ECOSPHERE

Disentangling the contributions of dispersal limitation, ecological drift, and ecological filtering to wild bee community assembly

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Abstract.   The species composition within communities is highly dependent on the rate of species immigration and whether immigrating species possess the functional traits required by the prevailing environmental conditions. Once established, random fluctuations in birth and death rates may reduce the diversity of ecologically equivalent species if local populations are not replenished by immigrating individuals. Consequently, three key processes drive community assembly: dispersal limitation, ecological filtering, and ecological drift. However, disentangling the relative contribution of these processes remains a challenge in community ecology. We used a binomial generalized linear mixed model to test whether the occurrences of solitary bees within 46 communities in southeast Norway were driven by (1) dispersal limitation, that is, the geographic distance to the nearest site where conspecifics occurred; (2) ecological filtering, that is, if forb species richness selected for non-Ericaceae-affiliated species; and (3) ecological drift, that is, if small, isolated communities were dominated by regionally common species. The regression slopes from the model for each potential driver of community composition were compared with those expected under a null model, in which species were treated as ecologically equivalent. Both dispersal limitation and ecological filtering influenced the probability of species occurring within communities. The occurrence of species decreased with elevation, and this relationship depended on the relative commonness of species and their floral preferences. For non-Ericaceae-affiliated species, the patterns of occurrence mirrored that expected under the null (neutral) model, resulting in the same patterns as would be expected under ecological drift. In contrast, the response of Ericaceae-affiliated species differed from what would be expected from the null model. Our results also indicate that processes leading to neutral dynamics in species compositions drive a large part of the gradient in species richness in Norwegian bee communities. These processes seem related to sampling effects so that large and interconnected communities have a higher probability of including regionally rare species than small, isolated communities. Our results suggest that targeting habitats—where the influence of ecological filtering is expected to be greater than that of neutral dynamics—can increase the success of habitat management plans aimed at promoting rare species.

Key words: bees; community assembly; deterministic processes; dispersal; ecological drift; ecological filtering; functional traits; stochastic processes.

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INTRODUCTION

Faced with current declines in species diversity (Dirzo et al. 2014), designing and implementing habitat management plans is required to conserve species-rich communities. Manipulating environmental conditions may promote rare species by alleviating the influence of ecological filters that select for, or against, organisms based on their functional response traits (Keddy 1992). Functional response traits and community assembly theory can help guide conservation planning by providing predictable outcomes of habitat restoration schemes (Laughlin 2014). However, local communities exist in a regional meta-community (Leibold et al. 2004) connected by dispersal of individuals (Ricklefs 2008). Within the meta-community, the immigration rate of species, stochastic processes—ecological drift (Hubbell 2001)—and the deterministic processes of ecological filtering act together to determine the outcome of community assembly (Vellend 2010). Meta-communities are themselves shaped by biogeographic processes related to speciation and historical migration and regional extinction events (Cornell and Harrison 2014) that can influence the relative commonness of species within the region and thereby the susceptibility of species to ecological drift (Vellend 2010). Identifying the relative influence of ecological filtering, dispersal limitation, and ecological drift on community assembly is therefore useful for the design of habitat management plans and for predicting their success.

Dispersal limitation may be an important determinant of local bee diversity. For instance, the abundance of foraging bees shows a more pronounced decrease with distance from source habitats than the more ephemerally distributed hoverflies (Syrphidae) (Jauker et al. 2009). Dispersal limitation may also explain why the probability of species colonizing restored field margins depends on the amount of source habitats in the surrounding landscape (Scheper et al. 2013). In the original formulation of the neutral theory of biodiversity (Hubbell 2001), dispersal rates are assumed neutral with regard to species identities. However, the fact that foraging ranges and nesting behavior determine the response of bees to habitat isolation (Williams et al. 2010) supports the idea that dispersal rates may be at least partly deterministic (Lowe and McPeek 2014). Tests of the influence of dispersal limitation should therefore account for potential trait-specific (i.e., deterministic) differences in dispersal rates among species.

The process of ecological (species) drift results in changes in the relative frequencies of species within a community owing to random changes in birth and death rates (Hubbell 2001). If communities are completely isolated, neutral theory predicts that ecological drift will lead to the mono-dominance of one species, with the probability of a species obtaining mono-dominance being equal to its relative commonness in the meta-community (Vellend 2010). In contrast, if immigration is unrestricted, communities should theoretically consist of a random sample of individuals from the regional species pool, with the relative abundance of species reflecting that of their regional commonness (Rosindell et al. 2011, Matthews and Whittaker 2014). Thus, high dispersal rates can slow down the process of ecological drift, which may explain why the species evenness within bee communities increases with habitat connectivity (Marini et al. 2014). In addition to dispersal rates, community size (i.e., number of individuals within a habitat) is expected to be negatively related to the magnitude of influence of ecological drift (Vellend 2010). This is because communities are assumed to be saturated with individuals (Alonso et al. 2006), and small communities therefore will contain smaller populations of regionally rare species, compared to large communities. Low abundance of floral resources (Hoiss et al. 2013) and wild bees (Hoiss et al. 2012) is characteristic of high-elevation communities. The influence of ecological drift may therefore increase with elevation. The probability of species occurring in communities should therefore decrease with elevation and the rate of decrease should be greatest for regionally rare species due to a reduction in community size and an increased isolation with elevation.

Since dispersal limitation, ecological filtering, and ecological drift can all influence community assembly, it is important to estimate the importance of each of these processes in the same analyses. However, disentangling their relative influence on community assembly remains a challenge (Logue et al. 2011). The analysis of β-diversity (ratio between γ—regional—and α—local—diversities) indices allows estimation of

the relative roles of dispersal limitation and ecological filtering by comparing changes in functional and species-based β-diversity indices along spatial gradients (Pavoine and Bonsall 2011). However, their interpretation may be challenging since patterns in β-diversity are attributable to different processes across spatial scales (Warren et al. 2014). Their interpretation is further hampered by β-diversity depending on both the local (α) and regional (γ) diversities, albeit this may be corrected for using null models (Chase and Myers 2011). Moreover, analyses of β-diversity indices have been criticized for confounding changes in the mean and the dispersion of β-diversity values along environmental gradients—due to the mean–variance relationships in community data; that is, species with a high mean abundance also tend to display a high variance in abundance (Warton et al. 2012). In addition to purely computational issues, the wide variety of indices available (Barwell et al. 2015) and the way data are standardized (or not) prior to analyses can complicate the comparison of results among studies.

