Landscape heterogeneity moderates temporal changes in floral resource diversity

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Data availability: The data and code for replicating the results are available via https://github.com/emmaliinamarjakangas/Floral-resource-diversity.

Abstract

Floral resource diversity supports pollination function and is increasingly threatened by global environmental change. Using long-term data on native insect-pollinated plants across 200 landscapes in southern Sweden, we assessed changes in taxonomic and functional diversity over 26 years in relation to land cover heterogeneity. Species richness declined significantly, while the three functional diversity measures (functional richness, functional evenness, and functional dispersion) remained stable, suggesting that declines are not particularly associated with certain floral trait combinations. This suggests some degree of functional resilience in floral trait composition despite ongoing species loss. However, spatial and temporal variation was substantial, with some landscapes experiencing increases in floral diversity, while others showing a decrease. Landscapes with greater land cover heterogeneity supported higher levels of floral resource diversity, but this diversity was found to decline over time, potentially due to reduced management of semi-natural grasslands and transfer to conifer plantations. Initial diversity did not buffer against losses but rather indicated higher potential for decline. Our findings highlight the complex interactions between landscape heterogeneity, biodiversity loss, and ecosystem function. Conserving structurally heterogeneous landscapes and maintaining diverse floral traits are critical to supporting pollinator communities under global change. Our study underscores the need for landscape-scale strategies to preserve pollination services and ecosystem resilience as the human pressures on biodiversity intensify.

Keywords: flower trait, functional diversity, land cover, land use, plant diversity, plant community, pollination, Sweden

Introduction

The functional diversity of floral resources is key to sustaining ecosystem resilience and the mutualistic interactions between plants and pollinators (Abrahamczyk et al., 2022; Blüthgen & Klein, 2011). Pollinators contribute to essential ecosystem services such as food production, biodiversity maintenance, and habitat stability by facilitating plant reproduction through pollen transfer (IPBES, 2016). In return, flowering plants provide critical floral resources, such as nectar, pollen, and materials for nest construction. Because a large proportion of flowering plant species (78% in the temperate zone and 94% in the tropics; Ollerton et al., 2011) depend on pollinators to some extent, maintaining a diverse set of floral traits is crucial for supporting a wide range of pollinator taxa.

Functional redundancy within plant communities, where multiple species share similar traits, can buffer pollination systems against species loss (Blüthgen & Klein, 2011). Yet, declines in pollinator populations raise concerns about the parallel loss of functional diversity in floral resources. Despite their relevance to reproduction and mutualisms, floral traits remain underused in studies of functional diversity, which more commonly emphasize vegetative traits such as leaf size, plant height, and seed mass (Díaz et al., 2015; E-Vojtkó et al., 2020).

Floral traits (e.g. shape, color, and nectar production) and their diversity mediate plant-pollinator interactions and pollinator visitation in flowering plants (Dellinger, 2020; Fornoff et al., 2017) and are especially important for understanding ecosystem functioning. For example, specialized floral morphologies may evolve in response to pollinator anatomy, such as floral spurs matching the length of pollinator tongues (Hodges & Arnold, 1995). Flower color, scent and floral display can also influence plant-pollinator interactions through the attraction of specific pollinator groups to the flower (Bradshaw & Schemske, 2003; Fenster et al., 2004; Junker & Parachnowitsch, 2015; Raguso, 2008). For example, crossing experiments on *Mimulus* have demonstrated that slight colour changes in flowers can influence pollinator’s floral preference (Bradshaw & Schemske, 2003). Nectar traits can also structure pollinator visitation, with higher nectar quantity and quality supporting broader pollinator communities (Nottebrock et al., 2017). Thus, floral trait diversity reflects the capacity of a plant community to sustain pollinator diversity.

