a gradient in floral diversity (from structurally simple, unproductive, Ericaceous shrub dominated; to structurally complex, productive, forb dominated), and we therefore only used species richness of forbs within treatment plots (mean = 10.56, min = 0, $Q_{25} = 5$, $Q_{50} = 7$, $Q_{75} = 16$, max = 30) to represent floral resource abundance and diversity.

Bees were sampled in 2013 throughout the entire flowering season, from snowmelt to the end of the foraging activity-season in September. We installed three flight interception traps within each treatment plot. All traps were placed along the northernmost end of the treatment plot to maximize sun exposure. The flight interception traps consisted of two transparent Plexiglas screens (370 mm × 210 mm) that formed a cross, with a funnel and collecting bottle attached to it. The collecting bottle was filled with a 50:50 mixture of green propylene glycol and a drop of detergent. Every month we collected the bottles and immediately replaced them with new ones. This procedure ensured a continuous, standardized sampling among all sites throughout the entire season. We pooled all specimens sampled within a treatment plot and used the treatment plots as our sampling unit in the statistical analyses.

Phylogenetic diversity indices

We constructed an ultrametric, polytomous, proxy of a phylogenic tree for the bee species collected in this study (Fig. S1) by clustering taxa according to published phylogenies (Danforth et al. 2013; Schmidt et al. 2015). Branch lengths were calculated following Grafen (1989) with the p-parameter set to 0.25 in order to place the divergence of bee families early in the phylogeny as these evolved early in the phylogenetic history of bees (Cardinal and Danforth 2013).

We calculated the four indices (Table 1) proposed by Helmus et al. (2007) as measures of the phylogenetic diversity of bees occurring within the treatment plots. The phylogenetic species variability (PSV) quantifies the

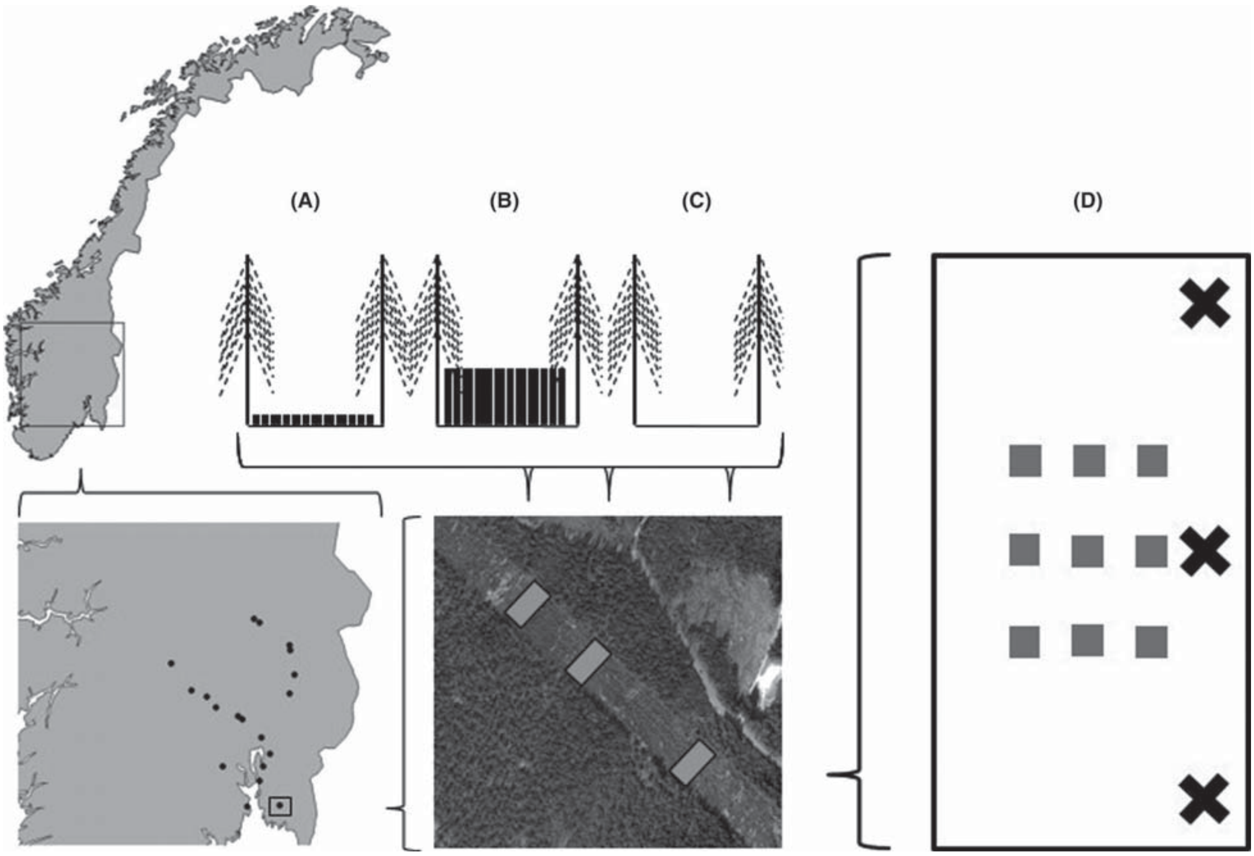


Figure 1. The geographic distribution of the 19 study sites located within power line clearings showing the three treatment plots (illustrated as cross-sections of the power line clearing); (A) Cut: all trees cut and left to decay in the clearing, (B) Uncut: uncleared control and (C) Cut + Remove: all trees cut and removed from the plot, thereby exposing the ground to direct sunlight. We sampled bees with three flight interception traps (black crosses) in each treatment plot (D), and plant data in the nine 1-m^2 subplots within each of the three treatment plots (gray boxes).

evolutionary distinctiveness of the species in a sample. The PSV equals one when all species in the community are equally unrelated to one another (i.e., the phylogeny is star shaped) and approaches zero as the species become increasingly related. The PSV is calculated as one minus the mean similarity in phylogenetic history (i.e., the mean off-diagonal values in a phylogenetic variance–covariance matrix). The phylogenetic species richness (PSR) is the phylogenetically corrected species richness. It is calculated as the species richness multiplied by the PSV. The phylogenetic species evenness (PSE) is the abundance-based PSV and is a measure of how evenly spread the individuals in a sample are, in terms of their evolutionary history. If all species have the same abundance, PSE equals PSV. Finally, the phylogenetic species clustering (PSC) is the PSV modified to provide information about how species in an assembly are clustered toward the tip of the phylogeny. The PSC approaches zero when the evolutionary distinctiveness of the nearest relatives in the community increases. A strength of the PSV-based indices is that they are standardized against a star-shaped phylogeny and therefore are not dependent on the regional species pool (Helmus et al. 2007). Prior to analyses, we removed all cleptoparasitic species from the data set as these species are highly host-specific and therefore co-occur with their hosts, although many of them (as in the case of the genus *Nomada*) are distantly related to their hosts. Including these species in the analyses could therefore obscure the effects of habitat conditions on the phylogenetic diversity of bee species assemblages. A total of 11 treatment plots were removed as they then contained fewer than two species, making it impossible to calculate the phylogenetic diversity indices. We used the picante library (Kembel et al. 2010) in R (R development core team 2014) to calculate the phylogenetic diversity indices (Table 1).

Functional diversity indices

To explore whether treatments differed with respect to functional diversity, we tested whether the bees trapped in the different treatment plots constituted only a subset of the functional groups from the local (site) species assemblage. The functional dissimilarity among bee species was quantified based on five life-history traits related to four main categories; foraging behavior, nesting behavior, month of emergence, as a measure of phenology, and the intertegular distance (ITD) as a measure of body size (Table S2). These traits were chosen as they are related to the responses of bees to disturbances (Williams et al. 2010; Sydenham et al. 2014; Forrest et al. 2015) and the ITD as it determines their foraging range (Greenleaf et al. 2007). We calculated four indices of functional diversity (i.e., FSSR, FDis, FEve, and CWM); the number of functionally distinct species (hereafter; functionally singular species richness; FSSR), which is the functional equivalent of species richness. To quantify the variation in trait values within treatment plots, we followed the approach of Forrest et al. (2015) and calculated the functional dispersion (FDis) of trait values. The functional evenness (FEve) was calculated to test how the skewness of trait values differed within and among sites (Villèger et al. 2008). Non-Euclidean distances, due to the inclusion of categorical traits, were corrected using the Cailliez correction (Forrest et al. 2015). We also calculated the community-weighted mean (CWM) trait value to test whether the attraction of bees to cleared sites depended on pollen specialization (i.e., polylectics vs. oligolectics), nesting behavior (i.e., above vs. belowground nesters), month of emergence, and body size (i.e., ITD). All the trait diversity indices were calculated using the FD library (Laliberte and Legendre 2010) in R. The indices were abundance-weighted as we were interested in the distribution of individuals, belonging to different functional groups, among treatment plots.

Table 1. Abbreviations used for phylogenetic (Helmus et al. 2007) and functional (Villèger et al. 2008) diversity indices used in this paper. See text for details.

	Abbreviation
Phylogenetic diversity[1]	
Phylogenetic species variability	PSV
Phylogenetic species richness	PSR
Phylogenetic species evenness	PSE
Phylogenetic species clustering	PSC
Functional diversity[2]	
Functionally singular species richness	FSSR
Functional dispersion	FDis
Functional evenness	FEve
Community-weighted mean	CWM
Proportion of oligolectics	None used
Proportion of aboveground nesters	None used
Intertegular distance (body size)	CWM ITD
Month of emergence	CWM emergence

[1] Cleptoparasites were excluded from analyses with phylogenetic diversity indices as response variables.

[2] The FDis, FEve, and CWM indices were abundance-weighted as we were interested in the preference of individuals for different treatment plots. Cleptoparasites were excluded in the analyses on the proportions of oligoletics and aboveground nesters.

Statistical analyses

We analyzed the effects of the treatments on the response variables by fitting a generalized linear mixed effect models (GLMM) using the R library lme4 (Bates et al. 2015). For each response variable, we first fitted a full model which included the treatment-specific interaction terms treatment × forb species richness, treatment × elevation, and the site-specific interaction term forb species richness × elevation as well as the main effect terms of each variable and site identity as a random effect. The number of successful trap-months (hereafter; sampling intensity) within each treatment plot was included as an offset variable to account for a difference in sampling intensity caused by destroyed traps (27 trap-months missing of 684). We first used chi-square tests in R to test whether including the sampling intensity significantly reduced the model deviance. If not, we refitted the model without sampling intensity as an offset variable. We then used likelihood ratio tests (LRTs) to conduct a sequential backward elimination of nonsignificant terms ($P > 0.05$, LRT statistics for all variables dropped from models as well as outputs from final models are listed in Tables S3, S5 and S6).

Analyses with either species richness or abundance of solitary bees as the dependent variable were run using GLMMs with Poisson-distributed errors and log-link functions. We analyzed the data both with and without cleptoparastic species (*i.e., Coelioxys, Nomada,* and *Sphecodes* spp.). Analyses with the PSR as the dependent variable were fitted using GLMMs with a Gamma distribution and a log-link function, whereas the PSV, PSE, and PSC were fitted using linear mixed effect models.

The analyses with the FSSR (Table 1) as the response variable were run using negative binomial GLMMs whereas linear mixed effect models were fitted to the FDis, CWM ITD, and the CWM emergence. The proportion of belowground nesting bees and oligolectics (i.e., pollen specialists) were fitted using GLMMs with binomial distributions and logit-link functions. Cleptoparasitic species were excluded from the single trait analyses on nesting behavior and lecty status as these species only indirectly depend on the resources sought by their hosts. We did not include sampling intensity as an offset variable in the analyses on proportions data, as these variables were already standardized by the abundance of bees within treatment plots and therefore readily comparable among treatments and sites. We tested for nonindependence among the main functional trait categories (ITD, lecty status, month of emergence, and nest location) possessed by each species ($n = 63$ species) using Spearman's rank correlation tests in the Hmisc (Harrell et al. 2015) library in R. This was carried out since the interpretation of analyses on individuals traits might be confounded by co-variation among traits.

Results

Influence of experimental treatments and habitat conditions on species richness and abundance

We collected a total of 617 individuals and 63 species of solitary bees. The species richness (incl. cleptoparasites) differed among treatment plots, but the magnitude depended on the forb species richness within plots. This shows that the effect of removing the debris after clearings was strongest in the most productive (i.e., floristically diverse) sites (Fig. 2, Tables 2 and S3). Results for bee species richness were similar when cleptoparasites were removed (Fig. 2, Table 2) and also for the abundance of bees, regardless of the inclusion/exclusion of cleptoparasites (Table 2). There was also a decrease of species richness with elevation, but this did not differ among treatments (Fig. S4). See Table S3 for likelihood ratio tests statistics for dropped variables and the full GLMM outputs for the final models.

Influence of experimental treatments and habitat conditions on phylogenetic diversity

The phylogenetic species richness (PSR) differed among treatments within sites, but the differences depended on the forb species richness within treatment plots and elevation (Fig. 2, Table 3). Inclusion of the interaction term treatment type × elevation (Table S5) significantly improved the model fit ($\chi^2 = 8.44$, $P < 0.038$) and was marginally significant (df = 2, LRT = 5.864, $P = 0.053$).

The increased PSR was not paralleled by a selective bias against specific taxonomic groups as neither the phylogenetic species variability (PSV) or evenness (PSE) varied systematically along the gradient in forb species richness, elevation, or among treatments (Table S5). In contrast, the phylogenetic species clustering (PSC) differed among treatments and increased with forb species richness in the Cut+Remove and Cut treatments but not in the Uncut treatment (Fig. 2, Table 3). Moreover, the significant

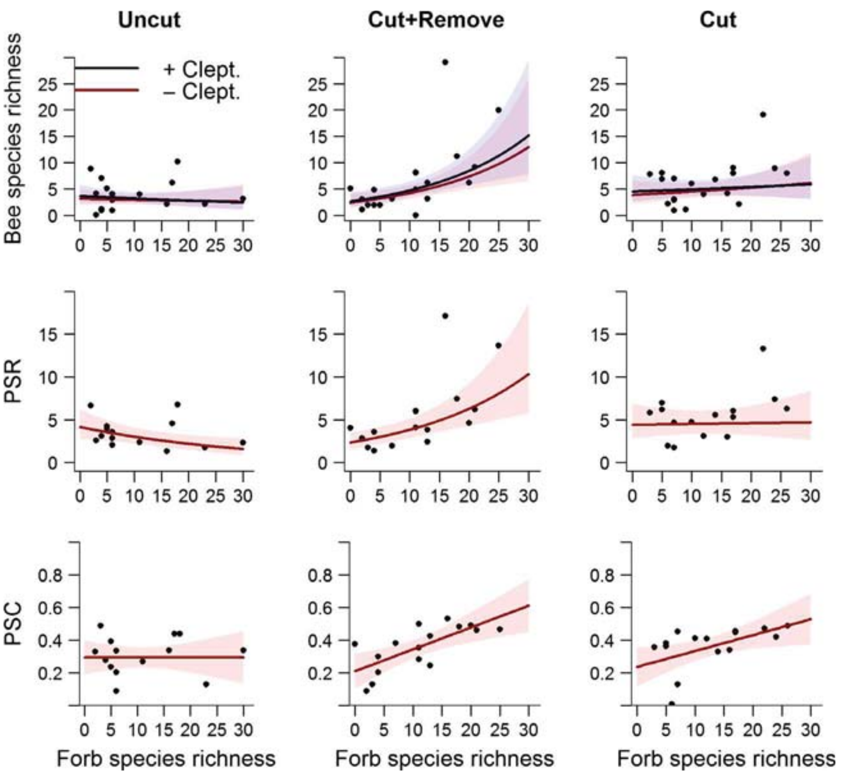


Figure 2. The effects of treatments (Uncut, Cut + Remove, and Cut) on the relationship between species richness, phylogenetic species richness (PSR), and phylogenetic species clustering (PSC) and forb species richness. The results were similar when cleptoparasites were excluded (- Clept.). Plots show fitted lines and 95% confidence intervals for GLMMs on the interaction term treatment × forb species richness (see text and Tables 2 and 3 for details).

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

interaction between forb species richness and elevation showed that the PSC increased with forb species richness and that the slope of this relationship increased with elevation (Table 3, Fig. S4). See Table S5 for likelihood ratio test statistics from the backward elimination of variables and full model outputs from the final models for PSR and PSC.

Influence of experimental treatments and habitat conditions on functional diversity

The functionally singular species richness (FSSR) increased with forb species richness in the Cut + Remove treatment whereas this relationship did not occur in the Cut and Uncut treatments (Fig. 3, Table 4). There was also a positive interaction between forb species richness and elevation, suggesting that the importance of forb species richness for FSSR increased with elevation (Fig. S4, Table 4).