An alternative approach to testing the influence of ecological filtering is to use generalized linear models (GLMs), because GLMs can account 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). The GLMM-based approach takes all species-by-site combinations, thereby allowing for statistical tests of how species-specific functional traits and site-specific environmental conditions influence the probability of species occurring locally. A merit of this approach is its intuitive response variable—probability of occurrence—which is comparable among studies. However, this framework has so far been limited to testing the influence of ecological filtering. Here, we expand on this approach and apply a novel analytical framework allowing the inclusion—and statistical tests—of the influence of dispersal limitation, ecological filtering, and ecological drift on the assembly of wild bee communities.

We here use a model system consisting of 46 wild bee communities sampled in power line clearings in southeast Norway to test whether dispersal limitation, ecological filtering, and

ecological drift influence community assembly. Wild bees are central place foragers with typical foraging ranges around 1–2 km (Greenleaf et al. 2007) and so depend on habitats where nesting and foraging resources are found within close proximity (Matheson et al. 1996) and tend to respond to environmental conditions at spatial scales of a few hundred meters (Steffan-Dewenter et al. 2002). For instance, elevational gradients act as an ecological filter on the diversity of wild bees by selecting for species with broad climatic tolerances (Hoiss et al. 2012), such as many *Bombus* species (Sydenham et al. 2015). In addition to climatic conditions, ecological filters also operate at the resource scale, and floral diversity is known to be an important filter on local bee diversity (Potts et al. 2003). Bees therefore provide excellent model organisms for studies of community assembly.

Understanding the drivers of bee diversity is of high importance due to their roles as wild plant and crop pollinators and because bee diversity is in decline in many parts of the world (Potts et al. 2010). Our study area is dominated by forests intersected with power line clearings, and mixed with patches of agricultural land, and dead wood (standing dead trees, stumps, snags, and logs) which accumulates along the edges of the power line clearings. Potential nest sites for aerial nesting bees in dead wood may therefore be more widely distributed within the study area than deep and sandy soils used by ground-nesting bees, which are restricted to thick moraine and river and marine sediments. Bees that nest below ground may therefore be more dispersal limited than bees that nest in dead wood. In our study system, the floral context ranges from ericaceous shrub-dominated to being dominated by forbs, providing resources for a broader spectrum of non-shrub-affiliated bees (Hanula et al. 2015, Sydenham et al. 2015). The gradient in forb species richness thereby provides a useful test of the influence of ecological filtering on community assembly, because higher forb diversity selects for non-Ericaceae-affiliated species.

We here tested whether the probability of species occurring in communities was related to:

1. Dispersal limitation: The mean probability of species occurring within a community decreases with increasing distance to the

nearest site where conspecifics occur. We expected that foraging ranges and nesting behavior would influence the degree of dispersal limitation experienced by species. We therefore also tested the statistical significance of the interaction terms *Distance to source habitat × Nesting behavior* and *Distance to source habitat × Foraging range*.

2. 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 since it is an important determinant of solitary bee diversity within our study system (Sydenham et al. 2015). We tested for the influence of ecological filters by testing the statistical significance of the interaction term *Forb species richness × Ericaceae affiliation*.

3. Ecological drift: The mean occurrence of a species increases with its relative commonness in the surrounding meta-community and decreases with elevation due to a reduction in community size with elevation. We also included the *Elevation × Relative commonness × Ericaceae affiliation* interaction, because we expected high-elevation sites to host smaller communities and therefore be more prone to ecological drift, and particularly so for species associated with forbs.

4. To show that observed patterns in species distributions are neutral, it is necessary to demonstrate that the observed patterns do not differ from those expected under a neutral null model (Vellend et al. 2014). We therefore tested whether the relationships between the occurrence of solitary bee species and the variables described in I-III differed from those expected if the distribution of bee species were neutral with regard to species traits.

Materials and Methods

Study system

We combined two datasets (Fig. 1) 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," four traps were installed in each site along the center of the power line clearing in each site ($n = 27$). As some traps were lost during the trapping season, we standardized the sampling intensity across sites by randomly removing one trap from the first and fourth sampling period from sites where traps had not been lost. We thereby included bee specimens collected from three traps in sampling periods one and four, and from four traps in sampling periods two and three (Sydenham et al. 2016*a*). The sites ($n = 19$) in "Dataset 2" were sampled during a field experiment with three treatment plots per site and three traps per treatment plot (Sydenham et al. 2016*b*). We conducted plant surveys within 1-m^2 subplots in each site. Subplots in "Dataset 1" were arranged in eight 5-m^2 rectangles placed 50 m 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 floral resource diversity; high values indicate floristically diverse sites, and low values are characteristic of Ericaceous shrub-dominated sites (Sydenham et al. 2015, 2016*b*). We combined site- and species-specific information from both datasets into four separate data frames: the species-by-site data frame; the species-by-trait data frame; the site-by-environmental conditions data frame; and the site-by-geographic coordinates data frame.