Globally, landscapes vary in their capacity to support diverse flowering plant communities depending on the degree of land cover heterogeneity. In highly heterogeneous landscapes, a mosaic of land cover types, such as semi-natural grasslands, pastures, and forest edges, supports a wide range of flowering plants with diverse phenology and interactions with pollinators (Ammann et al., 2024; Cavigliasso et al., 2022). In contrast, homogenized landscapes dominated by urban infrastructure or intensive agriculture often lack the structural and compositional diversity needed to support functionally diverse plant communities (McKinney, 2006; Pearse et al., 2018; Sánchez et al., 2022). Additionally, the remaining floral rich habitats in the landscape are fragmented and isolated, limiting dispersal of pollen and seeds (Aune et al., 2018; Billeter et al., 2008; Veen et al., 2009). As such, variation in land cover heterogeneity plays a central role in shaping the functional trait composition of flowering plant communities at the landscape scale.

The flowering plant community composition can change differently in different landscapes. For example in Sweden, plant species with high nectar production have increased in relative frequency over time, likely due to the spread of non-native ornamental species and increased primary productivity from nitrogen deposition and eutrophication (Hallman et al., 2022; Tyler et al., 2018). These changes may not benefit specialist pollinators reliant on native species. Moreover, in urban landscapes, species composition has changed and subsequently there has been a shift in functional traits from stress tolerant to disturbance tolerant species (Knapp et al., 2009; Petersen et al., 2021), altering the functional trait space in favor of generalist strategies.

Despite the documented loss of plant species richness across central and northern Europe (Eichenberg et al., 2021; Finderup Nielsen et al., 2019; Kindlund & Tyler, 2023; Sundberg, 2014), especially under agricultural intensification, it remains unclear how these changes have affected the diversity of floral traits that are important for plant-pollinator interactions. In conservation and management, the diversity of flowering plants has long been used as an indicator of pollinator diversity due to their strong correlation (Ebeling et al., 2008; Potts et al., 2003; Steffan-Dewenter & Tscharntke, 2001). In contrast, floral traits not only allow us to assess the diversity of plant species, but also their functional diversity and diversity of interacting functional groups. However, the limited availability of long-term data on flowering plant traits and distributions remains a key challenge. Consequently, we know little about whether declines in taxonomic diversity are paralleled by losses in the diversity of floral resources and, by extension, whether pollinators are experiencing declines in functionally relevant plant traits across different landscape types.

Here, we address this gap by analyzing long-term data on native flowering plant occurrences and pollination-related traits in 200 landscapes across southern Sweden between 1989 and 2015. By combining species-level trait information with land cover data, we evaluate temporal changes in both taxonomic and functional diversity of floral resources. We focus on native species, as specialist pollinators tend to rely on them even when non-native plants dominate the landscape (Pekos et al., 2025). A loss of native species richness can signal broader ecosystem shifts in situations when overall richness appears stable due to alien species introductions and spread. We provide a novel assessment of how floral resource diversity is changing over time and how these trends vary depending on land cover heterogeneity. By examining floral traits related to pollination, instead of the more commonly studied vegetative traits, we highlight a key functional dimension of plant communities directly tied to plant-pollinator interactions and reproductive success. Our study addresses two main questions: 1) How have the taxonomic and functional diversities of floral resources changed over time?; and 2) Do these temporal trends relate to land cover heterogeneity across landscapes? We predict a general decline in both taxonomic and functional diversity of floral resources over time, reflecting global patterns of biodiversity loss of native species and biotic homogenization (Daru et al., 2021). We also predict a weaker decline in functional diversity than in species richness, due to functional redundancy among species buffering the community against trait loss. Finally, we predict stronger declines in floral resource diversity in heterogeneous landscapes because they are made up of many smaller, unique habitat patches, and losing these patches can lead to the loss of the plants they support.