We found no systematic change in the FDis within or among sites (Table S6). However, the FEve decreased with forb species richness and increased with elevation so that the individuals sampled in treatment plots at high elevations with a low forb species richness had the most evenly distributed functional trait distributions (Fig. S4, Table 4). The CWM ITD of individuals increased with elevation and decreased with forb species richness (Fig. S4, Table 4). These responses were site-specific as no interactions occurred between the environmental variables and treatment (Table S6).

The proportion of belowground nesting bee individuals was lower in the two cleared treatment types than in the Uncut treatment (Fig. 4, Table 4), but was not related to elevation or forb species richness (Table S6). The proportion of pollen specialists (oligolectics) decreased with forb species richness and increased with elevation and these relationships were most pronounced in the Uncut treatment type, indicating an effect of treatment. However, the relationships between the proportion of oligolectic bees and the interaction terms treatment × forb species richness (Fig. 3, df = 2, LRT = 0.36, $P = 0.836$) and treatment × elevation (df = 2, LRT = 5.15, $P = 0.076$) were not significant when Ericaceae specialists were removed from the analysis. The CWM emergence increased with elevation in the Uncut treatment plots but decreased with elevation in the Cut + Remove and Cut treatment plots (Table 4, Fig. 3). The CWM emergence also decreased with forb species richness (Table 4, Fig. S4). See Table S6 for likelihood ratio test statistics from the backward elimination of variables and full model outputs from the final models fitted to the functional diversity indices.

Table 2. Likelihood ratio tests for final models on bee species richness and abundance. Models were fitted using Poisson GLMMs with the number of successful trap-months as an offset variable and site identity as a random effect. See Table S3 for LRT test statistics from the backward elimination of variables and model outputs from the final model.

Response	Explanatory terms	LRT	df	*P*
Species richness (incl. Cleptoparasites)	Elevation	7.55	1	0.006
	Treatment × Forb species richness	13.26	2	0.001
Species richness (excl. Cleptoparasites)	Elevation	7.10	1	0.008
	Treatment × Forb species richness	9.00	2	0.011
Bee abundance (incl. Cleptoparasites)	Elevation	4.88	1	0.027
	Treatment × Forb species richness	33.39	2	<0.001
Bee abundance (excl. Cleptoparasites)	Elevation	4.70	1	0.030
	Treatment × Forb species richness	27.20	2	<0.001

Discussion

The effect of habitat management on bee diversity was modified by the environmental context. The cleared treatment plots in power lines (treatments Cut and Cut + Remove) attracted more species and individuals than noncleared plots (Uncut) and this effect increased with forb species richness. Contrary to our expectations, the effect of treatments did not change with elevation, and the phylogenetic similarity among species increased following the clearing of power lines in plots with a high species richness of forbs. However, the increase in phylogenetic similarity was driven by a parallel packing of species within several taxonomic groups. This was also supported in that the Cut and Cut + Remove treatments were slightly less dominated by belowground nesting bees than the Uncut treatment and that the proportion of oligolectic individuals was more stable along the forb spe-

Table 3. Likelihood ratio tests for final models on the phylogenetic diversity within treatment plots in power line clearings. The phylogenetic species richness (PSR) was fitted using Gamma GLMMs with site identity as a random effect. The phylogenetic species clustering (PSC) was fitted using a linear mixed effect model. See Table S5 for LRT test statistics from the backward elimination of variables and model outputs from the final model.

Response	Explanatory terms	LRT	df	*P*
Phylogenetic species richness (PSR)	Treatment × Forb species richness	24.40	2	<0.001
	Treatment × Elevation	5.86	2	0.053
Phylogenetic species clustering (PSC)	Treatment × Forb species richness	7.61	2	0.022
	Forb species richness × Elevation	4.34	1	0.037

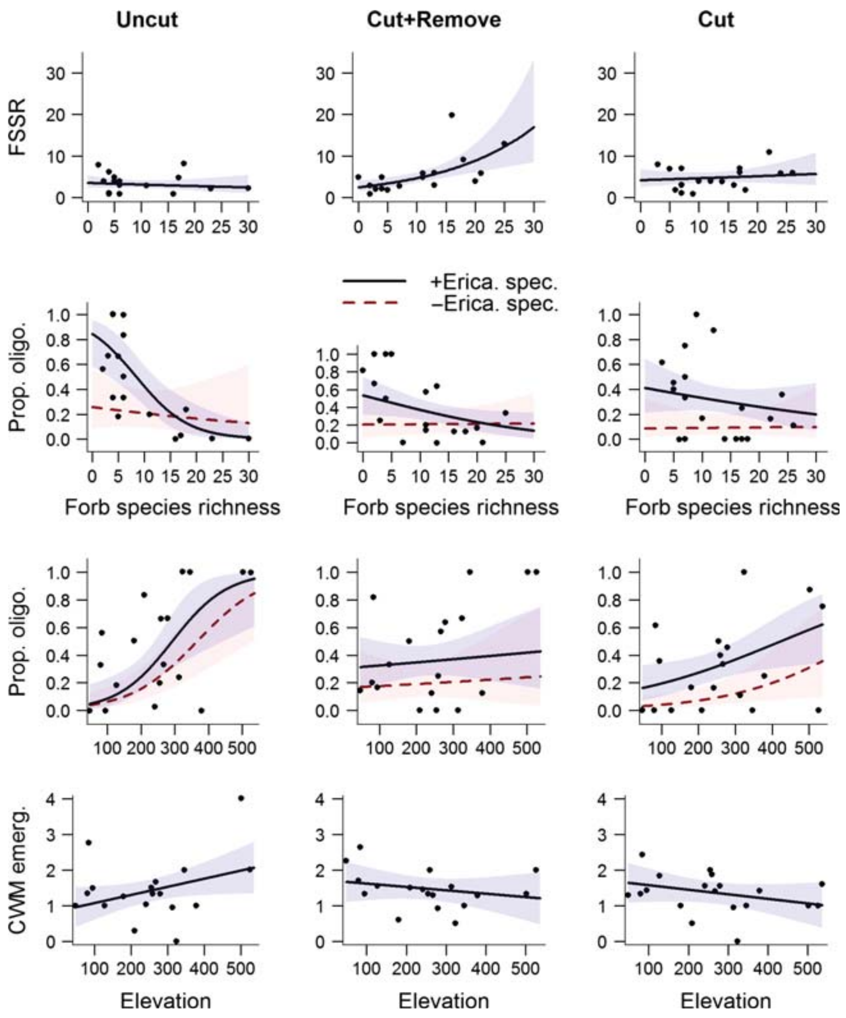


Figure 3. The effects of treatments (Uncut, Cut + Remove, and Cut) on the relationship between the functionally singular species richness (FSSR), proportion of oligolectics (prop. oligo.), and community-weighted mean month of emergence (CWM emerg.) and environmental conditions (forb species richness and elevation). Relationships are also shown when Ericaceae specialists were excluded from the analyses on Prop. Olig. (- Erica. spec.). Plots show fitted lines and 95% confidence intervals for GLMMs.

cies richness and elevation gradients in the two cleared treatments, compared to the Uncut treatment. There was a significant correlation among several of the trait categories (Table 5). Pollen specialists and aboveground nesters generally emerged later in the season, and pollen generalists tended to be smaller than pollen specialists. These interdependencies meant that the single trait analyses have to be interpreted in concert as some trait–environment relationships might have been confounded by other traits than the one being tested.

Influence of management practices on species richness and abundance of bees

The cleared treatment plots attracted more bee species and individuals from the local species pools than the noncleared plots, and the effect of clearing and debris removal was greatest in sites with a high species richness of forbs. In contrast, in the ericaceous shrub dominated (i.e., low forb species richness) sites, the treatment effect was negligible (Fig. 2, Table 2). This may indicate that bee species in our study preferred different successional stages, as previously shown for bees along temporal gradients in fire history (Moretti et al. 2009; Ricotta and Moretti 2011). In our system, this preference could be related to floral specialization in that Ericaceae-affiliated species are less affected by clearing regrowth than forb-affiliated species. For instance, the common Ericaceae specialist *Andrena lapponica* is frequently foraging on bilberry (*Vaccinium myrtillus*) in shaded *Picea abies* forests (pers. obs.), whereas the majority of solitary bees prefer sun-exposed areas in this ecosystem (Sydenham et al. 2014) with a diverse flora (Hanula et al. 2015; Sydenham et al. 2015). This suggests that forb-dominated power line clearings have a greater potential for boosting local bee diversity than those dominated by ericaceous shrubs.

In addition to the influence of clearing and floral diversity, elevation was negatively related to the species

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

richness and abundance of bees within treatment plots (Table 2, Table S3, Fig. S4). The species and functional diversity of wild bee species assemblages have previously been shown to decrease with elevation (Hoiss et al. 2012; Sydenham et al. 2015). In contrast to our expectations, the influence of elevation on bee species richness did not differ among the three experimental treatments (Fig. S4, Table 2). Scheper et al. (2013) found that the effect of habitat management in landscapes with little or no semi-natural habitats was negligible due to low species densities. The same may have occurred in the power line clearings at high elevations, where a low species richness in sites could mask potential differences in habitat quality among treatments.

Table 4. Likelihood ratio tests for final models on the functional diversity within treatment plots in power line clearings. The functionally singular species richness (i.e., FSSR; the number of functionally unique species) was fitted using a negative binomial GLMM whereas the functional evenness (FEve) and community-weighted mean body size of bee individuals (ITD) were fitted using linear mixed effect models. Analyses with the proportion of belowground nesting and oligolectic bee individuals were run using GLMMs with binomial distributions. See Table S6 for LRT test statistics from the backward elimination of variables and model outputs from the final model.

Response	Explanatory terms	LRT	df	*P*
Functionally singular species richness (FSSR)	Treatment type × Forb species richness	12.50	2	0.002
	Forb species richness × Elevation	5.14	1	0.023
Functional Evenness (FEve)	Forb species richness	12.65	1	<0.001
	Elevation	3.97	1	0.046
Mean body size of bee individuals (ITD)	Forb species richness	9.46	1	0.002
	Elevation	8.88	1	0.003
Proportion belowground nesting bee individuals	Treatment type	17.72	2	<0.001
Proportion of Oligolectic bee individuals	Treatment type × Forb species Richness	10.34	2	0.006
	Treatment type × Elevation	9.06	2	0.011
Mean emergence time of individuals	Forb species richness	4.92	1	0.027
	Treatment type × Elevation	10.95	2	0.004

Influence of management practices on the phylogenetic composition

The attraction of bee species to cleared plots with a high forb species richness also led to an increased phylogenetic species richness (PSR, Fig. 2), as would be expected as this index was correlated to species richness in our data set. We expected the phylogenetic species variability (PSV) and evenness (PSE) to change with forb species richness, treatment, or their interaction, as long-tongued bees prefer later successional habitats than distantly related short-tongued bees (Moretti et al. 2009; Ricotta and Moretti 2011), but we found no such relationships. That the phylogenetic species clustering (PSC) increased

Table 5. Spearman's rank correlations among the main functional trait categories. *P*-values are given in parenthesis. The body size of species (intertegular distance; ITD) and the month of emergence (Emergence) are numerical values. The Lecty status and Nest location are binary given the value 1 for polylectics and belowground nesters, respectively.

	Emergence	ITD	Lecty status
ITD	0.05 (0.70)	1	−0.33 (0.01)
Lecty status	−0.30 (0.02)	−0.33 (0.01)	1
Nest location	−0.35 (<0.01)	−0.03 (0.79)	−0.16 (0.22)

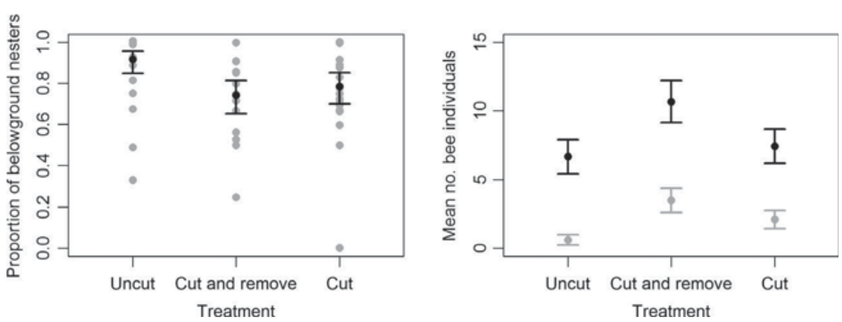


Figure 4. The proportion of belowground nesting bee individuals differed among treatment plots and was lowest in the two cleared treatment plots (Cut and Cut+Remove). Black dots and whiskers are predicted values and 95% CI limits. Gray dots are observed values. The right panel shows the mean number of belowground nesting (black) and aboveground nesting (gray) bee individuals per treatment type with 95% CI limits estimated using individual Poisson GLMs for each of the six nesting behavior–treatment combination. See Table 4 for test statistics.

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

with forb species richness in both clearing treatments, but not in the Uncut treatment (Table 3, Fig. 2), suggests that taxa did not discriminate between the clearing treatments and that most clades were present in areas that had plots with a high forb diversity. The preference for cleared treatment plots could be caused by the increased solar radiation in such plots, as sun exposure is an important determinant of solitary bee species richness in field margins along forest edges (Sydenham et al. 2014). In addition to increased local temperature, the direct sunlight could also increase the number of species flowering, and their flower density, in cleared plots, thereby increasing the diversity of foraging resources. As different taxa of bees tend to show distinct floral preferences (Potts et al. 2003), an increased diversity of floral resources could attract more species, from distantly related taxa, to the same treatment plot.

Influence of management practices on the functional diversity

The effects of treatments on the functional diversity of bees depended on elevation and on the forb species richness within plots. The response of the functional diversity of bees to habitat conditions may contrast that of species diversity if the habitat selects for bees with certain traits (Forrest et al. 2015). Indeed, while the response of the FSSR to treatments mirrored that of the species richness and PSR (Figs. 2 and 3, Tables 2–4) there were also trait-specific responses (Figs. 3 and 4, Table 4). We found a lower proportion of belowground nesting bees in the cleared plots despite these plots contained a larger area of sun exposed soil, which is attractive to nest seeking females (Potts et al. 2005). The preference for cleared plots may therefore have been driven mainly by foraging resources as floral diversity is an important driver of bee diversity (Potts et al. 2003). Moreover, differences among treatments in the relationships between the proportion of oligolectic bees and elevation and forb species richness were only significant when Ericaceae specialists were included in the analyses (Fig. 3). This suggests that Uncut treatment plots with a low diversity of foraging resources and at high elevations tended to be more dominated by Ericaceae specialists than the cleared plots. Oligolectics tended to emerge later in the season than polylectics (Table 5). That the CWM emergence increased with elevation in the Uncut treatment and decreased in two cleared treatment types (Fig. 3) may therefore have been caused by early emerging, polylectic, bees preferring the cleared plots at high elevations. At high elevations, this preference could be due to an earlier onset of flowering, resulting from increased sun exposure to the ground.

In addition to the effects of treatment, the functional diversity was also influenced by environmental conditions irrespective of treatments (Fig. S4). As the species richness decreased with elevation (Fig. S4), it surprised us that the FSSR increased with the interaction between elevation and forb species richness (Fig. S4). However, the decrease in functional evenness (FEve), with forb species richness and increase with elevation suggests an even trait distribution at high elevation sites with a high forb species richness. This could lead to an increased FSSR in treatment plots at high elevations areas with a diverse forb community. That the CWM ITD increases with elevation (Table 4, Fig. S4) was also found by Hoiss et al. (2012), who suggested that the relationship could be caused by large species being better at thermoregulating and able to fly under poorer weather conditions or that large species can forage over greater distances (Greenleaf et al. 2007). A decrease in CWM ITD with forb species richness was also found in another study in power line clearings in Norway (Sydenham et al. 2015), and was likely caused by sites with a high dominance of Ericaceous shrubs being species poor and dominated by the relatively large Ericaceae specialists (mean ITD = 2.67 ± 0.47 mm vs. 2.1 ± 0.75 mm). This could also explain why the mean month of emergence decreased with forb species richness (Fig. S4) as sites with a high species richness of forbs would be more likely to provide foraging resources for earlier emerging polylectics.

Implications for habitat management

Different types of habitats host-specific bee species assemblages (Murray et al. 2012). Thus, it should be of high conservation priority to develop habitat-type specific management strategies in potentially bee friendly habitats, such as power line clearings (Russell et al. 2005). In the European Union (EU), the implementations of such management plans in agricultural landscapes are motivated through the EU Agri Environmental Schemes. These include establishing flower-strips along field margins and restoring hedgerows, which increases local bee diversity (Kremen and M'Gonigle 2015). In contrast, no environmental schemes have been proposed for power line clearings that transect forests, although they cover vast areas and host diverse plant (Wagner et al. 2014; Eldegard et al. 2015), bee (Russell et al. 2005), and butterfly (Berg et al. 2013) species assemblages. However, the impact of management practices depends on the environmental context and is greatest in landscapes of intermediate complexity that contain source habitats from which species can recolonize restored areas (Scheper et al. 2013). Our findings are in agreement with Scheper et al. (2013) in that the largest increase in diversity occurs in sites with a high

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

species richness and they highlight the importance of testing management schemes under different environmental conditions prior to establishment.