The species-by-site data frame consisted of 46 sites and 58 bee species (Appendix S1: Table S1). The majority of species occurred with less than 20 individuals in the meta-community and occupied fewer than 10 sites. The majority of sites had fewer than 25 individuals and 10 species present (Appendix S1: Fig. S1). The species-by-trait data frame contained the mean intertegular distance (ITD), nesting behavior (above- vs. below-ground), and Ericaceous affiliation (specialists vs. non-specialists) for all species. Information on traits was 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. The maximum 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
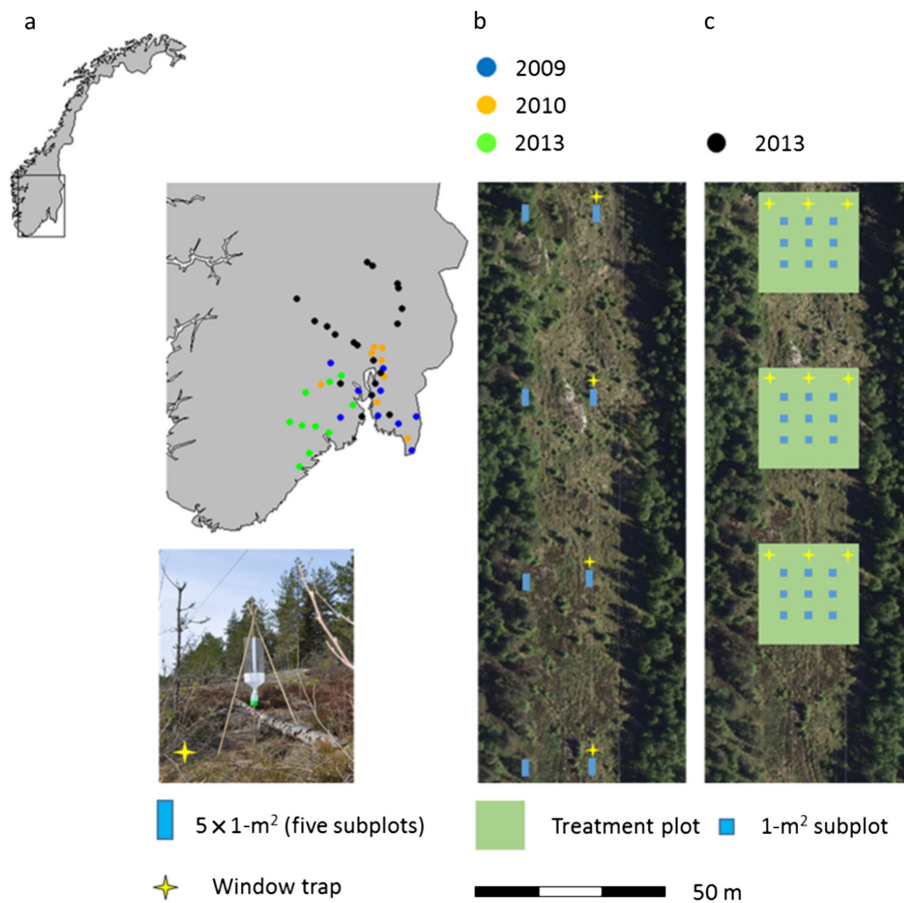
Fig. 1. The geographic distribution of study sites in southeast Norway (a). The location and sampling year of the 27 sites from "Dataset 1" are shown as blue, orange, and green circles (a, b). The location of the 19 sites from "Dataset 2" (sampled in 2013) is shown as black circles (a, c). Plant surveys were conducted within 1-m^2 subplots in all sites, but the spatial configuration of subplots differed between Dataset 1 and Dataset 2. In Dataset 2, bees were sampled within experimental treatment plots (c) and pooled at the site level. Each treatment plot was randomly allocated one of three experimental treatments: uncut (woody vegetation uncut), cut (woody vegetation cut), and cut + removal of debris (woody vegetation cut and removed from the treatment unit). Differences in sampling methodology were handled statistically in the analyses (see *Methods* for details).

ranges was skewed and only *Megachile nigriventris* was expected to be able to forage at distances >4 km from the nest (Appendix S1: Table S1, Fig. S2). There was no significant difference in the estimated foraging ranges between below-ground-nesting bees and above-ground-nesting bees (two-sample *t*-test; df = 28.7, *t* = 0.83, *P* = 0.413). Three species were Ericaceae specialists and accounted for 17% of the 901 individuals sampled.

The environment-by-site conditions 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). *Elevation* and *Forb species richness* were not correlated when both datasets were combined (Spearman's ρ = 0.03, *P* = 0.84) or within Dataset 1 (ρ = 0.15, *P* = 0.46) and Dataset 2 (ρ = −0.23, *P* = 0.35). We used the function sm.density.compare in the "sm" library (Bowman and Azzalini 2014) in R (R Development Core Team 2014) to apply a bootstrap test with 1000 samples to test whether 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* differed 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 (Appendix S1: Fig. S3). The differences in the density distributions of *Forb species richness* could be due to the sites in Dataset 2 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, Dataset 1 had 20 1-m^2 subplots placed along the center of the power line clearing, and 20 subplots situated along the edge. In contrast, Dataset 2 had 27 1-m^2 plant survey plots located in the center of the power line clearing, arranged in a regular grid. Since the diversity of forbs is higher in the center compared to that in the edge (Eldegard et al. 2015), this could have increased the detection rate in Dataset 2 compared to Dataset 1. This potential bias in the estimation of the resource diversity could influence the estimated relationship between the probability of bee species occurring in a site and forb species richness. We accounted for this potential bias in the statistical analyses. The location-by-site data frame contained the geographic coordinates for each site (WGS84 UTM32) used to calculate the geographic distance among all sites (Appendix S1: Fig. S4, min = 5.5 km, mean 98 km, max = 277.6 km).

Data preparation

We combined the four data frames into a single data frame that was used for the analyses (Appendix S1: Table S2). 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 and the environmental information for each site. For every species-by-site combination, we calculated the distance to the nearest site where a conspecific had been sampled. An increased geographic distance is often related to changes in environmental conditions between sites. Inferring dispersal limitation from geographic distances alone may therefore confound the influence of ecological filtering with that of dispersal limitation (Gilbert and Lechowicz 2004). However, this was accounted for in our *Distance to source habitat* variable as it quantifies the proximity to sites where the environmental conditions

required by a species are met, assuming that the presence of a species indicates habitat suitability. 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 overlapping geographic distances (Appendix S1: Fig. S5). 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 only site they occurred in.

The final variable in the data frame was the *Relative commonness* of each species in the metacommunity, calculated as: Relative commonness$_{ij}$ = $(sp_i - sp_{ij})/(sp_\Sigma - sp_{\Sigma j})$, where sp_i was the total abundance of the ith species ($n = 44$) across all j sites ($n = 46$); sp_{ij} was the number of individuals of the ith species in the jth site; sp_Σ was the total number of bee individuals sampled across all sites; and $sp_{\Sigma j}$ was the total number of bee individuals sampled in the jth site. The relative commonness thereby quantifies the relative contribution of individuals of the ith species to the entire bee fauna found outside a local community. If species are ecologically equivalent, the probability of species occurring locally should be proportionate to its relative commonness.

