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The role of past landscape structure and present management in seminatural grasslands for wild bee species richness and abundance

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Foreword

This thesis marks the end of a long journey where I have learned and experienced a lot. I have been lucky to have been surrounded by wonderful support and care, and I would like to thank them all.

I would like to thank Norwegian Institute for Nature Research (NINA), especially Graciela Rusch and Markus Sydenham, for the opportunity to have been a part of the “POLLILAND” project. I would like to thank Arnstein Staveløkk for identifying the bumblebees.

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Abstract

1. During the last century the area of semi-natural grasslands has been dramatically reduced in all European countries, including Norway. Semi-natural grasslands provide habitats for wild pollinators such as wild bees and are thus important to maintain. In this study I explored whether present management in semi-natural grasslands, as well as current and past landscape composition (amount of available bee habitat), had a significant effect on wild bee richness and abundance.
2. Wild bees were collected during the summer of 2019 in semi-natural grasslands in south-east Norway. I categorized the collected bees into different functional trait groups; sociality (solitary or social), nesting preference (aboveground or belowground) and size (small or large). I used available maps of early successional habitats that had been derived from satellite imagery, representing the potential bee habitat availability in landscapes in 1988 (i.e. past) and 2016 (i.e. present day).
3. I found no significant relationships between the reported management status or registered site importance status and the wild bee or functional group specific richness or abundance within semi-natural grasslands. Instead, I found that wild bee species richness and abundance were strongly related to the amount of available bee habitat in the surrounding landscape and how habitat availability had changed over time (decrease, no change or increase). Specifically, I found that bee diversity was greatest in semi-natural grasslands situated in landscapes with a large amount of high availability habitat. Furthermore, the importance of landscape conditions was greatest in dynamic landscapes where habitat availability had actually been reduced over the course of 30 years.
4. My study shows that past available bee habitat as well as current available bee habitat of semi-natural grasslands are an important factor for richness of some functional group of bees. Current management criteria for semi-natural grasslands in Norway are based upon historical cultural management practices. While this can be beneficial for wild bees, the nature of the relationship between availability of semi-natural grasslands and occurrence and abundance wild bees depends on both the current landscape context and temporal changes in the surrounding landscape.
5. *Conclusions and management implications.* This study show that some functional bee groups have a relationship with landscape changes, while others seems to mainly respond to present landscape conditions. The most species rich seminatural grassland are found in landscapes where forest encroachment during the past 30 years has led to a loss of bee habitat. The current criteria cover the historical cultural management practices of grassland farming; and added criteria covering wild bee abundance and richness in the semi-natural grasslands would be beneficial to better manage wild bee species.

Sammendrag

1. Slåttemarkene i Europa, så vel som i Norge, har opplevd en betydelig reduksjon i areal de siste 100 årene. Disse habitatene er viktige å ivareta, ettersom de er viktige habitater for villbier. I denne studien undersøkte jeg om dagens hevd av slåttemarker, så vel om tidligere landskap (tilgjengelig biehabitater), har en betydelig påvirkning for artsdiversitet og abundans for villbier.
2. Villbier ble samlet sommeren 2019 i slåttemarker Sørøst-Norge. Jeg klassifiserte de i forskjellige funksjonelle grupper; sosialitet (solitære eller sosiale), hekkepreferanse (over eller under bakken) og størrelse (små eller store). Jeg brukte tilgjengelige kart av tidlige suksesjonshabitater som hadde blitt hentet fra satellittbilder, for å representere potensielle biehabitater i landskaper i 1988 (m. a. fortid) og 2016 (m.a. nåtid).
3. Det ble ikke funnet noen signifikante relasjoner mellom hevdstatus og stedverdi og artsdiversitet og abundans av villbier. Jeg observerte en sterk korrelasjon mellom artsdiversitet og abundans og det tilgjengelige biehabitatet i nærliggende landskap og hvordan habitattilgjengeligheten hadde endret seg over tid (nedgang, ingen endring eller økning). Videre fant jeg at viktigheten av landskapet var mest vesentlig i dynamiske landskap hvor tilgjengelig biehabitat hadde blitt redusert i løpet av de siste 30 årene.
4. Min studie viser at fortidens tilgjengelig biehabitat så vel om dagens tilgjengelige biehabitater i slåttemarker er viktige faktorer for artsrikdommen for noen funksjonelle grupper for bier. Dagens kriterier for hevdstatus for slåttemarker er basert på den tradisjonelle driften av slåttemarker. Selv om denne typen drift kan ha positive effekter for villbier, så vil relasjonen mellom tilgjengelige slåttemarker og tilstedeværelsen av villbier avhenge både av dagens landskapsstruktur og temporære endringer i nærliggende landskap.
5. *Konklusjoner og forvaltningsimplikasjoner.* Denne studien viser at noen funksjonelle biegrupper er knyttet til landskapsendringer, mens andre er mer knyttet til dagens landskapsstruktur. De mest artsrike slåttemarkene er funnet i landskap hvor gjengroing de siste 30 årene har ført til et tap av biehabitat. Dagens forvaltningskriterier av slåttemarker dekker kun den tradisjonelle driften av slåttemarker. En ny tilleggskriteria som tar for seg artsdiversitet og abundans til villbier i slåttemarker vil være positivt for å bedre kunne forvalte villbier.

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Introduction

During the last century, researchers have documented a global decline in insect populations (Seibold et al., 2019). These declines are a major concern as insects provide essential ecological services such as food for insectivores, nutrient recycling and plant propagation (Gullan & Cranston, 2014). It is henceforth of great interest to invest in measurements to conserve insects.

Bees (Hymenoptera: Anthophila) constitute an ecologically important group of species, providing pollination services to both native flowers as well as agricultural crops. Over 80 percent of wild plant species (Ollerton et al., 2011) and 35 percent of global crop species are dependent on animal pollinators (Klein et al., 2007; Ollerton et al., 2011). Though many other insect groups are pollinators as well (e.g. butterflies, hoverflies and beetles) (Rader et al., 2016), bees are generally considered to be the most efficient pollinators (Garibaldi et al., 2013; McGrady et al., 2019). Several studies show that bee populations are in decline (Biesmeijer et al., 2006; Ghazoul, 2005; Martins et al., 2013; Scheper et al., 2014). Of the European bee species that could be assessed for the IUCN red list, 9.2 percent are threatened, but due to data deficiency, this number could be as high as 60.7 percent (Nieto et al., 2014).

Wild bees comprise a large and diverse group. In Europe alone, there are 1965 species (Nieto et al., 2014), 208 of these have been found in Norway (Artsdatabanken, 2019a). These bees are classified into six families: *Andrenidae*, *Apidae*, *Colletidae*, *Halictidae*, *Megachilidae* and *Melittidae* (Artsdatabanken, 2019a; Nieto et al., 2014). Depending on the different functional traits, these species can either have similar or different requirements to their surrounding habitat (Nieto et al., 2014). The most commonly used trait groups in studies of bee diversity and ecology are sociality (social or solitary bees), nesting preference (aboveground or belowground nesters) and body size (Williams et al., 2010). Classifying bees into these functional trait groups is useful for understanding and predicting how the bee diversity responds to environmental changes (Williams et al., 2010).

Providing habitats that are of high value to bees is essential to combat the decline in bee population (Nieto et al., 2014). Semi-natural grasslands provide important habitats for wild bees because of their diverse communities of flowering plant species as well as nesting sites (Kohler et al., 2008; Öckinger & Smith, 2007). Semi-natural grasslands used to be a common agricultural habitat type in Europe. However, the intensification of agricultural farming during the past century (Bullock et al., 2011) has resulted in a decrease in the area of semi-natural

grasslands of nearly 90 percent or more in several European countries, among these Norway (Bullock et al., 2011; Dahlström et al., 2008; Direktoratet for naturforvaltning, 2009).

To combat the continuing decline, European Union (EU) aims to restore former semi-natural grasslands (Olmeda et al., 2019). In Norway, the government started an action plan called “Handlingsplan for slåttemark” or “Action plan for semi-natural grasslands” (Direktoratet for naturforvaltning, 2009). The main management measure of this action plan was economic support to landowners at semi-natural grasslands with national and regional site value for carrying out management in the traditional low-intensity manner. This was done on a voluntarily basis. In 2015, close to 600 landowner used the economic support to maintain their semi-natural grasslands (Miljødirektoratet, 2016). As of today, a total of 2734 semi-natural grasslands are registered in a national database in Norway (Miljødirektoratet, 2020), compared to 1275 semi-natural grasslands in 2009 (Direktoratet for naturforvaltning, 2009).

Even though semi-natural grasslands contribute to insect diversity, creating new semi-natural grasslands is not necessarily the best course of action to conserve wild bee diversity (Concepción et al., 2012). In landscapes with few remnant areas of seminatural grassland, the establishment of flower rich habitat patches has little effect because low heterogeneity in the landscape (Scheper et al., 2013). Therefore, conserving the established semi-natural grasslands can have positive effects for conserving wild bee species (Ollerton et al., 2014). The spatial scale a bee travel within is related to their body size. Smaller bees and solitary bees have been shown to have a shorter dispersal range than larger bees and social bees (López-Urbe et al., 2019), making recolonization a possible long-term project. Most bee species forage within 1km radii of their nesting site (Greenleaf et al., 2007). While most solitary bee species will forage on a scale between 150m and 600m (Gathmann & Tscharntke, 2002), bumblebees can operate at a scale of several kilometers (Goulson & Stout, 2001). Moreover, solitary bee diversity has been shown to respond to environmental conditions within the surrounding landscape, at smaller spatial scales than bumblebees (Steffan-Dewenter et al., 2002). However, it is not always clear what the relevant spatial scale is, and the relevant scale is not necessarily the same for all groups of bees.

Bees have a rapid turnover rate and if they have suffered a loss in richness or abundance, they may only need a few years to reach a new equilibrium (Krauss et al., 2010). However, being that there is a large variety of bee species, recolonization rate could differ from species to species. A study done by Kremen et al. (2018), found a higher bee species richness in habitats that had been newly restored compared to when the habitats had aged. Similar results have been found for hedgerows as well (Kremen & M'Gonigle, 2015). Kremen et al. (2018) concluded that this could be due to the flower density of the sites. The higher the

flower richness, the lower the flower species abundance, the less specific nutrients for bees, and thus less bee richness diversity. This illustrates that the ecological quality of semi-natural grasslands as bee habitat is not necessarily related to the age of the area. As long as the habitat or surrounding landscape provide the resources required to sustain bee populations; nest sites, nest building materials and pollen and nectar as food sources (Westrich, 1996), recolonization is possible.

The amount of potential habitat patches in the surrounding landscape is an important determinant of wild bee diversity (Jauker et al., 2009; Le Féon et al., 2013; Öckinger & Smith, 2007). Research show that bee species will thrive better in semi-natural grasslands with close proximity to each other (Jauker et al., 2009; Öckinger & Smith, 2007). While the role of adjacent semi-natural grasslands is important, the role of past semi-natural grasslands must be recognized as well. Several studies have seen a connection between biodiversity and present and past landscape structure. While these studies have looked at plants (Bommarco et al., 2014; Helm et al., 2006; Lindborg & Eriksson, 2004), vertebrates (Brooks et al., 1999; Harding et al., 1998; Metzger et al., 2009), and other invertebrates (Dauber et al., 2006; Duan et al., 2019; Nakahama et al., 2018), little is known about how past landscape affects present day species richness and abundance of wild bees.

In this study I aimed to understand if current availability of bee habitat in the surrounding landscape, as well as changes in availability if bee habitat in the past 30 years, affects present bee diversity and community structure and whether or not different functional groups of bee species respond similarly to environmental changes

Specifically, I hypothesized that:

1. Bee community composition in semi-natural grasslands can be predicted based on the quality measures for semi-natural grasslands given by the governmental management agencies.
2. Bee community composition is not only dependent on present landscape composition, but also affected by the landscape alterations during the past 30 years.

From these hypotheses I predicted that:

1. There will be a high richness and abundance of wild bees, irrespective of functional guilds, in semi-natural grasslands with a high site value and high level of maintenance. By contrast, I expected a reduced richness and abundance of solitary bees, belowground nesting bees and small bodied bees, but higher richness of more robust bee species in semi-natural grasslands with a low site value and low level of maintenance.

2. Semi-natural grasslands situated in landscapes that have lost bee habitats during the past 30 years will host a lower richness and abundance of solitary bees, belowground nesting bees and small bodied bees. However, the richness and abundance of the robust bee species will be less affected by these landscape alterations.
3. Semi-natural grasslands situated in landscapes that have gained bee habitats during the past 30 years will host an equal richness and abundance of solitary bees, belowground nesting bees and small bodied bees. However, the richness and abundance of the robust bee species will be less affected by these landscape alterations.

Methods

Study site

A total of 32 sites (semi-natural grasslands) were located in three counties; Oslo, Viken and Innlandet (Fig. 1). The sites were chosen to ensure they encompassed gradients of landscape context, grassland size and elevation, as well as making it realistic for two field assistants to sample within a set amount of time. All sites were semi-natural grasslands that were either categorized as “nationally important”, “regionally important” or “locally important” (Direktoratet for naturforvaltning, 2009). They also had different levels of maintenance that could either be “well managed”, “low managed”, “not managed”, “fairly to heavily overgrown” and “poorly managed” (Miljødirektoratet, 2014). 20 sites had “national importance”, ten sites had “regional importance” and two sites had “local importance”. 14 sites were “well managed”, ten sites were “low managed”, five sites were “not managed”, one site was “fairly to heavily overgrown” and two sites were “poorly managed”. To ensure that we would have enough comparable data for the sites, we chose to pool the sites in the categories of regional and local importance into a new group; “regionally or locally important”. For maintenance, we pooled the categories “not managed”, “fairly to heavily overgrown” and “poorly managed”. In the final dataset, 25 sites were “nationally important” (A) and 12 sites were “regionally or locally important” (B). 14 sites were “well managed” (1), ten sites were “poorly managed” (2), and eight sites were “abandoned or altered sites” (3).

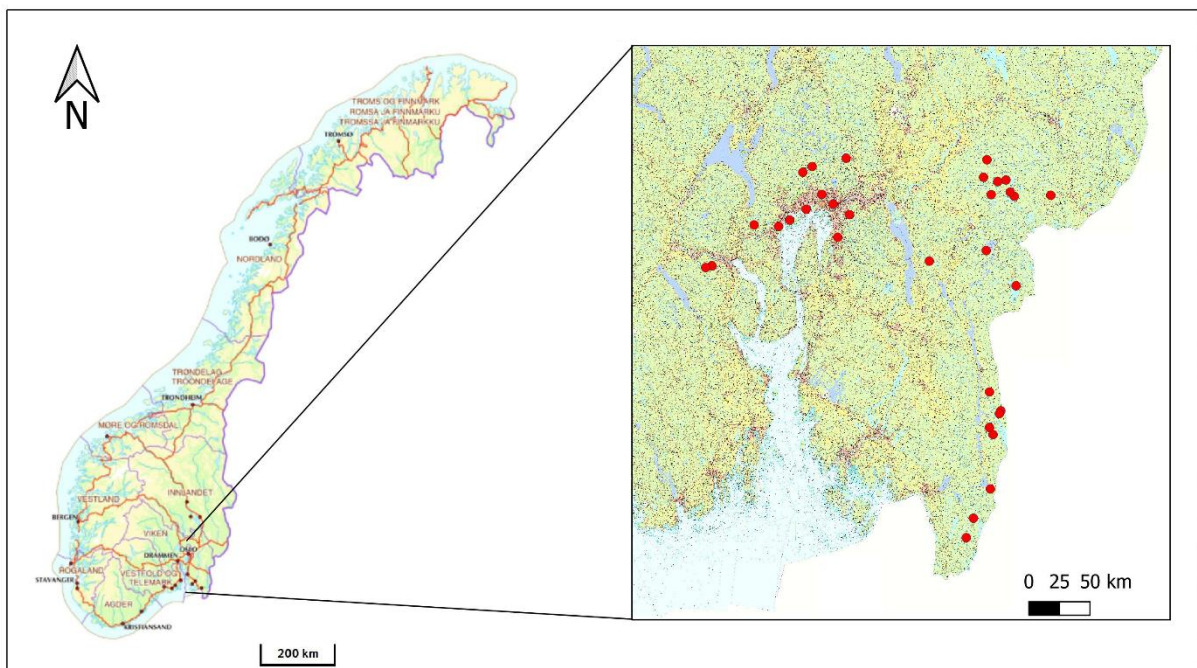


Figure 1. Map of study area in southeast Norway (QGIS Development Team, 2020). Red points indicate the geographic locations of the 32 study sites in semi-natural grasslands.

Study design

Bee sampling

Wild bees were collected using pan traps (Fig. 2) which is an effective method for bee sampling. Pan traps can gather large amounts of data in a short amount of time, as well as being cost efficient (Vrodljak & Samways, 2012; Westphal et al., 2008). Taking the attributes and the distance between each site into consideration, we decided that pan traps would be the most suitable sampling method as they allowed for parallel sampling across all sites.

The pan traps were plastic soup bowls coated with fluorescent white, fluorescent yellow or fluorescent blue following standard protocols (Westphal et al., 2008). These bowls were filled with water and a detergent to break the surface tension (in our case, a drop of liquid soap). I placed three bowls with the aforementioned colors close to each other and defined them as one trap.

All sites had three traps each that were distributed in different parts of the sites to compensate for heterogeneity, but always within the sunny parts of the sites. The traps were deployed at least 20 meters apart to reduce inter-trap competition (Droege et al., 2010). We leveled the bowls with the surrounding vegetation, to ensure that they were visible.

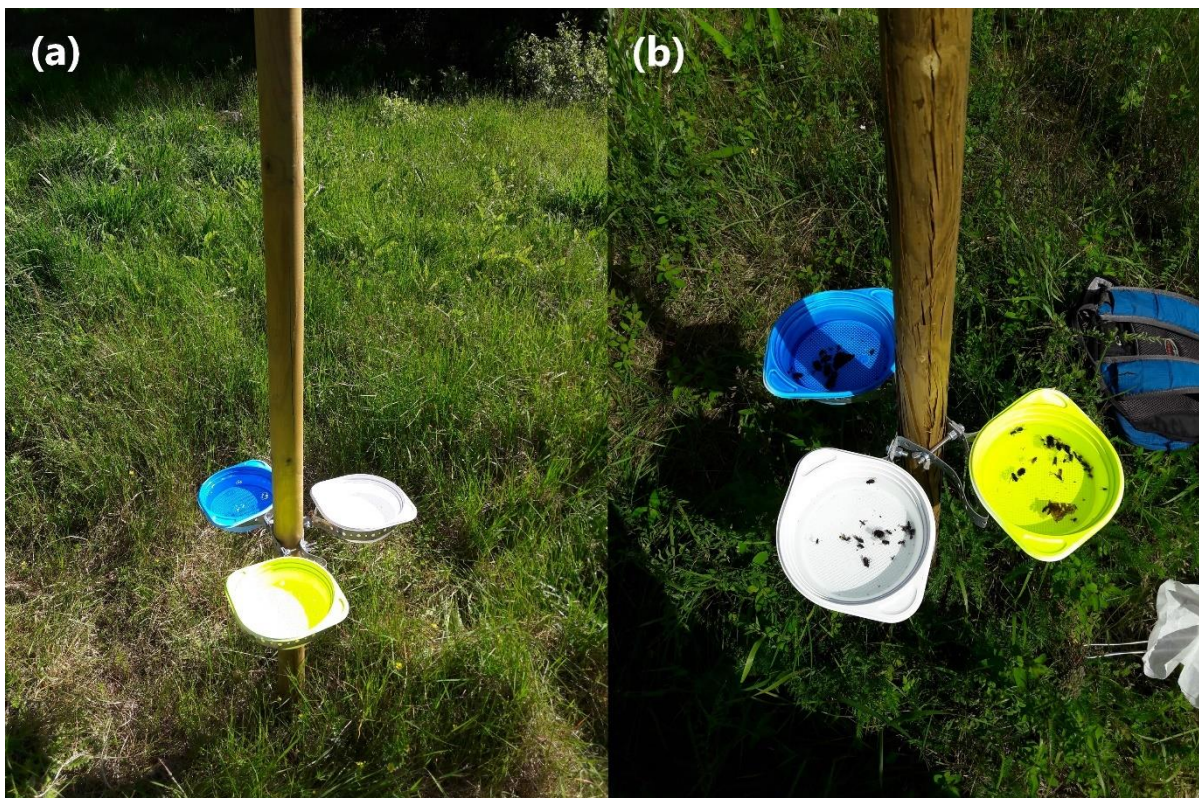


Figure 2. Pan traps in semi-natural grassland before (a) and after (b) 48-hour deployment time.

The bees were sampled during the summer of 2019. Pan traps were only placed out in sites on sunny days with temperatures above 15 degrees and with low wind conditions. To cover all sites simultaneously, traps were prepared and placed out in the sites by two fieldworkers simultaneously over four days. Two days were spent placing the traps, then the traps were out for 48 hours before using two days to collect the data. This process was repeated four times during the field season. Once in May (13th to 16th), once in June (21th to 24th) and twice in July (9th to 13th and 23th to 26th). The original plan was to sample in early June as well, but due to undesirable weather conditions this was not possible. One trap on two different sites had been tampered with during the last sampling, so these traps were re-deployed on the 26th to ensure a homogeneity in our samples.

Sampled bees were collected and stored in pure ethanol. Thereafter, the bees were brought to the lab where they would be pinned and labeled. Later, they would be identified to species level by Markus Sydenham (researcher, NINA). The only species not identified were those of the *Bombus sensu strictu* subgenus (*Bombus cryptarum*, *Bombus lucorum*, *Bombus magnus* and *Bombus terrestris*) as these cannot be reliably identified from morphological characteristics. The rest of the bumblebees were identified by Arnstein Staveløkk (researcher, NINA). The specimens are stored at the Norwegian Institute for Nature Research (NINA), Oslo, Norway.

Quantification of bee habitat

I used maps of early successional areas (i.e. potential bee habitats) derived from satellite imagery (Fig. 3). The maps were made available as part of an ongoing research project at NINA as a means to quantify the amount of early successional habitat within the landscape. Landsat satellite images were used to create the maps. The oldest map was made with images from 1984 to 1988 and the latter was made with images from 2012 to 2016. The use of images from different years ensured that the maps were free of disturbances (such as clouds). The result was maps with each pixel representing a 30m² area. Water bodies were used as control pixels to ensure that the maps would match one another. The maps were then analyzed in a Random Forest model that predicted bee habitat. By using Landsat and terrain data, it was possible to give each pixel a value between 1 and 0 indicating the probability of the raster pixels containing bee habitat (Venter et al., in prep.).

I used the bee habitat maps to estimate the available bee habitat within radii of 250, 500 and 1000m around each study site. By using buffer zones for each site, we were able to extract a percentage of habitat availability for bees both in 1988 and 2016. Given that most bees travel short distances (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007), we could get an indication of bee habitat availability within these buffer zones.

To determine if there had been an increase, decrease or no change in bee habitat availability between 1988 and 2016, I used the quantiles for each buffer zone. Quantiles are a statistical selection, where the cut will have a value that is the same or less as the quantile. I measured the decrease and increase in bee habitat by the 25th percentage extremes (quartiles), while the no change in bee habitat availability would be the value most close to zero.

Functional trait groups

I classified the collected bees according to three different functional traits. For each functional trait, grouping was based on sociality (social or solitary species), on nesting preference (Westrich, 2019) and body size (intertegular distance, ITD) (Roberts, n.d.).

Nesting preference was categorized as aboveground nesters or belowground nesters. Bee species capable of nesting both above and belowground were omitted from the analysis (six species).

The size of bees was categorized as either small or large. We separated all our bee ITD size into quantiles; ITD of 2,28mm was at the 50 percent quantile (median). Everything being 2,28mm or lower were classified as a small bee; anything above 2,28 mm were classified as a large bee.

Honeybees and cleptoparasitic bees were not included in the statistical analyses. This is due to honeybees being regarded as domesticated animals (Artsdatabanken, 2019b) and cleptoparasitic species being more dependent on their host rather than surrounding habitat (Artsdatabanken, 2019a).