Methods

Data

Study area. Scania, Sweden’s southernmost province (~11,000 km²), consists of calcareous clay plains and acidic uplands (Andersson & Weimarck, 1996; Persson & Tyler, 2007). Plains are dominated by agriculture with scattered deciduous forests, while uplands host forests and peatlands with some farming. About 33% of the land is forested and 63% is arable or grassland(Fridman et al., 2014), with forest cover increasing and grasslands declining over the past two centuries.

Plant occurrence data. We used presence-absence data for plant species in 200 randomly selected 2.5×2.5 km grid cells (hereafter, landscapes) across Scania, surveyed in 1989–2006 (period 1) and

2008–2015 (period 2) (Tyler et al., 2018, 2020). Landscapes containing >3,000,000 m² of water were excluded to ensure comparable sampling areas. We used two separate time periods instead of continuous yearly observations as each landscape has been surveyed twice but in varying times and durations within each study period. We followed the taxonomic nomenclature of The Plant List (*World Flora Online*, 2020). We identified native species using information from the Swedish Red List that comprises species assessments of 99% of the native vascular plant species (SLU Artdatabanken, 2020). From this set of species, we removed two apomictic complexes (274 microspecies of *Taraxacum spp.* and 729 microspecies of *Hieracium spp.*, except *Hieracium umbellatum*). We made this decision to avoid these two complexes, which due to minor local variations comprised 39% of the species in our dataset, having a disproportionally large influence on the results. In our final analysis, we aimed at only including plant species that contribute with pollen and/or nectar to pollinating insects. For this, we extracted information about pollen vectors from the plant trait databases BiolFlor and EcoFlora, accessed via R package TR8 (Bocci, 2015; Fitter & Peat, 1994; Klotz et al., 2002). We included any species, where insects were mentioned as pollen vectors in at least one of these databases, either alone or in combination with other vectors, unless the contribution of insects was specified as 'rare' or 'possible'. The final list comprised 609 species with 41,073 records in period 1, and 37,992 records in period 2.

Plant floral trait data. We compiled 11 floral traits related to pollination and reproductive success, following the design by Stefanaki et al. (2015): flower shape, flower depth, flower symmetry, corolla segmentation, reproductive unit, flower color, flower size, onset of flowering, flowering duration, flowering seasonality, and nectar production. For trait definitions, categories, and data sources, see Table 1 and Appendix S1. Trait data and metadata are openly available (Appendix S3).

Table 1. List and description of flower traits used in the study.

Trait name	Description	Levels	Source(s)
Flower shape	Functional shape of flowers	Bell, brush, disk, tube, disk-tube, funnel, flag, gullet, head, lip, trap	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; *LuontoPortti - NatureGate*

			Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Flower depth	Corolla tube length	Low-depth (<4mm), medium-depth (4-10mm), high-depth (>10mm)	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Flower symmetry	Number of floral symmetry axes	Radial symmetry, bilateral symmetry	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Corolla segmentation	Degrees of corolla (or perianth) segmentation	Sympetaly, choripetaly, semichoripetaly	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Reproductive unit	Functional reproductive unit of the inflorescence	Single flowers, flat/spherical, cylindrical	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Flower color	Dominant or most frequently occurring color of the flowers	White, yellow/cream, violet/purple/pink/red/brown/rose/lilac/magenta, blue, green	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Flower size	Length-width average of the exposed corolla surface in 2D-projection	Small (<10mm), medium (10-20mm), large (>20mm)	BioFlor, Ecoflora, LEDA (Bocci, 2015; Fitter & Peat, 1994; Kleyer et al., 2008; Klotz et al., 2002), floras (Lid & Lid, 2005; LuontoPortti - NatureGate Online Flora., 2020; Mossberg & Stenberg, 2014), and personal communication (T. Tyler)
Onset of flowering	A 2-week period when plant is first recorded to be flowering	Continuous numerical, based on flowering occurrence data. First 2-week period is in the first half of March and the last in the last half of October. Number of 2-week periods = 16.	(Tyler et al., 2021)