Statistical analyses

We used binomial GLMMs 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 dispersal 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 (min = 0.03, max = 5.69, mean = 0.91, SD = 1.02 km) and we expected that this could also influence their dispersal ability. We also included the interaction term *Distance to source habitat × Nesting behavior* to test whether below-ground-nesting bees were more dispersal limited than above-ground-nesting bees. We included the interaction term *Forb species richness × Ericaceae affiliation*, where *Ericaceae affiliation* was a categorical variable with two levels (Ericaceae affiliated

vs. non-Ericaceous affiliated). This allowed us to test whether changes in the probability of occurrence with *Forb species richness* depended on whether or not the species was affiliated with ericaceous shrubs and thereby whether *Forb species richness* acted as an ecological filter. The interaction term *Elevation × Relative commonness × Ericaceae affiliation* was included to test whether the influence of ecological drift increased with *Elevation* and whether this differed among trait groups.

We included the categorical variables *Species identity* (levels = 44), *Site identity* (46), *Study design* (2), and *Sampling year* (3) as random intercepts to account for variations in the mean probability of occurrence within each of these groups. We also included the interaction term *Forb species richness × Ericaceae affiliation* as a random slope for *Study design* to account for the differences in *Forb species richness* distributions between study designs. Following the syntax in Zuur et al. (2009), the full model was specified as:

$$\text{Presence of bee species}_i \text{ in site}_j \sim B(1, \pi_{(i,j)})$$

$$E(Y_{(i,j)}) = \pi_{(i,j)} \text{ and } \text{var}(Y_{(i,j)}) = \pi_{(i,j)} \times (1 - \pi_{(i,j)})$$

$$\text{Link} = \text{cloglog}$$

$$\text{link}(\pi_{(i,j)}) = \beta_0 + \beta_{Distance\,to\,source\,habitat\,(i,j)}$$
$$+ \beta_{Ericaceae\,affiliation\,(i)} + \beta_{Forb\,species\,richness\,(i)}$$
$$+ \beta_{Foraging\,range\,(i)} + \beta_{Nesting\,behavior\,(i)}$$
$$+ \beta_{Relative\,commonness\,(i,j)} + \beta_{Elevation\,(i)}$$
$$+ \beta_{Ericaceae\,affiliation\,(i)\times Forb\,species\,richness\,(j)}$$
$$+ \beta_{Foraging\,range\,(i)\times Distance\,to\,source\,habitat\,(i,j)}$$
$$+ \beta_{Nesting\,behavior\,(i)\times Distance\,to\,source\,habitat\,(i,j)}$$
$$+ \beta_{Relative\,commonness\,(i,j)\times Elevation\,(j)\times Ericaceae\,affiliation\,(i)}$$
$$+ \text{random intercept}_{Study\,design}$$
$$+ \text{random intercept}_{Site\,identity\,(j)}$$
$$+ \text{random intercept}_{Species\,identity\,(i)}$$
$$+ \text{random intercept}_{Sampling\,year\,(j)}$$
$$+ \text{random slope}_{Ericaceae\,affiliation\,(i)+Forb\,species\,richness\,(i)}$$
$$\scriptstyle +Ericaceae\,affiliation\,(i)\times Forb\,species\,richness\,(j)|Study\,design$$

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 scaled to zero means and unit deviance prior to analyses. We tested the influence of *Elevation* on the presence of single-site inhabitants in a separate GLMM analysis. We simplified models by first dropping random effects that increased the Bayesian Information Criterion. We then used likelihood ratio tests to conduct a backward elimination of non-significant ($P > 0.05$) fixed-effect terms (Crawley 2013).

The significant interaction terms *Distance to source habitat × Foraging range* (likelihood ratio (LRT) tests = 6.6, $P = 0.011$) and *Distance to source habitat × Nesting behavior* (LRT = 4.4, $P = 0.036$) suggested that dispersal limitation was a deterministic process as it differed among species depending on their functional traits. However, the significances of these interaction terms were biased due to the skewed density distribution of foraging ranges and specifically the presence of *M. nigriventris* with an estimated foraging range of 5.7 km and occurrences within three sites with *Distance to source habitats* of 127, 149.5, and 163 km (Appendix S1: Table S3). When *M. nigriventris* was removed from the model, neither the *Distance to source habitat × Foraging range* (df = 1, LRT = 0.02, $P = 0.900$) nor the *Distance to source habitat × Nesting behavior* (df = 1, LRT = 2.69, $P = 0.101$) was statistically significant. Due to the strong influence of this outlier, we removed *M. nigriventris* from the analyses, leaving 43 species in the final model.