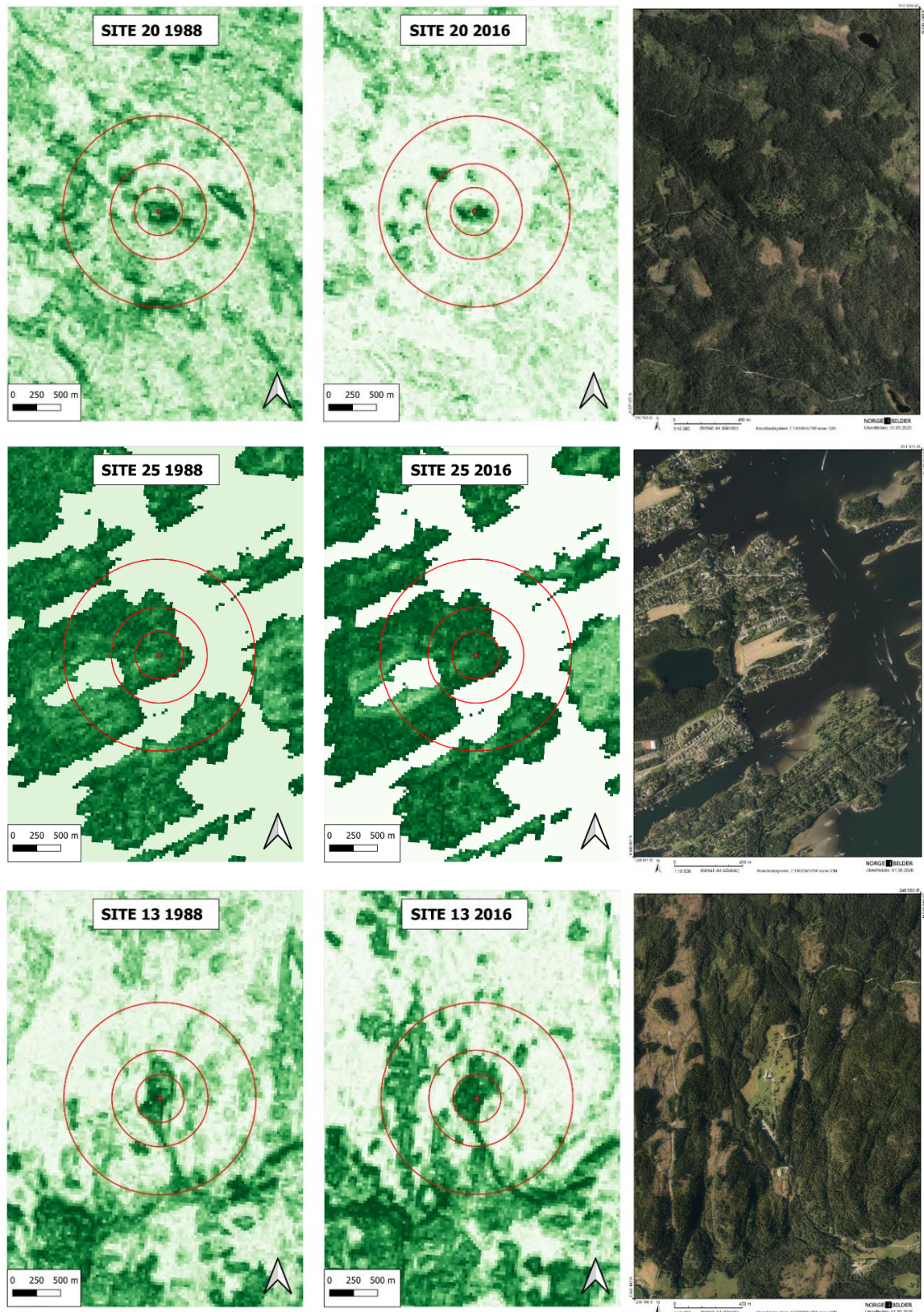


Figure 3. An example of the maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference. The uppermost maps are an example of decrease in bee habitat at a 1000m radius. The middle maps are an example of no change in bee habitat at a 1000m radius and the lower maps are an example of an increase in bee habitat at a 1000m radius (QGIS Development Team, 2020). For a complete overview of the sites, see Appendix I.

Data analysis

The statistical analyses were performed with R studio version 3.8.3 (RStudio Inc., 2019). To analyze if bee richness and abundance were influenced by changes in bee habitat and availability of bee habitat in the present surrounding landscape, I conducted two analyses. I used a Poisson generalized linear model (GLM) for the richness of bees. For the abundance of bees, I used a negative binomial generalized model (NBGLM) due to overdispersion. For the analyses of influence of available bee habitat on different measures of bee diversity, I carried out separate tests for the three different radii from site center; 250 meter, 500 meter and 1000 meter, to explore at which spatial scale I found the strongest relationships. The analyses were tested for six different functional trait groups; solitary bees, bumblebees, belowground nesting bees, aboveground nesting bees, small bees and large bees, as well as all the bees pooled together.

To analyze if bee richness and abundance differed between the site value (A or B) and among sites of different levels of management (1, 2 or 3), I conducted two analyses. For the richness I used a GLM model. The NBGLM model was utilized for the analyses of bee abundance to compensate for overdispersion as well. The analyses were tested for the aforementioned different functional bee groups. I also did one analysis with all the bees pooled together to see how the analysis would respond when the functional traits were not taken into consideration.

Results

A total of 2478 individuals consisting of 98 species of bees were collected (Fig. 4). Among these were 234 individuals of honeybees, and 127 individuals distributed across 16 species of cleptoparasitic bees (cuckoo bees). After excluding these species, I ended up with a dataset of 2117 individuals and 81 species belonging to different functional groups.

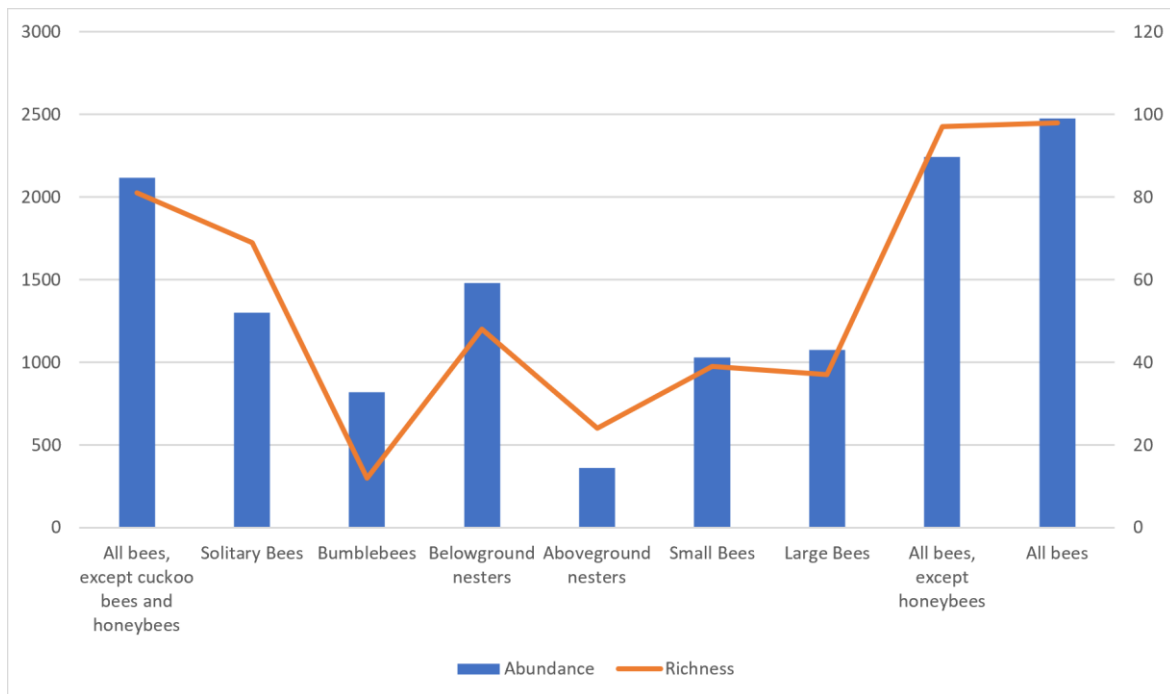


Figure 4. Abundance (2478 observed individuals) and richness (98 observed species) of collected bees recorded within different groups. Honeybees and cuckoo bees were excluded from all statistical analyses.

Bee richness and abundance in different categories of site value and maintenance level

Richness

When analyzing overall bee richness (i.e. all species, except cuckoo bees and honeybees) I found no relationship between overall bee richness and site value (A or B), nor any relationship between overall bee richness and level of management (1,2 or 3) (Table 1; Fig. 5). I did not find any significant impact of site value or level of management when testing for different functional trait responses from solitary bee richness (Table 2), bumblebee richness (Table 3), belowground nesting bee richness (Table 4), aboveground nesting bee richness (Table 5), small bee richness (Table 6) and large bee richness (Table 7).

Abundance

When analyzing overall bee abundance (i.e. all species, except cuckoo bees and honeybees), I found no relationship between overall bee abundance and site value (A or B), nor any relationship between overall bee abundance and level of management (1, 2 or 3) (Table 8; Fig 6). I did not find any significant impact of site value or level of different functional trait responses from solitary bee abundance (Table 9), bumblebee abundance (Table 10), belowground nesting bee abundance (Table 11), aboveground nesting bee abundance (Table 12), small bee abundance (Table 13) and large bee abundance (Table 14).

Landscape change and available bee habitat

Richness

I found that the relationship between solitary bee richness and availability of bee habitat in the current landscape depended on the degree of landscape change, both when considering available bee habitat within 250m and 500m radii (Table 15; $p_{250}=0.017$, $p_{500}=0.005$). A similar trend was also apparent when considering a radius of 1000m ($p_{1000}=0.009$). Solitary bee species richness increased with available bee habitat for sites situated in landscapes, in which the amount of bee habitat had decreased since 1988 (Fig. 7a; fig. 7d; fig 7g). In contrast, for sites situated in landscapes that have had no change or an increase in bee habitat, there was no clear relationship between solitary bee richness and current available habitat (Fig. 7b-c; Fig. 7e-f; F. 7h-i).

For bumblebee richness I found no clear relationship between current availability of bee habitat or the degree of landscape change (Table 16). Bumblebee richness neither decreased nor increased with available bee habitat for sites situated in landscapes, where the amount of bee habitat either had decreased, increased or experienced no change (Fig. 8a-i).

I found no relationship between belowground nesting bee richness and availability of bee habitat and degree of landscape change, when considering all radii (Table 17). Belowground nesting bee richness increased somewhat with available bee habitat for sites situated in landscapes, in which the amount of bee habitat had decreased since 1988 (Fig. 9a; fig. 9d; fig. 9g). In contrast, for sites situated in landscapes that have had no change or increase in bee habitat, there was no clear relationship between belowground nesting bee richness and current available habitat (Fig. 9b-c; Fig. 9e-f; Fig. 9h-i).

I found a strong relationship between richness of small bees and availability of bee habitat in the current landscape depended on the degree of landscape change, both when considering

available bee habitat within 250m, 500m radii (Table 19; $p_{250}=0.003$, $p_{500}=0.0005$) as well as 1000m radius ($p_{1000}=0.002$). A similar trend was also apparent when considering the relationship between small bee richness and the difference between the present available bee habitat and the past available bee habitat. This relationship was present at 250m, 500m and 1000m radii (Table 19; $p_{250}=0.009$, $p_{500}=0.002$, $p_{1000}=0.005$). Small bee richness increased with available bee habitat for sites situated in landscapes, in which the amount of bee habitat had decreased since 1988 (Fig. 11a; Fig. 11d; Fig. 11g). In contrast, there was no clear relationship for sites situated in landscapes that have had no change in bee habitat (Fig. 11b; Fig. 11h), but small bee richness decreased in sites situated in landscapes, where the amount of bee habitat had increased since 1988 (Fig. 11c; Fig. 11f; Fig. 11i).

The relationship between richness of large bees and availability of bee habitat in the current landscape depended on the current available bee habitat both when considering available bee habitat within 250m and 500m radii (Table 20; $p_{250}=0.042$, $p_{500}=0.049$). This trend was not apparent when considering a radius of 1000m ($p_{1000}=0.101$). I found no clear relationship between large bee richness and available bee habitat for sites situated in landscapes, where the amount of bee habitat had decreased, increased or had not changed since 1988 (Fig. 12a-c; Fig. 12d-i).

I found a relationship between overall bee richness and availability of bee habitat in the current landscape depended on the degree of landscape change, both when considering available bee habitat within 250m and 500m radii (Table 21; $p_{250}=0.037$, $p_{500}=0.03$). I found a similar, but not statistically significant trend ($p_{1000}=0.078$) when considering a radius of 1000m. However, I did find a relationship between overall bee richness and the present available bee habitat within a 250m radius (Table 21; $p_{250}=0.074$). Overall bee richness increased with available bee habitat for sites situated in landscapes in which the amount of bee habitat had decreased since 1988 (Fig. 13a; fig. 13d; fig. 13g), as well as sites situated in landscapes where the amount of bee habitat had no changes since 1988, at a 250m radius (Fig. 13b). In contrast, there was no clear relationship between overall bee richness for sites situated in landscapes that have not changed at 500m and 1000m radii, or increased in available bee habitat (Fig. 13c; Fig. 13e-f; Fig. 13h-i).

Abundance

For solitary bees, I found that the relationship between solitary bee abundance and availability of bee habitat in the current landscape depended on the degree of landscape change, when considering available bee habitat within a 250m radius (Table 22; $p_{250}=0.047$). I did not find a similar pattern when considering a radius of 500m and 1000m ($p_{500}=0.204$, $p_{1000}=0.452$). I found that solitary bee abundance increased with available bee habitat for

sites situated in landscapes, where the amount of bee habitat had decreased since 1988 (Fig. 14a; Fig. 14d; Fig. 14g). In contrast, for sites situated in landscapes that had not changed or increased in bee habitat, there was no clear relationship between solitary bee abundance and current available habitat (Fig. 14b-c; Fig. 14e-f; Fig. 14h-i).

I found that the relationship between bumblebee abundance and availability of bee habitat in the current landscape depended on the current available bee habitat, both when considering available bee habitat within 500m and 1000m radii (Table 23; $p_{500}=0.032$, $p_{1000}=0.035$). This trend was not significant when considering a radius of 250m ($p_{250}=0.095$). I found no clear relationship between bumblebee abundance and available bee habitat for sites situated in landscapes, where the amount of bee habitat had decreased, increased or not changed since 1988 (Fig. 15a-i).

For belowground nesting bees, I found no clear relationship between belowground nesting bee abundance and availability of bee habitat (Table 24). Nor was there any clear relationship between bumblebee abundance and available bee habitat for sites situated in landscapes, where the amount of bee habitat had decreased, increased or not changed since 1988 (Fig. 16a-i). This trend was also apparent when considering aboveground nesting bee abundance (Table 25; Fig. 17), small bee abundance (Table 26; Fig. 18) and large bee abundance (Table 27; Fig. 19).

I found no clear relationship between overall bee abundance and availability of bee habitat (Table 28). Nor was there any clear relationship between overall bee abundance and available bee habitat for sites situated in landscapes, where the amount of bee habitat had decreased, increased or not changed since 1988 (Fig. 20a-i).

Discussion

I studied wild bees in semi-natural grasslands to assess if bee diversity within this nature type depended on the: level of management; site value; and landscape conditions as well as historic changes in these landscape conditions. While bee species richness and abundance were strongly related to the amount of high habitat availability in the surrounding landscape and how this had changed over time, I found no support for my hypotheses related to how good management status or high site-specific value of meadows would promote bee diversity.

The amount of potential habitat in the surrounding landscape is an important determinant of wild bee diversity (Jauker et al., 2009; Le Féon et al., 2013; Öckinger & Smith, 2007). Local bee diversity increases with habitat conditions at a landscape scale for several reasons. This can be due to how different habitat patches contribute with complimentary resources such as nesting sites or foraging grounds (Westrich, 1996) and thus increase bee populations (Potts et al., 2005). I found that bee diversity in general, and for solitary bee diversity in particular, increased with the amount of bee habitat in the surrounding landscape with the strongest relationship at small spatial scales (i.e. 250m and 500m). This is line previous findings such as Steffan-Dewenter et al. (2002). In their study they had buffer radii from 250m up to 3000m, as 3000m is the known foraging range for honeybees. Their study found a positive relationship between richness and abundance of solitary bees and the proportion of semi-natural grasslands, where the radius of 250m was the most significant spatial scale. As the amount of bee habitat within the landscape decreases, the distance between patches will inevitably increase which may make species less likely to fly between patches in their search for resources.

Similar to my findings, Steffan-Dewenter et al. (2002) found that bumblebees did not have a relationship with the landscape context for any of the radii.. I found no effect of the amount of bee habitat within distances less than 500m on bumblebee diversity. It is not uncommon for bumblebees to fly far from their nesting site. One study by Goulson and Stout (2001) showed that when testing the home range of *Bombus terrestris*, they could fly as far as 9.8km. In my study, bumblebee abundance was not affected by the shortest radius, 250m, but it was affected at 500m and 1000m radii. Even though my largest radius was 1000m, they could respond to radii beyond that.

Because the nesting resource requirements of bees differ between below and above ground nesting bees, a variety of local habitat types are important to sustain wild bee diversity (Westrich, 1996). Having a variety of trees as well as shrubs in different sizes provides a heterogenous habitat able to provide for species with different functional traits

(Sjödin et al., 2008). Semi-natural grasslands can contribute with aboveground nesting materials, such as dead wood, stems, trees and shrubs (Forrest et al., 2015). I found that the species richness of aboveground nesting bees increased with the bee habitat availability at 250m and 500m radii. Shrubs and stems are plants that could fully mature in under 30 years. This could explain why my aboveground nesting bee richness did not have a relationship with the past landscape bee habitat availability. By only responding at the shorter radii, it could be that the aboveground nesting bee richness prefer to have the nesting source and foraging source in a closer proximity. This is supported by Williams et al. (2010) who found that aboveground nesting bees are more dependent on nesting substrates in close proximity and vulnerable to habitat fragmentation. As for belowground nesting bees, I found no relationship between the species richness or abundance of belowground nesting bees and the amount of landscape change during the past 30 years. Belowground nesting bees has been shown to be vulnerable to tillage (Williams et al., 2010). Tillage are not a management practice of semi-natural grasslands. This could explain the lack of relationship between belowground nesting bees and semi-natural grasslands, as their nesting ground would not be disturbed.

The most prominent results for the landscape change and available bee habitat models was from the small bees and large bees. I found a strong correlation between small bees and past landscape habitat availability compared to the larger bees, who were more dependent on present landscape habitat availability. The small bee species richness responded to all my spatial scales (250m, 500m and 1000m radii), as well as the change in bee habitat availability between 2016 and 1988 (250m, 500m and 1000m radii). The larger bee species richness responded to present landscape habitat availability at 250m and 500m radii, but not a 1000m radius. This is similar to Ekroos et al. (2013), who found that richness and abundance for bumblebees, a larger bee group, decreased with increasing distance to semi-natural grasslands. The foraging range of bees are strongly correlated to the intertegular distance (ITD) size of bees (Gathmann & Tschardt, 2002; Greenleaf et al., 2007). However, foraging range is not the same as dispersal range. Foraging is a frequent traveling range, while dispersal is a nest seeking range and may be longer. Even so, larger bodied has been shown to have a higher dispersal range than small bodied bees (López-Urbe et al., 2019). Small bees are more vulnerable to landscape change, as they have more restricting dispersal range.

My study shows that solitary bee species, small bee species and bee species overall have the most diverse communities in areas where the reduction in habitat availability is greatest, and where bee habitat has often been lost due to e.g. forest encroachment. This is in contrast to Krauss et al. (2009) who found that bees were more dependent on habitat area rather than the age of the habitat. Their study had an age gradient of over 120 years. They

suggest that their sites, limestone quarries, were “only of minor importance for wild bees” and that the bees have been able to recolonize such areas. The presence of small bees would also mean that they could act as a reservoir for reintroducing bee populations to nearby suitable habitats (Öckinger & Smith, 2007).

Several studies have found a positive relationship between different bee communities and semi-natural grasslands (Cusser et al., 2019; Ekroos et al., 2013; Kremen et al., 2018). My study shows that age as well as area is an important factor for some functional group richness, and the importance to observe bees as different groups rather than just one group or group them together, to fully understand the semi-natural landscapes importance.

Perhaps the most counterintuitive results from my own study, is that there was an overall higher presence of bee species in sites situated in landscapes that have experienced a decrease in available bee habitat availability during the last 30 years. These results were similar for the solitary bee richness (Fig. 7a; Fig. 7d; Fig. 7g), small bee richness (Fig. 11a; Fig. 11d; Fig. 11g) as well as the overall richness (Fig. 13a; Fig. 13d; Fig. 13g). This trend could most likely be explained by the location of the sites that have experienced this decrease over the past 30 years. Several of the sampled sites were located in urban areas close to the sea level. It is common to find more bee species in regions at a low elevation (Sydenham et al., 2015). My habitat availability and landscape change model does not take meters above sea level (m a.s.l.) into account, due to m a.s.l. being strongly correlated with the radii of the sites (Correlation coefficient: -0.8). However, if the landscapes with the largest decrease in bee habitat availability are in areas with low elevation, my results could indicate a high wild bee richness and abundance in landscapes with low elevation. This would also indicate that these areas are vulnerable to habitat loss. These indications invite to further research.

Nonetheless, my results indicate that areas with the largest presence of bees are in areas with the largest decrease of bee habitat availability in landscapes (e.g. reforestation) during the past 30 years. While these sites have the largest bee diversity, these sites are also the most vulnerable landscape change.

Semi-natural grasslands act as a local source of different habitats and support wild bees with different life traits (Potts et al., 2005). Therefore, the management of semi-natural grasslands are essential to best maintain these qualities. Generally, it is intuitive to conclude that the better the management level a semi-natural grassland has, the better bee habitat availability it provides. Wild bee richness has been found to have a negative relationship with landscapes with low grassland coverage, but not with landscapes with medium or high grassland coverage (Jauker et al., 2009). Jauker et al.'s (2009) study suggest that landscapes with medium grassland coverage could be sufficient enough to support wild bee richness. Similar results were found by Söderström et al. (2001), who looked at bumblebees in semi-natural grasslands in Sweden. They found that the bumblebee richness decreased with increasing grazing intensity. However, these results were not found by Sjödin et al. (2008). Unlike the two previous studies, Sjödin et al. (Sjödin et al., 2008) found no discernible difference in bee richness and abundance among the different levels of management.

I found no relationship between level of management and wild bee richness nor abundance in my study. In contrast, Steffan-Dewenter and Leschke (2003) found that abandoned semi-natural grasslands would hold a higher level of aboveground nesting bee species, as the volume of dead wood would not be cleared. While my results could indicate a higher number of aboveground nesting bees in abandoned sites (Fig. 5d; Fig. 6d), none of my results were significant enough to fully support that statement. One reason for the lack of results could be that flower distribution rather than level of management is a more crucial predictor. Both Sjödin et al. (2008) and Söderström et al. (2001) found that bee presence in semi-natural grasslands were related to the flower composition at a local scale.

Another reason for the lack of results could be the criteria for the level of management in Norway, which are determined by the degree of overgrowth (Miljødirektoratet, 2014). Well managed semi-natural grasslands have no level of overgrowth. Low managed means that it is not being well managed enough to prevent overgrowth, and no management means it has begun to overgrow with plants such as *Hypericum macalatum* and *Filipendula ulmaria* beginning to dominate the field. Fairly to heavily overgrown is when the semi-natural grassland is overgrown, but not so severely that the semi-natural grassland loses its value. Lastly, poorly managed is when the semi-natural grassland is treated wrongly, one example being overgrazing of fields. These criteria are more based on historical cultural management practices of semi-natural grasslands rather than the biological diversity aspect. While these two categories can intertwine and relate, level of management is not necessarily the best measurement for predicting the presence of wild bee abundance and richness.

Norwegian semi-natural grasslands are categorized by site value; national importance (A), regional importance (B) and local importance (C). These values are based off “DN-håndbok 13-2007”, a habitat mapping tool for the Norwegian government (Miljødirektoratet, 2014). The site values are based on several different factors, such as size, indicator plant species (such as: *Arnica montana*, *Gentianella campestris* and *Scorzonera humilis*), plant species richness, threatened plant species, closeness to other cultural landscapes and continuous management (Miljødirektoratet, n.d.). For full overview, see Appendix II (Table A1). In two cases, insects had been mapped, but among these, only one bumblebee species was observed (*Bombus humilis* in site 37). The semi-natural grasslands are mapped and valued with the historical cultural management in mind.

While this is not directly correlated to wild bee richness and abundance, this might not be negative for wild bees. Le Féon et al. (2013) found a positive relation between long-term grasslands and solitary bee abundance. This trend of having a positive relation between semi-natural grasslands and insect abundance can be seen in other studies as well (Ekroos et al., 2013; Söderström et al., 2001). However, as seen in my study, while mapping the value after the historical cultural management could have beneficial effects for insects, and moreover bees, the relationship between these two are not given. To better conserve bee species, semi-natural grasslands should also be mapped and valued with criteria that benefits the wild bees.

Except for the bumblebee abundance, none of my other functional groups abundance responded to my landscape change and available bee habitat models. One possible explanation could be that while wild bee richness depends on changes in bee habitat availability in the semi-natural grasslands, the wild bee abundance are dependent on the flower composition. This is in accordance with previously conducted studies such as Cusser et al. (2019), Rasran et al. (2018) and Ollerton et al. (2011). Unfortunately, data on floral resources were not available for my study sites. Future studies should aim to assess if the evaluation of semi-natural grasslands captures the floral diversity within sites.

Conclusions and management implications

This study shows that some functional bee groups have a relationship with historic landscape changes, while others seem to mainly respond to present landscape conditions. Larger bees and aboveground nesting bees are more affected by the present landscape habitat availability, while smaller bees and solitary bees are more affected by the past landscape habitat availability. Wild bees are a diverse group of species with different life traits, and thus respond differently to landscape conditions. Different bees with different life traits can affect each other when grouped into one model, possibly leading to a loss of important information. When conducting bee studies, it would be strongly advised to split the wild bees into groups, to better understand their requirements.