Flowering duration	Number of 2-week periods when plant is recorded to be flowering	Continuous numerical, based on flowering occurrence data. Minimum = 2, maximum = 14.	Newly compiled for this study
Flowering seasonality	Flowering occurrence in the first half of April (Spring), in the first half of July (Summer), and in the first half of September (Autumn)	For each category (Spring, Summer, Autumn) a separate binary dummy variable: Yes and No. Each species may belong to 0–3 categories.	(Tyler et al., 2021)
Nectar production	Yearly production of nectar (sugar) and pollen (protein) per species and area.	Continuous numerical. Minimum = 1, maximum = 7.	(Tyler et al., 2021)

Land cover data. We used CORINE Land Cover data (version 2000; (European Union's Copernicus Land Monitoring Service information, 2000) at 100 m resolution covering all study landscapes. We reclassified the original 44 land cover categories into broader categories: arable land, forest (coniferous, deciduous, and mixed), natural open land, urban, water, wetland, and other open land (Appendix S1, Table S1, Figures S1-S2). To do this, we overlaid the CORINE data with our landscape grid cells using R package sf (Pebesma, 2018), calculated the area of each land cover class within each landscape, and then summed areas by land cover category. We quantified land cover heterogeneity per landscape using Shannon's diversity index using the original CORINE land cover categories (R package vegan; Oksanen et al., 2013). Land cover heterogeneity varied across the study region (Appendix S1, figure S3).

Quantifying taxonomic and functional diversity

We measured floral resource diversity using four metrics per landscape and time period: species richness, and three functional diversity metrics: functional richness, evenness, and dispersion (Laliberté & Legendre, 2010; Villéger et al., 2008). In general, functional diversity measures represent trait combinations in multidimensional space. In case of decreasing functional diversity, unique combinations of traits are lost in the plant community, which makes functional diversity a useful way to assess the effects of plant composition changes on pollinators in an ecologically relevant way. We calculated the functional diversity metrics using the dbFD function in R package FD (Laliberté et al., 2014). For this, we calculated Gower distances based on traits in Table 1 with equal weighting. Functional richness for multiple traits represents the amount of functional space filled by the community and is calculated as the volume of the n-dimensional convex hull. Functional dispersion represents the mean distance of individual species' trait values to the centroid of all species' (trait mean) in the community. Functional evenness is calculated based on the minimum spanning tree that links the species in the functional trait space. That is, functional evenness measures the regularity of species along this tree in the trait space (Villéger et al., 2008). In the context of our study system, temporal increase in functional evenness would indicate that trait values are more evenly distributed across species. While this may sound positive, it also implies a loss of species with rare or extreme trait values that might support specialist pollinators. Similarly, an increase in functional dispersion would indicate that remaining species are more divergent from the average trait profile of the community. This could reflect a shift toward more trait outliers and marginal species, potentially supporting novel or rare interactions, or alternatively indicating instability in the plant community structure. Together these three functional diversity measures encompass the different dimensions of functional diversity (Magneville et al., 2022). We found a strong correlation between species richness and functional richness ($r = 0.93$), but not among other metrics (Appendix S1, Tables S2–S3). Because we suspect that landscapes with high initial floral resource diversity (diversity in period 1) will be better able to buffer changes over time, we also tested for correlation between initial diversity values and changes in diversity. Finally, we computed absolute and proportional differences in category occurrences in trait frequency changes between periods (Appendix S2, Table S1).

Statistical modeling

We used linear mixed effects models (R package lme4; (Bates et al., 2015) to model temporal changes in the four diversity metrics and used land cover heterogeneity and time period as the main predictors. This was done with interaction terms to capture temporal effects of heterogeneity. We included landscape identity as a random effect. Each model used one diversity metric as the response variable. Analyses and figures were produced using R v4.3.0 (R Core Team, 2024).