Determining whether stochastic processes drive changes in observed patterns of community composition requires the use of null models (Vellend et al. 2014). We therefore tested whether the regression slopes from the final model differed from those expected if species were ecologically equivalent. We simulated 200 neutral meta-communities, each consisting of 46 sites and the 43 species from the original dataset. Each simulated meta-community was generated by shuffling the individuals in the original meta-community data frame while maintaining total site (row) and species (column) abundance. We combined the 200 simulated datasets with the observed dataset and added two categorical variables: *Data source*, that is, simulated vs. original data, and *DatasetID*, that is, meta-community identity with a separate identifier for each of the 201 datasets. We specified the GLMMs with the interaction terms: *Ericaceae affiliation × Forb species richness × Data sources;*
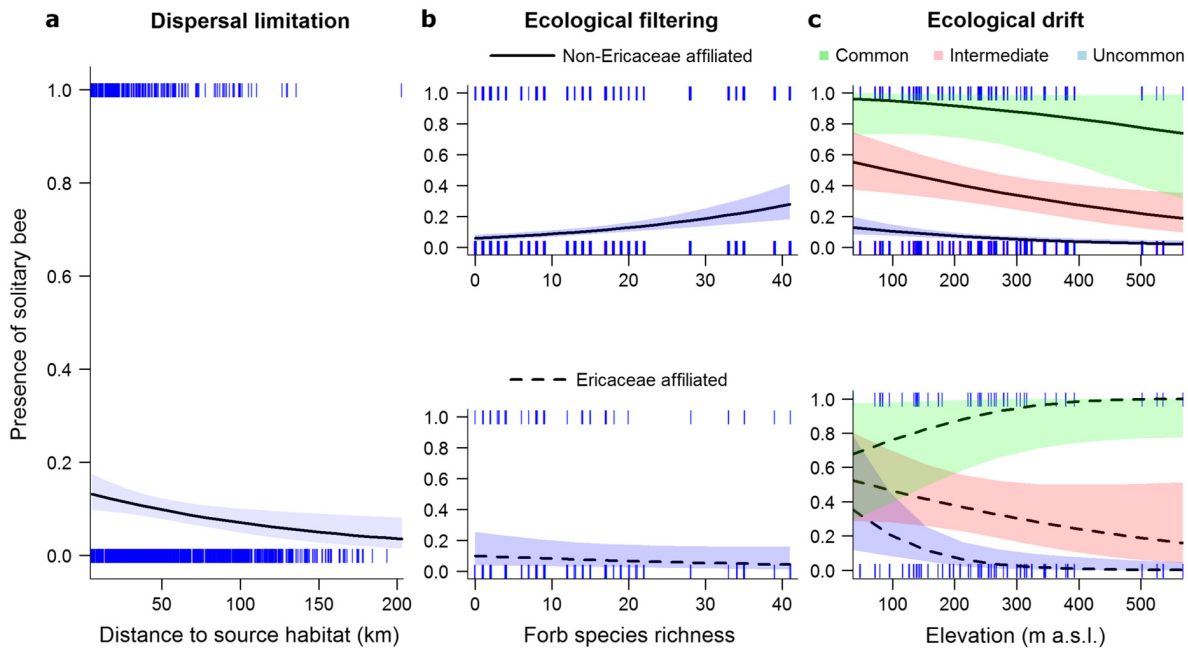
Fig. 2. Estimated relationships from binomial generalized linear mixed model on the presence of solitary bee species in 46 power line clearings as a function of the (a) distance to source habitat, (b) *Ericaceae affiliation × Forb species richness*, and (c) *Ericaceae affiliation × Relative commonness × Elevation*. The influence of the interaction *Relative commonness × Elevation* is plotted at three difference levels of relative commonness (low = blue; intermediate = pink; and high = green). Binomial ticks show the observed presences and absences at each level of the explanatory variables. Green, blue, and red shaded regions show 95% confidence intervals. See Table 1 for model output.

Distance to source habitat × Data sources; and *Elevation × Relative commonness × Data sources × Ericaceae affiliation,* and all lower-order interaction terms and their main effect terms. We used the random-effects structure from the final models from the analysis on the original (empirical) data, but with the random-effects terms (species identity and site identity) nested within each dataset (i.e., 200 simulated and 1 empirical).

Results

Both stochastic and deterministic processes influenced the occurrence of solitary bee species within communities.

The final model included the main effect term *Distance to source habitat* (LRT = 6.27, $P = 0.012$), showing that the estimated probability of a species occurring within a community decreased from 13.2% to 3.5% as the distance to the nearest source habitat increased from 5.5 to 203 km (Fig. 2a,

Table 1). The significant interaction term *Ericaceae affiliation × Forb species richness* (LRT = 14.81, $P < 0.001$) showed that as the species richness of forbs increased from 0 to 41, ecological filtering decreased the occurrence of Ericaceae-affiliated species from 10.1% to 4.2% and increased the occurrence of non-Ericaceae-affiliated species from 5.8% to 27.9% (Fig. 2b, Table 1). The interaction term *Elevation × Relative commonness × Ericaceae affiliation* (LRT = 5.11, $P = 0.024$) showed that the probability of species occurring locally decreased with *Elevation*, but especially so for species with no *Ericaceae affiliation* and a low *Relative commonness* (Fig. 2c, Table 1). When the *Relative commonness* was held constant at the highest level, the estimated probability of occurrence decreased with *Elevation* for non-Ericaceae-affiliated species, whereas it increased for Ericaceae-affiliated species (Fig. 2c). The occurrence of the rarest species within our study area (i.e., single-site inhabitants) decreased with *Elevation* (Fig. 3, Table 1).

Table 1. Analysis of the presence of solitary bee species within power line clearings in southeast Norway.

GLMM species occurring in >1 site				
Fixed effects	β	SE	z	P
Intercept	−2.258	0.121	−18.69	<0.001
Forb species richness	0.455	0.093	4.88	<0.001
Ericaceae affiliated	−0.285	0.497	−0.57	0.566
Distance to source habitat	−0.252	0.097	−2.61	0.009
Elevation	−0.426	0.116	−3.66	<0.001
Relative commonness	0.737	0.081	9.06	<0.001
Forb species richness × Ericaceae affiliated	−0.696	0.181	−3.85	<0.001
Elevation × relative commonness	0.050	0.054	0.93	0.351
Ericaceae affiliated × Elevation	−0.690	0.438	−1.58	0.115
Ericaceae affiliated × relative commonness	0.081	0.188	0.43	0.665
Ericaceae affiliated × elevation × relative commonness	0.326	0.146	2.23	0.026
Random effects	σ	SD	Obs.	Groups
Site identity (intercept)	0.243	0.493	1978	46
Species identity (intercept)	0.089	0.299		43
GLMM on species occurring in 1 site				
Fixed effects	β	SE	z	P
Intercept	−4.550	0.578	−7.86	<0.001
Elevation	−1.292	0.435	−2.97	0.003
Random effects	σ	SD	Obs.	Groups
Site identity (intercept)	0.224	0.474	664	46

Notes: GLMM, generalized linear mixed model. Results from binomial GLMMs. The first model was run with species occurring in at least two sites. A separate model was run with the presence of single-site occupants as response variable and elevation as a covariate. All numerical variables were scaled to zero means and unit variance prior to analyses. *Megachile nigriventris* was excluded from the analyses as it was an influential outlier (see Appendix S1: Table S1).
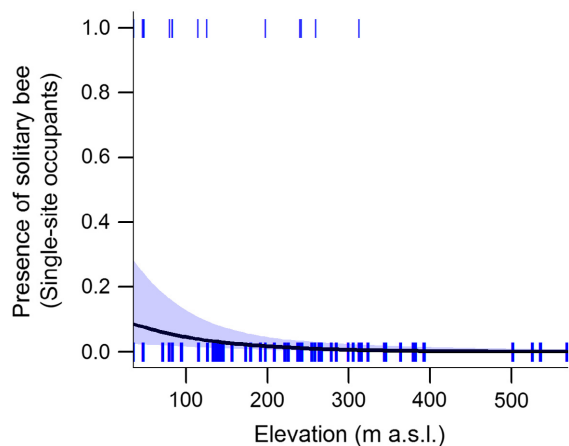

Fig. 3. Estimated relationships from binomial generalized linear mixed model on the probability of single-site inhabitants as a function of elevation. Binomial ticks show the density of observed presences and absences at each level of the explanatory variables. The blue shaded region shows 95% confidence intervals. See Table 1 for model output.