That the most species rich semi-natural grasslands are found in landscapes where forest encroachment during the past 30 years has led to a loss of bee habitat is encouraging as it suggests that these grasslands still contain some of the bee diversity that was historically present in these landscapes. However, because bee diversity in these landscapes also increases with the present day proportion of bee habitat, management schemes should focus on restoring semi-natural grasslands in these landscapes. In order to assess the quality of semi-natural grasslands as wild bee habitat, there is a need for new assessment criteria. While semi-natural grasslands and insect diversity and abundance are related, the current Norwegian criteria for this habitat does not reflect this relation. The current criteria cover the historical cultural management practices of grassland farming; and added criteria covering wild bee abundance and richness in the semi-natural grasslands would be beneficial to better manage wild bee species.

Tables

Semi-natural grasslands with site value and level of maintenance

Table 1. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Overall Sampled (81 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3= Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.778	0.072	38.590	<0.001
Site Value B	0.055	0.186	0.298	0.766
Poorly Managed Sites	0.055	0.122	0.453	0.651
Abandoned or altered sites	-0.037	0.193	-0.191	0.849
Site Value B x Poorly Managed Sites	-0.132	0.246	-0.537	0.591
Site Value B x Abandoned or altered sites	0.191	0.274	0.697	0.486
Site Value x Level of Management				0.446

Table 2. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Solitary Bees (69 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.435	0.085	28.502	<0.001
Site Value B	0.007	0.225	0.032	0.974
Poorly Managed Sites	0.130	0.142	0.916	0.360
Abandoned or altered sites	-0.372	0.230	-0.162	0.871
Site Value B x Poorly Managed Sites	-0.197	0.295	-0.620	0.503
Site Value B x Abandoned or altered sites	0.269	0.328	0.820	0.412
Site Value x Level of Management				0.296

Table 3. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Bumblebees (12 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	1.540	0.134	11.528	<0.001
Site Value B	0.164	0.330	0.498	0.618
Poorly Managed Sites	-0.154	0.244	-0.632	0.527
Abandoned or altered sites	-0.036	0.359	-0.101	0.919
Site Value B x Poorly Managed Sites	0.059	0.448	0.131	0.895
Site Value B x Abandoned or altered sites	0.006	0.501	0.011	0.991
Site Value x Level of Management				0.990

Table 4. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Belowground Nesting Bees (48 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.303	0.091	25.224	<0.001
Site Value B	0.049	0.237	0.206	0.837
Poorly Managed Sites	-0.034	0.160	-0.212	0.832
Abandoned or altered sites	-0.163	0.259	-0.627	0.531
Site Value B x Poorly Managed Sites	-0.120	0.318	-0.378	0.705
Site Value B x Abandoned or altered sites	0.253	0.360	0.705	0.481
Site Value x Level of Management				0.541

Table 5. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Aboveground Nesting Bees (24 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	1.253	0.154	8.119	<0.001
Site Value B	0.000	0.408	0.000	1.000
Poorly Managed Sites	0.288	0.244	1.179	0.238
Abandoned or altered sites	0.357	0.352	1.014	0.311
Site Value B x Poorly Managed Sites	-0.094	0.511	-0.183	0.855
Site Value B x Abandoned or altered sites	0.033	0.547	0.060	0.952
Site Value x Level of Management				0.962

Table 6. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Small bees (39 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.114	0.099	21.614	<0.001
Site Value B	0.111	0.250	0.445	0.656
Poorly Managed Sites	0.163	0.163	0.999	0.318
Abandoned or altered sites	-0.435	0.317	-1.372	0.170
Site Value B x Poorly Managed Sites	-0.274	0.329	-0.831	0.406
Site Value B x Abandoned or altered sites	0.597	0.410	1.455	0.146
Site Value x Level of Management				0.063

Table 7. Parameter estimates, test statistics and associated p-values from the GLM analysis on Richness for Large bees (37 observed species) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.015	0.105	19.115	<0.001
Site Value B	-0.143	0.297	-0.482	0.630
Poorly Managed Sites	-0.143	0.192	-0.746	0.455
Abandoned or altered sites	0.236	0.252	0.936	0.349
Site Value B x Poorly Managed Sites	0.181	0.388	0.466	0.641
Site Value B x Abandoned or altered sites	0.032	0.400	0.080	0.937
Site Value x Level of Management				0.875

Table 8. Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Overall Sampled (2117 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	4.220	0.133	31.630	<0.001
Site Value B	-0.231	0.356	-0.648	0.517
Poorly Managed Sites	-0.355	0.233	-1.523	0.128
Abandoned or altered sites	0.043	0.353	0.122	0.903
Site Value B x Poorly Managed Sites	0.493	0.466	1.060	0.289
Site Value B x Abandoned or altered sites	0.424	0.518	0.819	0.413
Site Value x Level of Management				0.559

Table 9. Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Solitary Bees (1300 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	3.722	0.158	23.554	<0.001
Site Value B	-0.181	0.421	-0.429	0.668
Poorly Managed Sites	-0.326	0.277	-1.179	0.238
Abandoned or altered sites	-0.097	0.420	-0.232	0.817
Site Value B x Poorly Managed Sites	0.396	0.552	0.718	0.473
Site Value B x Abandoned or altered sites	0.573	0.614	0.933	0.351
Site Value x Level of Management				0.639

Table 10. Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Bumblebees (817 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	3.283	0.171	19.190	<0.001
Site Value B	-0.313	0.460	-0.680	0.496
Poorly Managed Sites	-0.402	0.302	-1.334	0.182
Abandoned or altered sites	0.228	0.448	0.509	0.611
Site Value B x Poorly Managed Sites	0.651	0.602	1.082	0.279
Site Value B x Abandoned or altered sites	0.225	0.664	0.338	0.735
Site Value x Level of Management				0.542

Table 11. Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Belowground Nesting Bees (1478 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.079	0.155	13.460	<0.001
Site Value B	-0.375	0.442	-0.847	0.397
Poorly Managed Sites	0.433	0.254	1.707	0.088
Abandoned or altered sites	0.560	0.375	1.494	0.135
Site Value B x Poorly Managed Sites	0.237	0.547	0.434	0.665
Site Value B x Abandoned or altered sites	0.635	0.590	1.077	0.282
Site Value x Level of Management				0.544

Table 12. Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Aboveground Nesting Bees (361 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.

	Estimate	Std. Error	z	p
Intercept	2.079	0.155	13.460	<0.001
Site Value B	-0.375	0.442	-0.847	0.397
Poorly Managed Sites	0.433	0.254	1.707	0.088
Abandoned or altered sites	0.560	0.375	1.494	0.135
Site Value B x Poorly Managed Sites	0.237	0.547	0.434	0.665
Site Value B x Abandoned or altered sites	0.635	0.590	1.077	0.282
Site Value x Level of Management				0.559

Table 13. *Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Small Bees (1030 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.*

	Estimate	Std. Error	z	p
Intercept	3.507	0.160	21.862	<0.001
Site Value B	-0.249	0.429	-0.579	0.563
Poorly Managed Sites	-0.301	0.281	-1.072	0.284
Abandoned or altered sites	-0.268	0.430	-0.623	0.533
Site Value B x Poorly Managed Sites	0.111	0.565	0.197	0.844
Site Value B x Abandoned or altered sites	0.898	0.627	1.432	0.152
Site Value x Level of Management				0.318

Table 14. *Parameter estimates, test statistics and associated p-values from the NBGLM analysis on Abundance for Large Bees (1074 observed individuals) in different categories of site value (A=Nationally important, B=Regionally or Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). P-value of Site Value x Level of Management is derived from a likelihood ratio test.*

	Estimate	Std. Error	z	p
Intercept	3.539	0.154	22.960	<0.001
Site Value B	-0.243	0.413	-0.588	0.556
Poorly Managed Sites	-0.432	0.272	-1.591	0.112
Abandoned or altered sites	0.268	0.404	0.664	0.506
Site Value B x Poorly Managed Sites	0.826	0.539	1.531	0.126
Site Value B x Abandoned or altered sites	0.051	0.597	0.086	0.931
Site Value x Level of Management				0.215

Landscape change and available bee habitat analysis

Table 15. *Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Solitary Bees (69 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.154	0.254	8.487	<0.001
Current habitat	0.673	0.387	1.741	0.082
Change in habitat	4.298	2.282	1.883	0.060
Current habitat x Change in habitat	-9.469	3.954	-2.395	0.017
<u>500m</u>				
Intercept	2.298	0.208	11.036	<0.001
Current habitat	0.494	0.349	1.413	0.158
Change in habitat	3.741	1.639	2.283	0.022
Current habitat x Change in habitat	-10.274	3.648	-2.816	0.005
<u>1000m</u>				
Intercept	2.369	0.202	11.733	<0.001
Current habitat	0.379	0.351	1.081	0.280
Change in habitat	3.926	1.698	2.312	0.021
Current habitat x Change in habitat	-10.731	4.133	-2.596	0.009

Table 16. *Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Bumblebees (12 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	1.304	0.416	3.133	0.002
Current habitat	0.391	0.635	0.616	0.538
Change in habitat	-0.670	3.192	-0.210	0.834
Current habitat x Change in habitat	-1.168	5.564	-0.210	0.834
<u>500m</u>				
Intercept	1.333	0.342	3.896	<0.001
Current habitat	0.312	0.571	0.546	0.585
Change in habitat	-1.808	2.475	-0.731	0.465
Current habitat x Change in habitat	1.825	5.624	0.325	0.746
<u>1000m</u>				
Intercept	1.281	0.336	3.811	<0.001
Current habitat	0.401	0.576	0.697	0.486
Change in habitat	-2.798	2.449	-1.143	0.253
Current habitat x Change in habitat	4.458	6.242	0.714	0.475

Table 17. Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Belowground Nesting Bees (48 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.207	0.276	8.003	<0.001
Current habitat	0.266	0.425	0.626	0.532
Change in habitat	3.971	2.429	1.635	0.102
Current habitat x Change in habitat	-7.378	4.245	-1.738	0.082
<u>500m</u>				
Intercept	2.279	0.226	0.226	<0.001
Current habitat	0.161	0.161	0.385	0.676
Change in habitat	2.930	2.930	1.777	0.099
Current habitat x Change in habitat	-6.941	4.023	-1.725	0.084
<u>1000m</u>				
Intercept	2.313	0.221	10.460	<0.001
Current habitat	0.095	0.389	0.243	0.808
Change in habitat	2.983	1.826	1.634	0.102
Current habitat x Change in habitat	-7.230	4.546	-1.591	0.112

Table 18. Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Aboveground Nesting Bees (24 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	0.444	0.454	0.979	0.328
Current habitat	1.626	0.670	2.426	0.015
Change in habitat	0.731	3.813	0.192	0.848
Current habitat x Change in habitat	-6.923	6.484	-1.068	0.286
<u>500m</u>				
Intercept	0.814	0.364	2.233	0.026
Current habitat	1.181	0.590	2.002	0.045
Change in habitat	1.991	2.766	0.720	0.472
Current habitat x Change in habitat	-9.122	6.030	-1.513	0.130
<u>1000m</u>				
Intercept	0.954	0.351	2.716	0.007
Current habitat	0.979	0.590	1.659	0.097
Change in habitat	1.838	2.832	0.649	0.516
Current habitat x Change in habitat	-8.065	6.779	-1.190	0.234

Table 19. Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Small Bees (39 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.266	0.295	7.687	<0.001
Current habitat	0.060	0.457	0.131	0.896
Change in habitat	7.021	2.703	2.598	0.009
Current habitat x Change in habitat	-13.829	4.720	-2.930	0.003
<u>500m</u>				
Intercept	2.352	0.248	9.470	<0.001
Current habitat	-0.119	0.429	-0.277	0.782
Change in habitat	5.956	1.951	3.053	0.002
Current habitat x Change in habitat	-15.232	4.362	-3.492	0.0005
<u>1000m</u>				
Intercept	2.314	0.236	9.785	<0.001
Current habitat	-0.084	0.423	-0.199	0.842
Change in habitat	5.694	2.007	2.838	0.005
Current habitat x Change in habitat	-15.362	4.891	-3.141	0.002

Table 20. Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Large Bees (37 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	1.385	0.328	4.225	<0.001
Current habitat	1.003	0.492	2.037	0.042
Change in habitat	-1.462	2.600	-0.562	0.574
Current habitat x Change in habitat	0.184	4.491	0.041	0.967
<u>500m</u>				
Intercept	1.529	0.264	5.788	<0.001
Current habitat	0.850	0.431	1.972	0.049
Change in habitat	-1.653	1.969	-0.840	0.401
Current habitat x Change in habitat	1.761	4.438	0.397	0.700
<u>1000m</u>				
Intercept	1.623	0.261	6.214	<0.001
Current habitat	0.724	0.441	1.642	0.101
Change in habitat	-1.885	1.985	-0.950	0.342
Current habitat x Change in habitat	3.287	4.997	0.658	0.511

Table 21. Parameter estimates, test statistics and associate p-values for the GLM analysis of Richness for Overall Sampled (81 observed species) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.511	0.217	11.589	<0.001
Current habitat	0.589	0.330	1.784	0.074
Change in habitat	2.644	1.850	1.430	0.153
Current habitat x Change in habitat	-6.706	3.212	-2.088	0.037
<u>500m</u>				
Intercept	2.626	0.178	14.776	<0.001
Current habitat	0.437	0.298	1.467	0.142
Change in habitat	2.041	1.361	1.499	0.134
Current habitat x Change in habitat	-6.611	3.050	-2.167	0.030
<u>1000m</u>				
Intercept	2.658	0.173	15.368	<0.001
Current habitat	0.384	0.299	1.282	0.200
Change in habitat	1.823	1.388	1.314	0.189
Current habitat x Change in habitat	-6.044	3.425	-1.765	0.078

Table 22. Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Solitary Bees (1300 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	3.528	0.484	7.292	<0.001
Current habitat	0.445	0.748	0.595	0.552
Change in habitat	6.674	3.866	1.726	0.084
Current habitat x Change in habitat	-13.509	6.795	-1.988	0.047
<u>500m</u>				
Intercept	3.553	0.408	8.719	<0.001
Current habitat	0.330	0.693	0.477	0.633
Change in habitat	2.695	3.076	0.876	0.381
Current habitat x Change in habitat	-8.959	7.060	-1.269	0.204
<u>1000m</u>				
Intercept	3.621	0.408	8.871	<0.001
Current habitat	0.190	0.718	0.265	0.791
Change in habitat	1.806	3.169	0.570	0.569
Current habitat x Change in habitat	-6.080	8.088	-0.752	0.452

Table 23. Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Bumblebees (817 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.418	0.523	4.625	<0.001
Current habitat	1.343	0.805	1.669	0.095
Change in habitat	-0.536	4.112	-0.130	0.896
Current habitat x Change in habitat	-2.208	7.212	-0.306	0.760
<u>500m</u>				
Intercept	2.367	0.414	5.721	<0.001
Current habitat	1.496	0.698	2.142	0.032
Change in habitat	-4.375	3.114	-1.405	0.160
Current habitat x Change in habitat	8.090	7.146	1.132	0.258
<u>1000m</u>				
Intercept	2.458	0.392	6.277	<0.001
Current habitat	1.439	0.682	2.110	0.035
Change in habitat	-5.624	3.017	-1.864	0.062
Current habitat x Change in habitat	14.273	7.723	1.848	0.065

Table 24. Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Belowground Nesting Bees (1478 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	3.510	0.483	7.274	<0.001
Current habitat	0.692	0.746	0.928	0.354
Change in habitat	6.153	3.857	1.595	0.111
Current habitat x Change in habitat	-11.592	6.779	-1.710	0.087
<u>500m</u>				
Intercept	3.444	0.412	8.366	<0.001
Current habitat	0.730	0.669	1.044	0.296
Change in habitat	-0.548	3.108	-0.176	0.860
Current habitat x Change in habitat	0.030	7.141	0.004	0.997
<u>1000m</u>				
Intercept	3.565	0.403	8.851	<0.001
Current habitat	0.574	0.707	0.812	0.417
Change in habitat	-1.482	3.124	-0.474	0.635
Current habitat x Change in habitat	5.126	7.994	0.641	0.521

Table 25. *Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Aboveground Nesting Bees (361 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000 m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	1.634	0.496	3.292	0.001
Current habitat	1.259	0.758	1.662	0.097
Change in habitat	1.462	3.919	0.373	0.709
Current habitat x Change in habitat	-10.168	6.829	-1.489	0.136
<u>500m</u>				
Intercept	1.940	0.401	4.839	<0.001
Current habitat	0.903	0.674	1.339	0.181
Change in habitat	3.316	3.027	1.096	0.273
Current habitat x Change in habitat	-13.187	6.844	-1.927	0.054
<u>1000m</u>				
Intercept	1.888	0.412	4.587	<0.001
Current habitat	0.965	0.715	1.350	0.177
Change in habitat	1.626	3.192	0.510	0.610
Current habitat x Change in habitat	-10.370	7.995	-1.297	0.195

Table 26. *Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Small Bees (1030 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	3.348	0.517	6.476	<0.001
Current habitat	0.326	0.799	0.408	0.683
Change in habitat	6.240	4.114	1.517	0.129
Current habitat x Change in habitat	-14.023	7.232	-1.939	0.053
<u>500m</u>				
Intercept	3.274	0.432	7.578	<0.001
Current habitat	0.386	0.734	0.525	0.600
Change in habitat	2.456	3.258	0.754	0.451
Current habitat x Change in habitat	-9.268	7.470	-1.241	0.215
<u>1000m</u>				
Intercept	3.262	0.432	7.552	<0.001
Current habitat	0.410	0.759	0.541	0.589
Change in habitat	1.313	3.351	0.392	0.695
Current habitat x Change in habitat	-5.835	8.546	-0.683	0.495

Table 27. *Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Large Bees (1074 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	2.814	0.471	5.977	<0.001
Current habitat	1.198	0.726	1.651	0.099
Change in habitat	1.258	3.732	0.337	0.736
Current habitat x Change in habitat	-3.777	6.551	-0.576	0.564
<u>500m</u>				
Intercept	2.888	0.389	7.422	<0.001
Current habitat	1.122	0.659	1.703	0.089
Change in habitat	-2.363	2.936	-0.805	0.421
Current habitat x Change in habitat	4.247	6.743	0.630	0.529
<u>1000m</u>				
Intercept	3.041	0.378	8.041	<0.001
Current habitat	0.916	0.662	1.384	0.166
Change in habitat	-3.496	2.927	-1.194	0.232
Current habitat x Change in habitat	9.934	7.495	1.325	0.185

Table 28. *Parameter estimates, test statistics and associate p-values for the NBGLM analysis of Abundance for Overall Sampled (2117 observed individuals) as a function of current available bee habitat and change in available bee habitat in the surrounding landscape (from 2016 to 1988). Amount of bee habitat – and habitat change – were quantified for three different radii (250m, 500m, and 1000m) surrounding each study site.*

Radii	Estimate	Std. Error	z	p
<u>250m</u>				
Intercept	3.719	0.411	9.051	<0.001
Current habitat	0.865	0.635	1.363	0.173
Change in habitat	3.508	3.248	1.080	0.280
Current habitat x Change in habitat	-8.833	5.706	-1.548	0.122
<u>500m</u>				
Intercept	3.722	0.346	10.766	<0.001
Current habitat	0.868	0.587	1.478	0.139
Change in habitat	-0.261	2.607	-0.100	0.920
Current habitat x Change in habitat	-1.979	5.986	-0.331	0.741
<u>1000m</u>				
Intercept	3.789	0.343	11.058	<0.001
Current habitat	0.791	0.601	1.316	0.188
Change in habitat	-1.383	2.654	-0.521	0.602
Current habitat x Change in habitat	2.464	6.782	0.363	0.716

Figures

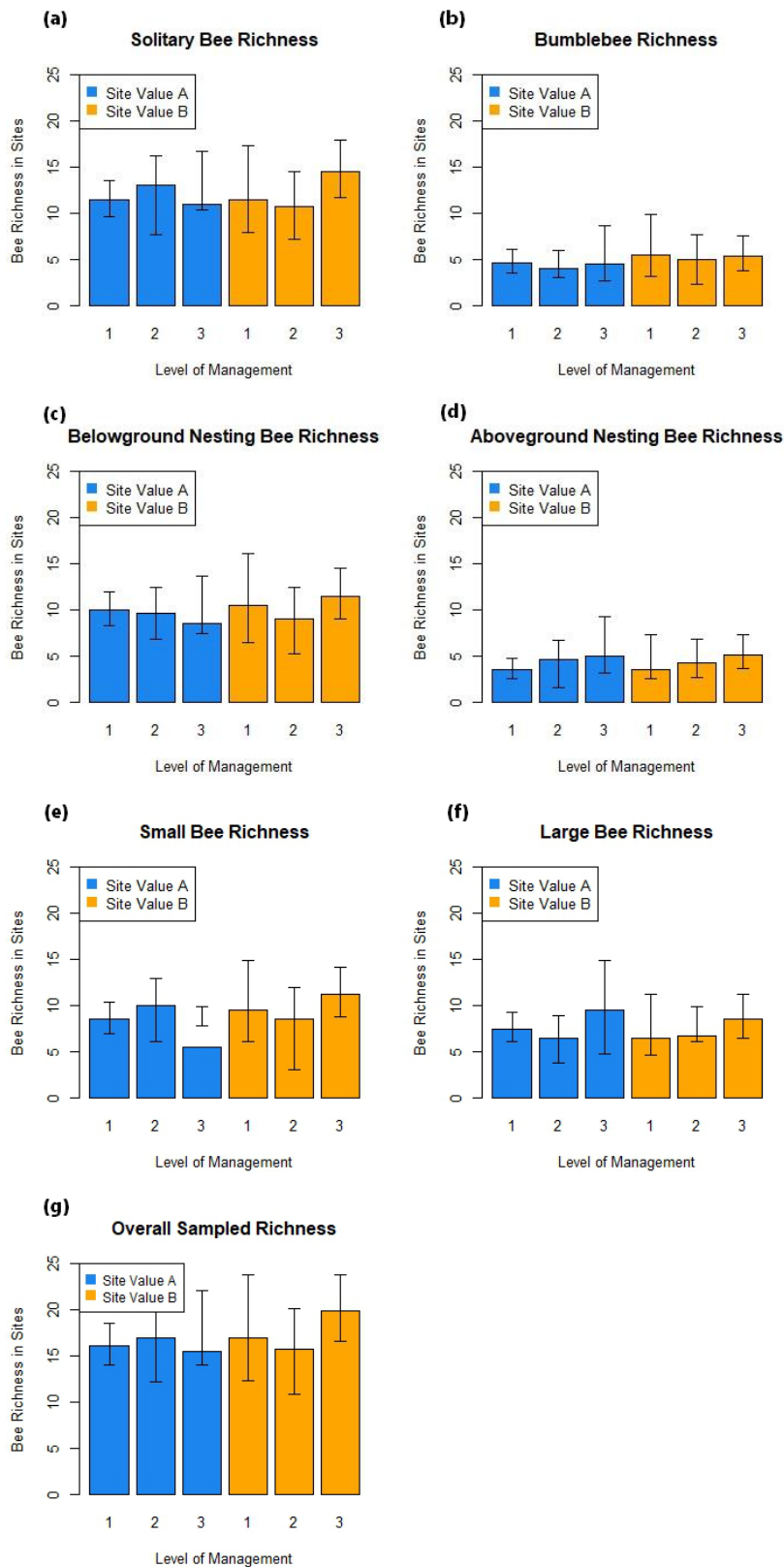


Figure 5. Richness of bees in semi-natural grasslands, in different subsets of the bee community, for different combinations of site value (A=Very important, B=Important/Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). Bars are observed averages per site and error bars are standard error.