Results

Spatial variation in species richness and floral resource diversity

Distributions of the measures describing floral resource diversity were largely similar in both study periods with high variation in floral resource diversity among landscapes (Figure 1). For example, on average(±sd) in period 1, 222(±47) species were recorded across the landscapes, while in period 2, 205(±53) species were recorded across the landscapes.

How have the taxonomic and functional diversities of floral resources changed over time? Overall, we observed a statistically significant decline in species richness over time (Figures 1d, and 2d). Functional richness tended to decrease, and functional evenness and dispersion tended to increase over time, although these changes were not statistically significant (Figures 1a-c, 2a-c). Although there was a general decline in floral resource diversity, changes over time varied greatly among sites (distribution contains both positive and negative values in Figure 2). Across the study region, the largest declines in floral resource diversity were observed in the forest-dominated upland north and northeastern parts, and these changes were only significant when measuring floral resource diversity with species richness metrics (Figure 3). The largest increases in functional richness and species richness occurred on the agricultural plains in the southwestern part of the study region (Figure 3). Specifically, functional richness and species richness declined most in study landscapes dominated by forest and remained largely stable in study landscapes dominated by arable land (Appendix S2, Figure S1). Initial diversity and change in diversity correlated negatively, indicating that declines were most prominent in areas with high initial diversity ($r_{\text{Functional richness}} = -0.16$, $r_{\text{Functional evenness}} = -0.33$, $r_{\text{Functional dispersion}} = -0.43$, $r_{\text{Species richness}} = -0.25$) (Appendix S2, Figure S2).