Our findings suggest that changes in management practices, that is, removing debris after clearing, create a preferred habitat for bees and whether these translate into an increased pollen provisioning for offspring may enhance bee diversity in power line clearings. However, it should be noted that this study was limited to the diversity of solitary bees, and the suggested management advice might have different effects on other organisms. In order to mitigate negative effects on, for example, the local diversity of decomposers, the woody debris could be left on site, but collected in heaps, thereby creating a heterogeneous environment that benefits both bees and organisms that depend on dead wood. Moreover, the responses measured in this study are likely to be a mixture of population-level responses occurring at the site level, and behavioral-level responses occurring within sites. Future studies of bees should aim to test whether behavioral-level responses, such as those documented in this study, manifest themselves at the population level.

One of our treatments mimicked an labor-intensive management practice with removal of woody debris from the area after management clearing. Unless the debris is harvested and sold for biofuels or other products, removing the woody debris will increase the net cost of clearing the power line clearings. The most cost-effective solution would be to allocate this treatment to sites where the benefit is expected to have the greatest positive effect on bee diversity. Our results show that the largest effect is gained in areas with a relatively high forb diversity. In boreal forest landscapes, these are typically areas with a high site productivity and low soil moisture. Moreover, as the decrease in species richness and abundance with elevation was not affected by management practice, managers should remove debris primarily at low elevations as these areas have the highest bee diversity. Logistically, this will likely reduce the cost of intensified management as low elevational sites are generally more easily accessible.

Acknowledgments

We wish to thank Greina Trefelling AS for clearing the treatment plots. Irene B. Hermansen, Jenny Lorange, Celin M. H. Olsen, Randy G. Lange, and Adrian Rasmussen for assistance with field and laboratory work. This study was funded by Statnett.

Data Accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qj4h3

Conflict of Interest

None declared.

References

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear mixed-effect models using Eigen and S4. R package version 1.1-8, http://CRAN.R-project.org/package=lme4.

Berg, Å., K. Ahrné, E. Öckinger, R. Svensson, and J. Wissman. 2013. Butterflies in semi-natural pastures and power-line corridors – effects of flower richness, management, and structural vegetation characteristics. Insect Conserv. Divers. 6:639–657.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48:1079–1087.

Cardinal, S., and B. N. Danforth. 2013. Bees diversified in the age of the eudicots. Proc. R. Soc. B 280:20122686. http://dx.doi.org/10.1098/rspb.2012.2686

Danforth, B. N., S. Cardinal, C. Praz, E. A. B. Almeida, and D. Michez. 2013. The impact of molecular data on our understanding of bee phylogeny and evolution. Annu. Rev. Entomol. 58:57–78.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

Eldegard, K., Ø. Totland, and S. M. Moe. 2015. Edge effects on plant communities along power-line clearings. J. Appl. Ecol. 52:871–880.

Forrest, J. R. K., R. W. Thorp, C. Kremen, and N. M. Williams. 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. J. Appl. Ecol. 52:706–715.

Grafen, A. 1989. The phylogenetic regression. Philos. Trans. R. Soc. London [Biol] 326:119–57.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.

Hanula, J. L., S. Horn, and J. J. O'Brien. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? For. Ecol. Manage. 348:142–152.

Harrell, F. E. Jr with contributions from C. Dupont and many others. 2015. Hmisc: Harrell Miscellaneous. *R package version 3.16-0*, https://cran.r-project.org/web/packages/Hmisc.

Helmus, M. R., T. J. Bland, C. K. Williams, and A. R. Ives. 2007. Phylogenetic measures of Biodiversity. Am. Nat. 169: E68–E83.

Hoiss, B., J. Krauss, S. G. Potts, S. Roberts, and I. Steffan-Dewenter. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proc. R. Soc. B Biol. Sci. 279:4447–4456.

Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biol. Conserv. 141:2632–2640.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, et al. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Kremen, C., and L. K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. J. Appl. Ecol. 52:602–610.

Laliberte, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecol. Appl. 23:829–839.

Moretti, M., F. De Bello, S. P. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. J. Anim. Ecol. 78:98–108.

Murray, T. E., U. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown, and R. J. Paxton. 2012. Local-scale factors structure wild bee communities in protected areas. J. Appl. Ecol. 49:998–1008.

Nieto, A., S. P. M. Roberts, J. Kemp, P. Rasmont, M. Kuhlmann, M. García Criado, et al. 2014. European red list of bees. Publication Office of the European Union, Luxembourg.

Noordijk, J., K. Delille, A. P. Schaffers, and K. V. Sýkora. 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142:2097–2103.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. Science 346:1360–1362.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology, 84:2628–2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, et al. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol. Entomol., 30:78–85.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25:345–353.

R development core team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricotta, C., and M. Moretti. 2011. CMW and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167:181–188.

Russell, K., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. Biol. Conserv. 124:133–148.

Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, et al. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss–a meta-analysis. Ecol. Lett. 16:912–920.

Schmidt, S., C. Schmid-Egger, J. Morinière, G. Haszprunar, and P. D. N. Hebert. 2015. DNA Barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea *partim*). Mol. Ecol. Resour. 15:985–1000.

Shine, R., E. G. Barrot, and M. J. Elphick. 2002. Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. Ecology 83:2808–2815.

Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432.

Stoate, C., A. Báldi, P. Beja, N. Boatman, I. Herzon, A. Van Doorn, et al. 2009. Ecological impacts of early 21st century agricultural change in Europe–a review. J. Environ. Manage. 91:22–46.

Sydenham, M. A. K., K. Eldegard, and Ø. Totland. 2014. Spatio-temporal variation in species assemblages in field edges: seasonally distinct responses of solitary bees to local habitat characteristics and landscape conditions. Biodivers. Conserv. 23:2393–2414.

Sydenham, M. A. K., S. R. Moe, Ø. Totland, and K. Eldegard. 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? Ecography 38:140–153.

Villèger, S., N. W. H. Mason, and D. Muillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

Wagner, D. L., K. J. Metzler, S. A. Leicht-Young, and G. Motzkin. 2014. Vegetation composition along a New England transmission corridor and its implications for other trophic levels. For. Ecol. Manage. 327:231–239.

Williams, N. M., E. E. Crone, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol. Conserv. 143:2280–2291.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21:213–223.

© 2016 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. Annu. Rev. Ecol. Evol. Syst. 42:1–22.

Wojcik, V. A., and S. Buchmann. 2012. Pollinator conservation and management on electrical transmission and roadside rights-of-way: a review. J. Pollinat. Ecol. 7:16–26.

Wong, B. B. M., and U. Candolin. 2015. Behavioural responses to changing environments. Behav. Ecol. 26:665–673.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The hypothesized phylogenetic tree used in this study.

Table S2. List of functional traits used in this study and their assignment to species.

Table S3. Backward elimination of variables and final model outputs from analyses of species richness and abundance.

Figure S4. Influences of environmental conditions on the bee diversity in treatment plots.

Table S5. Backward elimination of variables and final model outputs from analyses of phylogenetic diversity.

Table S6. Backward elimination of variables and final model outputs from analyses of functional diversity.

Supplementary material for paper IV

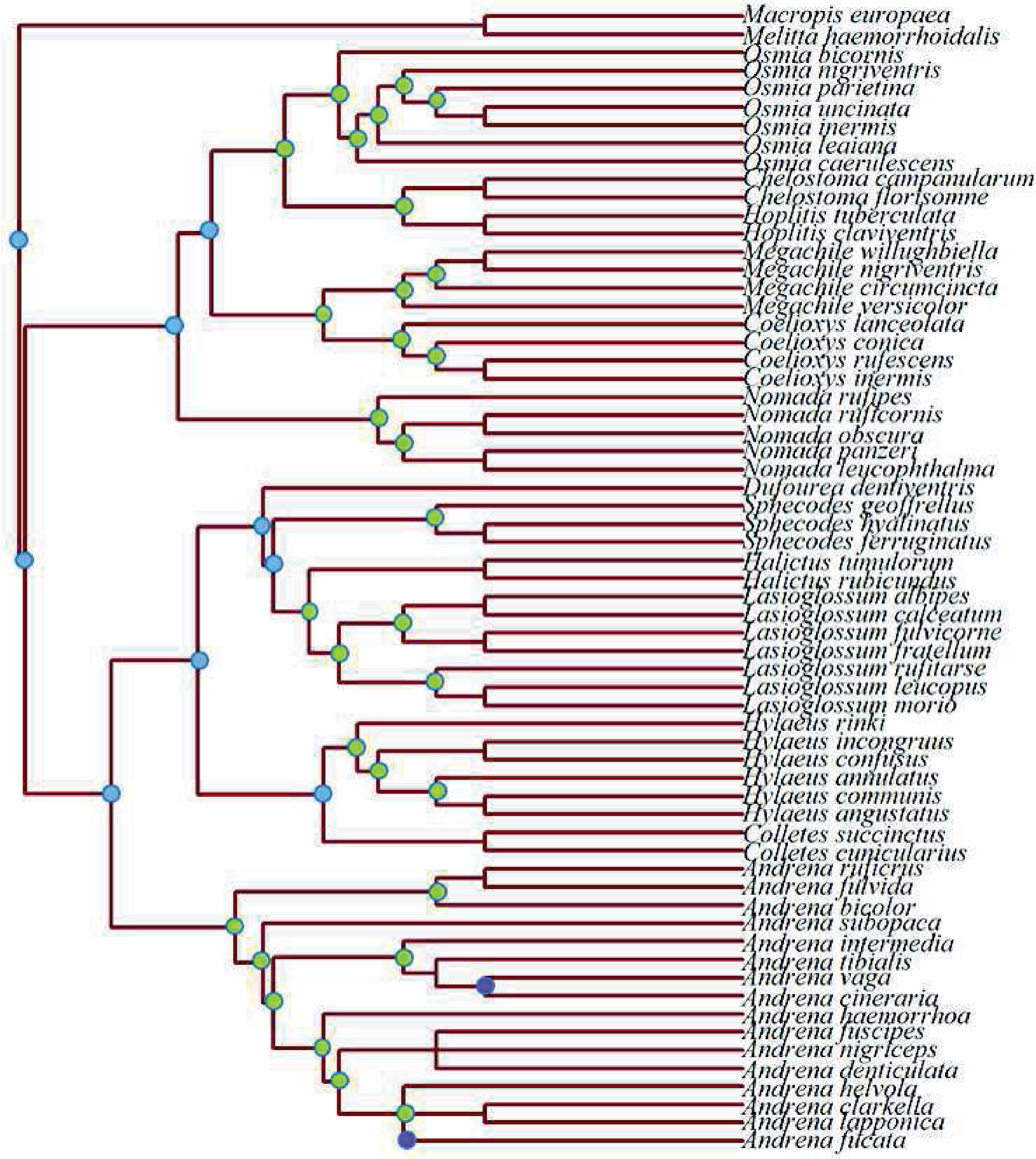


Figure S1. The hypothesized phylogenetic relationships among solitary bees sampled in power line clearings. The tree was structured by clustering taxa according to Danforth et al (2013; Blue dots) and Schmidt et al. (2015; Green dots). If species were not included in the phylogeny of Schmidt et al (2015) we placed them according to their subgeneric affiliation (Purple dots).

Table S2.1. Summary table of the functional traits included in this study. Cleptoparasites were assigned the exact same trait values as their hosts since they indirectly depend on these.

Trait category	Variable type	Trait range
Foraging behaviour		
Pollen specialist	Factor	Yes vs. No
Host plants for specialists		
Asteraceae	Factor	Yes vs. No
Campanulaceae	Factor	Yes vs. No
Fabaceae	Factor	Yes vs. No
Lysimachia	Factor	Yes vs. No
Raununculus	Factor	Yes vs. No
Salix	Factor	Yes vs. No
Ericaceae	Factor	Yes vs. No
Nesting behaviour		
Above vs. below ground	Factor	Yes vs. No
Clepto-parasitic	Factor	Yes vs. No
Host genus for clepto-parasites	Factor	*Andrena, Anthophora, Lasioglossum, Megachile*
Phenology		
Emergence	Numeric	March = 0, April = 1, May = 2, June =3, July = 4, August = 5.
Body size	Numeric	Mean = 2.17, min = 1, max = 4 mm

Table S2.2 The trait values assigned to each species. Species were designated as either polylectic (Poly = 1) or oligolectic (Poly = 0). For oligolectics we also specified the taxonomic affiliation of plants pollen is collected from. Species were also assigned a trait according to their nesting behaviour; i.e. below ground nesters (Nestbelow = 1) vs. above ground nesters (Nestbelow = 0). The month of emergence for species was included as a numerical variable (Table S2.1). Cleptoparasites were assigned an extra trait value according to the genera of their hosts (Clepto). We measured the intertegular distance (ITD) up to 10 female individuals of each species. We then used the mean ITD for each species, rounded to the nearest mm to account for measurement errors.

Species	Poly	Oligo	Nestbelow	Emergence	Clepto	ITD
Andrena bicolor	1	FALSE	1	April	FALSE	2
A. cineraria	1	FALSE	1	April	FALSE	3
A. clarkella	0	Salix	1	March	FALSE	3
A. denticulata	0	Asteraceae	1	July	FALSE	2
A. fucata	1	FALSE	1	April	FALSE	2
A. fulvida	1	FALSE	1	May	FALSE	2
A. fuscipes	0	Ericaceae	1	August	FALSE	2
A. haemorrhoa	1	FALSE	1	April	FALSE	3
A. helvola	1	FALSE	1	April	FALSE	2
A. intermedia	0	Fabaceae	1	June	FALSE	2
A. lapponica	0	Ericaceae	1	May	FALSE	3
A. nigriceps	1	FALSE	1	June	FALSE	2
A. ruficrus	0	Salix	1	March	FALSE	2
A. subopaca	1	FALSE	1	April	FALSE	2
A. tibialis	1	FALSE	1	April	FALSE	3
A. vaga		Salix	1	March	FALSE	3
Chelostoma campanularum	0	Campanulaceae	0	July	FALSE	1
C. florisomne	0	Raununculus	0	May	FALSE	2
Coelioxys conica	1	FALSE	0	May	Megachile	3
C. inermis	1	FALSE	0	May	Megachile	2
C. lanceolata	1	FALSE	0	June	Megachile	3
C. rufescens	1	FALSE	1	June	Anthophora	3
Colletes cunicularius	0	Salix	1	March	FALSE	3
C. succinctus	0	Ericaceae	1	August	FALSE	3
Dufourea dentiventris	0	Campanulaceae	1	July	FALSE	2
Halictus rubicundus	1	FALSE	1	April	FALSE	2
H. tumulorum	1	FALSE	1	April	FALSE	1
Hoplitis claviventris	1	FALSE	0	June	FALSE	2
H. tuberculata	1	FALSE	0	June	FALSE	2
Hylaeus angustatus	1	FALSE	0	June	FALSE	1
H. annulatus	1	FALSE	0	June	FALSE	1

H. communis	1	FALSE	0	May	FALSE	1
H. confusus	1	FALSE	0	May	FALSE	1
H. incongruus	1	FALSE	0	May	FALSE	2
H. rinki	1	FALSE	0	June	FALSE	1
Lasioglossum albipes	1	FALSE	1	April	FALSE	2
L. calceatum	1	FALSE	1	March	FALSE	2
L. fratellum	1	FALSE	1	April	FALSE	1
L. fulvicorne	1	FALSE	1	March	FALSE	2
L. leucopus	1	FALSE	1	April	FALSE	1
L. morio	1	FALSE	1	April	FALSE	1
L. rufitarse	1	FALSE	1	April	FALSE	1
Macropiseuropaea	0	Lysimachia	1	July	FALSE	3
Megachile circumcincta	1	FALSE	0	May	FALSE	3
M. nigriventris	0	Fabaceae	0	June	FALSE	4
M. versicolor	1	FALSE	0	May	FALSE	3
M. willughbiella	1	FALSE	0	June	FALSE	3
Melitta haemorrhoidalis	0	Campanulaceae	1	July	FALSE	3
Nomada leucophthalma	1	FALSE	1	March	Andrena	2
N. obscura	1	FALSE	1	March	Andrena	2
N. panzeri	1	FALSE	1	March	Andrena	2
N. ruficornis	1	FALSE	1	March	Andrena	2
N. rufipes	1	FALSE	1	July	Andrena	2
Osmia bicornis	1	FALSE	0	April	FALSE	3
O. caerulescens	1	FALSE	0	May	FALSE	2
O. inermis	1	FALSE	0	May	FALSE	2
O. leaiana	0	Asteraceae	0	June	FALSE	3
O. nigriventris	1	FALSE	0	April	FALSE	3
O. parietina	1	FALSE	0	May	FALSE	2
O. uncinata	1	FALSE	0	April	FALSE	2
Sphecodes ferruginatus	1	FALSE	1	May	Lasioglossum	2
S. geoffrellus	1	FALSE	1	May	Lasioglossum	1
S. hyalinatus	1	FALSE	1	April	Lasioglossum	1

Table S3.1 Backward elimination of variables from the full models. Response variables were: The species richness (incl. cleptoparasites), species richness (excl. cleptoparasites), bee abundance (incl. cleptoparasites) and bee abundance (excl. cleptoparasites) abbreviated as SR_{incl}, SR_{excl}, Ab_{incl} and $Ab_{excl.}$, respectively. The explanatory variables in the full models were: Treatment type, Forb species richness, Elevation, Treatment type × Forb species richness, Treatment type × Elevation, Forb species richness × Elevation and log(Number of Trap months) was included as an offset variable. In the first step (step 1) the full model was tested against a full model where the offset variable was excluded by comparing the deviance statistics between the models using χ^2 tests. The offset variable was included if it decreased the deviance , and dropped if that increased the deviance. Variables with p-values > 0.05 were dropped from the model. Outputs from the final models are shown in table S3.2.