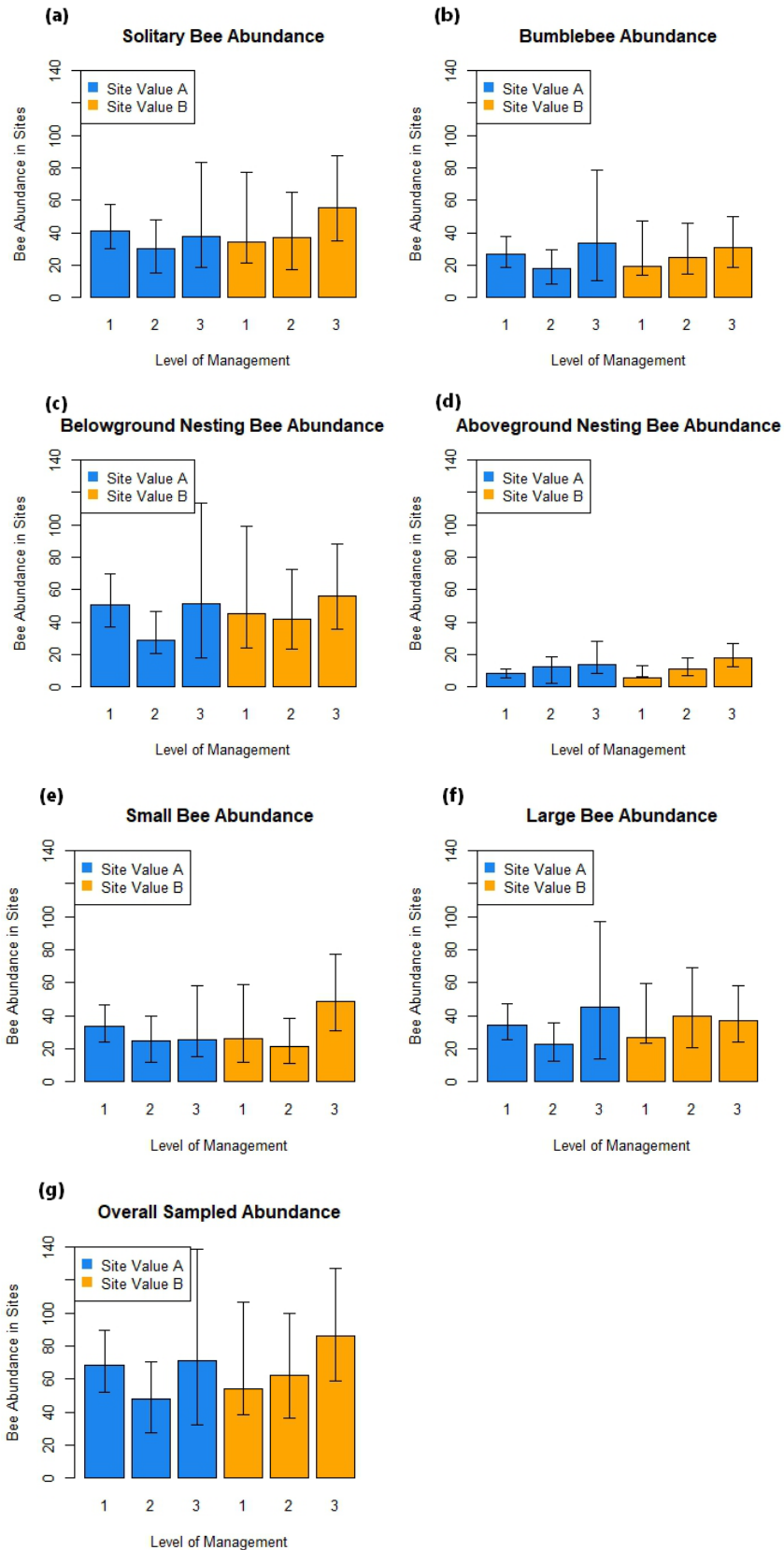


Figure 6. Abundance of bees in semi-natural grasslands, in different subsets of the bee community, for different combinations of site value (A=Very important, B=Important/Locally important) and level of management (1=Well managed, 2=Poorly managed, 3=Abandoned or altered sites). Bars are observed averages per site and error bars are standard error.

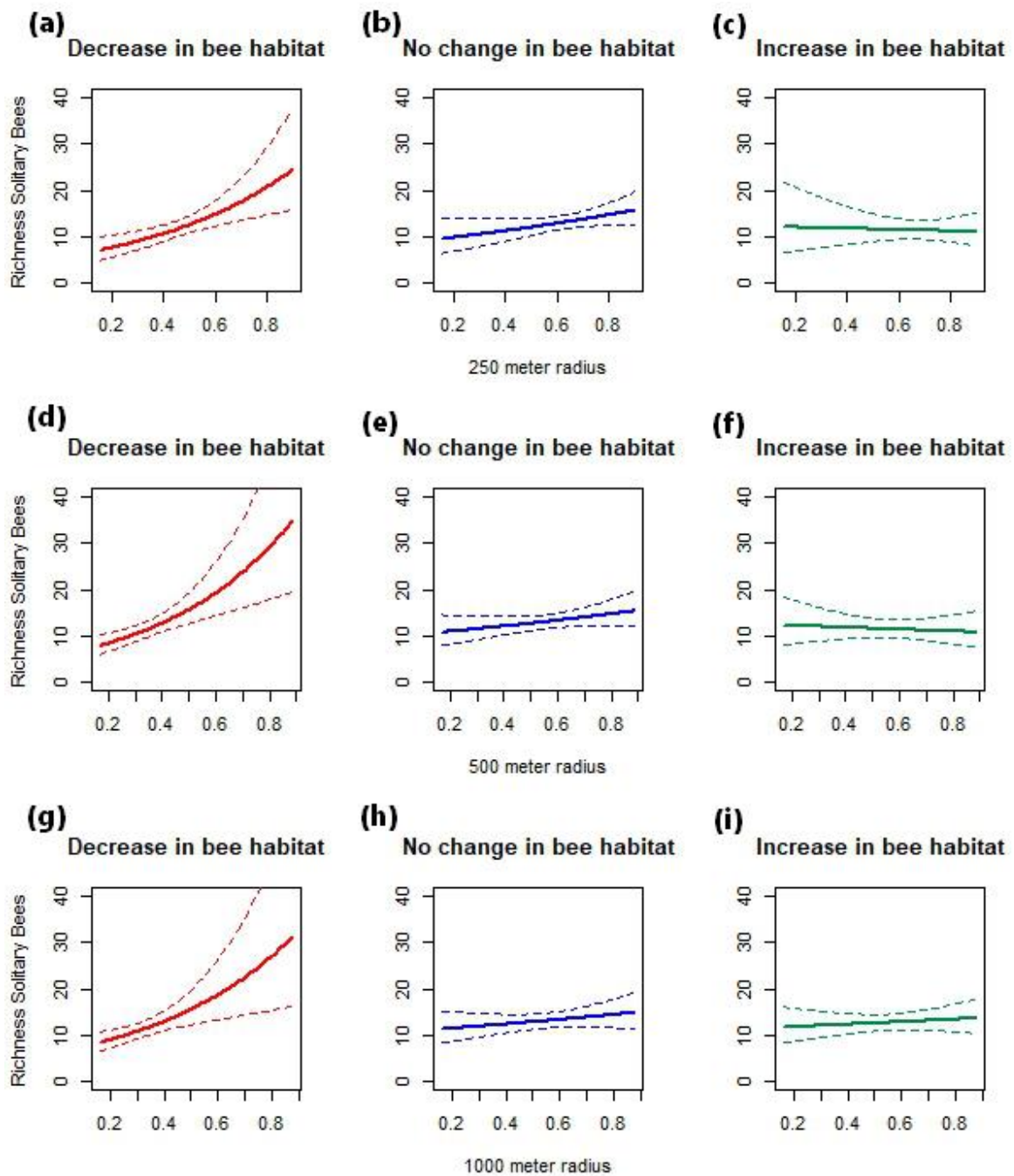


Figure 7. Estimated relationship between Solitary Bee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

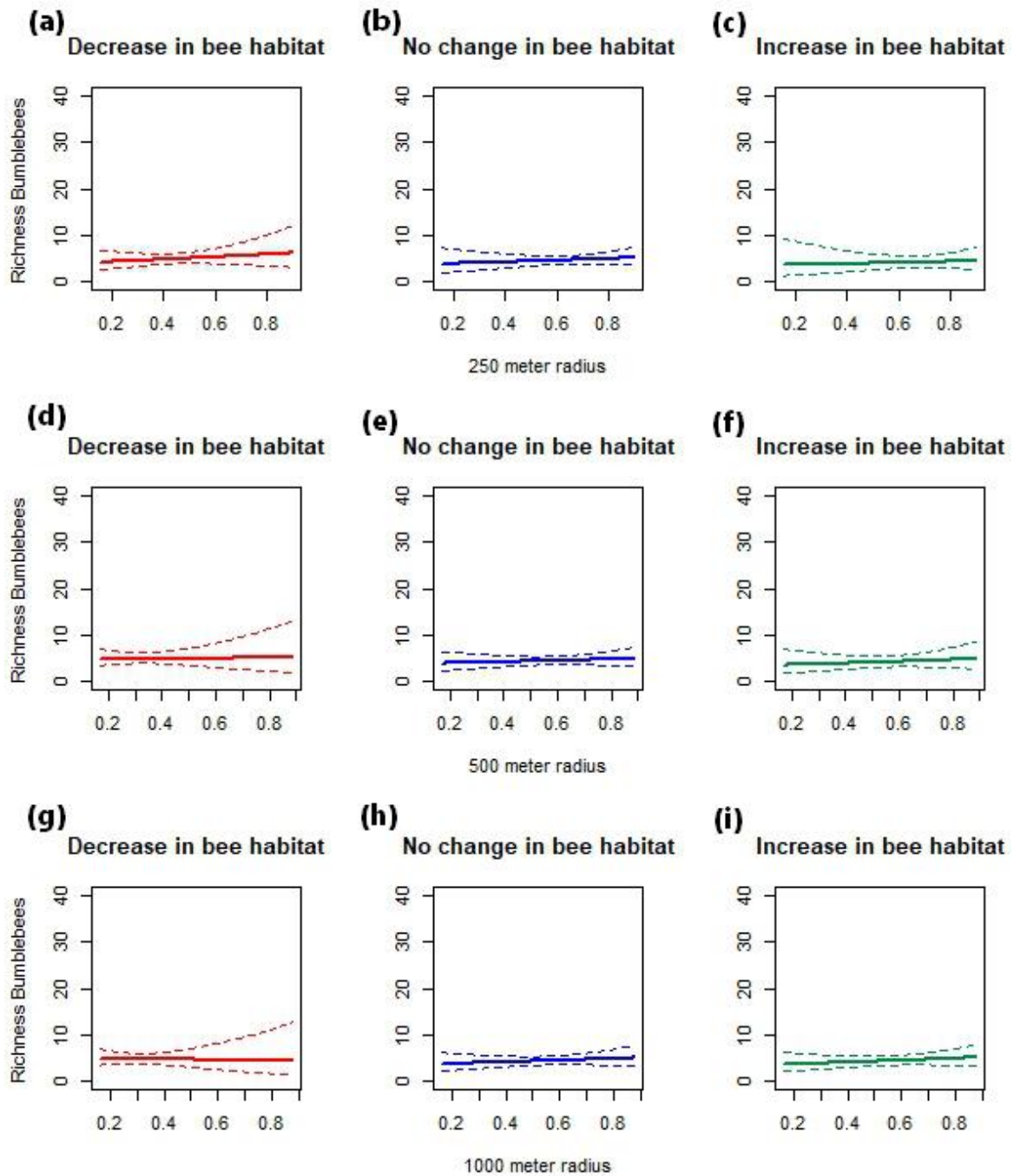


Figure 8. Estimated relationship between Bumblebee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

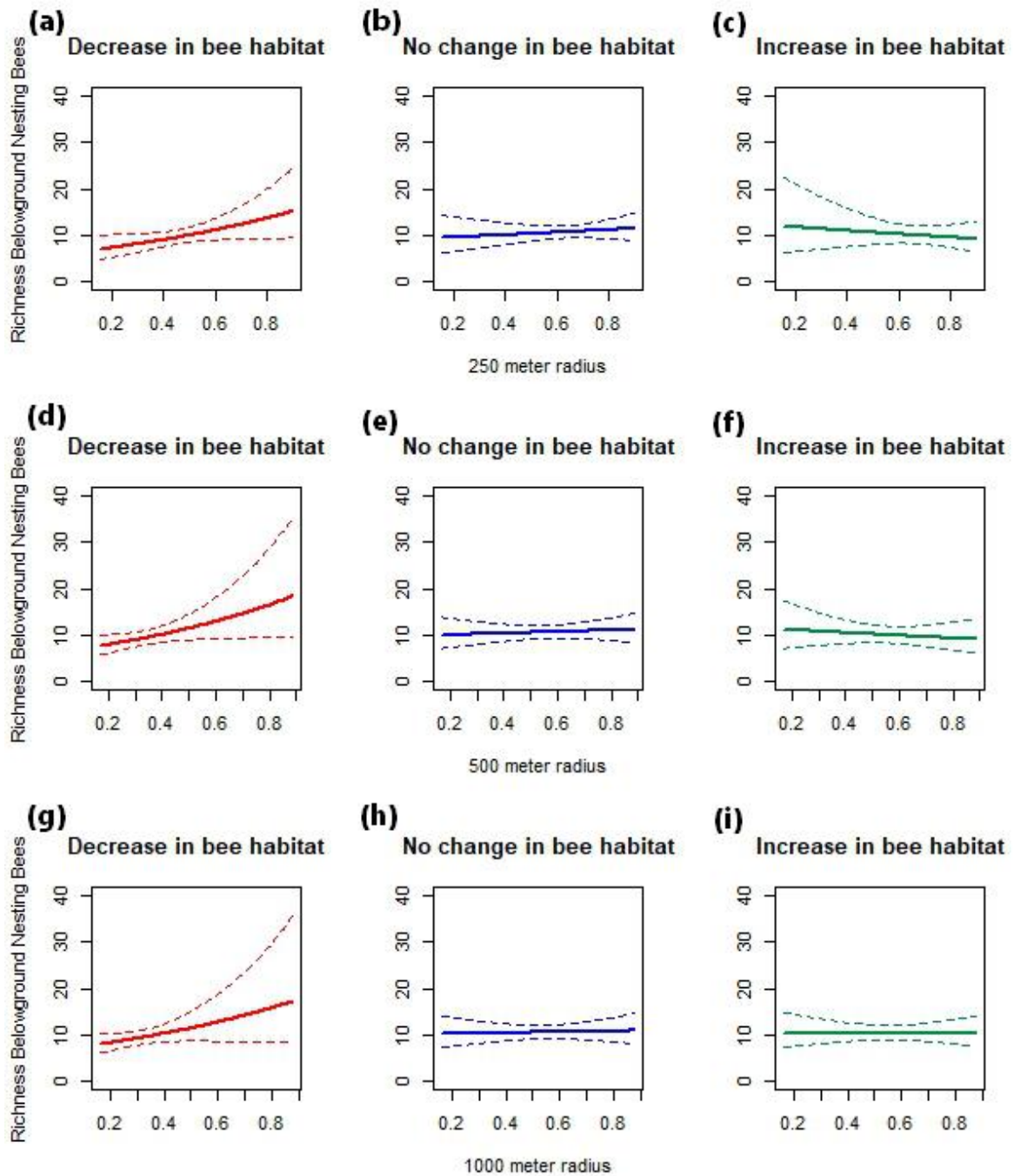


Figure 9. Estimated relationship between Belowground Nesting Bee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

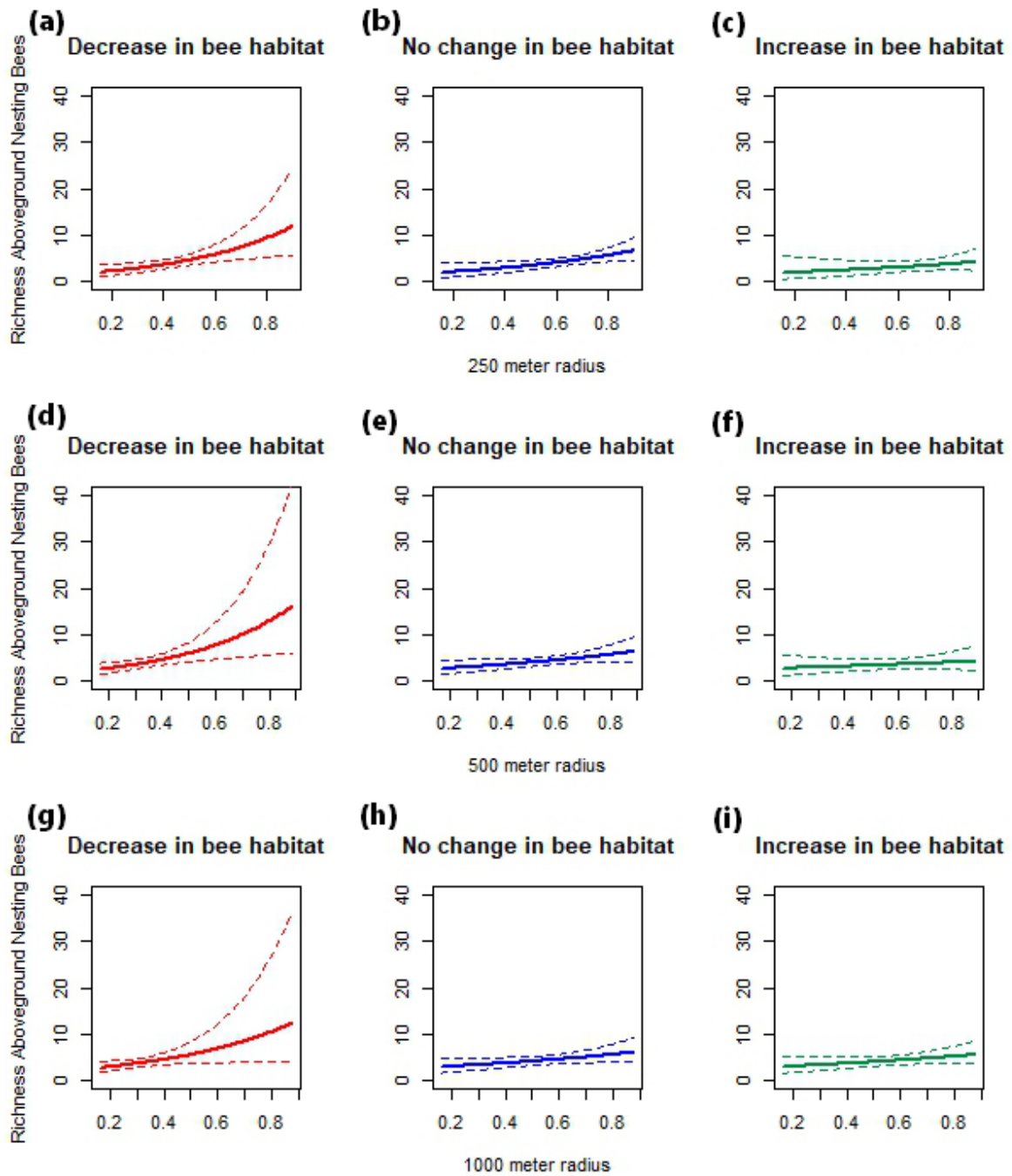


Figure 10. Estimated relationship between Aboveground Nesting Bee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

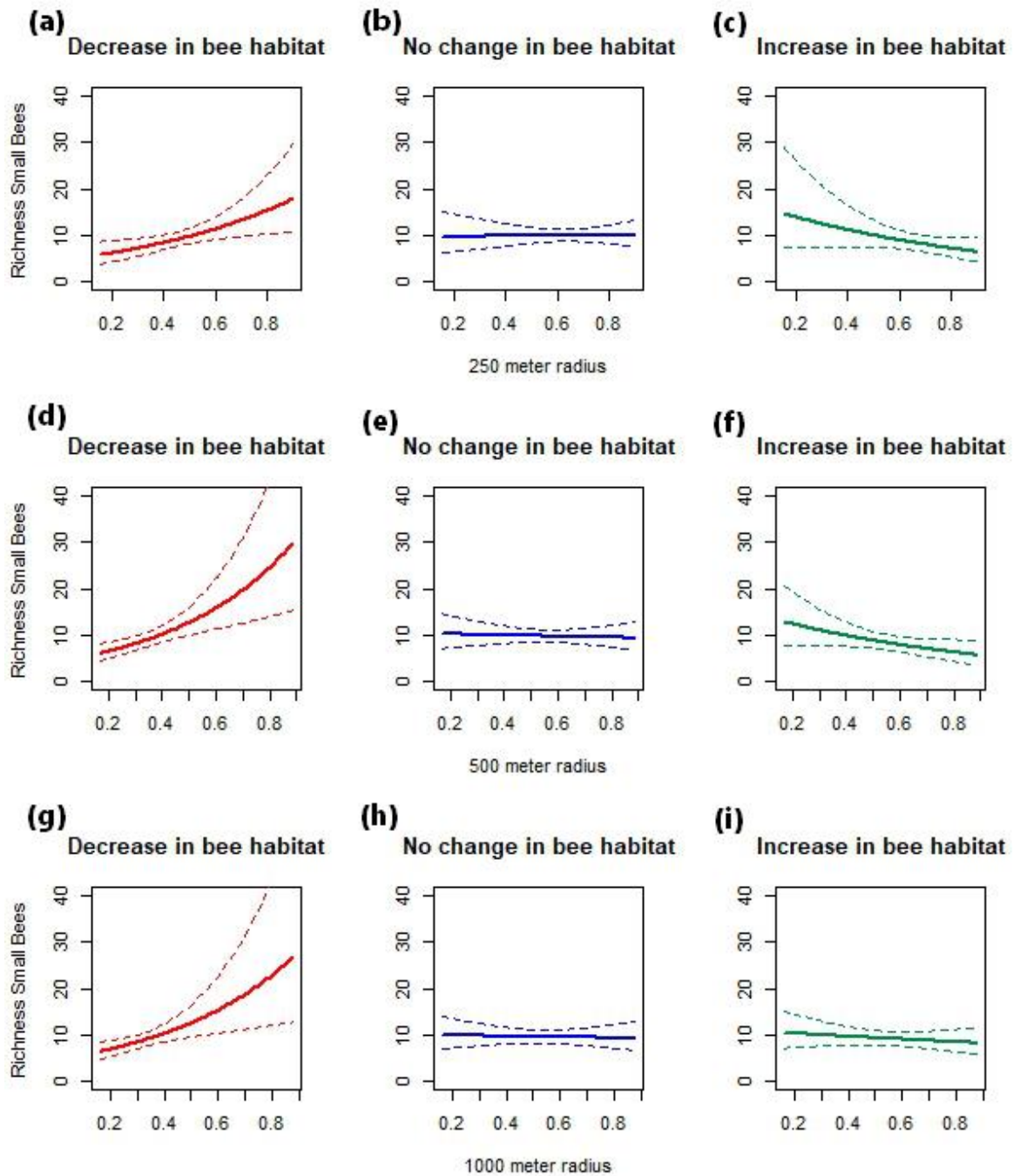


Figure 11. Estimated relationship between Small Bee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

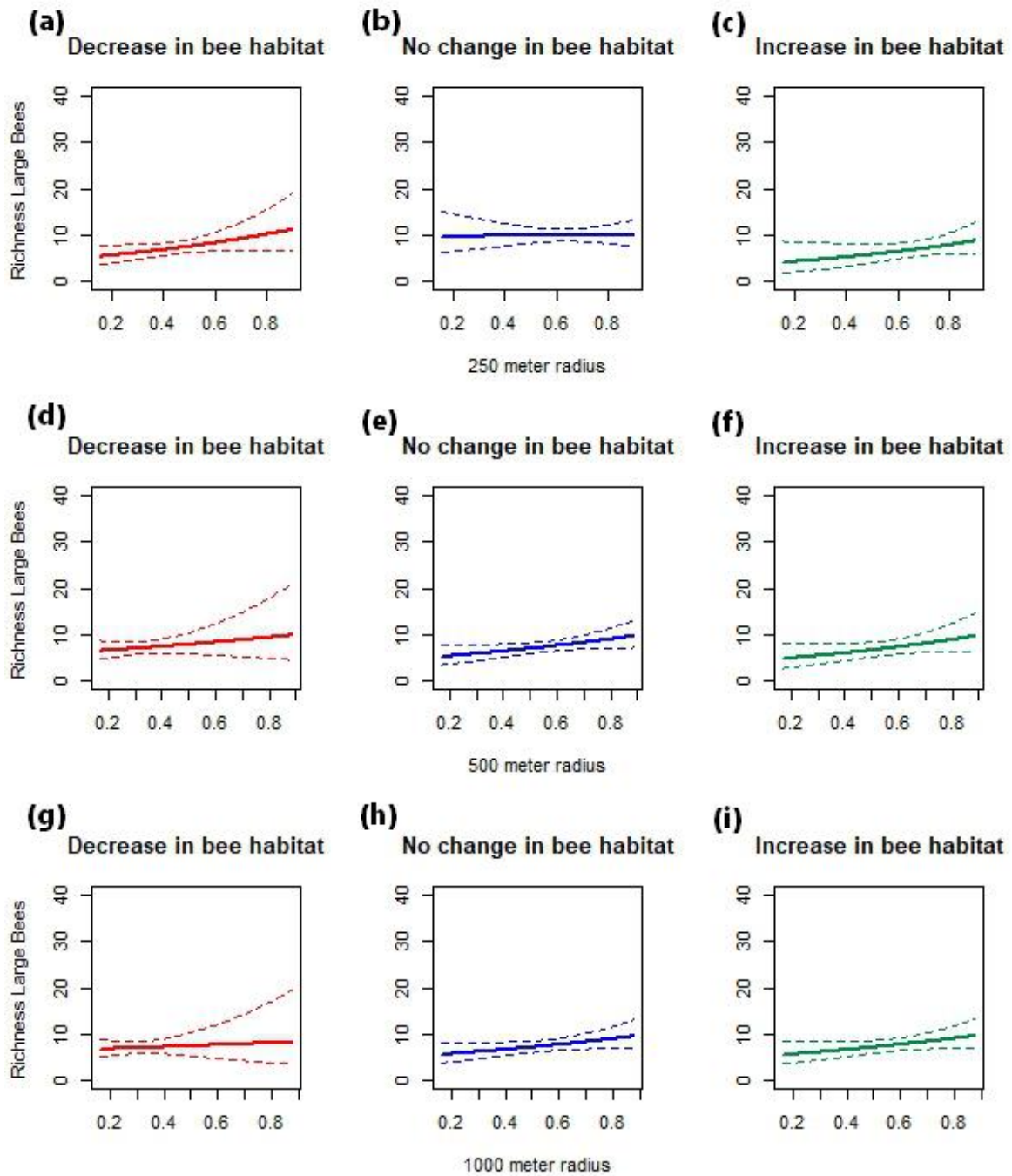


Figure 12. Estimated relationship between Large Bee Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