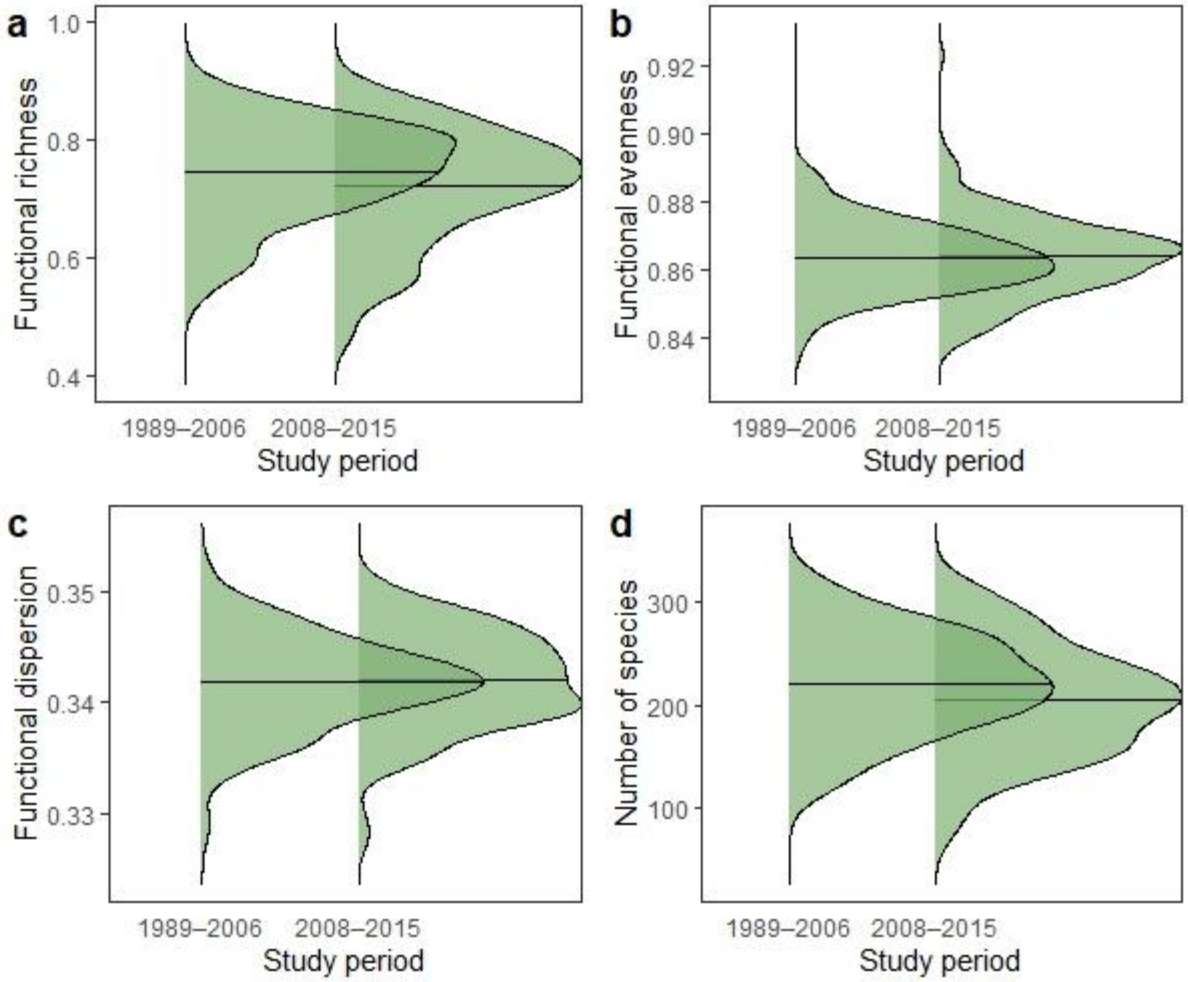

Figure 1. Distribution of functional and taxonomic diversity values of floral resource plant species (y-axes) in two time periods (x-axis) in southern Sweden. The horizontal lines indicate the study period-specific mean values.