Response	Explanatory and offset variables	LRT for variable	step
$SR_{incl.}$	Offset variable: *included*	$\chi^2 = 0.67$, $p < 0.001$	1
	Treatment type × Elevation	df = 2, LRT = 0.20, p = 0.906	2
	Forb species richness × Elevation	df = 1, LRT = 3.08, p = 0.079	3
$SR_{excl.}$	Offset variable: *included*	$\chi^2 = 0.35$, $p < 0.001$	1
	Treatment type × Elevation	df = 2, LRT = 0.15, p = 0.928	2
	Forb species richness × Elevation	df = 1, LRT = 2.70, p = 0.101	3
$AB_{incl.}$	Offset variable: *included*	$\chi^2 = 6.50$, $p < 0.001$	1
	Treatment × Elevation	df = 2, LRT = 1.495, p = 0.473	2
	Forb species richness × Elevation	df = 1, LRT = 1.53, p = 0.217	3
$AB_{excl.}$	Offset variable: *included*	$\chi^2 = 6.02$, $p < 0.001$	1
	Treatment × Elevation	df = 2, LRT = 1.170, p = 0.557	2
	Forb species richness × Elevation	df = 1, LRT = 1.10, p = 0.293	3

Table S3.2 Final model outputs from Generalized Linear Mixed effect Models (GLMMs) on the species richness and abundance of solitary bees in power line clearings. Models were run with Poisson distributed errors and a log-link function.

Bee species richness (*Including cleptoparasites)*	β	SE	z	P
Intercept (Uncut)	-0.455	0.333	-1.37	0.172
Cut-Remove	-0.328	0.296	-1.11	0.268
Cut	0.206	0.29	0.71	0.477
Forb Rich	-0.014	0.018	-0.76	0.446
Elevation	-0.003	0.001	-2.83	0.005
Cut-Remove × Forb Rich	0.072	0.022	3.35	0.001
Cut × Forb Rich	0.023	0.021	1.09	0.274
Random effects:	σ	SD	Obs.	Sites
Site identity	0.209	0.458	57	19
Bee species richness (*Excluding cleptoparasites)*	β	SE	z	P
Intercept (Uncut)	-0.641	0.341	-1.882	0.060
Cut-Remove	-0.262	0.305	-0.858	0.391
Cut	0.207	0.300	0.692	0.489
Forb Rich	-0.007	0.019	-0.356	0.722
Elevation	-0.002	0.001	-2.648	0.008
Cut-Remove × Forb Rich	0.063	0.022	2.854	0.004
Cut × Forb Rich	0.022	0.021	1.046	0.295
Random effects:	σ	SD	Obs.	Sites
Site identity	0.197	0.444	57	19
Bee abundance (*Including cleptoparasites)*	β	SE	z	P
Intercept (Uncut)	0.198	0.421	0.471	0.638
Cut-Remove	-0.292	0.234	-1.244	0.213
Cut	0.338	0.231	1.466	0.143
Forb Rich	-0.025	0.014	-1.763	0.078
Elevation	-0.003	0.001	-2.294	0.022
Cut-Remove × Forb Rich	0.076	0.016	4.75	< 0.001
Cut × Forb Rich	0.005	0.015	0.319	0.75
Random effects:	σ	SD	Obs.	Sites
Site identity	0.577	0.759	57	19
Bee abundance (*Excluding cleptoparasites)*	β	SE	z	P
Intercept (Uncut)	0.083	0.427	0.195	0.846
Cut-Remove	-0.268	0.238	-1.129	0.259
Cut	0.326	0.235	1.388	0.165
Forb Rich	-0.019	0.014	-1.310	0.190
Elevation	-0.003	0.001	-2.235	0.025
Cut-Remove × Forb Rich	0.070	0.016	4.342	0.000
Cut × Forb Rich	0.004	0.015	0.252	0.801

Random effects:	σ	SD	Obs.	Sites
Site identity	0.585	0.765	57	19

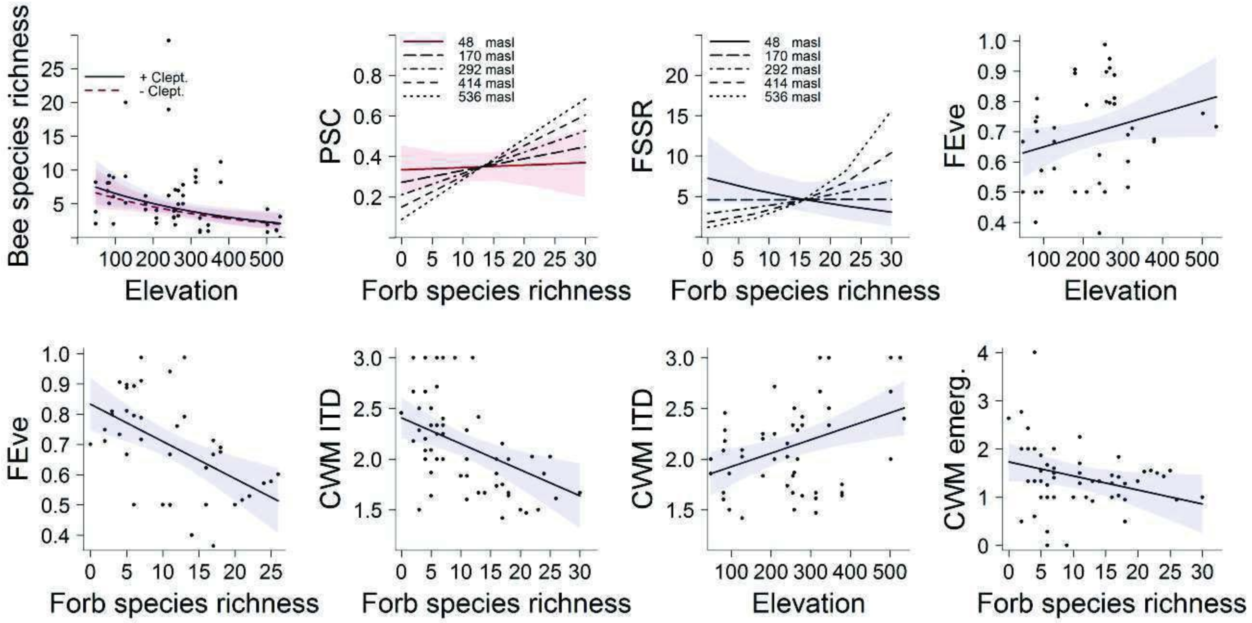


Figure S4. The relationship between environmental conditions and the species richness, phylogenetic species clustering (PSC), functionally singular species richness (FSSR), functional eveness (FEve), community weighted mean body size (CWM ITD) and emergence (CWM emerg.). Months of emergence were coded as a numeric so that March = 0, April = 1, May = 2, June = 3, July = 4 and August = 5. Plots show results from GLMMs and 95% CI's.

Table S5.1 Backward elimination of variables from the full models. Response variables were: The phylogenetic species richness (PSR), the phylogenetic species variability (PSV), the phylogenetic species evenness (PSE) and the phylogenetic species clustering (PSC). The variables in the full models were: Treatment type, Forb species richness, Elevation, Treatment type × Forb species richness, Treatment type × Elevation, Forb species richness × Elevation and the log(Number of Trap months) was included as an offset variable. In the first step (step 1) the full model was tested against a full model where the offset variable was excluded by comparing the deviance statistics between the models using χ^2 tests. The offset variable was included if it decreased the deviance, and dropped if it increased the deviance. Variables with p-values > 0.05 were dropped from the model. Outputs from the final models are shown in table S5.2. Note that for the PSR the interaction term Treatment type × Elevation was included in the analyses, despite not being significant at the 0.05 level, since its inclusion significantly improved the model fit ($\chi^2 = 8.44$, $p < 0.038$) compared to a model where Treatment type × Elevation and Elevation (df = 1, LRT = 2.572, p = 0.109) were removed.

Response	Explanatory and offset variable	LRT for variable	step
PSR	Offset variable: *included*	$\chi^2 = 1.27$, $p < 0.001$	1
	Forb species richness × Elevation	df = 1, LRT = 0.013, p = 0.909	2
	Treatment type × Elevation	df = 2, LRT = 5.864, p = 0.053	3*
	Elevation	df = 1, LRT = 2.572, p = 0.109	4
PSV	Offset variable: *Dropped*	$\chi^2 = 24.402$, $p < 0.001$	1
	Treatment type × Forb species richness	df = 2, LRT = 1.269, p = 0.530	2
	Forb species richness × Elevation	df = 1, LRT = 0.444, p = 0.505	3
	Treatment type × Elevation	df = 2, LRT = 1.568, p = 0.457	4
	Elevation	df= 1, LRT = 0.003, p = 0.955	5
	Treatment type	df = 2, LRT = 1.522, p = 0.467	6
	Forb species richness	df = 1, LRT = 2.533, p = 0.112	7
PSE	Offset variable: *Dropped*	$\chi^2 = 18.76$, $p < 0.001$	1
	Treatment type × Elevation	df = 2, LRT = 0.154, p = 0.912	2
	Forb species richness × Elevation	df = 1, LRT = 0.682, p = 0.409	3
	Treatment type × Forb species richness	df = 2, LRT = 2.252, p = 0.324	4
	Forb species richness	df = 1, LRT = 0.261, p = 0.609	5
	Treatment type	df = 2, LRT = 3.835, p = 0.147	6
	Elevation	df = 1, LRT = 2.189, p = 0.139	7
PSC	Offset variable: *Dropped*	$\chi^2 = 17.007$, $p < 0.001$	1
	Treatment type × Elevation	df = 2, LRT = 1.864, p = 0.394	2

Table S5.2. The effects of experimental treatment and habitat conditions on the phylogenetic diversity of bees sampled in treatment plots. The experimental treatments mimicked three different management practices (Uncut, Cut, and Cut-Remove, Fig. 1). Forb Rich = the species richness of forbs within the treatment plot. The Phylogenetic Species Richness and the difference between the species richness and PSR were fitted using generalized linear mixed effects models (GLMM) with Gamma distributions and log-link functions. The Phylogenetic species clustering was fitted with linear mixed models (See main text for Likelihood test statistics).

Phylogenetic Species Richness (PSR)	β	SE	t	p
Intercept (Uncut)	-1.060	0.328	-3.230	0.001
Cut-Remove	-0.008	0.240	-0.034	0.973
Cut	0.462	0.264	1.754	0.079
Forb Rich	-0.032	0.012	-2.576	0.010
Elevation	<0.001	0.001	0.126	0.900
Cut-Remove × Forb Rich	0.082	0.014	5.855	<0.001
Cut × Forb Rich	0.034	0.013	2.627	0.009
Cut-Remove × Elevation	-0.002	0.001	-2.612	0.009
Cut × Elevation	-0.002	0.001	-1.858	0.063
Random effects:	σ	SD	Obs.	Sites
Site identity	0.113	0.336	46	18
Residual	0.099	0.315		
Phylogenetic species clustering (PSC)	β	SE	t	
Intercept (Uncut)	0.407	0.073	5.616	
Forb Rich	-0.009	0.006	-1.480	
Cut-Remove	-0.084	0.071	-1.179	
Cut	-0.058	0.076	-0.759	
Elevation	-0.001	0.0003	-1.937	
Cut-Remove × Forb Rich	0.013	0.005	2.525	
Cut × Forb Rich	0.010	0.005	1.812	
Forb rich × Elevation	3E-05	1E-05	2.020	
Random effects:	σ	SD	Obs.	Sites
Site	0.0004	0.020	46	18
Residuals	0.012	0.110		

Table S6.1 Backward elimination of variables from the full models. Response variables were: The functional species richness (FSR), the functional dispersion (FDis), the functional evenness (FEve), the community weighted mean body size (ITD), the proportion of below ground nesters (Below) and the proportion of pollen specialists (Oligo.). The variables in the full models were: Treatment type, Forb species richness, Elevation, Treatment type × Forb species richness, Treatment type × Elevation, Forb species richness × Elevation and the log(Number of Trap months) was included as an offset variable. In the first step (step 1) the full model was tested against a full model where the offset variable was excluded by comparing the deviance statistics between the models using χ^2 tests. The offset variable was included if it decreased the deviance , and dropped if that increased the deviance. Variables with p-values > 0.05 were dropped from the model. Outputs from the final models are shown in table S6.2.

Response	variable	LRT for variable	step
FSR	Offset variable: *included*	$\chi^2 = 1.67$, p < 0.001	1
	Treatment type × Elevation	df = 2, LRT = 0.37, p = 0.83	2
FDis	Offset variable: *Dropped*	$\chi^2 = 28.79$, p < 0.001	1
	Treatment type × Forb species richness	df = 2, LRT = 0.959, p = 0.619	2
	Treatment type × Elevation	df = 2, LRT = 1.688, p = 0.430	3
	Forb species richness × Elevation	df = 1, LRT = 1.599, p = 0.206	4
	Elevation	df = 1, LRT = 2.622, p = 0.105	5
	Forb species richness	df = 1, LRT = 2.766, p = 0.096	6
	Treatment type	df = 1, LRT = 3.806, p = 0.149	7
FEve	Offset variable: *Dropped*	$\chi^2 = 4.00$, p < 0.001	1
	Forb species richness × Elevation	df = 1, LRT = 0.229, p = 0.632	2
	Treatment type × Elevation	df = 1, LRT = 0.770, p = 0.680	3
	Treatment type × Forb species richness	df = 2, LRT = 1.486, p = 0.476	4
	Treatment type	df = 2, LRT = 2.523, p = 0.283	5
ITD	Offset variable: *Dropped*	$\chi^2 = 1.502$, P < 0.001	1
	Treatment type × Forb species richness	df = 2, LRT = 1.185, p = 0.553	1
	Treatment type × Elevation	df = 2, LRT = 1.408, p = 0.495	2
	Treatment type	df = 2, LRT = 1.269, p = 0.53	3
	Forb species richness × Elevation	df = 1, LRT = 0.352, p = 0.553	4
% Below	Offset variable: *Not included*	NA	1
	Treatment type × Elevation	df = 2, LRT = 0.049, p = 0.976	2
	Forb species richness × Elevation	df = 2, LRT = 1.206, p = 0.272	3
	Elevation	df = 1, LRT = 0.379, p = 0.538	4
	Treatment type × Forb species richness	df = 2, LRT = 5.037, p = 0.081	5
	Forb species richness	df = 2, LRT = 0.003, p = 0.958	6
% Oligo.	Offset variable: *Not included*	NA	1
	Forb species richness × Elevation	df = 1, LRT = 3.355, p = 0.067	2
Emergence	Offset variable: *included*	Df = 12, $\chi^2 = 0.379$, p < 0.001	1
	Treatment type × Forb species richness	Df = 2, LRT = 0.432, p = 0.806	2
	Forb species richness × Elevation	Df = 1, LRT = 2.37, p = 0.123	3

Table S6.2 Outputs from final mixed effect models on the functional diversity within treatment plots. See Table 3 for LRT test statistics and text for details.