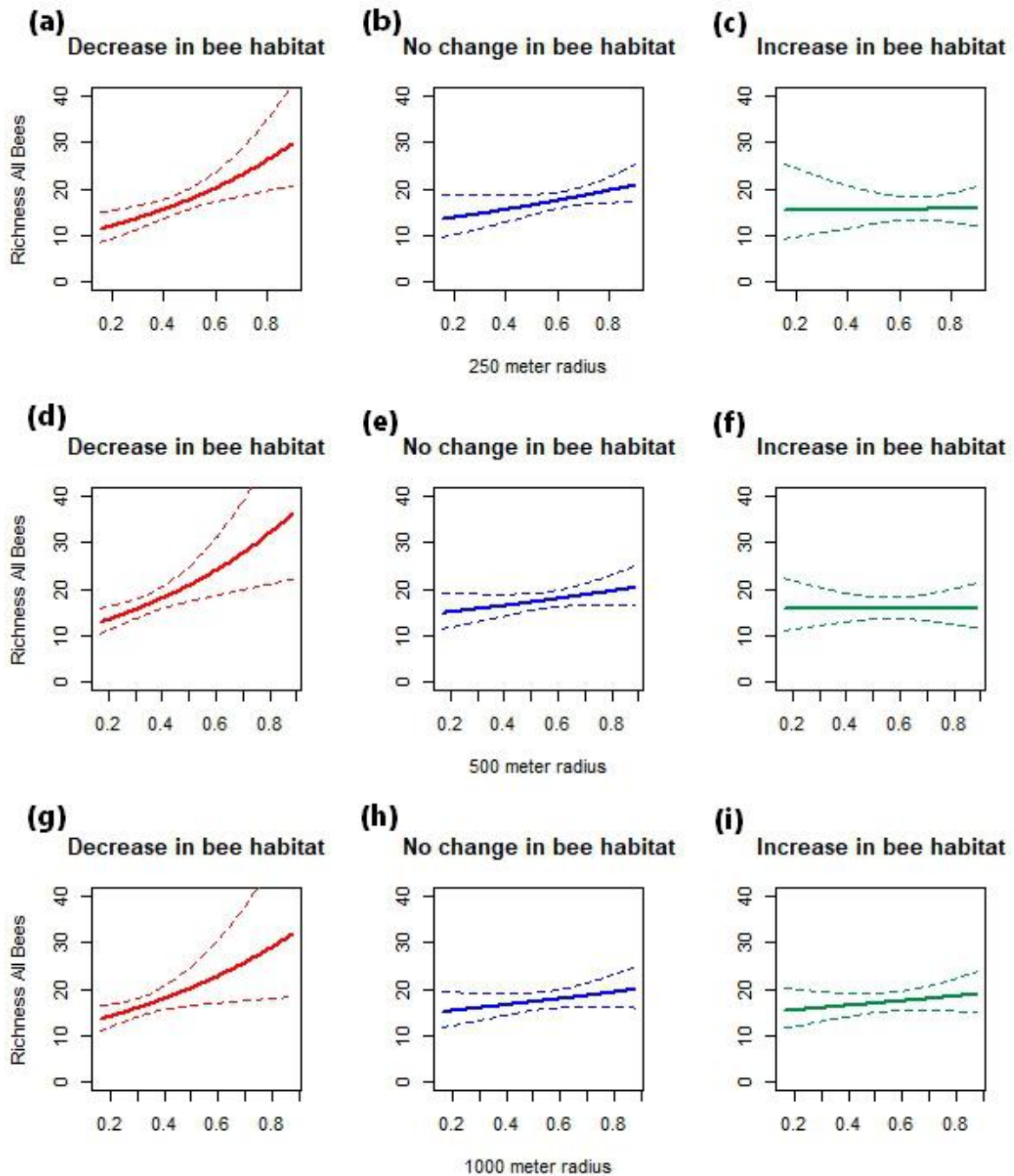


Figure 13. Estimated relationship between Overall Sampled Richness and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

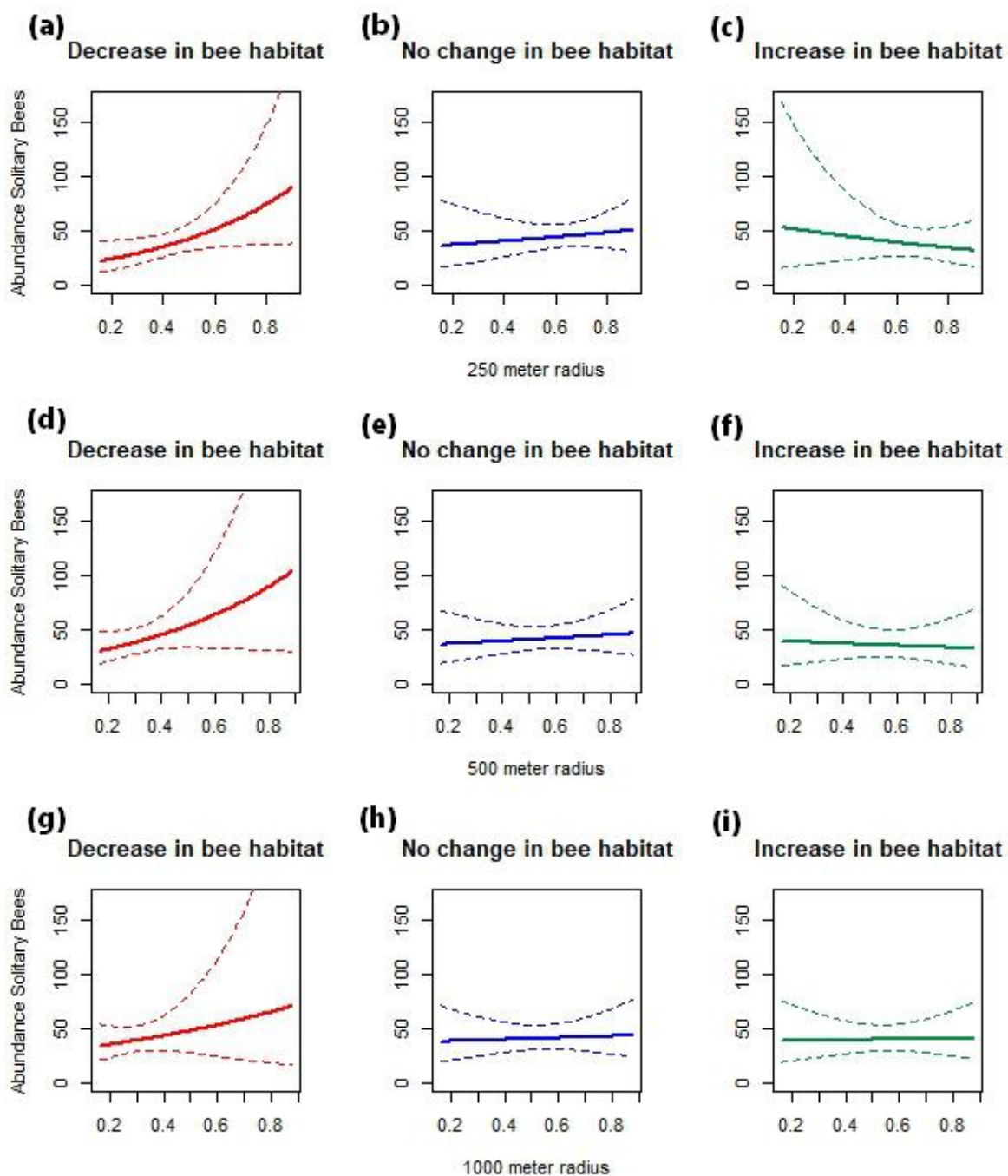


Figure 14. Estimated relationship between Solitary Bee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

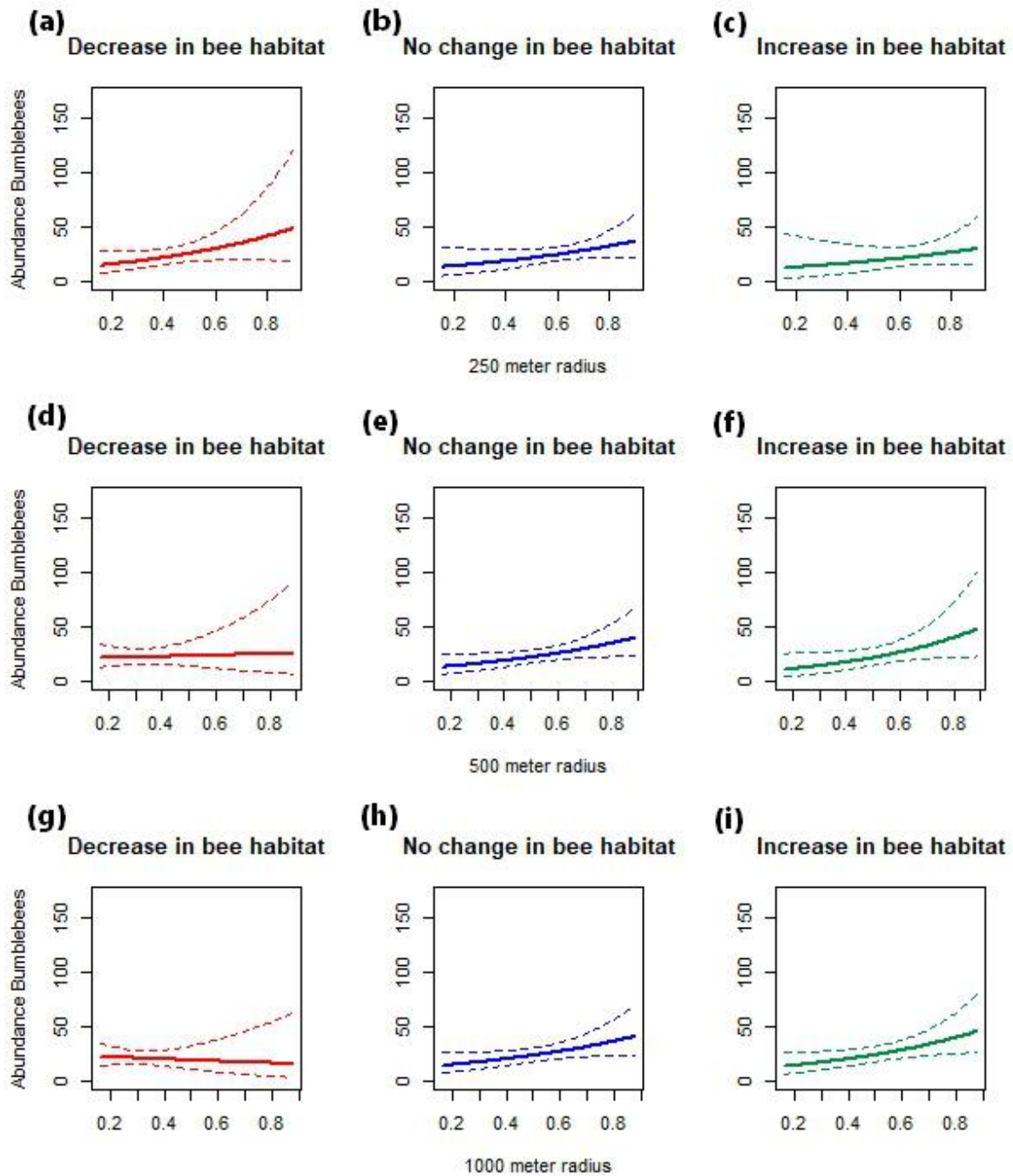


Figure 15. Estimated relationship between Bumblebee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

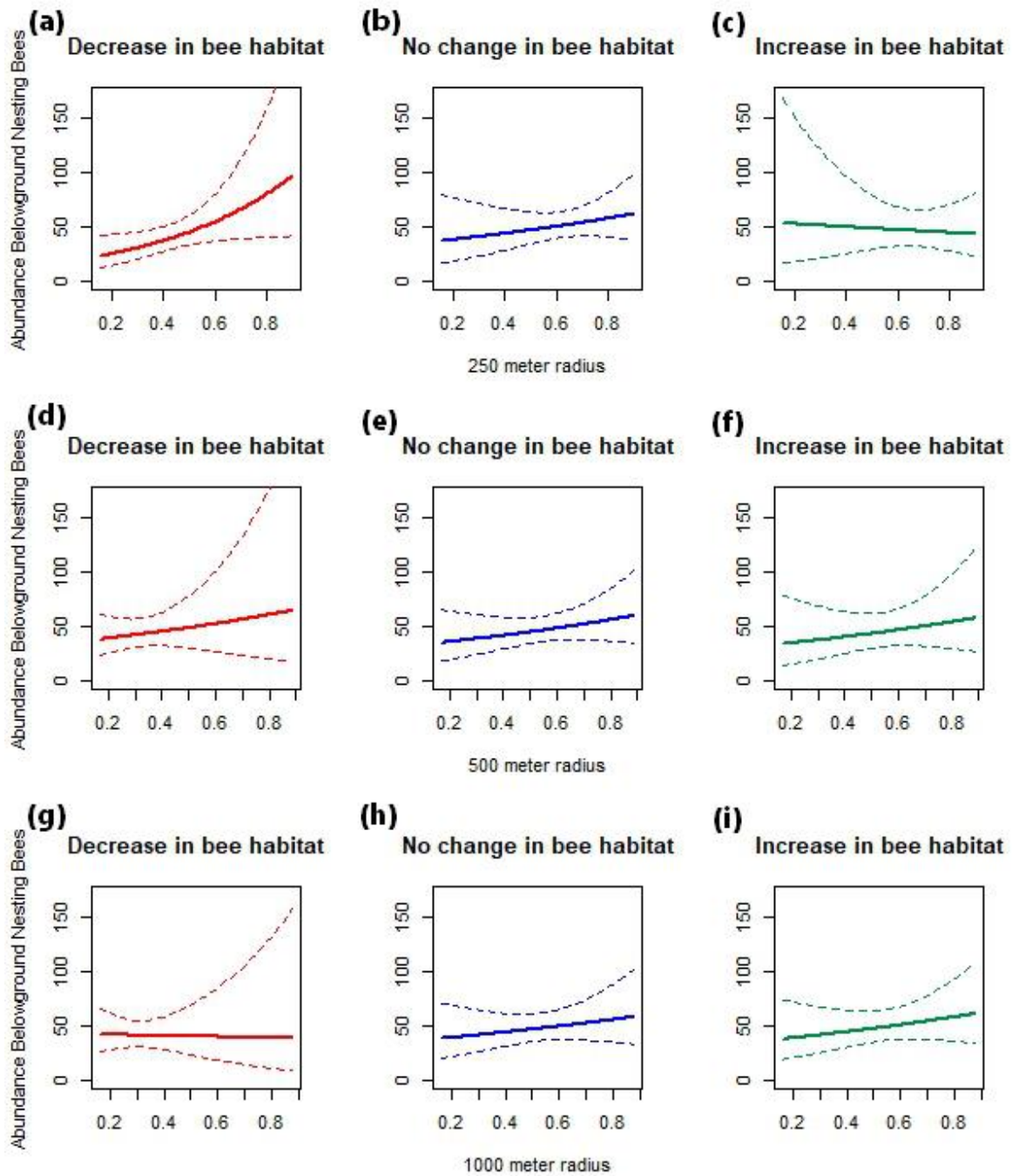


Figure 16. Estimated relationship Belowground Nesting Bee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

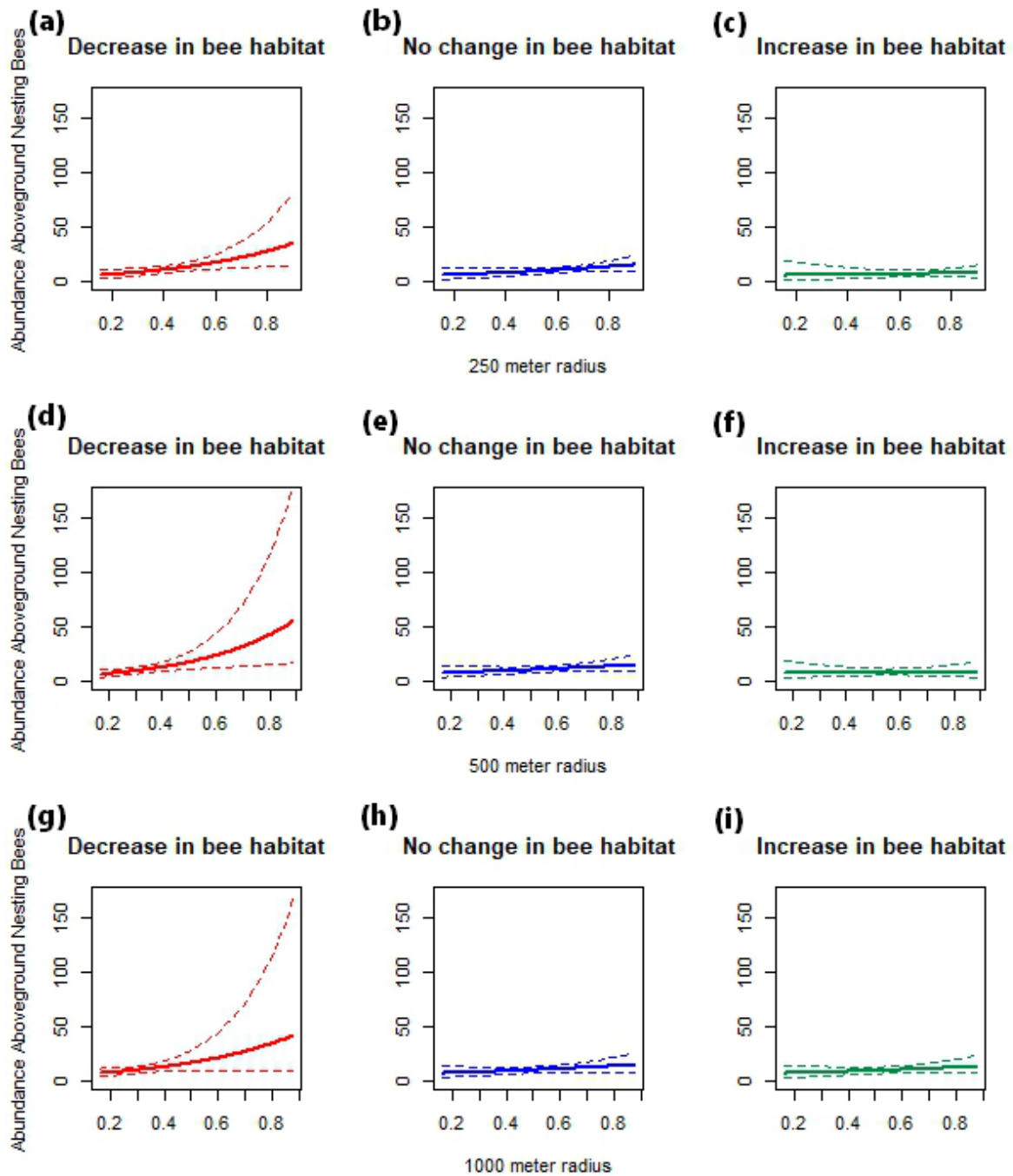


Figure 17. Estimated relationship between Aboveground Nesting Bee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

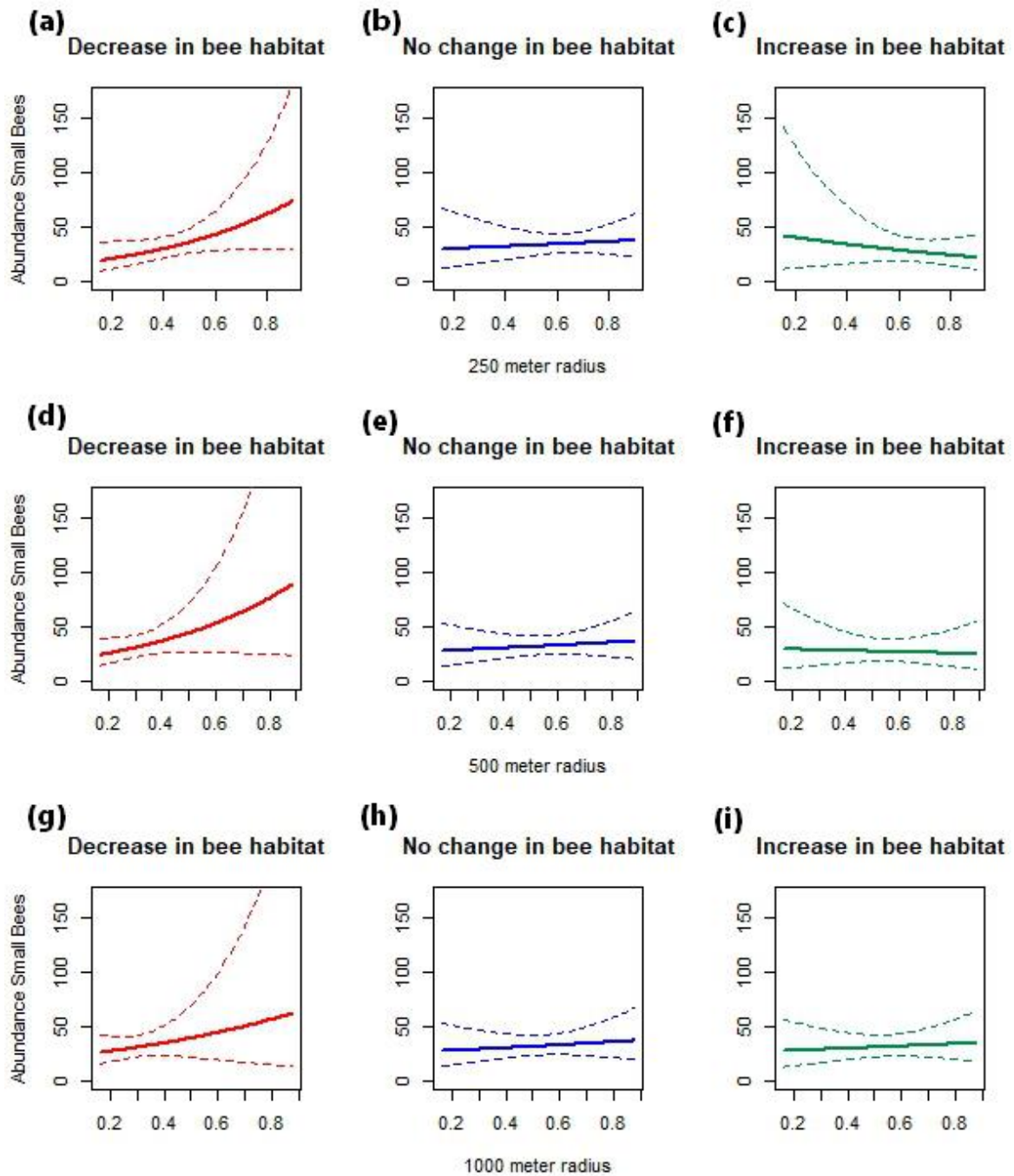


Figure 18. Estimated relationship between Small Bee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

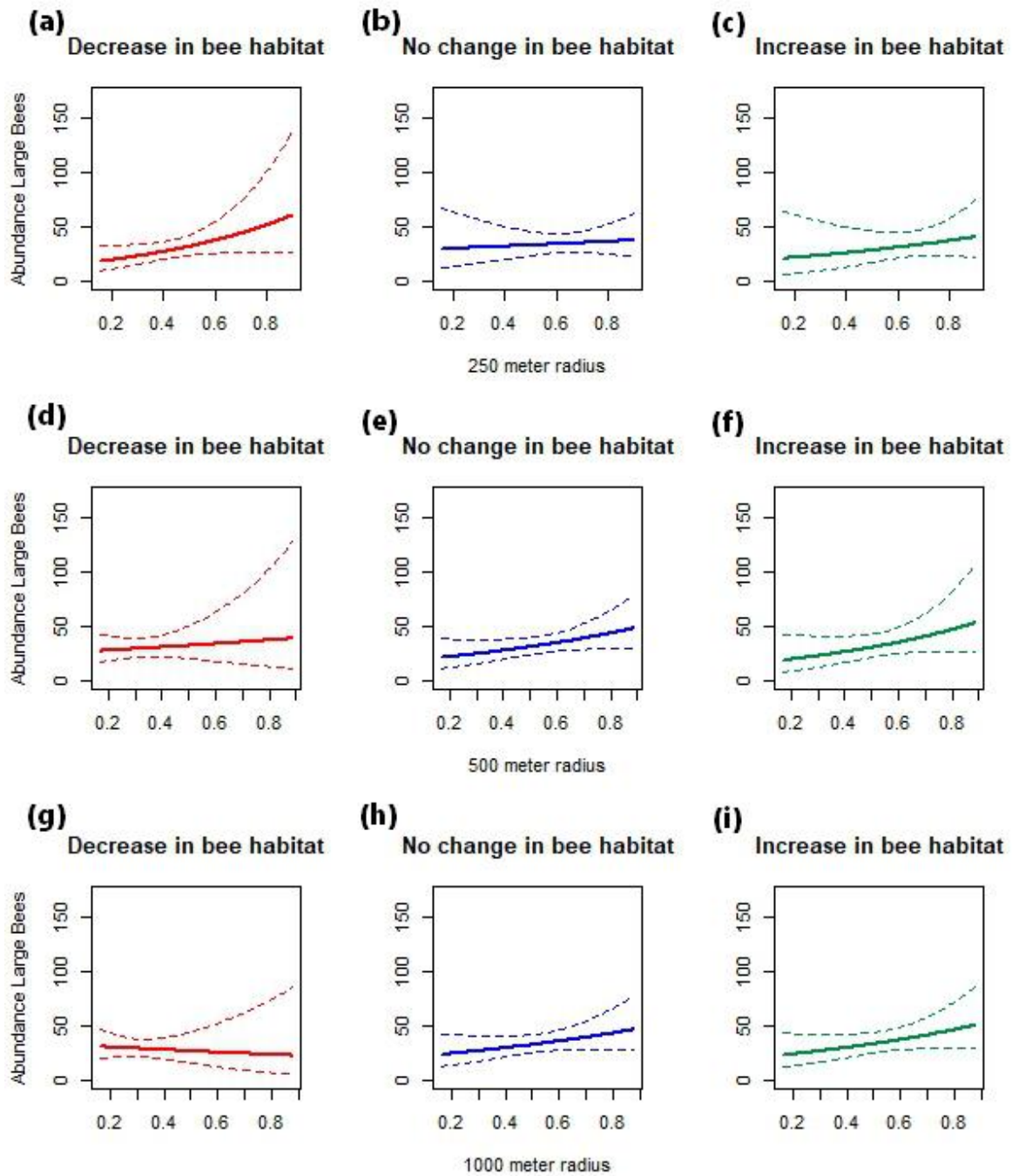


Figure 19. Estimated relationship between Large Bee Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