The comparisons of the regression slopes from the empirical community dataset and the slopes from the 200 simulated neutral meta-communities showed that the life-history traits of bees are related to patterns of community assembly that differ from those expected under a neutral model. The interaction term *Data source × Distance to source habitat* showed that, compared to the empirical communities, the simulated neutral communities were less dispersal limited (Fig. 4a, Table 2). The interaction term *Data source × Ericaceae affiliation × Forb species richness* showed that the increase in occurrence of non-Ericaceae-affiliated species with forb species richness mirrored that expected if species were ecologically neutral (Fig. 4b, Table 2). In contrast, the negative relationship between Ericaceae-affiliated species and *Forb species richness* contrasted the pattern expected under the neutral model, showing that ecological filtering did indeed structure the bee communities within our study region.
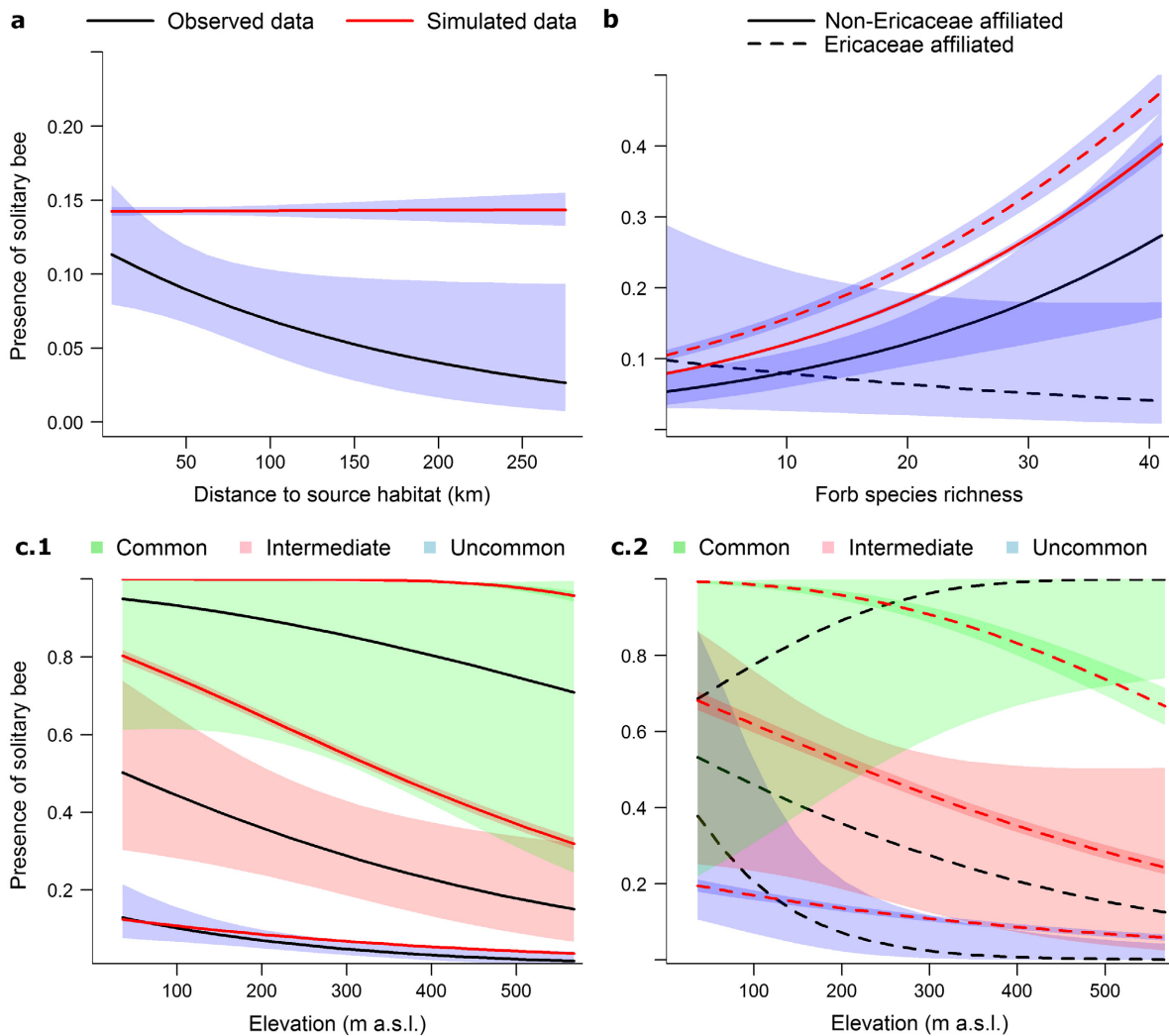
Fig. 4. Estimated regression slopes from the binomial generalized linear mixed model showing slopes for the empirical data (black lines) and from the simulated data (red lines) on bee occurrence as a function of distance to source habitat (a). The occurrence of solitary bee species along the gradient in forb species richness (b) and elevation (c.1–2) was estimated for both non-Ericaceae-affiliated species (solid lines) and for Ericaceae-affiliated species (dashed lines). Along the elevational gradient, the occurrence of solitary bee species was estimated with the relative commonness held constant at low, intermediate, and high values. The estimated slopes for Ericaceae- and non-Ericaceae-affiliated species along the elevational gradients are plotted in two separate graphs (c.1 and c.2) for visual purposes. Green, blue, and red shaded regions show 95% confidence intervals. See Table 2 for model output.