Functionally singular species richness (FSSR)	β	SE	z	p
Intercept (Uncut)	-1.188	0.212	-5.593	<0.001
Forb species richness	-0.012	0.018	-0.688	0.491
Cut-Remove	-0.355	0.296	-1.199	0.231
Cut	0.173	0.292	0.591	0.554
Elevation (standardized to achieve convergence)	-0.522	0.165	-3.161	0.002
Cut-Remove × Forb species richness	0.077	0.023	3.352	0.001
Cut × Forb species richness	0.023	0.022	1.015	0.310
Forb species richness × Elevation (standardized)	0.033	0.013	2.494	0.013
Random effects:	σ	SD	Obs.	Sites
Site identity	0.071	0.266	55	19
Functional evenness (FEve)	β	SE	z	
Intercept (Uncut)	0.749	0.058	13.008	
Forb species richness	-0.012	0.003	-3.937	
Elevation	0.0004	0.0002	1.997	
Random effects:	σ	SD	Obs.	Sites
Site identity	0.001	0.023	40	17
Residuals	0.018	0.134		
Mean body size of bee individuals (ITD)	β	SE	t	
Intercept	2.067	0.157	13.136	
Forb species richness	-0.026	0.007	-3.528	
Elevation	0.001	0.0004	3.087	
Random effects	σ	SD	Obs.	Sites
Site	0.034	0.184	55	19
Residual	0.092	0.304		
Proportion of below ground nesters	β	SE	z	p
Intercept (Uncut)	2.413	0.350	6.888	<0.001
Cut-Remove	-1.358	0.356	-3.811	<0.001
Cut	-1.109	0.370	-2.997	0.003
Random effects	σ	SD	Obs.	Sites
Site	0.269	0.518	55	19
Proportion of Oligolectic individuals	β	SE	z	p
Intercept (Uncut)	-1.451	0.766	-1.896	0.058
Cut-Remove	1.327	0.810	1.638	0.101
Cut	-0.036	0.793	-0.046	0.963
Forb species richness	-0.199	0.059	-3.357	0.001
Elevation	0.012	0.004	3.026	0.002

Cut-Remove × Forb species richness	0.133	0.059	2.266	0.023
Cut × Forb species richness	0.165	0.057	2.893	0.004
Cut-Remove × Elevation	-0.011	0.004	-2.729	0.006
Cut × Elevation	-0.008	0.004	-1.926	0.054
Random effects	σ	SD	Obs.	Sites
Site identity	0.412	0.642	55	19
CWM emergence time	β	SE	t	
Intercept (Uncut)	-1.288	0.356	-3.624	
Cut-Remove	0.867	0.336	2.582	
Cut	0.855	0.335	2.551	
Forb species richness	-0.029	0.014	-2.125	
Elevation	0.002	0.001	2.012	
Cut-Remove × Elevation	-0.003	0.001	-2.736	
Cut × Elevation	-0.004	0.001	-3.108	
Random effects	σ	SD	Obs.	Sites
Site identity	0.210	0.458	55	19
Residual	0.218	0.467		

Paper V

Assessing the roles of stochastic and deterministic processes on the assembly of bee communities

Markus A.K. Sydenham[1], Stein R. Moe[1], Michael Kuhlmann[2], Simon G. Potts[3], Stuart P.M. Roberts[4], Ørjan Totland[1] and Katrine Eldegard[1]

[1]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.B. 5003, NO-1432 Ås, Norway.*

[2]*Zoological Museum, University of Kiel, Hegewischstr. 3, D-24105 Kiel, Germany*

[3]*Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Reading University, Reading, RG6 6AR, UK*

[4]*Visiting Research Fellow, Reading University, Reading, RG6 6AR, UK*

Corresponding author: markus.sydenham@nmbu.no

Abstract

Both stochastic and deterministic processes drive community assembly. The relative influence of stochastic processes, i.e. dispersal and ecological drift, may determine how predictable the outcome of habitat management is. Since these processes operate at several spatial scales, understanding the determinants of local biodiversity requires syntheses among hierarchies of biological organization. We build on previous approaches testing the role of ecological filtering and develop a novel framework to characterize the influence of dispersal limitation and ecological drift. Using wild bee communities as an example, we show that the probability of species occurring within communities is dispersal limited. Moreover, regionally abundant species were relatively more likely to occur at high elevations than less abundant species suggesting that the role of ecological drift increases with elevation. In addition to stochastic processes, ecological filtering also influenced community assembly by selecting for species based on their floral preferences.

Our results show that an appreciation of stochastic processes can help inform decisions about habitat management. Specifically, the outcome of habitat management may be more predictable in areas of favorable climatic conditions. Moreover, the analytical framework we have developed here is scalable to the population and biogeographic levels and so can facilitate a synthesis among biological hierarchies.

Keywords: Bees, community assembly, deterministic processes, dispersal, drift, stochastic processes

Introduction

Understanding the distribution of species diversity requires syntheses among hierarchies of biological organization (Jenkins and Ricklefs 2011) and that communities are understood in a regional context (Ricklefs 2008). Communities are embedded in a network of other communities, i.e. the metacommunity, connected through the dispersal of species (Leibold et al. 2004). Within this network, community assembly is influenced by both stochastic processes, related to immigration and ecological drift, as well as deterministic processes of ecological filtering (Fig. 1, Vellend (2010). Faced with current declines in species diversity (Dirzo et al. 2014) the development of habitat management plans is required in order to conserve species rich communities. Identifying the influence of both stochastic and deterministic processes on community assembly is essential for the design of habitat management plans and predicting their success. However, disentangling the relative importance of these two processes remains a challenge (Logue et al. 2011).

β-diversity indices allow estimating the relative roles of dispersal limitation and ecological filtering (Pavoine and Bonsall 2011). However, their interpretation and the comparison of results from different study systems may be challenging since; patterns in β-diversity are attributable to different processes across spatial scales (Warren et al. 2014) and the wide variety of indices available (Barwell et al. 2015); inter-site dissimilarity indices have been criticized for introducing statistical artefacts due to the mean-variance relationships in community data (Warton et al. 2012). An alternative approach to testing the influence of ecological filtering is to use generalized linear models, since GLMs are better at accounting for mean-variance relationships (Warton et al. 2015). Similarly generalized linear mixed effect models (GLMMs), have recently been used to test how functional traits influence the occurrence of bee species (Kremen and M'Gonigle 2015). However, the univariate approach has so far been limited to testing the influence of ecological filtering. Here we expand on this approach and suggest a novel analytical framework allowing the inclusion of the influence of stochastic processes. We use this framework to test if dispersal limitation, ecological drift as well as ecological filtering influence the assembly of bee communities.

Stochastic processes may be important determinants of bee diversity, and communities at northern latitudes in the northern hemisphere may be especially susceptible since they are on the limits of the distributional range of many species (Nieto et al. 2014). They therefore provide a good model system for testing the combined influence of stochastic and deterministic processes on community assembly. For instance, that foraging ranges and nesting behavior determine the response of bees to habitat isolation (Williams et al. 2010), suggests dispersal limitation could influence bee community assembly and supports the idea that dispersal rates may be partly deterministic (Lowe and McPeek 2014). Indeed, as central place foragers, bees show more pronounced distance decay functions from source habitats than the more ephemerally distributed hoverflies (Syrphidae) (Jauker et al. 2009).

The influence of dispersal limitation can be assessed through increases in species turnover among sites with increasing distances (Anderson et al. 2011). Communities that are connected through species dispersals should have a more similar species composition than sites that are unconnected (Leibold et al. 2004). In the approach proposed in this paper, we follow this rationale. However, estimating the species turnover among sites within a metacommunity results in a multivariate matrix that includes all inter-site distances, which is unsuited for univariate analyses. We therefore create a univariate variable *'Distance to source habitat'* that allows estimating the average probability of a species being present in a local community as a function of the geographic distance to the nearest community where the species occurs. For each species by site combination, we calculate the distance to the nearest site where that species occurs. A strength of this approach is that it allows the inclusion of interaction terms between functional traits hypothesized to influence dispersal limitation and the geographic distance to the nearest conspecific. Our proposed variable, the *'Distance to source habitat'* thereby characterizes the influence of the proximity of suitable habitat patches on the occurrence of species and allows the influence of dispersal limitation to be characterized using univariate GLMMs within existing frameworks (Kremen and M'Gonigle 2015).

If communities are not connected through the dispersal of species, neutral theory predicts that ecological (species) drift will lead to the mono-dominance of one species. In contrast, if immigration is unrestricted, communities consist of a random sample of individuals from the regional species pool (Rosindell et al. 2011). Bee diversity often declines with elevation (Hoiss et al. 2012), and communities at high latitudes are usually more dissimilar than those at low latitudes suggesting a higher degree of habitat isolation (Sydenham et al. 2015). The probability of species occurring in favorable conditions should therefore mirror their regional abundance, whereas the relative probability of occurrence should be lower in high elevation sites due to too a lower abundance (Hoiss et al. 2013) and a more patchy distribution of resources.

To explore the relative importance of dispersal limitation, ecological drift and ecological filtering we use a model system of solitary bee communities comprising 44 species, from 46 sites in southeastern Norway (Fig. 2). The sites encompassed gradients in elevation, latitude and from being dominated by Ericaceous shrubs too being dominated by forbs, providing resources for a broader spectrum of bees (Hanula et al. 2015, Sydenham et al. 2015). We tested if the probability of species occurring in communities was related to:

(I) Dispersal limitation; the mean occurrence of a species decreases with increasing distance to the nearest site where conspecifics occur. Dispersal limitation may be non-neutral in that rate of decrease in occurrence with distance among sites depends on foraging range and nesting behavior.

(II) Ecological drift; the mean occurrence of a species increases with its abundance in the surrounding metacommunity and this positive relationship is strongest at high elevations due to ecological drift.

(III) Ecological filtering; the mean occurrence of non-Ericaceae affiliated species increases with the species richness of forbs, whereas the mean occurrence of Ericaceae affiliated species decreases. We selected this specific trait and ecological filter combination as it has previously been shown to be an important determinant of solitary bee diversity within our study system (Sydenham et al. 2015).

Materials and Methods

We combined two datasets on solitary bees in power line clearings (sites) where bees had been sampled using flight-interception traps installed following snowmelt (April/May), emptied four times during the trapping season and removed in the early autumn (August/September). In 'Dataset 1', 3, 4, 4 and 3 traps per site were sampled during the first, second third and fourth sampling period, respectively. The sites in 'Dataset 2' were sampled during an experiment with three treatment plots per site and three traps per treatment plot (Fig. 2, Supplementary methods). Plant surveys were conducted within $1m^2$ subplots. Subplots in 'Dataset 1' were arranged in eight $5m^2$ rectangles placed 50 meters apart along the direction of the power line clearing. In 'Dataset 2' nine subplots were sampled in each of the three treatment units. We used the species richness of forbs within sites as a proxy for resource diversity; high values indicate floristically diverse sites, and low values are characteristic of Ericaceous shrub dominated sites (Sydenham et al. 2015). Estimated maximum foraging ranges (Supplementary methods), nesting behavior (above- vs. below-ground) and Ericaceous affiliation (specialists vs. non-specialists) for all species were obtained from the European pollinator database established during the ALARM and STEP projects and maintained by M.K., S.G.P. and S.P.M.R.

We combined site and species-specific information into one dataset (Table 1, Supplementary methods). We used binomial GLMMs in the lme4 [18] library in R [19] with the presence of species within sites as response variable. Functional traits were; the numerical variable *Foraging range* and the categorical variables *Ericaceae affiliation* and *Nesting behavior*. The *Forb species richness* and *Elevation* for each site were included as ecological filters. We included the interaction terms *Distance to source habitat* × *Foraging range, Distance to source habitat* × *Nesting behavior, Forb species richness* × *Ericaceae affiliation* and *Elevation* × *Regional abundance* and their main effect terms as fixed effects. *Species identity, Site identity, Study design* and *Sampling year* were included random intercept terms. *Forb species richness* × *Ericaceae affiliation* was included as a random slope to account for the differences in plant survey protocols between study designs. The binomial GLMM was fitted with the complementary log-log link due to imbalances in the number of presence and absences (Zuur et al. 2009). All numerical variables were centered to zero means. We excluded fourteen species from the analysis since they only occurred within single sites and their *Distance to source habitat* therefore returned missing values. We tested the influence of *Elevation* on the presence of single-site inhabitants in a separate GLMM analysis (Supplementary methods). We simplified models by first dropping random effects that increased the Bayesian Information Criterion (BIC). We then used likelihood ratio tests to conduct a backward elimination of fixed effect terms. One species was an influential outlier and we refitted the final model without this species (Supplementary methods).

Results

Our combined studies included 885 individuals from 44 species of solitary bees. The estimated probability of a species occurring within communities decreased from 13.5% to 3.2% as the distance to the nearest source habitat increased from 5.5 to 203 km (Fig. 3, table 2), irrespectively of foraging range or nesting behavior (Supplementary methods). Ecological drift was most pronounced at high elevations as the interaction term *Elevation* × *Regional abundance* showed that the probability of regionally rare species occurring in communities decreased more rapidly with elevation than it did for regionally common species (Fig. 3, table 2). Ecological filtering decreased the occurrence of Ericaceae specialists from 13.7% to 5.9% and increased the occurrence of non-Ericaceae affiliated species from 5.6% to 27.9% as the species richness of forbs increased from zero to 41. The probability of occurrence of single-site inhabitants decreased with elevation (Fig. 3, table 2).

Discussion

By expanding on approaches that test the influence of ecological filtering (Kremen and M'Gonigle 2015, Warton et al. 2015) we show that both stochastic and deterministic processes influenced the assembly of bee communities (Fig. 3, table 2).

The probability of species occurring in sites decreased with the distance to the nearest site where their habitat conditions were met suggesting that bee communities are dispersal limited. That dispersal limitation is an important process in the assembly of bee communities is supported by that the similarity in species composition decreases with geographic distance among similar habitats (Murray et al. 2012). However, it was somewhat surprising that foraging ranges and nesting behavior did not influence the dispersal limitation in our study system, since these traits have been shown to influence the vulnerability of bees to habitat isolation more generally (Williams et al. 2010). It may be that the inter-site distances in our study were too large (≥5.5 km) to account for trait specific responses to dispersal limitation or that foraging ranges are not a consistent proxy for dispersal capability (Murray et al. 2009). For instance, *Colletes hederae* and other species have, within recent years, crossed distances greater than their predicted foraging ranges and colonized the British Isles from continental Europe.

The decrease in species occurrences with elevation depended on their regional abundance. Bee communities at high elevation have previously been shown to consist of a few widely distributed lowland (e.g. *Lasioglossum calceatum*) and montane (e.g. *L. fratellum*) species (Hoiss et al. 2012). Our results suggests that pure sampling effects could also explain the under-representation of rare lowland species at high elevations, where single-site occupants (mainly lowland species) were also less likely to occur (Fig. 3, table 2), suggesting an increased role of ecological drift under unfavorable environmental conditions.

The role of stochastic processes in community assembly could have important bearings for conservation planning if the success of habitat management practices is less predictable in areas with harsh environmental conditions. For instance, the effect size of agri-environmental schemes on promoting local bee diversity depends on the availability of source habitats in the surrounding landscape suggesting (Scheper *et al.* 2013) suggesting that connectivity among sites should be considered in habitat management plans.

The approach used here allows estimating the influence of stochastic and deterministic processes on community assembly. A strength of focusing on species abundances (Warton et al. 2015) or occurrences (Kremen and M'Gonigle 2015), instead of multivariate diversity indices is that the framework is reducible to meta-population ecology as analyses can be restricted to single species. Moreover, differences in the metacommunity abundance among species are related to biogeographic processes since speciation events and long distance dispersal may explain the commonness (i.e. abundance) of species and clades within regions (Warren et al. 2014). In addition to elucidating the relevance of stochastic processes for conservation management, the approach used in this paper therefore also allows for a heuristic link between meta-population ecology and biogeography and thereby provides a step towards a reductionist community ecology.

Acknowledgements

We thank L.D. Häusler, I.B. Hermansen and J. Lorange for assistance with field and laboratory work. STATNETT funded the field and laboratory work for this study. The contribution by S.G.P. was made in the framework of the European Union (EU) FP7 projects LIBERATION (grant 311781) and STEP (grant 244090).

Literature cited

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita and K. F. Davies. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters **14**:19-28.

Barwell, L. J., N. J. Isaac and W. E. Kunin. 2015. Measuring β-diversity with species abundance data. Journal of Animal Ecology. **84**: 1112-1122.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac and B. Collen. 2014. Defaunation in the Anthropocene. Science **345**:401-406.

Hanula, J. L., S. Horn and J. J. O'Brien. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? Forest Ecology and Management **348**:142-152.

Hoiss, B., J. Gaviria, A. Leingärtner, J. Krauss and I. Steffan-Dewenter. 2013. Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. Diversity and Distributions **19**:386-395.

Hoiss, B., J. Krauss, S. G. Potts, S. Roberts and I. Steffan-Dewenter. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proceedings of the Royal Society B-Biological Sciences **279**:4447-4456.

Jauker, F., T. Diekoetter, F. Schwarzbach and V. Wolters. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology **24**:547-555.

Jenkins, D. G. and R. E. Ricklefs. 2011. Biogeography and ecology: two views of one world. Philosophical transactions of the Royal Society B: Biological sciences **366**:2331-2335.

Kremen, C. and L. K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. Journal of Applied Ecology **52**:602-610.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law and D. Tilman. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters **7**:601-613.

Logue, J. B., N. Mouquet, H. Peter, H. Hillebrand and M. W. Group. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology & Evolution **26**:482-491.

Lowe, W. H. and M. A. McPeek. 2014. Is dispersal neutral? Trends in Ecology & Evolution **29**:444-450.