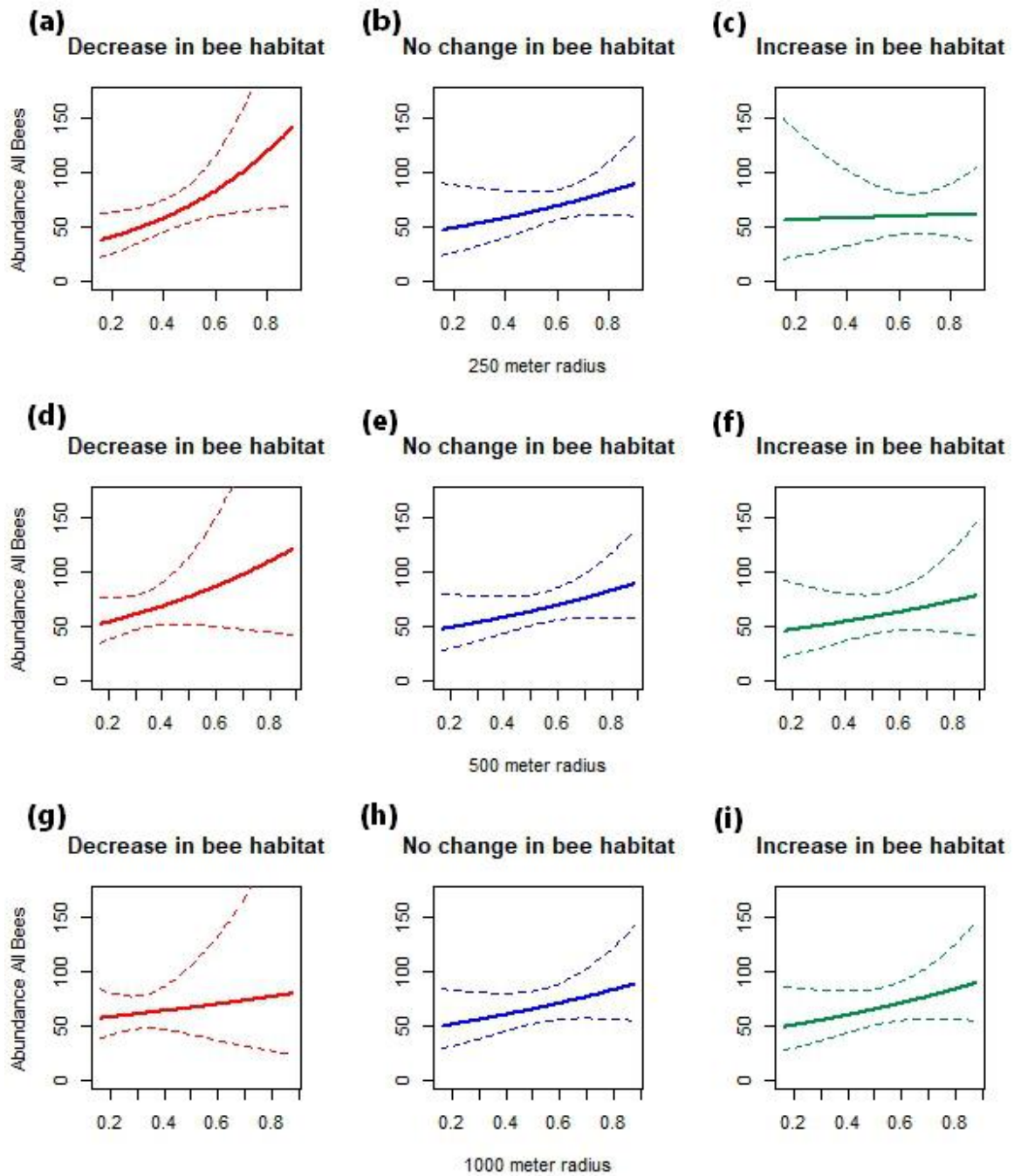


Figure 20. Estimated relationship between Overall Sampled Abundance and the amount of currently (year 2016) available bee habitat, ranging from 0 (no habitat) to 1 (100% of land cover is bee habitat) in sites of three different levels of landscape change; decrease, no change or increase in bee habitat from 1988 to 2016). Bee habitat was quantified within three different radii (250m, 500m or 1000m).