The *Ericaceae affiliation* also influenced the interacting influences of *Elevation* and *Relative commonness* on the probability of occurrence. Specifically, the four-way interaction *Elevation × Relative commonness × Ericaceae affiliation × Data source* showed that for non-Ericaceae-affiliated species, the decrease in occurrence with *Elevation* mirrored that expected under the neutral model (Fig. 4c.1). Indeed, when Ericaceae-affiliated species were excluded from the analysis, the three-way interaction term *Elevation × Relative commonness × Data source* was not significant (z-value = −1.295, P = 0.195). In contrast, for *Ericaceae-affiliated* species, the interacting influence of *Relative commonness*

Table 2. Analysis of the probability of species occurring within power line clearings in southeast Norway, as compared to in simulated communities.

Fixed effects	β	SE	z	P
Intercept	−2.318	0.154	−15.02	<0.001
Ericaceae affiliated	−0.252	0.579	−0.43	0.664
Forb species richness	0.472	0.117	4.02	<0.001
Data source	0.428	0.155	2.76	0.006
Distance to source habitat	−0.193	0.097	−1.99	0.047
Elevation	−0.460	0.139	−3.31	0.001
Relative commonness	0.732	0.112	6.54	<0.001
Ericaceae affiliated × forb species richness	−0.716	0.185	−3.87	<0.001
Ericaceae affiliated × data source	0.526	0.580	0.91	0.365
Forb species richness × data source	0.019	0.117	0.16	0.872
Data source × distance to source habitat	0.194	0.097	2.00	0.046
Data source × elevation	0.143	0.139	1.03	0.305
Data source × relative commonness	0.224	0.112	1.99	0.046
Elevation × relative commonness	0.059	0.055	1.06	0.288
Ericaceae affiliation × elevation	−0.715	0.447	−1.60	0.109
Ericaceae affiliation × relative commonness	0.119	0.245	0.49	0.628
Ericaceae affiliation × forb species Richness × data source	0.697	0.185	3.77	<0.001
Data source × elevation × relative commonness	−0.074	0.056	−1.34	0.181
Ericaceae affiliation × data source × elevation	0.718	0.447	1.61	0.108
Ericaceae affiliation × data source × relative commonness	−0.445	0.246	−1.81	0.070
Ericaceae affiliation × elevation × relative commonness	0.344	0.150	2.29	0.022
Ericaceae affiliation × data source × elevation × relative commonness	−0.341	0.151	−2.27	0.023
Random effects	σ	SD	Obs.	Groups
*Site identity	DatasetID* (intercept)	0.465	0.682	393,116	9246
*Species identity	DatasetID* (intercept)	0.249	0.499		8546

Notes: Results from binomial generalized linear mixed models. Significant interaction terms that include *Data source* indicate a difference in the estimated slopes between the empirical community dataset and the 200 simulated community datasets.

and *Elevation* differed from that expected if species were ecologically neutral (Fig. 4c.2, Table 2), and when non-Ericaceae-affiliated species were excluded from the analysis, the three-way interaction *Elevation × Relative commonness × Data source* was statistically significant (z-value = −2.757, P = 0.006).

Discussion

By expanding on approaches that test the influence of ecological filtering (Kremen and M'Gonigle 2015, Warton et al. 2015)—by also including dispersal limitation and ecological drift—we here show that both deterministic and stochastic processes influenced the assembly of bee communities (Figs. 2–4, Tables 1 and 2).

The probability of species occurring in sites decreased with the distance to the nearest site where their habitat conditions were met (i.e., conspecifics occurred), suggesting that the bee communities we have studied are dispersal limited

(Fig. 2a). Improving our understanding of the role of dispersal limitation in community assembly is essential to improving habitat management schemes since the success of these schemes depends on the surrounding landscape composition (Scheper et al. 2013). Our finding that dispersal limitation is an important process in the assembly of bee communities agrees with previous studies, which have shown that the similarity in species composition among similar habitats decreases with geographic distance (Murray et al. 2012). In contrast to our expectations, foraging ranges and nesting behavior did not influence the dispersal limitation in our study system, although these traits have been shown to influence the vulnerability of bees to habitat isolation more generally (Williams et al. 2010). Our findings therefore suggest that dispersal limitation is neutral with regard to these species traits within our study system. However, 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 (http://www.bwars.com/content/colletes-hederae-mapping-project).

The influence of *Distance to source habitat* on the probability of species occurring within communities differed between the empirical and the simulated datasets (Fig. 4a, Table 2). The observed influence of dispersal limitation was therefore not driven by our study region containing a single cluster of sites with large community sizes (i.e., number of individuals), which would have resulted in similar patterns for the empirical and simulated data. In contrast, our findings suggest that solitary bee species occur in several spatially aggregated populations within the forested landscape of southeast Norway. Spatial aggregation of bee species in clusters within a region has also been found in agricultural landscapes (Rollin et al. 2015). A possible explanation for these patterns is that nesting and/or foraging resources are not homogeneously distributed across the landscape. Soil characteristics are spatially aggregated in our study system due to the dependency of geological sedimentations on the topology and geological history of the landscape (https://www.geonorge.no/). The spatial aggregation of species within our region may therefore be related to the spatial aggregation of soil deposits, which determine the floral characteristics (i.e., deep fertile soils are dominated by forbs, and shallow nutrient-poor soils are dominated by ericaceous shrubs). Dispersal among communities may therefore mainly occur within such archipelagos of "islands" of suitable habitats, whereas the dispersal among these "archipelagos" is hampered by an "ocean" of ecological filters (i.e., a lack of suitable floral resources).