Murray, T. E., U. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown and R. J. Paxton. 2012. Local-scale factors structure wild bee communities in protected areas. Journal of Applied Ecology **49**:998-1008.

Murray, T. E., M. Kuhlmann and S. G. Potts. 2009. Conservation ecology of bees: populations, species and communities. Apidologie **40**:211-236.

Nieto, A., S. P. M. Roberts, J. Kemp, P. Rasmont, M. Kuhlmann, M. García Criado, J. C. Biesmeijer, P. Bogusch, H. H. Dathe, P. De la Rúa, T. De Meulemeester, M. Dehon, A. Dewulf, F. J. Ortiz-Sánchez, P. Lhomme, A. Pauly, S. G. Potts, C. Praz, M. Quaranta, V. G. Radchenko, E. Scheuchl, J. Smit, J. Straka, M. Terzo, B. Tomozii, J. Window and D. Michez. 2014. European Red List of bees. Publication Office of the European Union, Luxembourg.

Pavoine, S. and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews **86**:792-812.

Ricklefs, R. E. 2008. Disintegration of the ecological community. The American Naturalist **172**:741-750.

Rosindell, J., S. P. Hubbell and R. S. Etienne. 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology & Evolution **26**:340-348.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G. and Kleijn, D. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss–a meta-analysis. Ecology letters, **16**: 912-920.

Sydenham, M. A. K., S. R. Moe, Ø. Totland and K. Eldegard. 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? Ecography **38**:140-153.

Vellend, M. 2010. Conceptual synthesis in community ecology. The Quarterly Reviews of Biology **85**:183-206.

Warren, D. L., M. Cardillo, D. F. Rosauer and D. I. Bolnick. 2014. Mistaking geography for biology: inferring processes from species distributions. Trends in Ecology & Evolution **29**:572-580.

Warton, D. I., B. Shipley and T. Hastie. 2015. CATS regression – a model-based approach to studying trait-based community assembly. Methods in Ecology and Evolution **6**:389-398.

Warton, D. I., S. T. Wright and Y. Wang. 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution **3**:89-101.

Williams, N. M., E. E. Crone, R. L. Minckley, L. Packer and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation **143**:2280-2291.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.

Tables and Figures

Table 1. The original data frames required for the analyses and description of the variables they include. The derived data frame contains all species$_{1\ldots j}$-site$_{1\ldots k}$ combinations and thereby $j\times k$ rows.

Original data frames	**Rows**	**Columns**	**Description**
Community data frame	Site$_{1\ldots k}$	Species$_{1\ldots j}$	Abundances of species$_j$ in site$_k$
Traits data frame	Species$_{1\ldots j}$	Functional trait$_{1\ldots t}$	Trait$_t$ values for species$_j$
Environment data frame	Site$_{1\ldots k}$	Environmental variable$_{1\ldots e}$	Ecological filters$_e$ and site information for site$_k$
Spatial data frame	Site$_{1\ldots k}$	Spatial coordinates	Geographic position of site$_{1\ldots k}$
Columns in derived data frame	**Description**		**Range in this study**
Presence	Presence/absence of the jth species in the kth site		Mean = 0.17 of sites occupied per species
Local abundance	Abundance of the jth species in the kth site		Mean = 0.44 (range: 0; 37)
Species identity	Identifier of the jth species		44 species
Site identity	Identifier of the kth site		46 sites
Study design	Grouping factors for Dataset 1 and 2		Dataset 1; 27 sites, Dataset 2; 19 sites
Sampling year	Grouping factor for sites for sampling years		2009; 9 sites, 2010; 8 sites, 2013; 29 sites
Species traits	tth trait of the jth species (one column per trait)		Nesting behavior; % Above ground = 69% Foraging range: Mean = 0.84 km (range: 0.05;5.7)
Environmental condition	eth environmental variable value for the kth site (one column for each variable)		Forb species richness; Mean = 13.5 (range = 0; 41) Elevation; Mean = 248 m (range: 36; 568)
Distance to source habitat	Distance from the kth site to the nearest site where the jth species was found. For single-site occupants the calculation of this variable returns a missing value.		Mean = 52 km (range: 5.5; 203)
Metacommunity abundance	Abundance of the jth species across all sites.		Mean = 20.11 individuals (range: 2; 124)
Regional abundance	Metacommunity abundance – Local abundance		Mean = 19.68 individuals (range: 1; 124)

Table 2. Results from binomial GLMM on the presence of solitary bee species within power line clearings in southeast Norway (See text and Supplementary methods for details).

GLMM species occurring in > 1 site	β	s.e.	z	p
Intercept	-2.283	0.129	-17.71	<0.001
Forb species richness	0.465	0.097	4.82	<0.001
Ericaceae affiliated	0.071	0.294	0.24	0.809
Distance to source habitat	-0.275	0.102	-2.70	0.007
Elevation	-0.460	0.119	-3.88	<0.001
Regional abundance	0.723	0.074	9.75	<0.001
Forb species richness × Ericaceae affiliated	-0.703	0.186	-3.78	<0.001
Elevation × Regional abundance	0.098	0.046	2.14	0.033
Random effects	σ	s.d.	obs.	groups
Site identity (intercept)	0.264	0.514	1978	46
Species identity (intercept)	0.091	0.301		43
GLMM on species occurring in 1 site	β	s.e.	z	p
Intercept	-4.550	0.578	-7.86	<0.001
Elevation	-1.292	0.435	-2.97	0.003
Random effects	σ	s.d.	obs.	groups
Site identity (intercept)	0.224	0.474	664	46

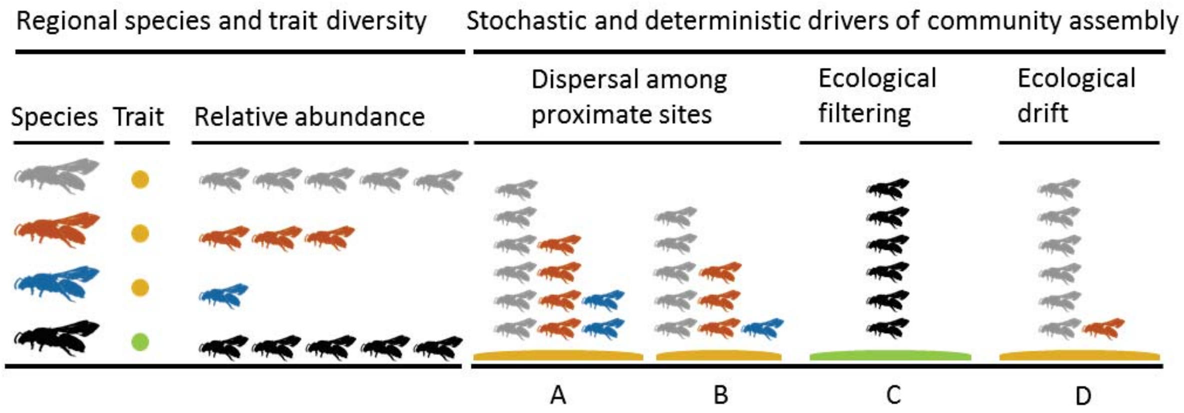


Figure 1. The hypothesis of how stochastic and deterministic processes drive community assembly within habitats (A-D). Species within the regional species pool are characterized by traits that define their habitat affiliation as well as their relative abundance compared to other species. Dispersal connects proximate communities in areas of similar habitat conditions. The absolute abundance of individuals may differ between sites due to differences in habitat size (A>B) but the relative abundance of species remains the same. Ecological filtering only allow the subset of species that possess the traits required by the environment to establish in sites (C). If habitats are isolated (D), ecological drift will eventually lead to the mono-dominance of the regionally most common species.

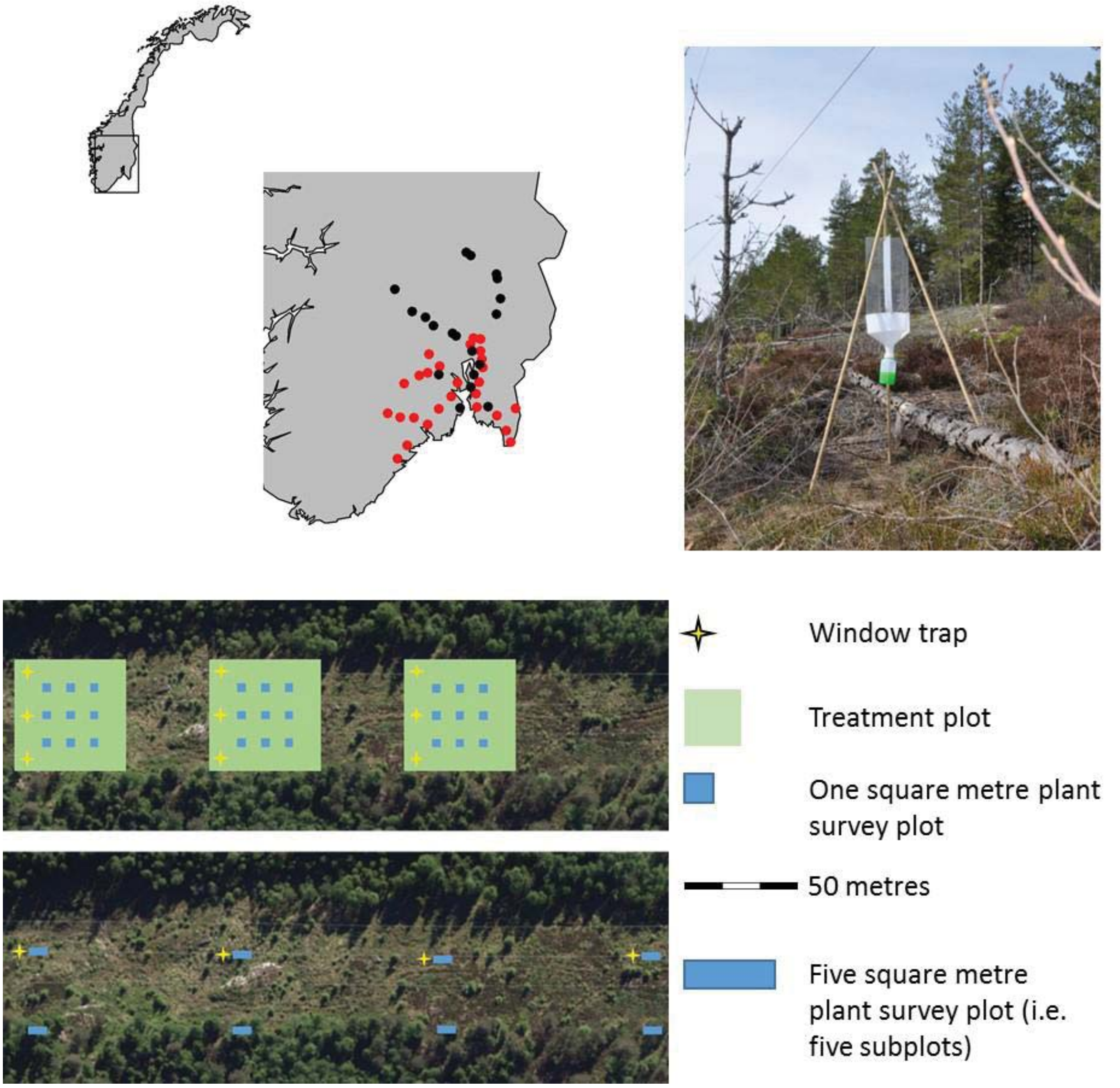


Figure 2. Map of study area marking the location of the 27 sites from ‘Dataset 1’ (red circles). 9, 8 and 10 sites were sampled in 2009, 2010 and 2013, respectively. The 19 sites from ‘Dataset 2’ (black circles) were sampled in 2013. Bees were sampled using window traps with four and nine traps installed in sites from ‘Dataset 1’ and ‘Dataset 2’, respectively (Supplementary methods).

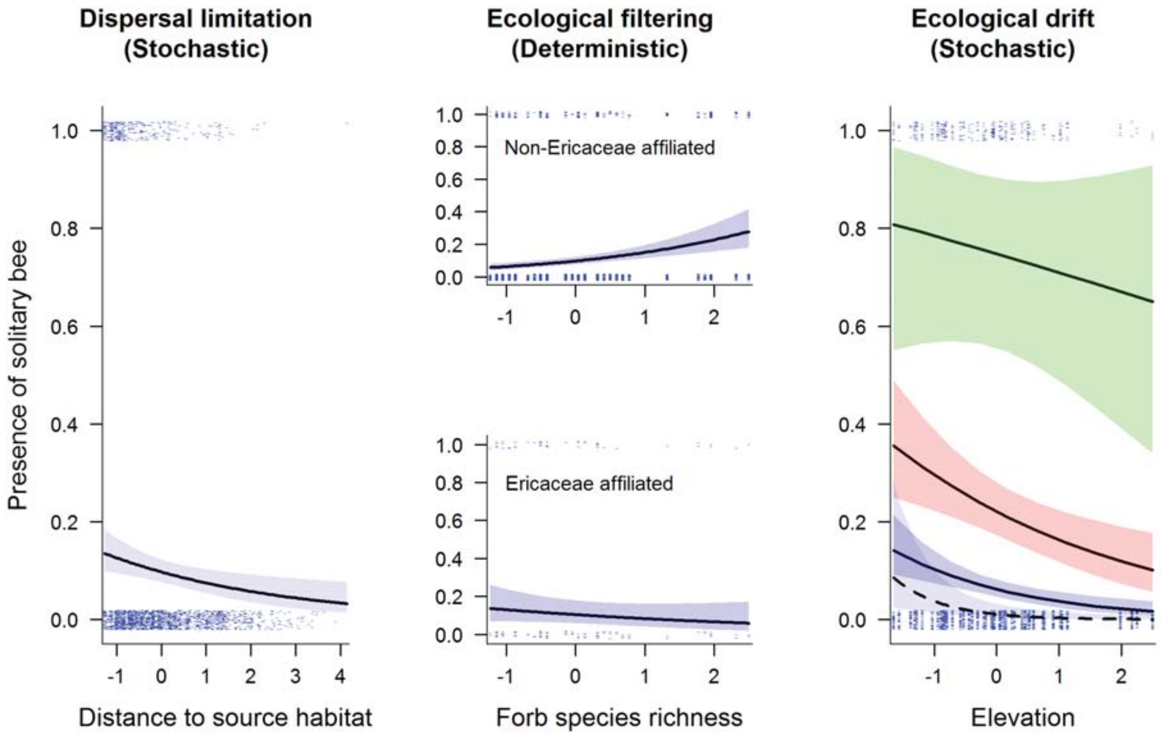


Figure 3. Binomial GLMM on the presence of solitary bee species in 46 power line clearings as a function of the *Distance to source habitat*, *Ericaceae affiliation* × *Forb species richness* and *Regional abundance* × *Elevation*. The influence of the interaction *Regional abundance* × *Elevation* is plotted at three difference levels of *Regional abundance* (lowest = blue, intermediate = pink, highest = green). The presence of single-site inhabitant decreased with elevation (dashed line). Polygons show 95% CI's.

Supplementary material for paper V

This document describes the characteristics of the datasets used in the analyses, the backward elimination procedure used to generate the final model presented in the main text (Fig. 3, Table 2) and the additional analysis on single-site occupants.

Data collection

Dataset 1 consisted of nine sites sampled in 2009, eight in 2010 and ten in 2013. Dataset 2 consisted of 19 sites sampled in 2013. Plant surveys were conducted within 1-m^2 subplots within each site (Fig. 2). We visually estimated the total cover of all vascular plant species found within subplots and calculated the species richness of forbs for each site. The elevation of each site was determined from Ar5 digital maps (http://www. skogoglandskap.no/temaer/ar5).

Community data frame:

A total of 46 sites and 58 bee species were sampled (Table S1). The majority of species occurred with less than 20 individuals in the metacommunity and occupied fewer than 10 sites, the majority of sites had fewer than 25 individuals and 10 species present (Fig. S1).

Functional trait data frame:

The functional traits data frame contained the mean intertegular distance (ITD) and foraging range of each bee species as well as the nesting biology as a categorical variable. The foraging range was estimated from the equation; foraging range = $10^{-1.363+ 3.366\times\log10(ITD)}$ (Greenleaf et al. 2007). The distribution of foraging ranges was skewed and only *Megachile nigriventris* was expected to be able to forage at distances greater than four kilometres from the nest (Table S1). There was also a slightly larger number of below ground nesting bees but both nest trait groups contained ≥ 22 species. There was no significant difference in the estimated foraging ranges between below ground nesting bees and above ground nesting bees (Two-sample t-test; d.f. = 28.7, t = 0.83, p = 0.413). Three species were Ericaceae specialists and accounted for as much as 17% of the 901 individuals sampled (Fig. S2). We focused on the Ericaceae affiliated and non-Ericaceae affiliated species, including other oligolectics, since species within these two groups have been shown to have different habitat preferences (Hanula et al. 2015). In particular, the proportion of Ericaceae affiliated species has been shown to increase with the dominance of Ericaceous shrubs (Sydenham et al. 2015).