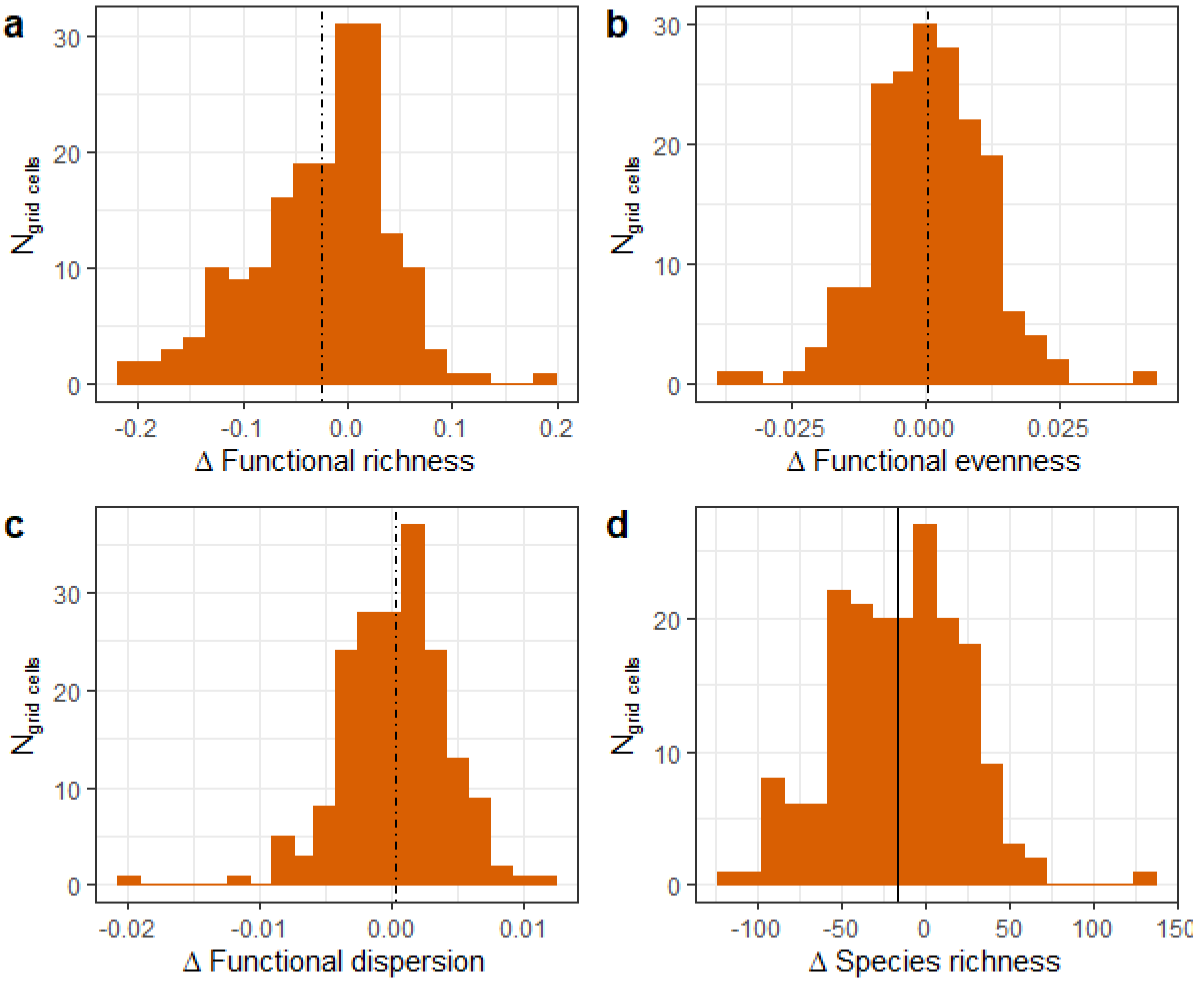

Figure 2. Change in the diversity of floral resource plant species over time in southern Sweden. Vertical lines indicate the average change value. Significant change is indicated with continuous line and non-significant changes with dashed lines (see Table 2 for the detailed model summaries).