We found a strong influence of ecological filtering on the assembly of bee communities (Fig. 2b). The probability of non-Ericaceae-affiliated species occurring within communities increased with the species richness of forbs, whereas the probability of Ericaceae-affiliated species occurring decreased (Fig. 2b, Table 1). As only three of the 43 species included in the final model, namely *Andrena lapponica*, *A. fuscipes*, and *Colletes succinctus*, are affiliated with ericaceous shrubs, these results show that bee diversity in our system increased with forb species richness. The influence of forb species richness on the diversity of wild bees in forested systems has also been documented in North America (Hanula et al. 2015), suggesting that the forb–shrub gradient may be a widespread ecological filter in forested ecosystems. Moreover, in a subset of the sites ($n = 17$) included in this study, we have previously shown that the proportion of Ericaceae specialists in the community decreased with forb diversity (Sydenham et al. 2015). However, using changes in the proportionate contribution of specific trait groups as an indicator of ecological filtering is problematic because the error distributions may vary among trait groups and because differences in community size are not accounted for (Reitan and Nielsen 2016). By following the approach of Kremen and M'Gonigle (2015), we were able to account for different error distributions between trait groups (e.g., the 95% confidence intervals for the estimated slopes differ among trait groups in Fig. 2). By using the approach adopted in this paper, we were able to demonstrate that the outcome of ecological filtering was realized through the contrasting responses of each trait group to the ecological filter (Fig. 2b, Table 1). Our comparison of how forb species richness influenced the probability of species occurring within the empirical communities and the simulated communities, respectively, showed that non-Ericaceae-affiliated species showed the same positive response to forb species richness as would be expected if species were ecologically neutral. In contrast, the response of Ericaceae-affiliated species showed the opposite response than what would be expected if their probability of occurring within communities was related to their regional commonness (Fig. 4b, Table 2). These results show that forb species richness was related to a general increase in community size, whereas Ericaceae-affiliated species were selected against along this gradient and that forage availability thereby acts as a deterministic filter on bee diversity within our system.

Bee communities at high-elevation sites have previously been shown to consist of a few widely distributed lowland (e.g., *Lasioglossum calceatum*) and montane (e.g., *L. fratellum*) species that possess life-history traits associated with cold tolerance (Hoiss et al. 2012). We found that the

probability of occurrence within communities decreased with elevation, but that the rate of decrease depended on both the relative commonness and *Ericaceae affiliation* of species (Fig. 2c). Since both species richness and abundance decrease with elevation (Hoiss et al. 2012, Marini et al. 2012), sampling effects alone could lead to a lower probability of observing relatively rare species at high-elevation sites, resulting in community compositions similar to those predicted under ecological drift (i.e., the mono-dominance of regionally common species). Within our elevation range (36–568 m a.s.l.), the decrease in species occurrences with elevation was most pronounced for bees that were relatively uncommon within our region (Fig. 2c, Table 1). However, non-Ericaceae-affiliated species and Ericaceae-affiliated species showed contrasting responses to elevation when the relationships were estimated for the most common species (Fig. 2c). For the non-Ericaceae-affiliated species, changes in occurrence with elevation and relative commonness mirrored those found for the neutral communities (Fig. 4c.1). In contrast, for the Ericaceae-affiliated species, changes in occurrence with elevation differed from those of the neutral communities (Fig. 4c.2). Our results suggest that sampling effects alone could indeed explain the under-representation of rare lowland, forb-affiliated species at high elevations, where single-site occupants (mainly lowland species) were also less likely to occur (Fig. 3, Table 1). These findings suggest an increased role of ecological drift at high elevations where the density of floral resources is low. A potential explanation for why we did not find similar patterns for the Ericaceae-affiliated species is that the density of ericaceous shrubs (i.e., *Vaccinium myrtillus*) can be high even at the highest elevations within our study area. *Andrena lapponica*, which forages on ericaceous shrubs, is therefore not likely to experience the same decrease in "habitat size" with elevation that non-Ericaceae-affiliated species do.

We have here focused on the patterns in species occurrences that are driven by processes operating at the meta-community scale (i.e., dispersal, filtering, and ecological drift sensu Vellend 2010). However, biogeographic processes also influence the species diversity within meta-communities. For instance, re-colonizations (i.e., re-introductions to the meta-community) of previously extinct bee species have recently been documented in the UK (Ollerton et al. 2014). Differences in the regional commonness of species may be related to biogeographic processes as the abundance of species tends to decrease with distance from the center of their distributional range (Bell 2001), and the diversity of taxa is often highest near their point of origin (e.g., Hines 2008, Hedtke et al. 2013, Kayaalp et al. 2013). Biogeographic processes may therefore assert a strong influence on meta-community dynamics since the regional abundance of a species (i.e., relative commonness) is related to its susceptibility to ecological drift (Figs. 2c and 4c). In northern regions, such as our study system, the imprint of such biogeographic processes on meta-community structure of bees may be particularly important due to the relatively young age (~10,000 yr) of the species pool and the fact that southern Norway is on the northern limit of the distributional range of many species. Thus, the role of stochastic processes in community assembly may differ among regions.

The role of stochastic processes in community assembly could have important implications for conservation planning if the success of habitat management practices is less predictable where environmental conditions reduce the density of resources. For instance, Scheper et al. (2013) found a low effect size of agri-environmental schemes on promoting local bee diversity in landscapes with a low availability of source habitats. These findings show the importance of retaining large source habitats within cultivated landscapes and that conservation planning should aim to promote the connectivity among such source habitats and restored habitats.

Conclusions

Our findings show that the functional response of bees to environmental conditions is deterministic and driven by ecological filters related to resource availability. However, within trait groups, species may be ecologically neutral in terms of their responses to ecological gradients. The probability of a species occurring within a patch of suitable habitat is therefore related to their commonness in the region, and the distance to the nearest suitable patch of habitat, and effectively determined by stochastic processes. This is

particularly so for rare species whose presence is hard to predict even in favorable habitats. Studies on community assembly should therefore aim to identify the roles of both stochastic and deterministic processes.

In addition to elucidating the relevance of stochastic processes for conservation management, our approach and the "relative commonness" variable used in this paper also allow for a heuristic link between meta-community ecology and biogeography. Estimating the relationship between the relative commonness of species, and thereby their susceptibility to ecological drift, and their biogeography may allow for an analytical link between community assembly and biogeography. The approach used in this paper is limited to studying the mean probability of occurrence, and as such, it does not explicitly account for the variance in occurrences between similar sites. Testing how the variance in occurrence is related to community size, ecological filtering, and habitat isolation would require a distance-based framework (e.g., beta diversity) and would be complementary to the univariate framework used in this study. The univariate approach used here does therefore not make multivariate approaches redundant, but rather adds a complementary test of the processes behind the assembly of ecological communities.

Acknowledgments

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Supporting Information

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