Environmental data frame:

The environmental data frame contained the numerical variables *Forb species richness* and *Elevation* and the categorical variable *Study design* with two levels (Dataset 1 vs. Dataset 2). We used a Spearman's rank correlation to test for correlations between *Elevation* and *Forb species richnes*s. The variables were not correlated when both datasets were combined (rho = 0.03, p = 0.84) or when the relationship was tested individually for Dataset 1 (rho = 0.15, p = 0.46) and Dataset 2 (rho = -0.23, p = 0.35). We used the function sm.density.compare in the 'sm' library (Brownman and Azzalini 2014) in R to apply a bootstrap test with 1000 samples to test if the density distributions of *Elevation* and *Forb species richness* were similar for both datasets. The density distribution of *Elevation* did not differ between the two datasets (p = 0.46). However, the density distributions of *Forb species richness* were not equal between the two datasets (p = 0.02) and there was a higher proportion of sites with more than 10 species of Forbs in Dataset 2 than in Dataset 1 (Fig. S3).

The differences in the density distributions of *Forb species richness* could be due to the sites in Dataset 2 actually having a richer flora than sites in Dataset 1, in which case the two datasets would complement each other by extending the gradient in floral diversity. However, the plant survey protocol differed between the two datasets (Fig. 2). Dataset 1 had 20 1-m^2 plant plots placed along the centre of the power line clearing, and a parallel set of 20 plant plots situated along the edge. In contrast, Dataset 2 had 27 plant survey plots located in the centre of the power line clearing, arranged in a regular grid. This could have increased the detection rate of Forbs in Dataset 2 compared to Dataset 1 since the diversity of plants is higher in the centre compared to in the edge (Eldegard et al. 2015). This potential bias in the estimation of the resource diversity within clearings could influence the relationship between the estimated probability of species occurring in a site and the forb species richness within the site. We accounted for this in the statistical analyses (see below).

Spatial data frame:

The spatial data frame contained the geographic coordinates for each site (WGS84 UTM32). This was used to calculate the geographic distance among all sites (Fig. S4, min = 5.5 km, mean 98 km. max = 277.6 km).

Statistical analyses

We combined the four data frames into a single data frame that was used for the analyses (Table 1). The data frame contained all possible species-by-site combinations and the presence or absence of each species within each site. It also contained the trait information for each species as well as the environmental information for each site. We combined the geographic distances among sites with the presence of each species in sites to calculate the distance from each site to the nearest site in which the focal species had been sampled. We assumed that a species being present in a site indicated that the habitat requirements for that species were met within foraging range of that particular site. The distance between the focal site and the nearest site hosting the focal species was used as a proxy for the distances from a site to the nearest source population of each species. Species were present within sites distanced within the entire spatial extent of the study (Fig. S5) showing that suitable habitats for bees were not situated in remotely distanced clusters of sites. Importantly the density distributions of '*Distance to source habitat*' from sites in which the focal species was both present and absent overlapped. Our study area thereby included sites with suitable and unsuitable habitat conditions at a variety of geographic distances (Fig. S5).

The final variable in the data frame was the total number of individuals of each species found in the metacommunity, outside the focal site, and was calculated as the total number of individuals observed for each species minus the number of that species found within the focal site.

We used binomial generalized linear mixed effect models in the lme4 (Bates et al. 2015) library in R (R development core team 2014) to build a full model allowing us to test the influence of migration limitation, ecological filtering and ecological drift on the average probability of a species occurring in a site. We included the interaction term *Distance to source habitat* × *Foraging range* since the foraging range of bees varied among the species sampled (Fig. S2) and we expected that this could also influence their migration ability and hence the distance decay rate in the probability of occurrence. We also included the interaction term *Distance to source habitat* × *Nesting behaviour* to test if the nesting resources sought by bees made them more migration limited. This was done since the study area was dominated by forests, with dead wood (standing dead trees, stumps, snags and logs) accumulating along the edges of the power line clearings. Dead wood may therefore be more widely distributed within the study area than deep and sandy soils, which are restricted to river and marine sediments. Bees that nest below ground may therefore experience a more aggregated distribution of nest sites than above ground nesting bees, which nest in dead wood or in cavities found above ground.

We included the interaction term *Forb species richness* × *Ericaceae specialist* where *Ericaceae specialists* was a categorical variable with two levels (i.e. Ericaceae specialist vs. non-Ericaceous affiliated). This allowed us to test if changes in the probability of occurrence with *Forb species richness* depended on whether or not the species was affiliated with Ericaceous shrubs and thereby if *Forb species richness* acted as an ecological filter.

The interaction term *Elevation* × *Regional abundance* was included to test if the influence of Ecological drift increased with *Elevation*, since species richness and abundance decreases with elevation, and since species found at high elevations tend to have broader distributional ranges (Hoiss et al. 2012) which may be caused by elevation acting as an ecological filter. However, since the species, functional and phylogenetic composition in bee species assemblages is usually less predictable at high latitudes (which correlates with elevation) (Sydenham et al. 2015), it may also be a sampling effect if the probability of observing regionally rare species decreases as less individuals are present. The latter would be a neutral process with an end result equivalent of that of ecological drift (Hubbel 2001, Rosindell et al. 2011).

We included the categorical variables *Species identity*, *Site identity*, *study design* and *Sampling year* as random intercepts to account for variations in the mean probability of occurrence within each of these random effects. We also included the interaction term *Forb species richness* × *Ericaceae specialist* as a random slope for *Study design* to account for the differences in *Forb species richness* distributions between study designs. This allowed us to account for differences between study designs in the relationships between the *Forb species richness* × *Ericaceae specialist* interaction and the average probability of a species occurring within a site. We removed 14 species that only occurred within a single site from the dataset, leaving 44 species for the analyses. This was done since including these species produced missing values for the *Distance to source habitat* when the focal site was the one site they occurred in. Their inclusion would thereby produce a missing value in the GLMM for the only site they occurred in, and inflated the number of absences in the analysis. Following Zuur et al. (2009) the full model was specified as:

$\text{Presence of bee species}_i \sim B(1, \pi_i)$

$E(Y_i) = \pi_i$ and $var(Y_i) = \pi_i \times (1 - \pi_i)$

$link = cloglog$

$$link(\pi_i) = \beta_{distance\ to\ source\ habitat} + \beta_{Ericaceae\ specialist} + \beta_{forb\ species\ richness} + \beta_{Home\ range} + \beta_{Ericaceae\ specialist \times Forb\ species\ richness} + \beta_{Foraging\ range \times Distance\ to\ source\ habitat} + \beta_{Nesting\ behaviour \times Distance\ to\ source\ habitat} + \beta_{Regional\ abundance \times Elevation} + \text{random intercept}_{Study\ design} + \text{random intercept}_{Site\ identity} + \text{random intercept}_{Species\ identity} + \text{random intercept}_{Sampling\ year} + \text{random slope}_{Ericaceae\ specialist + Forb\ species\ richness + Ericaceae\ specialist \times Forb\ species\ richness\ \ by\ Study\ design}$$

We simplified the model by first dropping random effects that did not account for a significant amount of variation by comparing the Bayesian Information Criterion (BIC) between the full model and the simplified model. We continued with the simplification of random effect terms until the BIC increased following the removal of a random effect (i.e. the full model provided a better fit to the data that the simplified model). We then used likelihood ratio tests and subjected the resulting model to backward elimination of fixed effects terms until all variables were significant ($p \leq 0.05$).

The random intercept *Sampling year* accounted for <0.001 of the variance and removing this variable reduced the BIC value ($\Delta BIC = -7.61$, $BIC_{complex\ model} \sim 1569$, $BIC_{reduced\ model} \sim 1561$) and *Sampling year* was dropped from the model. The variance accounted for by the random slope *Forb species richness* × *Ericaceae specialists* was <0.001. Reducing the interaction term to its main effect terms reduced the BIC value ($\Delta BIC = -30.46$, $BIC_{complex\ model} \sim 1561$, $BIC_{reduced\ model} \sim 1531$) and it was dropped from the model. At the next step we removed the random slope

Forb species richness since it only accounted for 0.001 of the variance and excluding this random effect reduced the BIC value (ΔBIC = -22.78, $\text{BIC}_{\text{complex model}}$ ~ 1531, $\text{BIC}_{\text{reduced model}}$ ~ 1508). At the next step we removed the random intercept term *Study design* as it only accounted for 0.001 of the variance and its removal did not increase the BIC value (ΔBIC = -0.002). We then removed the random slope term *Ericaceae specialist* as the variance accounted for by the differences in slopes between study designs was only 0.002 for Non-Ericaceae affiliated species and 0.010 for Ericaceae specialists and its removal reduced the BIC value (ΔBIC = -22.82, $\text{BIC}_{\text{complex model}}$ ~ 1508, $\text{BIC}_{\text{reduced model}}$ ~ 1485). The fact that all random effect terms, both intercepts and slopes, associated with study design were dropped from the model suggests that the differences in study designs did not influence the variance structure in model. We then removed the random intercept term *Species identity* as this accounted for 0.12 of the variance, compared to the 0.25 accounted for by the random intercept *Site identity*. However, removing *Species identity* increased the BIC value by 2.39 and it was therefore included in the model.

The LRT test showed that all variables contributed to explaining the presence of species within local communities (Table S2). However, the estimated influence of *Distance to source habitat* × *Foraging range* was biased due to the unequal density distribution of foraging ranges and specifically the presence of *Megachile nigriventris* with an estimated foraging range of 5.69 kilometres and occurrences within three sites separated by 127, 149.5 and 163 kilometres. We corrected for this bias in two ways.

We first ran the same model but excluded *M. nigriventris* from the analyses and rescaled the variables to zero means, which reduced the influence of *Distance to source habitat* × *Foraging range* (d.f. = 1, LRT = 0.04, p = 0.849). We therefore first excluded the interaction term from the model and thereafter the non-significant fixed effect term *Foraging range* (d.f. = 1, LRT = 0.14, p = 0.71). The interaction term *Distance to source habitat* × *Nesting behaviour* was not significant (d.f. = 1, LRT = 3.09, p = 0.079) and was dropped from the model followed by the exclusion of *Nesting behaviour* (d.f. = 1, LRT = 0.01, p = 0.99). The final model when *M. nigriventris* was excluded from the dataset therefore included the main effect term *Distance to source habitat* and the interaction terms *Forb species richness* × *Ericaceae specialist* and *Elevation* × *Regional abundance* (Table S2).

As an alternative approach, we included *M. nigriventris* in the analysis, but corrected for biased estimates of the influence of *Distance to source habitat* × *Foraging range*by transforming the *Foraging range* variable. The density distribution was skewed towards short home ranges (25th quantile = 152 metres, 50th quantile = 514 metres, 75th quantile = 1,093 metres). We therefore assigned all foraging ranges larger than the third quantile the same value (1,093 metres) so that all species with foraging ranges larger than one kilometre were treated equally. This transformed variable was called *Density corrected Foraging range*. We rescaled all numerical variables to zero means and reran the final model from the analyses on the untransformed data (where *M. nigriventris* had been included), but this time using the transformed foraging range variable. The interaction term *Distance to source habitat* × *Density corrected Foraging range* was not significant (d.f. = 1, LRT = 3.11, p = 0.078) and was dropped from the model followed by dropping of the main effect term *Density corrected Foraging range* (d.f. = 1, LRT = 0.86, p = 0.354). The final model included the interaction terms *Forb species richness* × *Ericaceae specialist*, *Distance to source habitat* × *Nesting behaviour* and *Elevation* × *Regional abundance* (Table S1). *M. nigriventris* was an influential outlier whose presence in the analyses led to the inclusion of the *Distance to source habitat* × *Foraging range* interaction term in the original model, and the *Distance to source habitat* × *Nesting behaviour* in the *Foraging range* density corrected model (Table S2). We therefore present the results from the model where *M. nigriventris* was excluded from the analyses, as this was the most parsimonious model.

The 14 species that were single site occupants (Table S1) and therefore removed from the analyses were all mainly lowland species (except from *O. inermis*). We therefore ran an additional analysis to test if the probability of observing these species decreased with *Elevation*. We fitted the presence of the species using a binomial GLMM with a cloglog link function. The centred *Elevation* was included as a fixed effect and *Site identity* as a random effect. *Species identity* was excluded as a random effect as this improved model fit ($\Delta \text{BIC} = -6.47$, $\text{BIC}_{\text{complex model}} \sim 147$, $\text{BIC}_{\text{reduced model}} \sim 141$). The estimated probability of observing single site occupants decreased from 9% to *c.* 0% with *Elevation* (df = 1, LRT = 9.63, p 0.002) following the same pattern as species with a low regional abundance in general (Fig. 3, Table 2).

Literature cited

Amiet, F., Müller, A. and Neumeyer, R. 1999. Fauna Helvetica 4. Apidae 2: Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha, Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., Herrmann, M., Müller, A. and Neumeyer, R. 2001. Fauna Helvetica 6. Apidae 3: Halictus, Lasioglossum, Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F., Herrmann, M., Müller, A. and Neumeyer, R. 2004. Fauna Helvetica 9. Apidae 4: Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis, Centre Suisse de Cartographie de la Faune (CSCF).

Amiet, F. 2007. Fauna Helvetica 20. Apidae 5: Ammobates, Ammobatoides, Anthophora, Blastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa, Centre Suisse de Cartographie de la Faune (CSCF).

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. lme4: Linear mixed-effect models using Eigen and S4. R package version 1.1-8, http://CRAN.R-project.org/package=lme4.

Bowman, A. W. and Azzalini, A. 2014. R package ‘sm’: nonparametric smoothing methods (Version 2.2-5.4). R package version 2.2-5.4, http://CRAN.R-project.org/package=sm.

Eldegard, K., Totland, Ø. and Moe, S.R. 2015 Edge effects on plant communities along power line clearings. Journal of Applied Ecolology. **52**: 871-880.

Greenleaf, S. S., Williams, N. M., Winfree, R. and Kremen, C. 2007. Bee foraging ranges and their relationship to body size. Oecologia **153**: 589-596.

Hanula, J. L., Horn, S. and O’Brien, J. J. 2015. Have changing forests conditions contributed topollinator decline in the southeastern United States? Forest Ecology and Management **348**: 142-152.

Hoiss, B., Krauss, J., Potts, S. G., Roberts, S. and Steffan-Dewenter, I. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. P Roy Soc B-Biol Sci **279**: 4447-4456.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography, Princeton University Press.

R development core team. 2014. R: A Language and Environment for Statistical Computing. Version: 3.1.0. Vienna, Austria, R Foundation for Statistical Computing.

Rosindell, J., Hubbell, S. P. and Etienne, R. S. 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in ecology & evolution **26**: 340-348.

Schmid-Egger, C. and Scheuchl, E. 1997. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band 3: Schlüssel der Arten der Familie Andrenidae. (Velden, Germany: Eigenverlag.

Sydenham, M. A. K., Moe, S. R., Totland, Ø. and Eldegard, K. 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? Ecography **38**: 140-153.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R, Springer Science & Business Media.

Table S1. List of species sampled in 46 power line clearings in south-eastern Norway. For each species, the table shows the number of sites that the species occurred in (Presences), the total abundance, i.e. number of individuals in the metacommunity, and the species' functional traits. ITD = mean intertegular distance (body size). Species marked in bold were excluded from the analyses as they only occurred within a single site. Specimens were identified using regional identification keys (Schmid-Egger and Scheuchl 1997, Amiet et al. 1999-2004, Amiet 2007) and voucher specimens are stored in the entomology collection at the Norwegian University of Life Sciences', Department of Ecology and Natural Resource Management.