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Appendix I

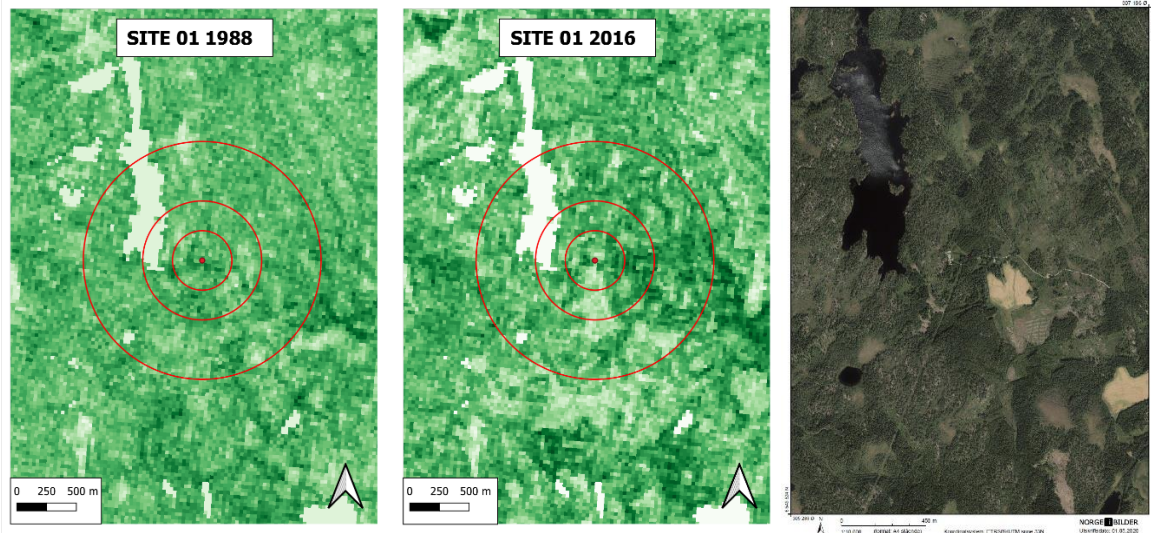


Figure A1. Site 1 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

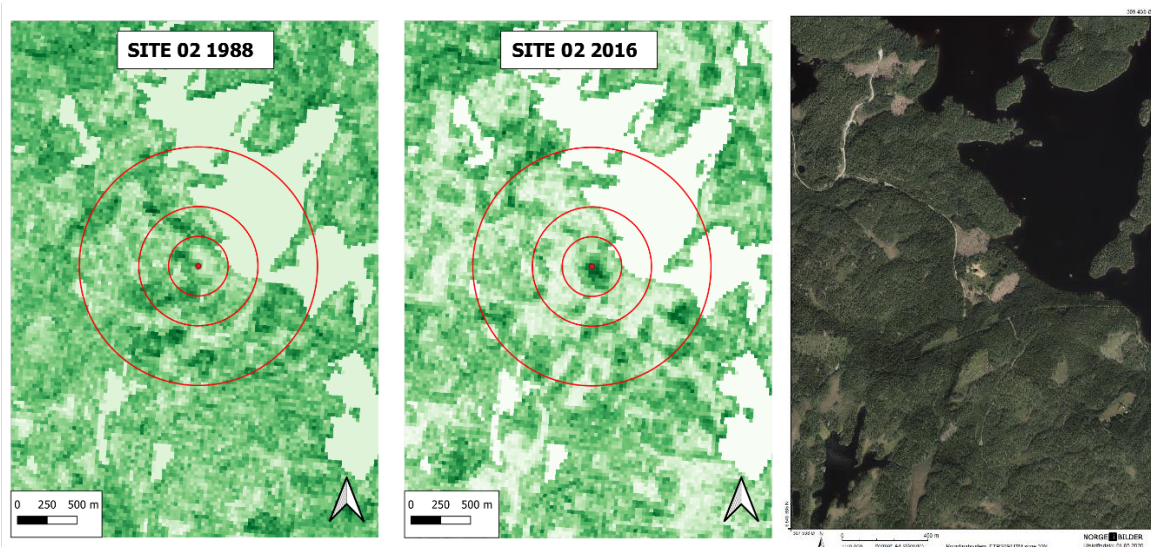


Figure A2. Site 2 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

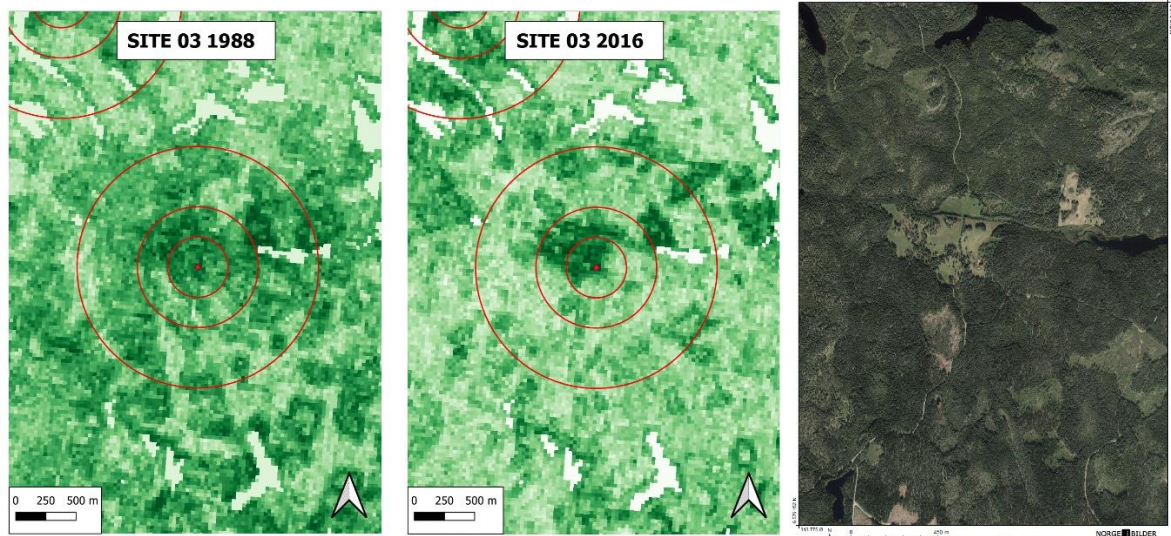


Figure A3. Site 3 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

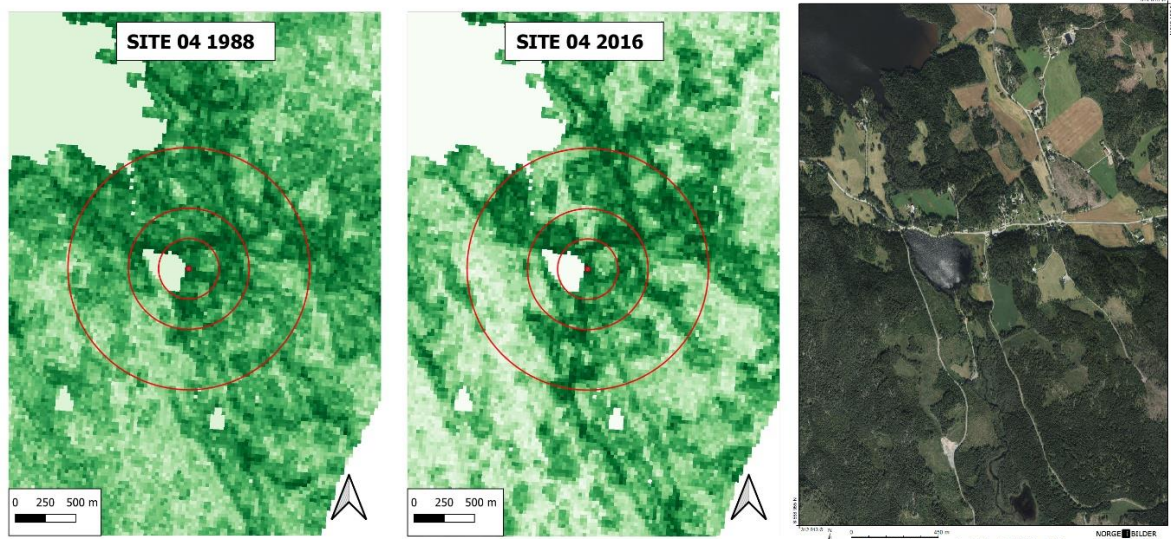


Figure A4. Site 4 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

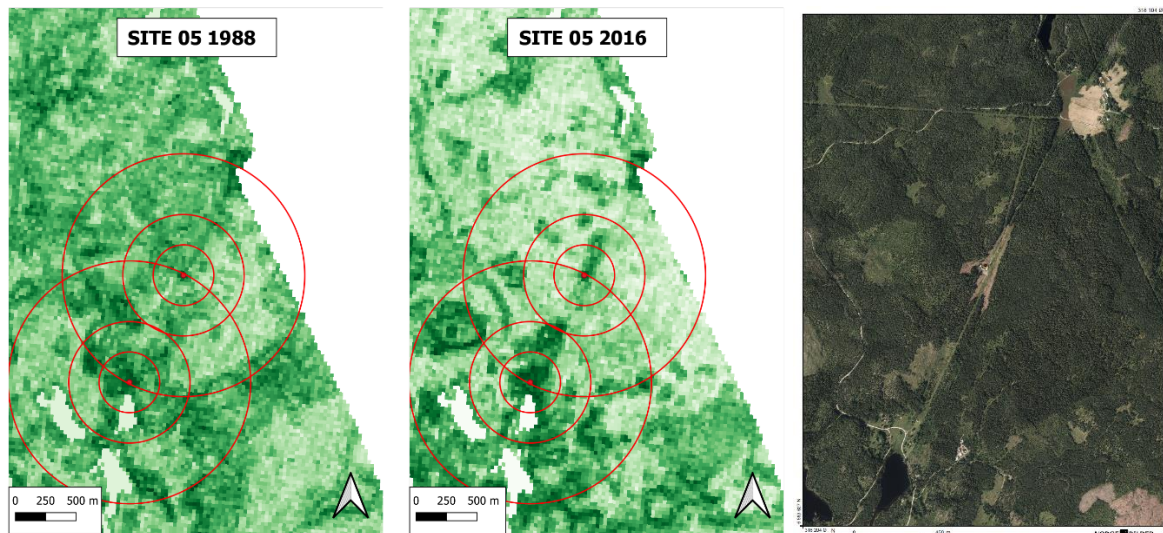


Figure A5. Site 5 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

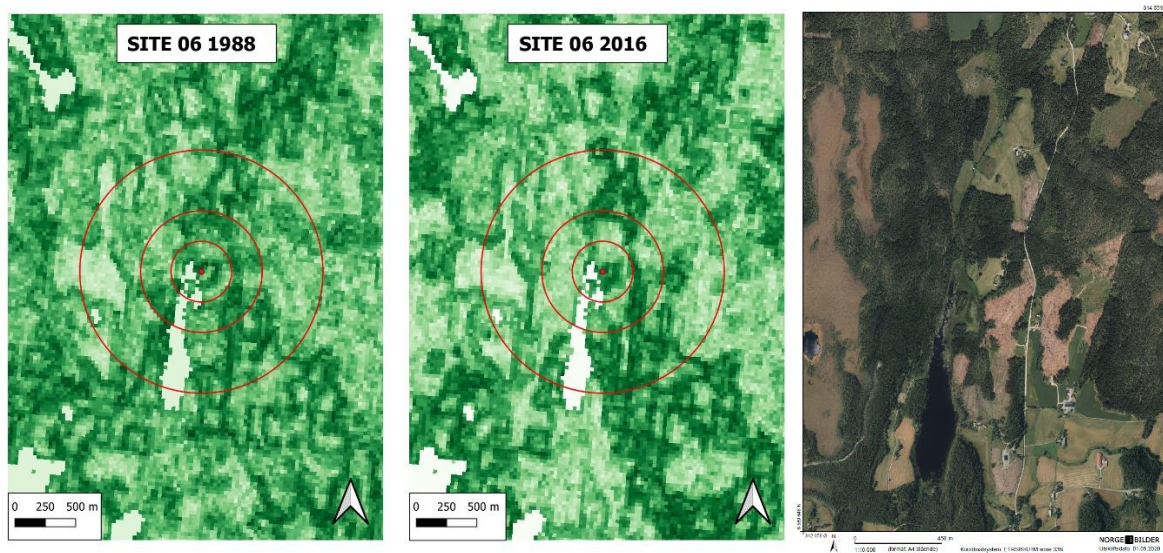


Figure A6. Site 6 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

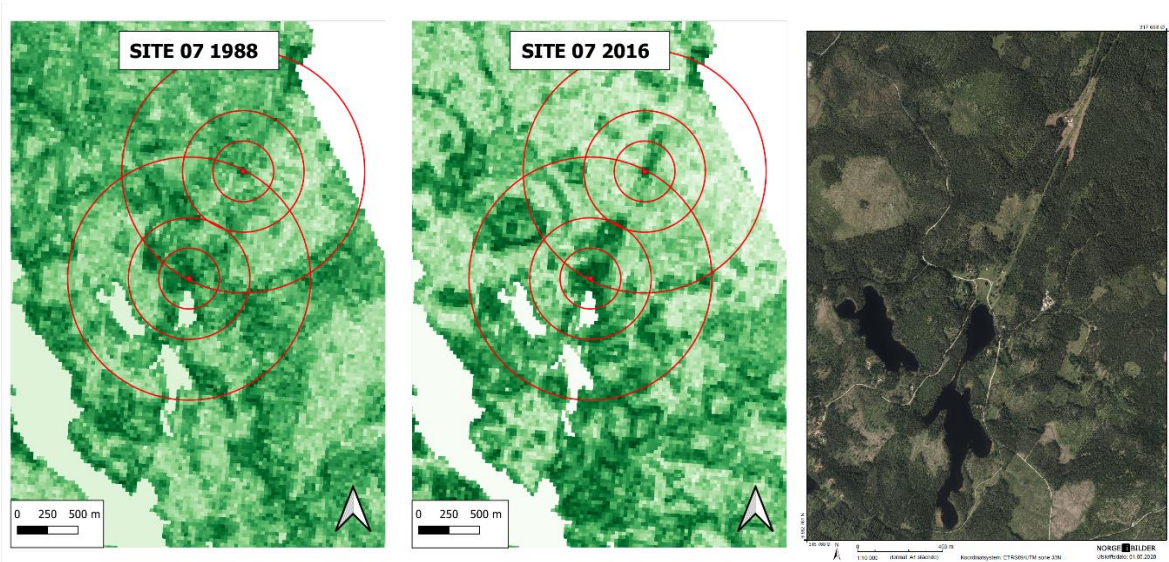


Figure A7. Site 7 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

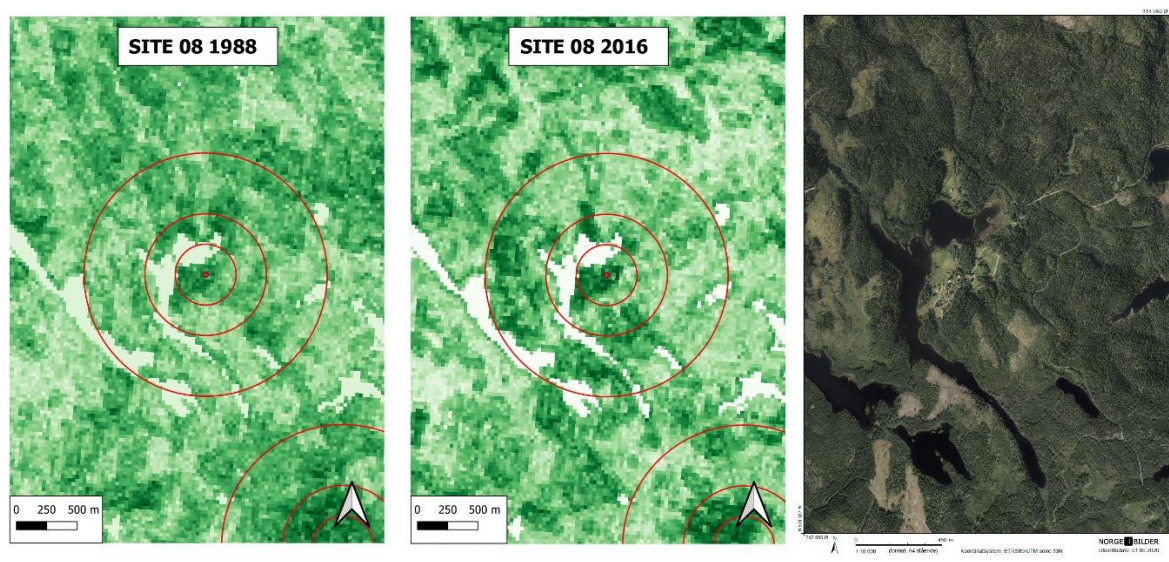


Figure A8. Site 8 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

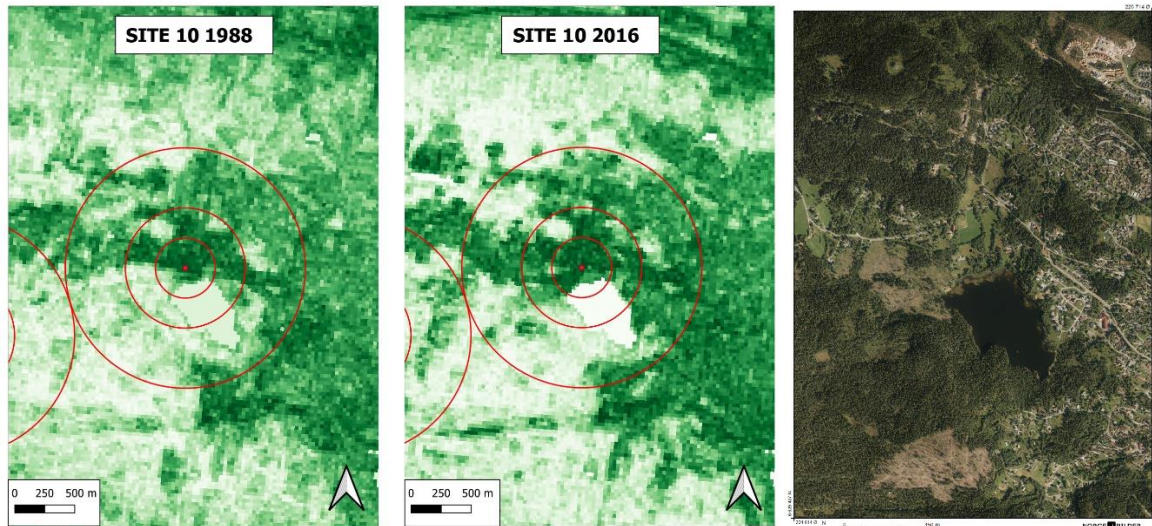


Figure A9. Site 10 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

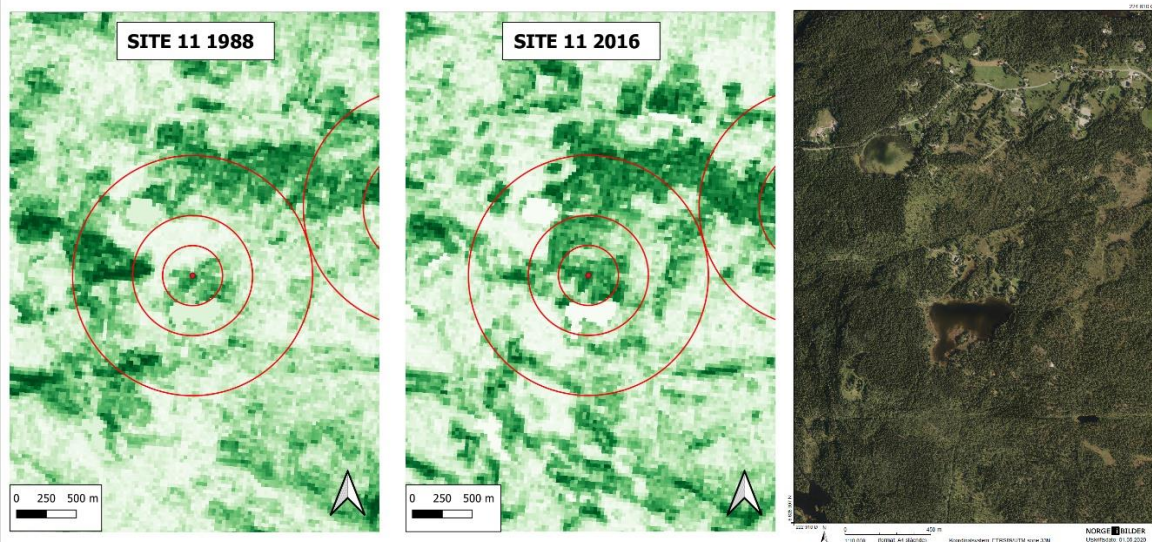


Figure A10. Site 11 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

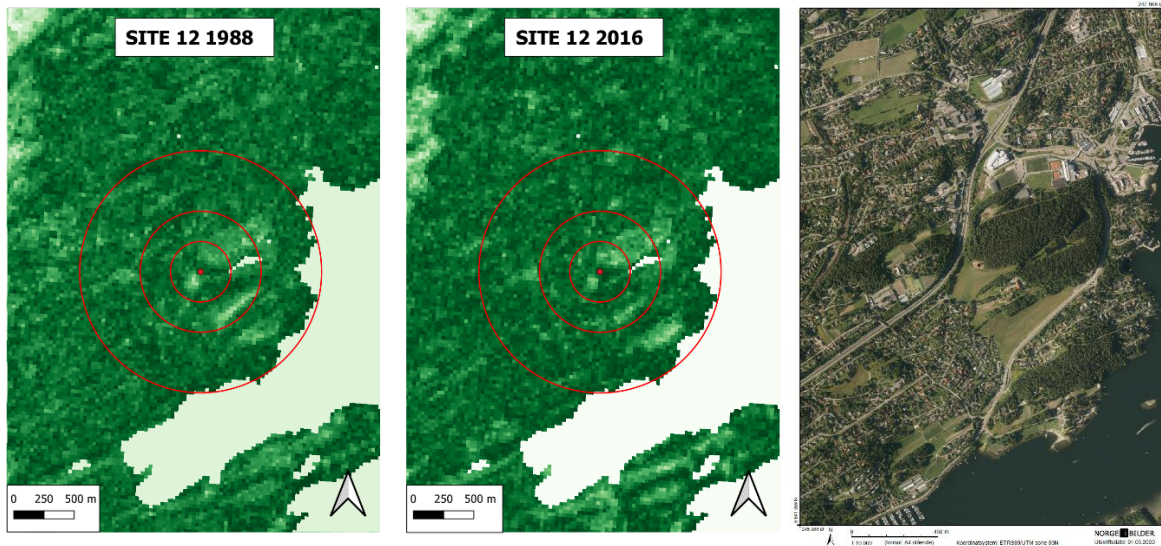


Figure A11. Site 12 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

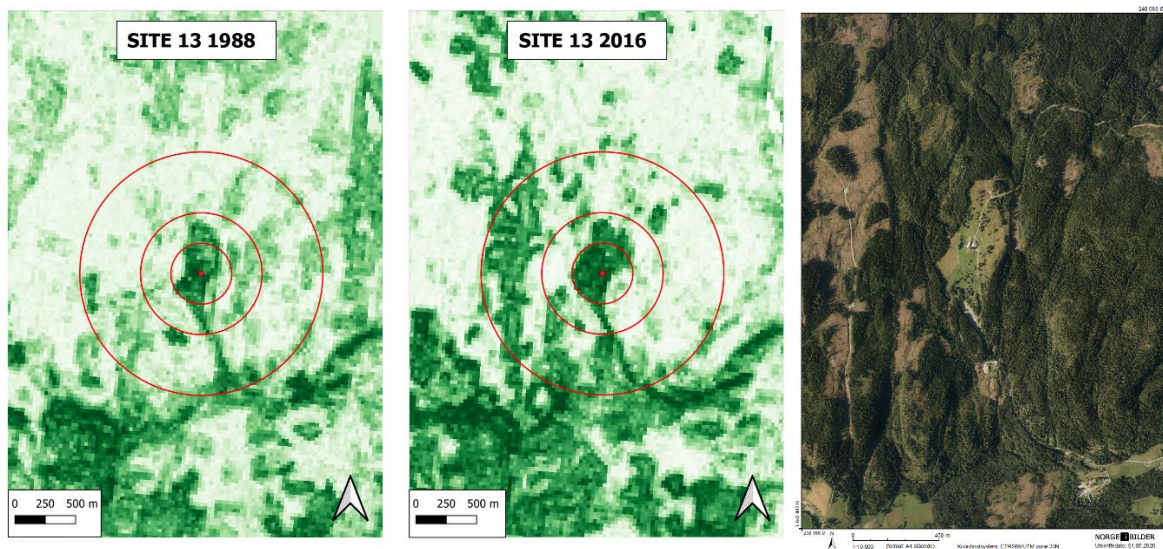


Figure A12. Site 13 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

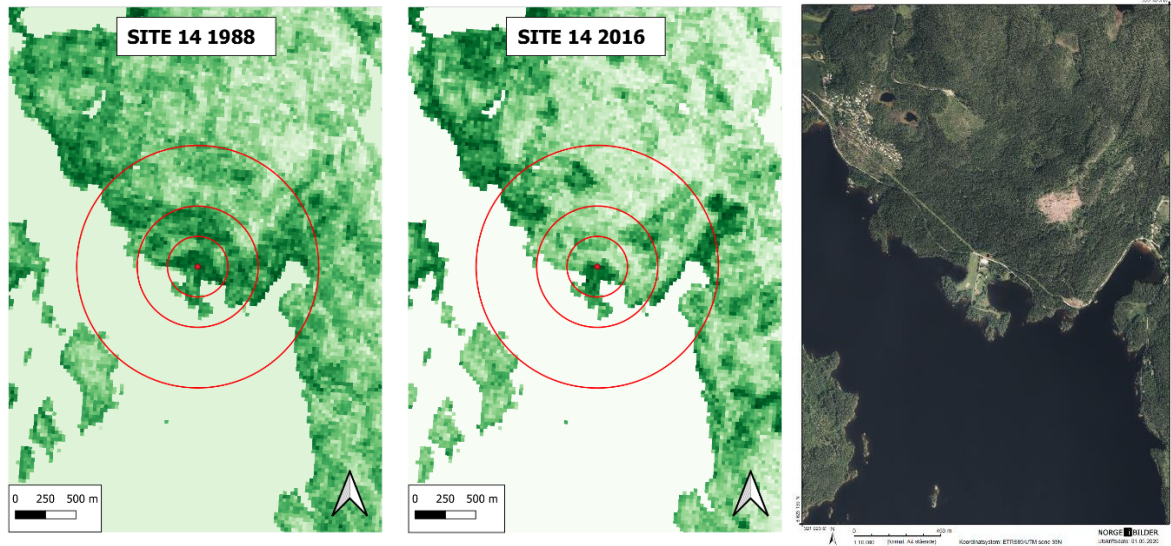


Figure A13. Site 14 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

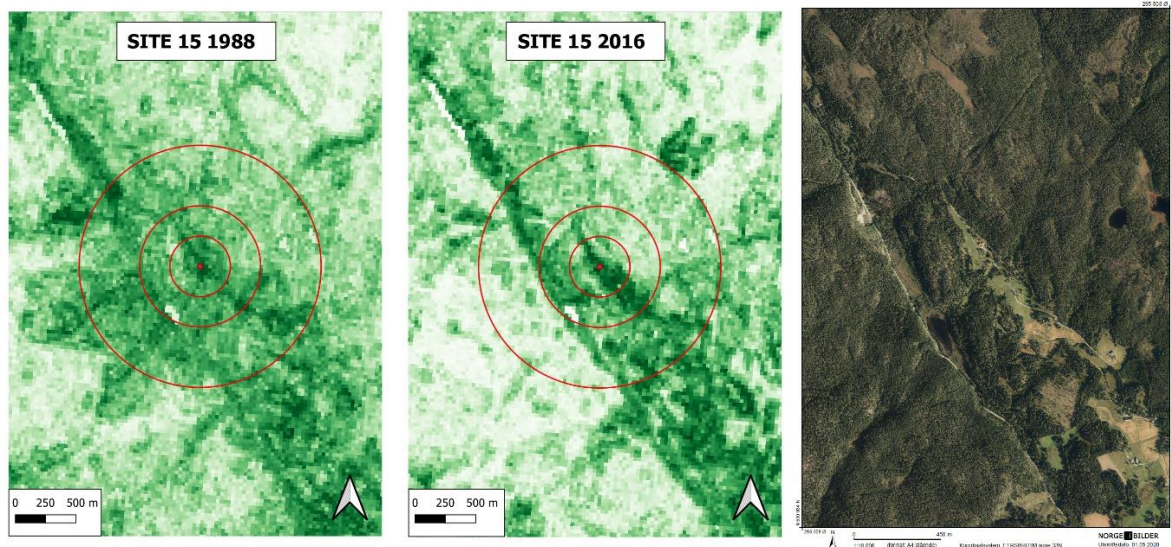


Figure A14. Site 15 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

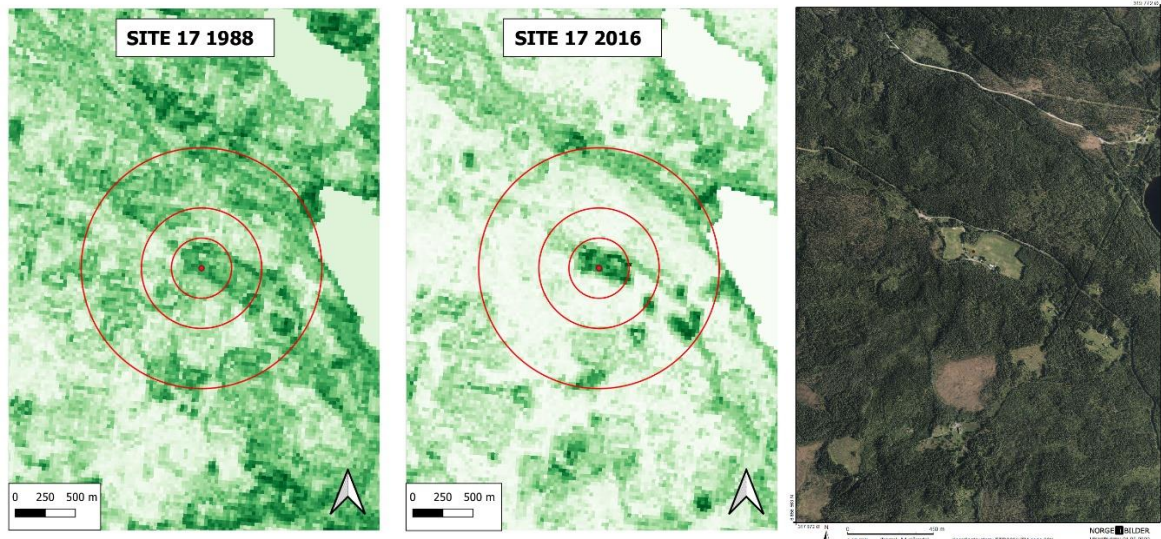


Figure A15. Site 17 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

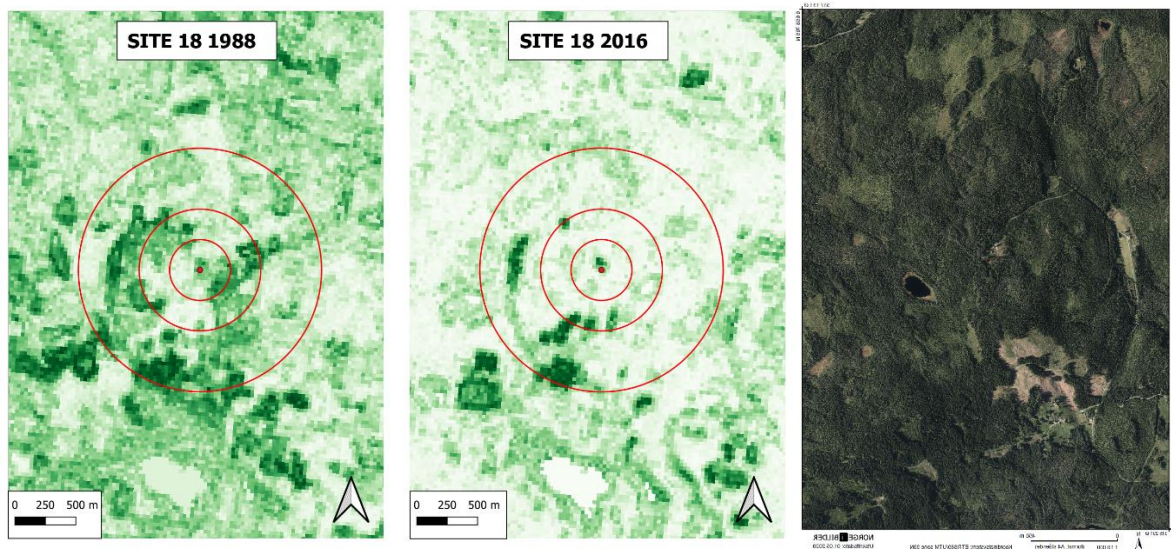


Figure A16. Site 18 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

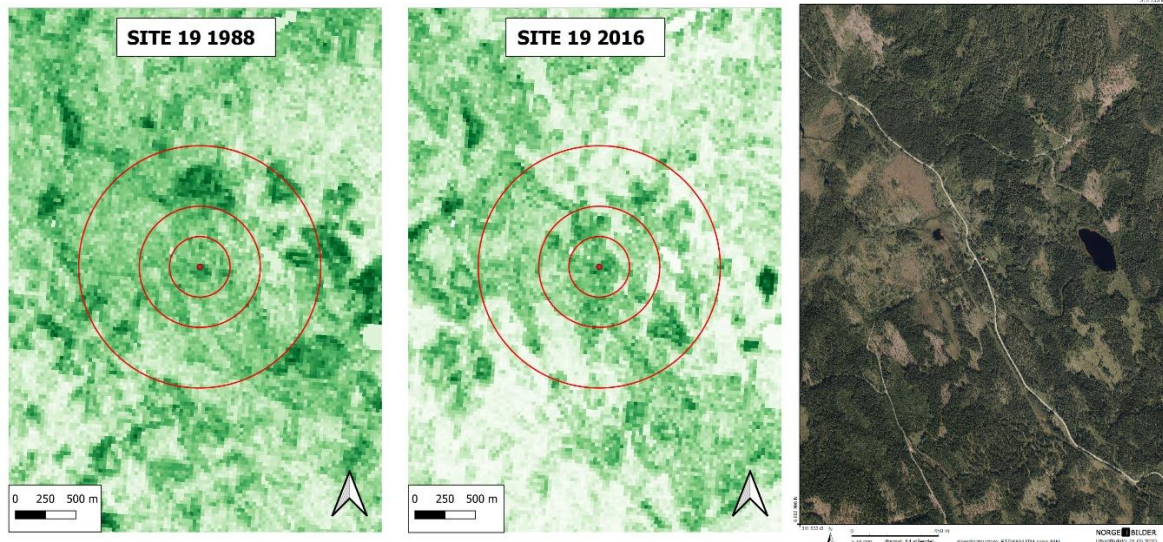


Figure A17. Site 19 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

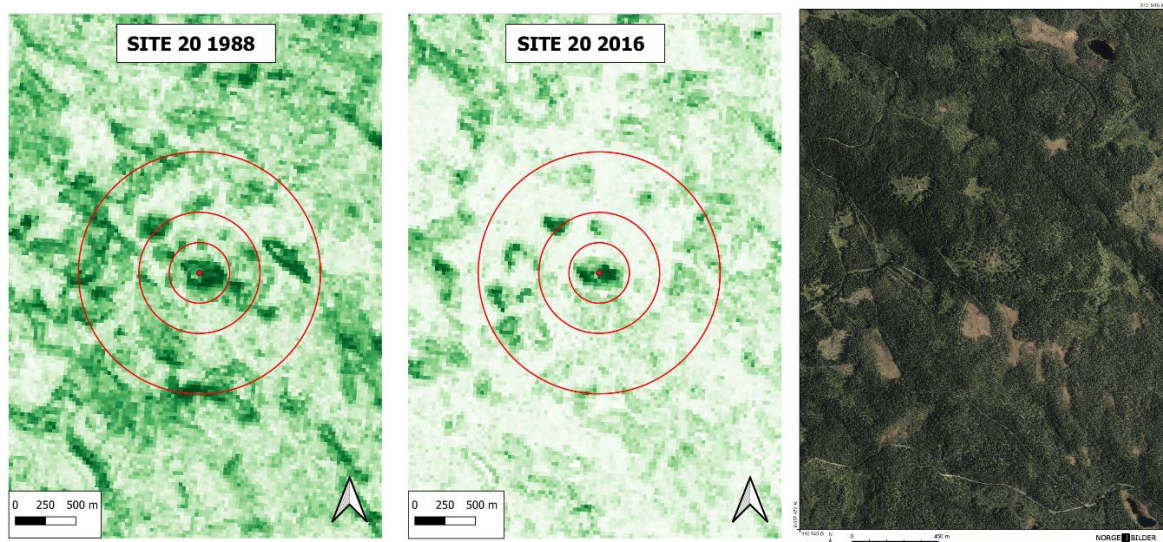


Figure A18. Site 20 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

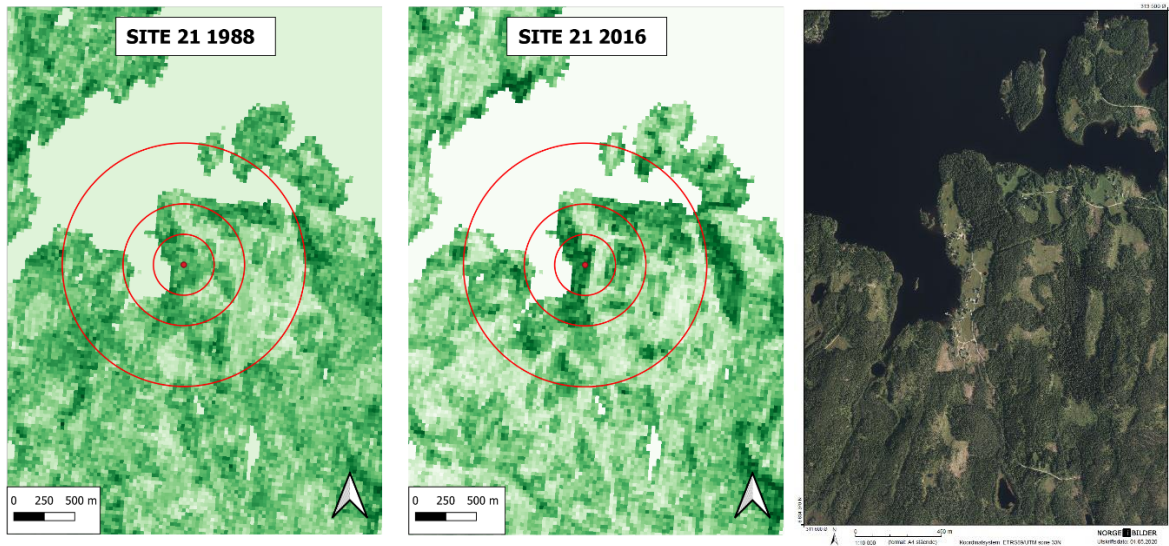


Figure A19. Site 21 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

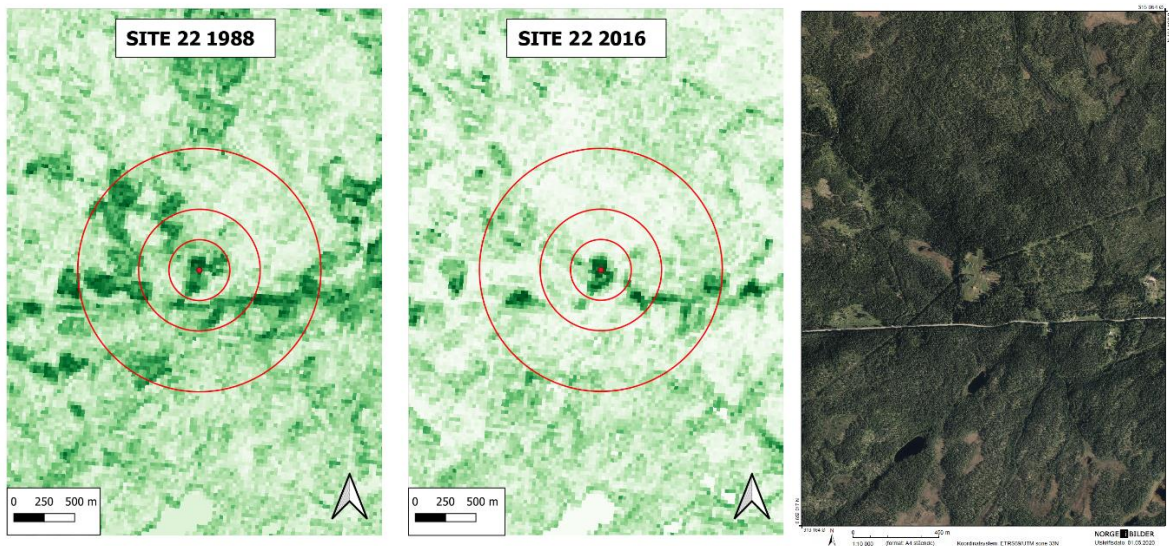


Figure A20. Site 22 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

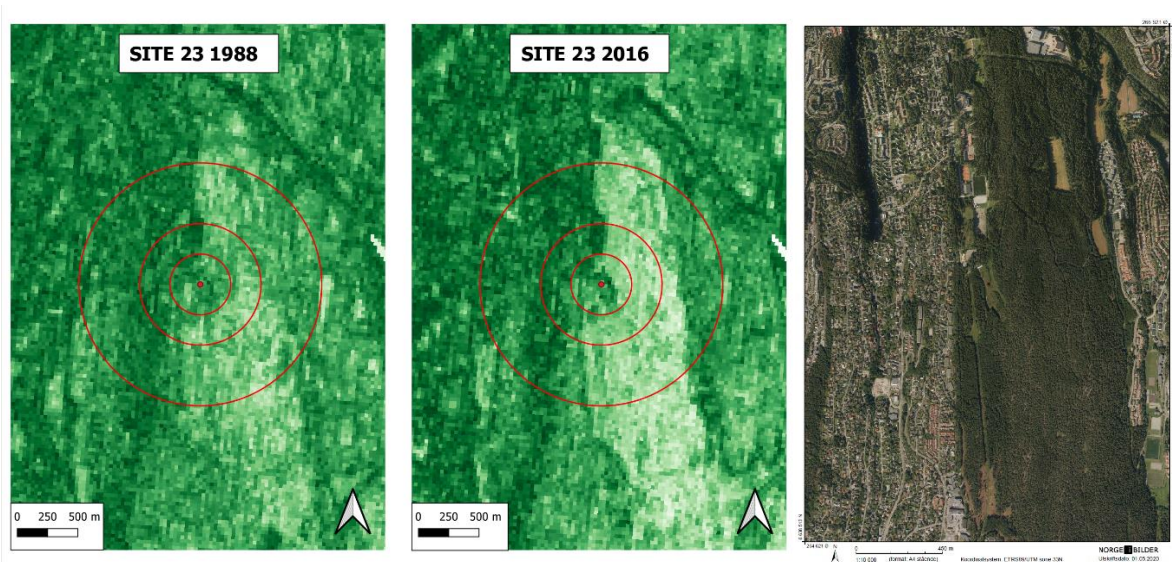


Figure A21. Site 23 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

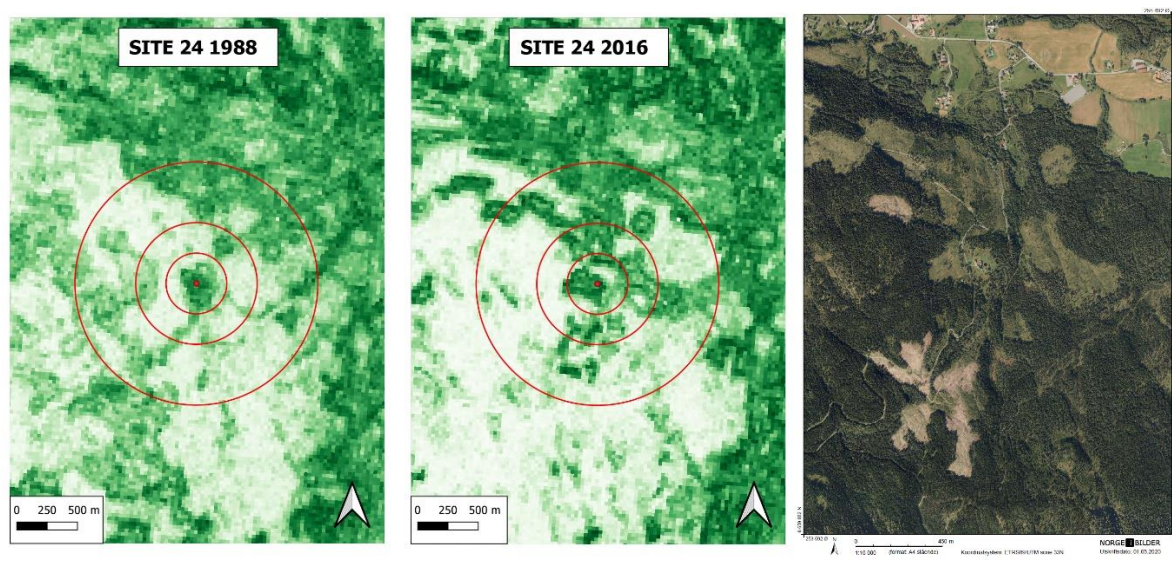


Figure A22. Site 24 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

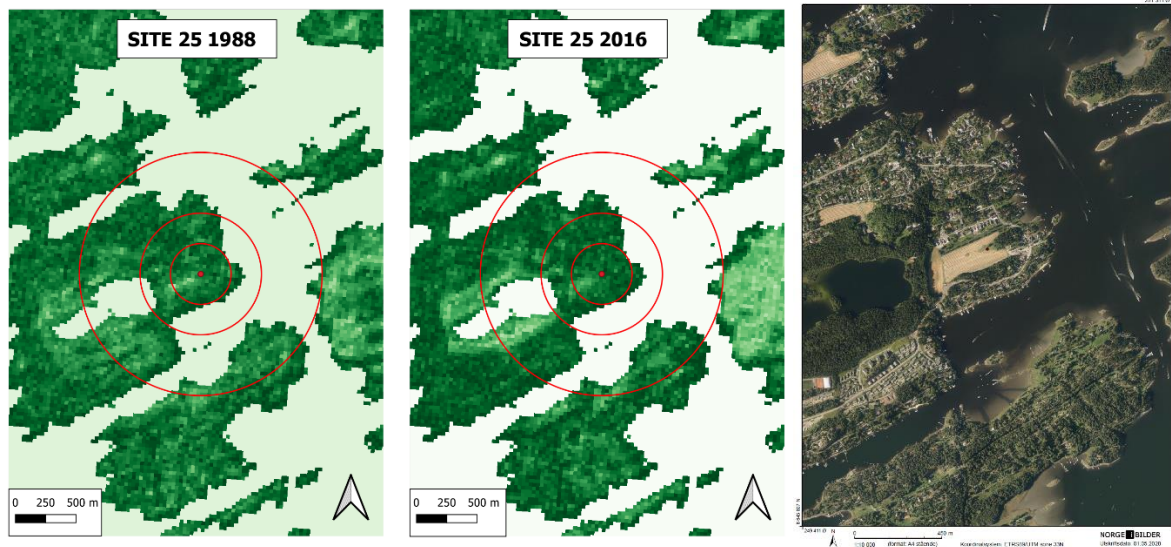


Figure A23. Site 25 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

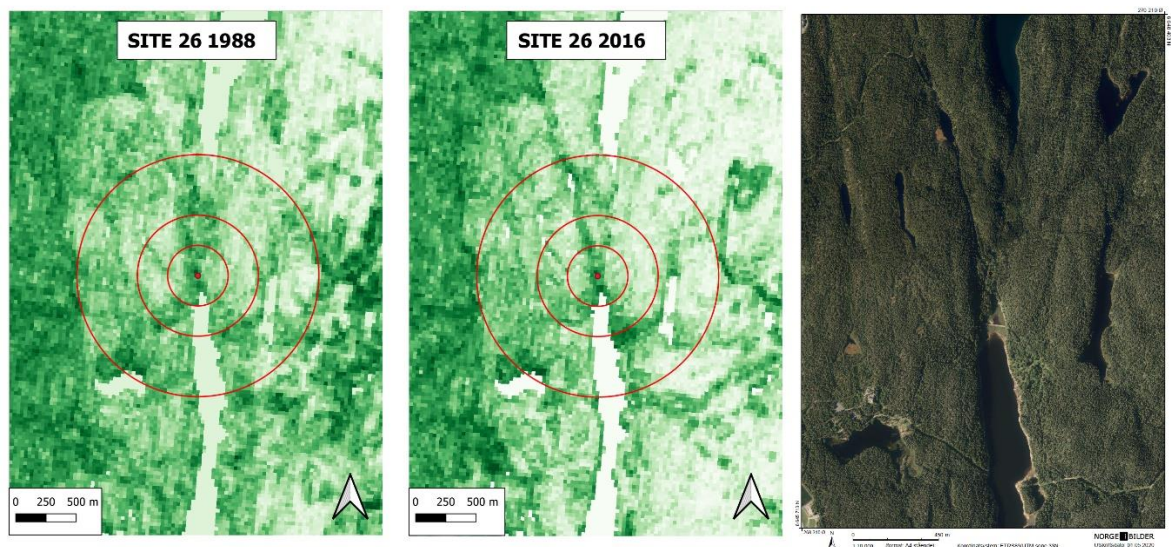


Figure A24. Site 26 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

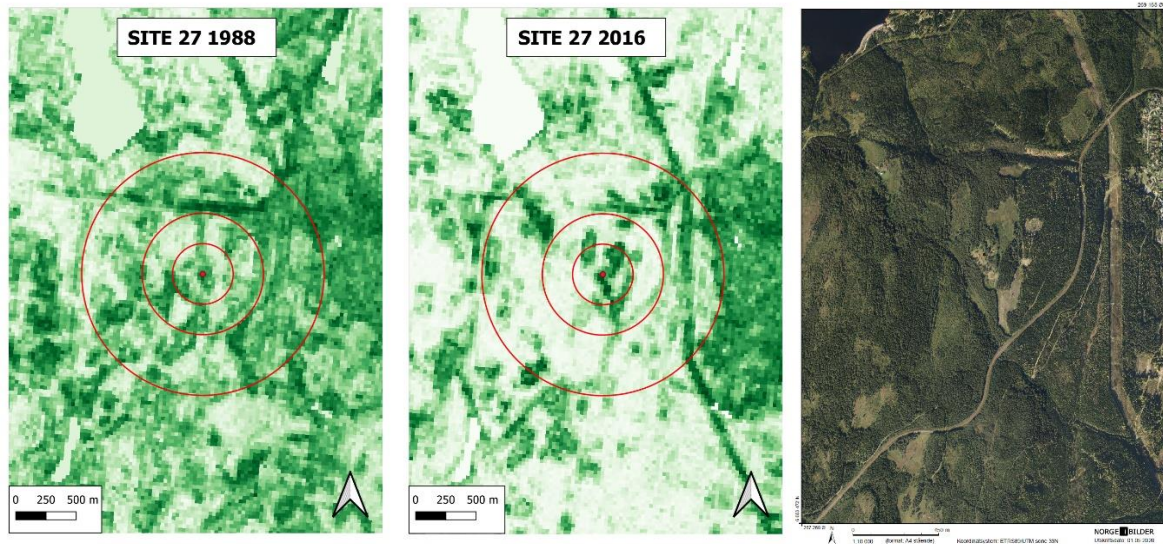


Figure A25. Site 27 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

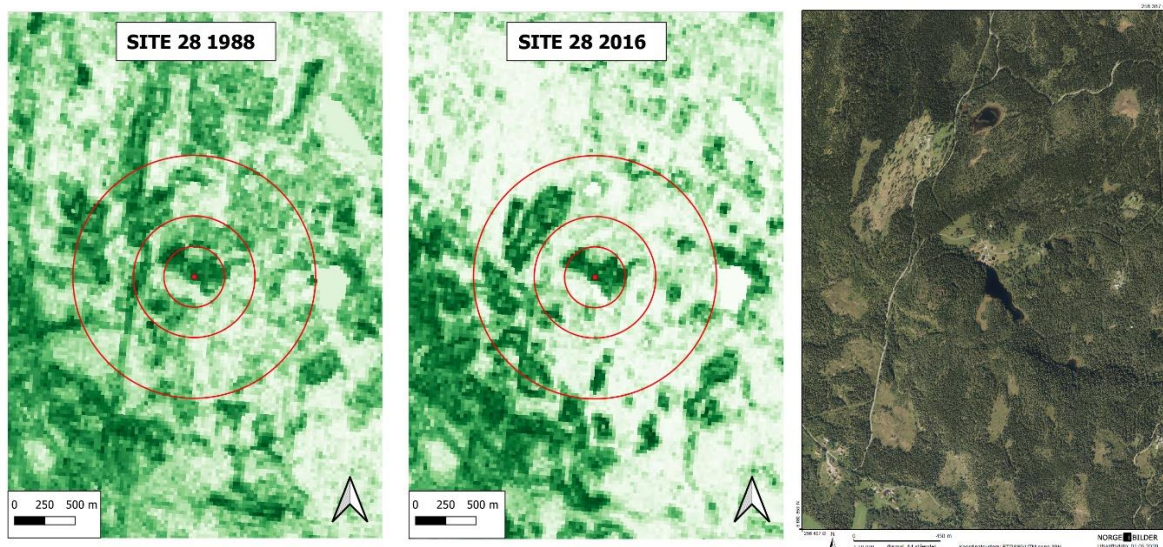


Figure A26. Site 28 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

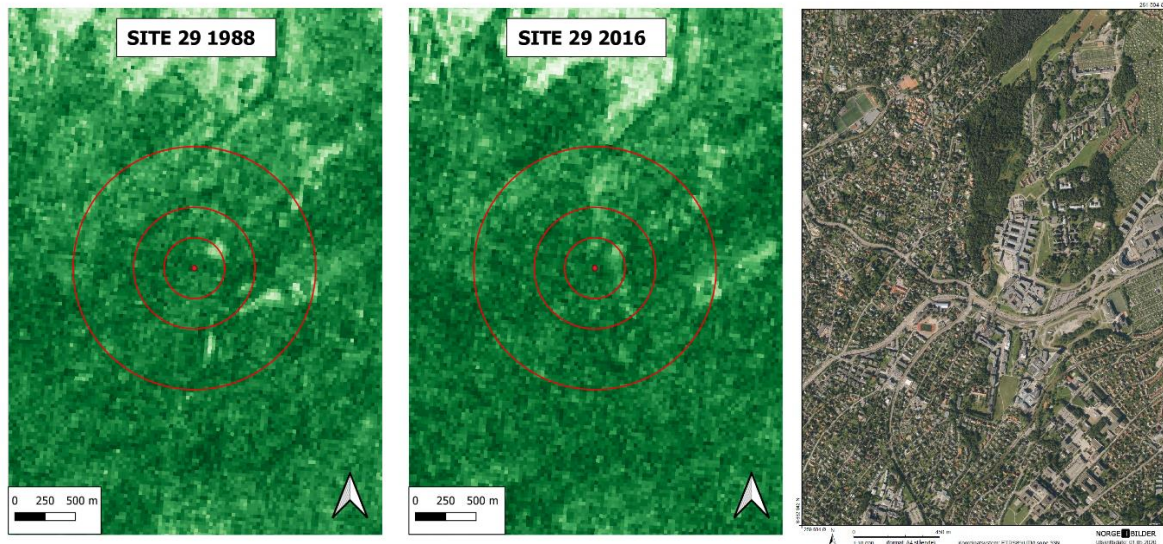