Species	Presences	Total abundance	Ericaceae affiliation	Nesting behaviour	ITD
Andrena bicolor	2	2	None	Below ground	2.05
Andrena carantonica	3	4	None	Below ground	2.76
Andrena cineraria	3	18	None	Below ground	2.78
Andrena clarkella	17	40	None	Below ground	3.17
Andrena denticulata	2	2	None	Below ground	2.13
Andrena fucata	19	36	None	Below ground	2.28
Andrena fulvida	6	13	None	Below ground	2.24
Andrena fuscipes	9	27	Oligolectic	Below ground	2.03
Andrena haemorrhoa	7	16	None	Below ground	2.58
Andrena helvola	5	7	None	Below ground	2.17
Andrena intermedia	**1**	**1**	**None**	**Below ground**	**1.83**
Andrena lapponica	36	124	Oligolectic	Below ground	2.58
Andrena nigriceps	**1**	**2**	**None**	**Below ground**	**2.54**
Andrena ruficrus	3	4	None	Below ground	1.96
Andrena subopaca	20	102	None	Below ground	1.48
Andrena tibialis	**1**	**1**	**None**	**Below ground**	**2.93**
Andrena vaga	2	6	None	Below ground	2.85
Andrena wilkella	**1**	**1**	**None**	**Below ground**	**2.16**
Colletes cunicularius	3	3	None	Below ground	3.63

Colletes daviesanus	2	2	None	Below ground	2.46
Colletes succinctus	3	5	Oligolectic	Below ground	2.95
Hylaeus angustatus	7	9	None	Above ground	1.06
Hylaeus annulatus	14	29	None	Above ground	1.47
Hylaeus brevicornis	2	2	None	Above ground	1.02
Hylaeus communis	14	30	None	Above ground	1.7
Hylaeus confusus	34	119	None	Above ground	1.36
Hylaeus hyalinatus	3	7	None	Above ground	1.33
Hylaeus incongruus	2	3	None	Above ground	1.43
Hylaeus rinki	5	5	None	Above ground	1.15
Dufourea dentiventris	**1**	**1**	**None**	**Below ground**	**1.55**
Halictus rubicundus	10	17	None	Below ground	2.1
Halictus tumulorum	2	3	None	Below ground	1.46
Lasioglossum albipes	6	20	None	Below ground	1.63
Lasioglossum calceatum	7	27	None	Below ground	1.8
Lasioglossum fratellum	24	65	None	Below ground	1.43
Lasioglossum fulvicorne	2	4	None	Below ground	1.32
Lasioglossum leucopus	12	44	None	Below ground	1.12
Lasioglossum morio	4	7	None	Below ground	1.01
Lasioglossum punctatissimum	**1**	**1**	**None**	**Below ground**	**1.3**
Lasioglossum rufitarse	6	32	None	Below ground	1.37
Anthidium punctatum	**1**	**1**	**None**	**Above ground**	**2.71**
Chelostoma campanularum	**1**	**2**	**None**	**Above ground**	**0.93**
Chelostoma florisomne	6	16	None	Above ground	1.75
Hoplitis claviventris	**1**	**1**	**None**	**Below ground**	**1.95**
Hoplitis tuberculata	2	2	None	Above ground	2.24
Megachile circumcincta	**1**	**1**	**None**	**Below ground**	**3.35**
Megachile nigriventris	3	3	None	Above ground	4.26

Megachile versicolor	2	2	None	Above ground	3.06
Megachile willughbiella	**1**	**1**	**None**	**Above ground**	**3.6**
Osmia bicornis	2	2	None	Above ground	3.1
Osmia caerulescens	2	2	None	Above ground	2.48
Osmia inermis	**1**	**1**	**None**	**Above ground**	**3.12**
Osmia leaiana	2	3	None	Above ground	2.69
Osmia nigriventris	9	12	None	Above ground	3.31
Osmia parietina	5	5	None	Above ground	2.14
Osmia uncinata	4	4	None	Above ground	2.07
Macropis europaea	**1**	**1**	**None**	**Below ground**	**2.52**
Melitta haemorrhoidalis	**1**	**1**	**None**	**Below ground**	**2.74**

Table S2. Likelihood Ratio Test statistics from binomial GLMMs on the presence of solitary bee species within power line clearings, with *Megachile nigriventris* included in the analyses, and when excluded from the analyses to account for biases in the estimated influence of the interaction term '*Distance to source habitat × Foraging range*'.

	d.f.	LRT	p-value
M. nigriventris included in the analyses			
Ericaceae specialist × Forb species richness	1	15.5	<0.001
Distance to source habitat × Foraging range	1	6.4	0.011
Distance to source habitat × Nesting behaviour	1	5.2	0.022
Elevation × Regional abundance	1	4.5	0.034
M. nigriventris excluded from the analyses			
Distance to source habitat	1	7.49	0.006
Forb species richness × Ericaceae specialist	1	16.09	<0.001
Elevation × Regional abundance	1	4.60	0.032
M. nigriventris included in the analyses (Foraging range density corrected)			
Ericaceae specialist × Forb species richness	1	15.86	<0.001
Distance to source habitat × Nesting behaviour	1	5.5	0.019
Elevation × Regional abundance	1	4.2	0.040

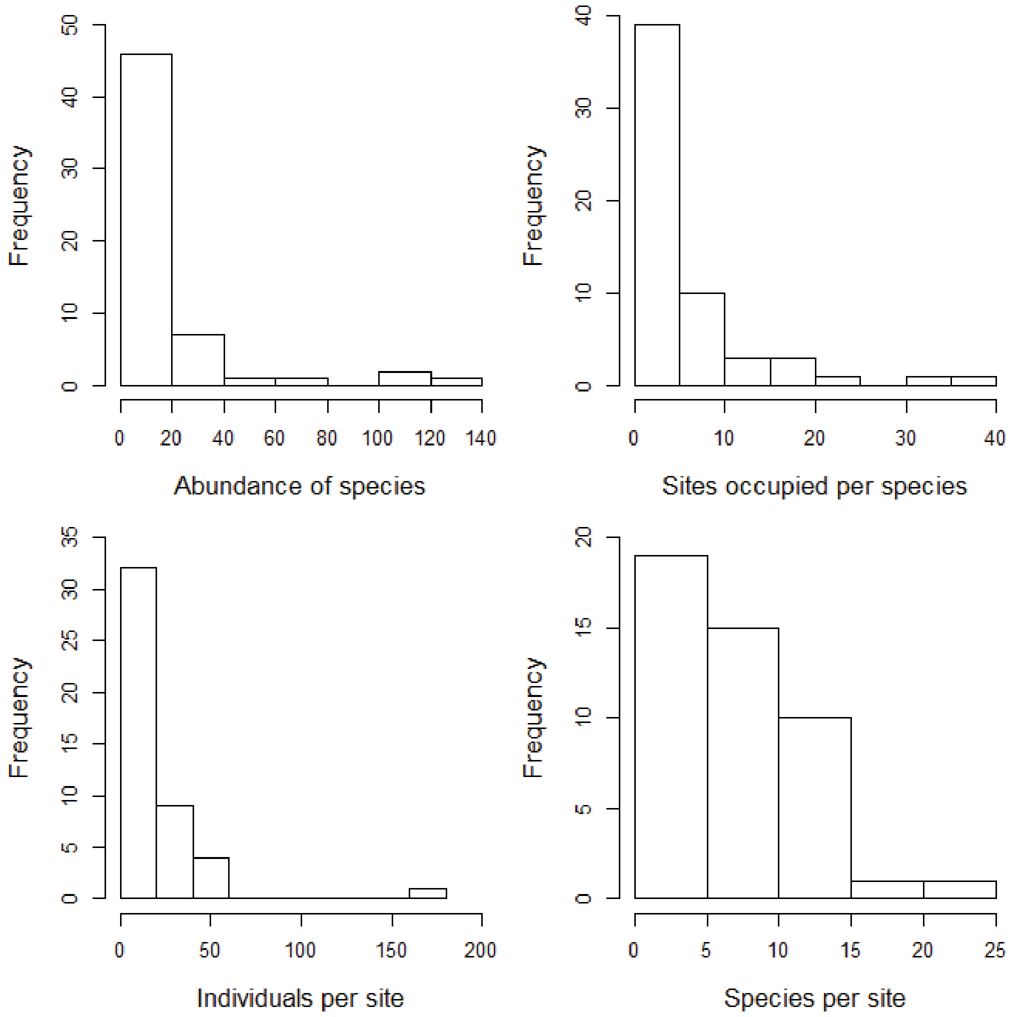


Figure S1. The distribution of abundances, the number of sites occupied by species and the number of individuals and species sampled per site.

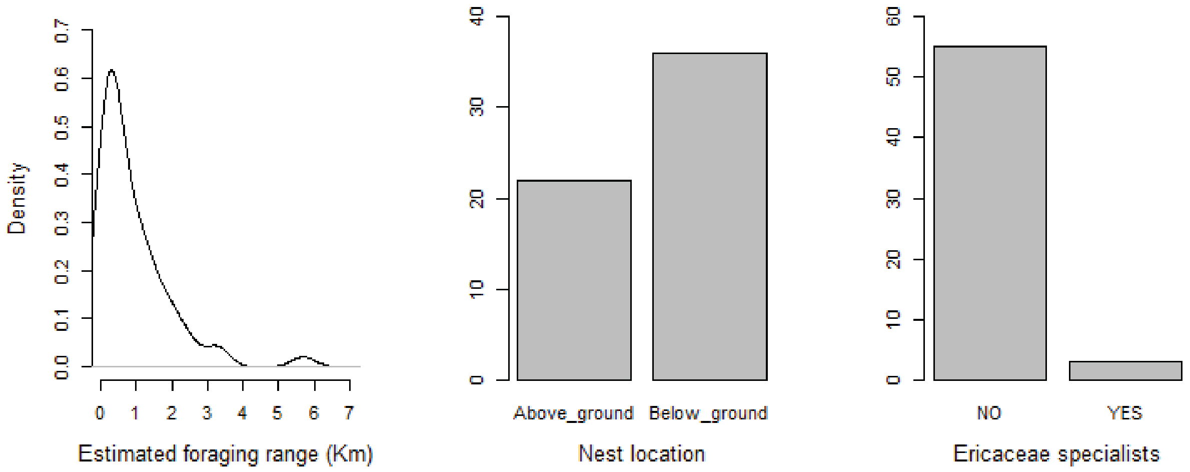


Figure S2. The distribution of functional traits among the 58 species of solitary bees sampled in 46 power line clearings in southeast Norway (Fig. 2). The foraging range was estimated from the body size of bees and used as a proxy for dispersal capability in the analyses.

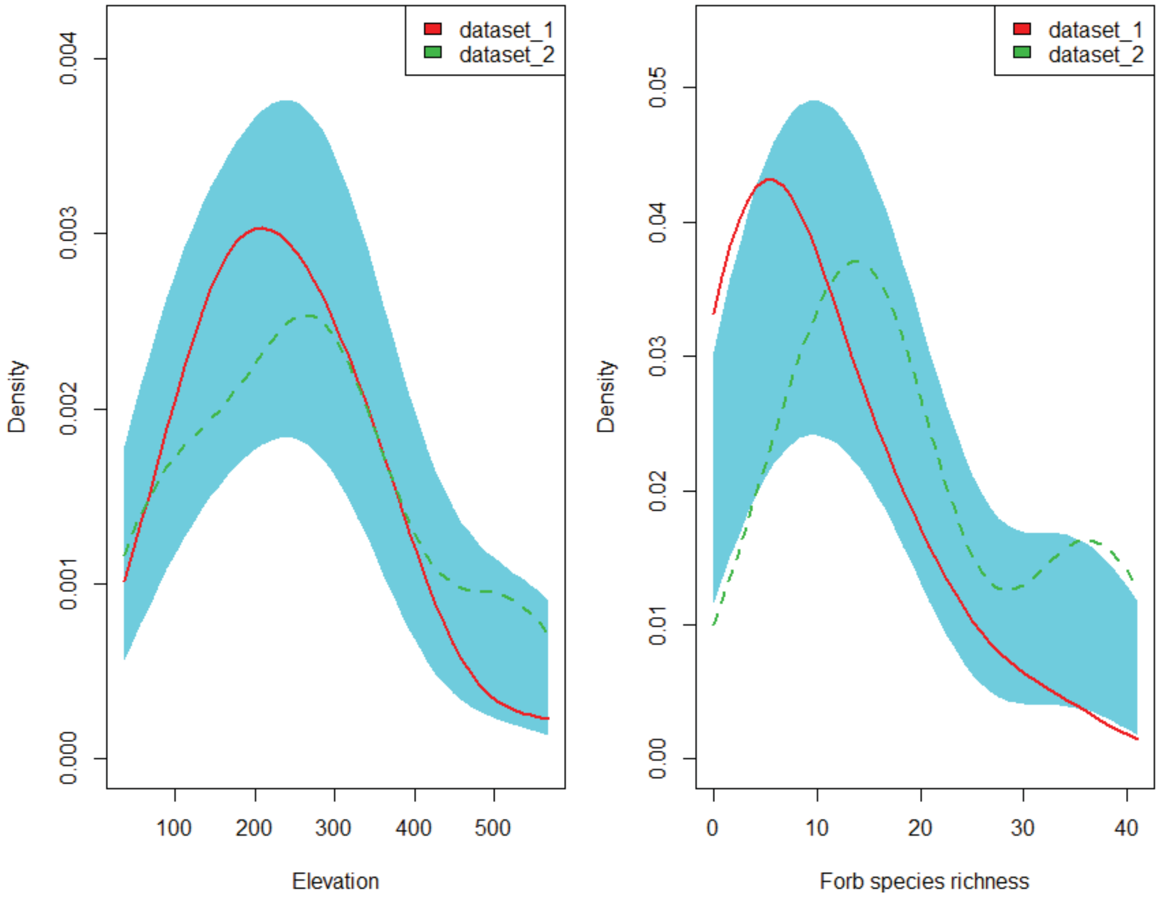


Figure S3. The density distributions of *Elevation* and *Forb species richness* within each of the two datasets. The blue bands mark the lower and upper bounds from the boot strapped reference distribution.

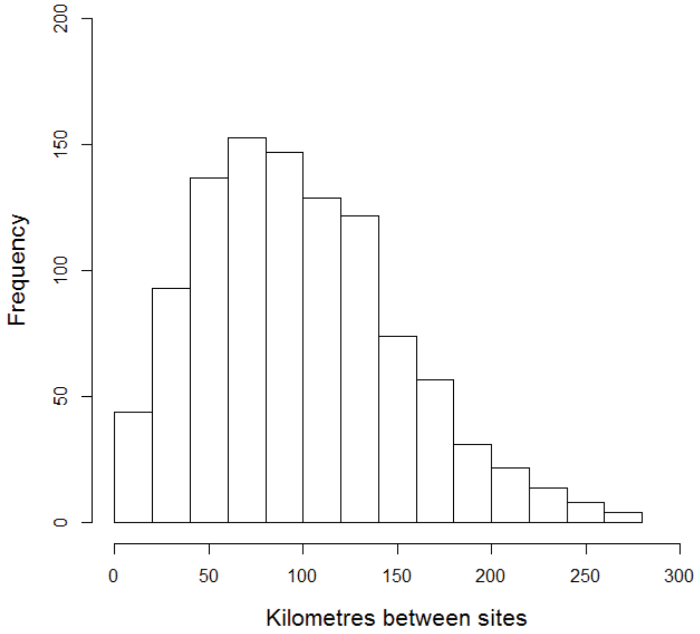


Figure S4. The distribution of geographic distances between the 46 sites included in this study (Fig. 2).

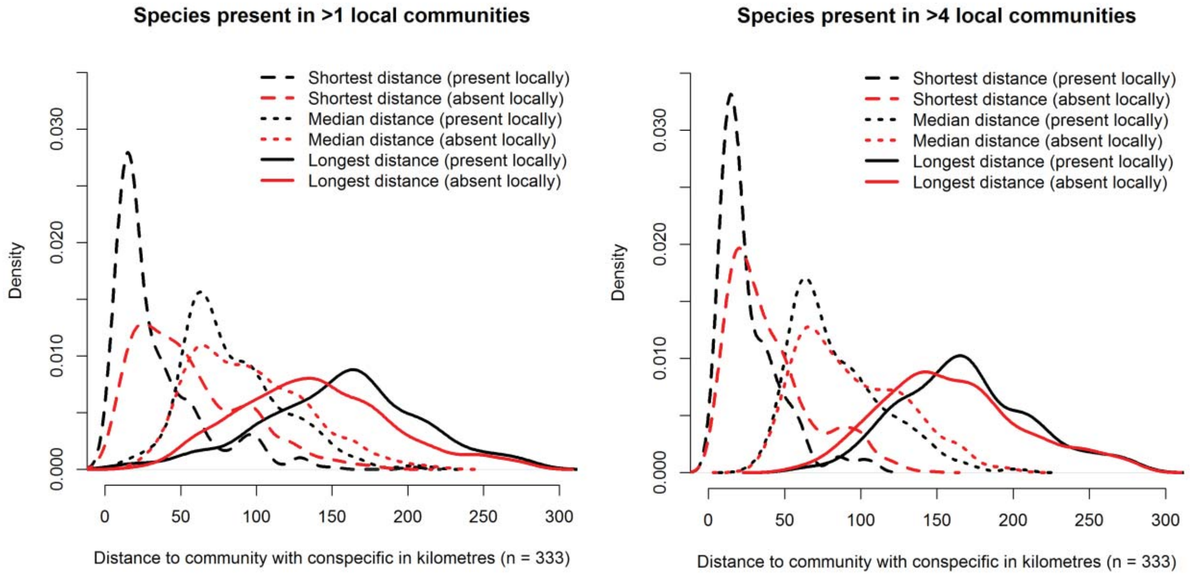


Figure S5. The density distributions of the distances from local sites to sites where the focal species was found (i.e. source habitats). Distances are calculated from sites where the focal species was either present or absent as well as for the shortest, median and longest distances between source habitats. Density distributions were calculated when all species that occurred in >1 site were included and when species occurring in <5 sites were excluded.

ISBN: 978-82-575-1352-8
ISSN: 1894-6402

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no