Figure A27. Site 29 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

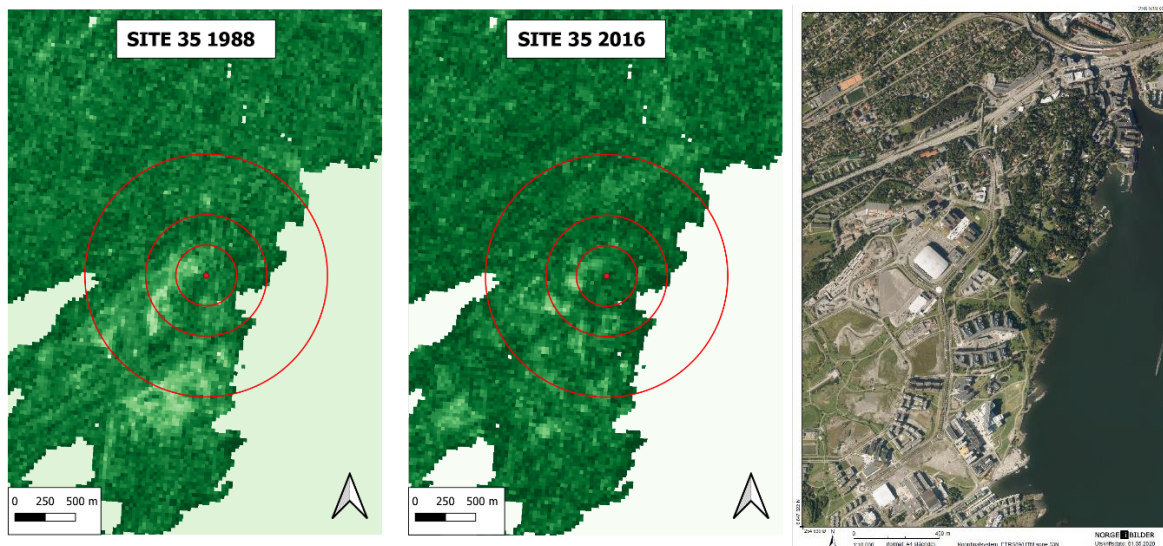


Figure A28. Site 35 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

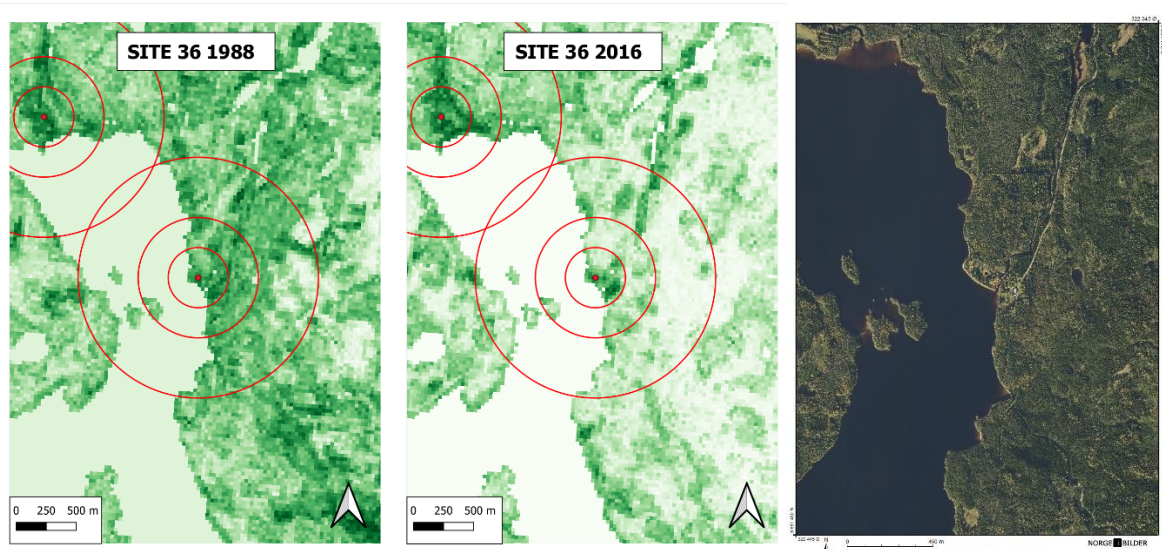


Figure A29. Site 36 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

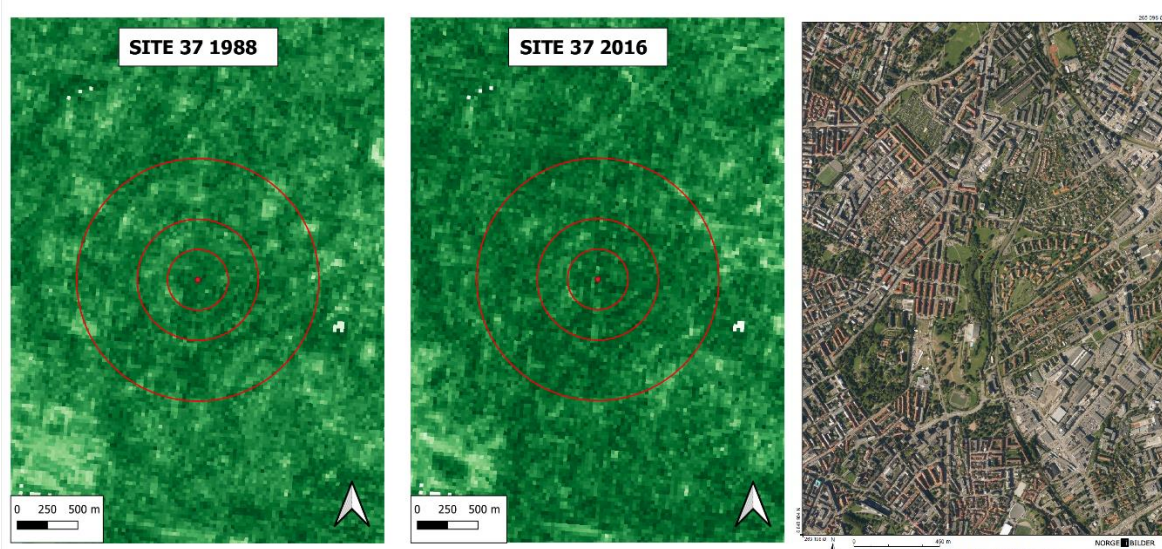


Figure A30. Site 37 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

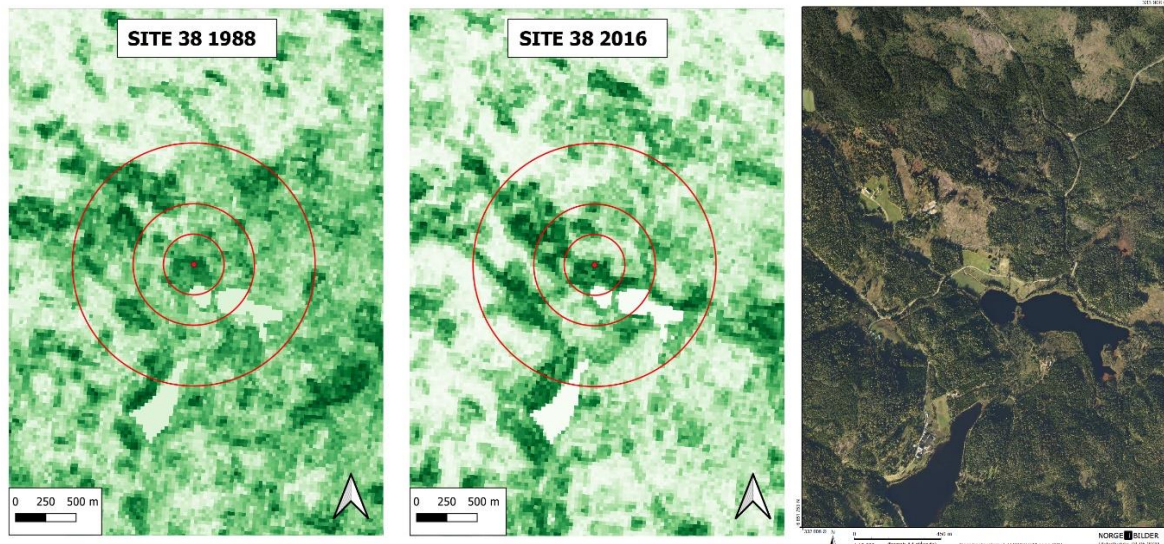


Figure A31. Site 38 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2016 as reference (QGIS Development Team, 2020).

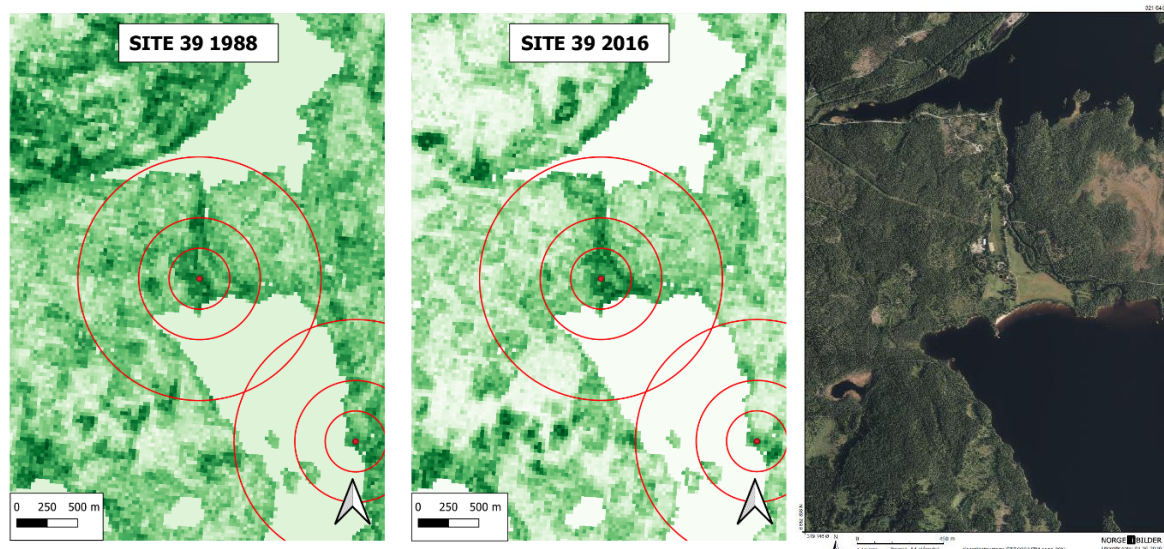


Figure A32. Site 39 with maps of early successional areas from 1984-1988 and 2012-2016 (to the left). Increased saturation indicates increasing probability of bee habitat. To the right is a satellite image from 2015 as reference (QGIS Development Team, 2020).

Appendix II

Table A1: Overview over sites, their registered id number and the web site with all the registered information.

Site	Semi-natural grassland ID	Web site
POLLI01	BN00069612	https://faktaark.naturbase.no/?id=BN00069612
POLLI02	BN00069656	https://faktaark.naturbase.no/?id=BN00069656
POLLI03	BN00109794	https://faktaark.naturbase.no/?id=BN00109794
POLLI04	BN00106173	https://faktaark.naturbase.no/?id=BN00106173
POLLI05	BN00038337	https://faktaark.naturbase.no/?id=BN00038337
POLLI06	BN00106180	https://faktaark.naturbase.no/?id=BN00106180
POLLI07	BN00038339	https://faktaark.naturbase.no/?id=BN00038339
POLLI08	BN00038219	https://faktaark.naturbase.no/?id=BN00038219
POLLI10	BN00085764	https://faktaark.naturbase.no/?id=BN00085764
POLLI11	BN00083539	https://faktaark.naturbase.no/?id=BN00083539
POLLI12	BN00047755	https://faktaark.naturbase.no/?id=BN00047755
POLLI13	BN00092283	https://faktaark.naturbase.no/?id=BN00092283
POLLI14	BN00038104	https://faktaark.naturbase.no/?id=BN00038104
POLLI15	BN00066317	https://faktaark.naturbase.no/?id=BN00066317
POLLI17	BN00092291	https://faktaark.naturbase.no/?id=BN00092291
POLLI18	BN00025396	https://faktaark.naturbase.no/?id=BN00025396
POLLI19	BN00025398	https://faktaark.naturbase.no/?id=BN00025398
POLLI20	BN00025436	https://faktaark.naturbase.no/?id=BN00025436
POLLI21	BN00066322	https://faktaark.naturbase.no/?id=BN00066322
POLLI22	BN00066311	https://faktaark.naturbase.no/?id=BN00066311
POLLI23	BN00093643	https://faktaark.naturbase.no/?id=BN00093643
POLLI24	BN00093621	https://faktaark.naturbase.no/?id=BN00093621
POLLI25	BN00088912	https://faktaark.naturbase.no/?id=BN00088912
POLLI26	BN00064416	https://faktaark.naturbase.no/?id=BN00064416
POLLI27	BN00113396	https://faktaark.naturbase.no/?id=BN00113396
POLLI28	BN00087207	https://faktaark.naturbase.no/?id=BN00087207
POLLI29	BN00064224	https://faktaark.naturbase.no/?id=BN00064224
POLLI35	BN00100175	https://faktaark.naturbase.no/?id=BN00100175
POLLI36	BN00066307	https://faktaark.naturbase.no/?id=BN00066307
POLLI37	BN00064442	https://faktaark.naturbase.no/?id=BN00064442
POLLI38	BN00058687	https://faktaark.naturbase.no/?id=BN00058687
POLLI39	BN00066308	https://faktaark.naturbase.no/?id=BN00066308



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