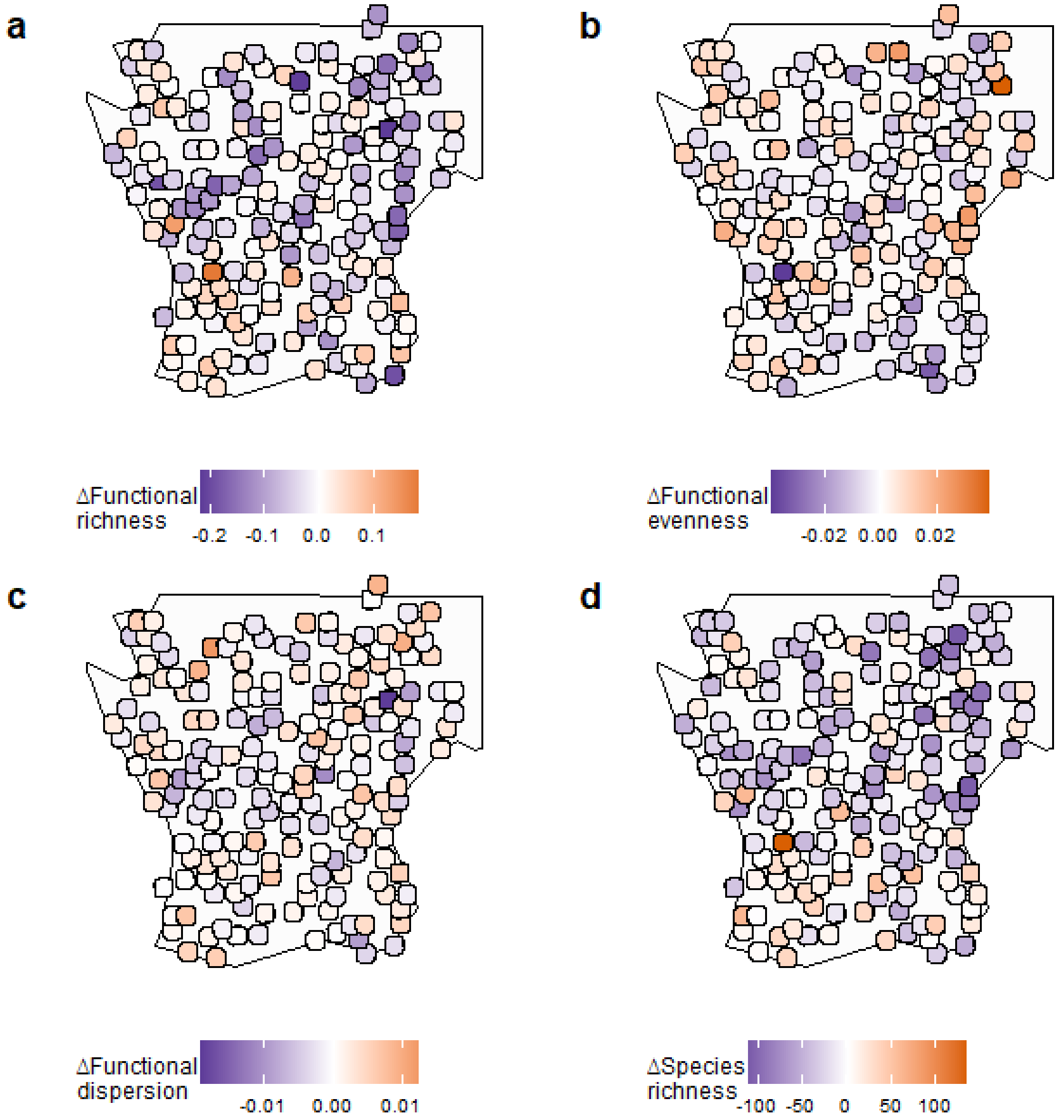

Figure 3. Spatial variation in floral resource diversity change of native floral resource plant species across southern Sweden. The color gradient illustrates the change, such that blue corresponds to decrease in diversity measure, while orange corresponds to increase in diversity measure. Note that positive values of functional evenness change reflect decreases in functional diversity. The size of the grid cells has been increased for illustrative purposes.

Do floral resource diversity trends relate to land cover heterogeneity? Land cover heterogeneity helped explain the variation in diversity change over time. Specifically, we found that the landscapes with greater heterogeneity experienced greater loss of species richness over time than the more homogenous landscapes (Table 2, Figure 4d). Similar, but only marginally statistically significant patterns were observed for the functional richness measure (Table 2, Figure 4a). According to the model, functional evenness and functional dispersion of floral resource plant species did not change over time (Table 2).

Table 2. Linear mixed effect model summary on relationships between floral resource diversity and land cover heterogeneity over time. Each cell includes the model estimate and standard error values. Each column represents a model with a different diversity measure as the response variable. Study period 1 was set as the reference category for the factorial Study period variable. Land cover heterogeneity was measured as Shannon diversity across land cover types (see Methods). Bolded estimates indicate statistically significant effects ($p < 0.05$).

	Response variable (estimate ± SE)			
	Functional richness	**Functional evenness**	**Functional dispersion**	**Species richness**
Intercept	**0.692 ± 0.014**	**0.862 ± 0.002**	**0.341 ± 0.0007**	**189.944 ± 7.883**
Study period	-0.0087 ± 0.011	0.00004 ± 0.002	0.00005 ± 0.0007	-5.459 ± 6.174
Land cover heterogeneity	**0.061 ± 0.014**	0.002 ± 0.002	0.0010 ± 0.00007	**35.548 ± 7.820**
Study period * Land cover heterogeneity	-0.019 ± 0.011	-0.0005 ± 0.002	0.0002 ± 0.00007	**-12.707 ± 6.124**

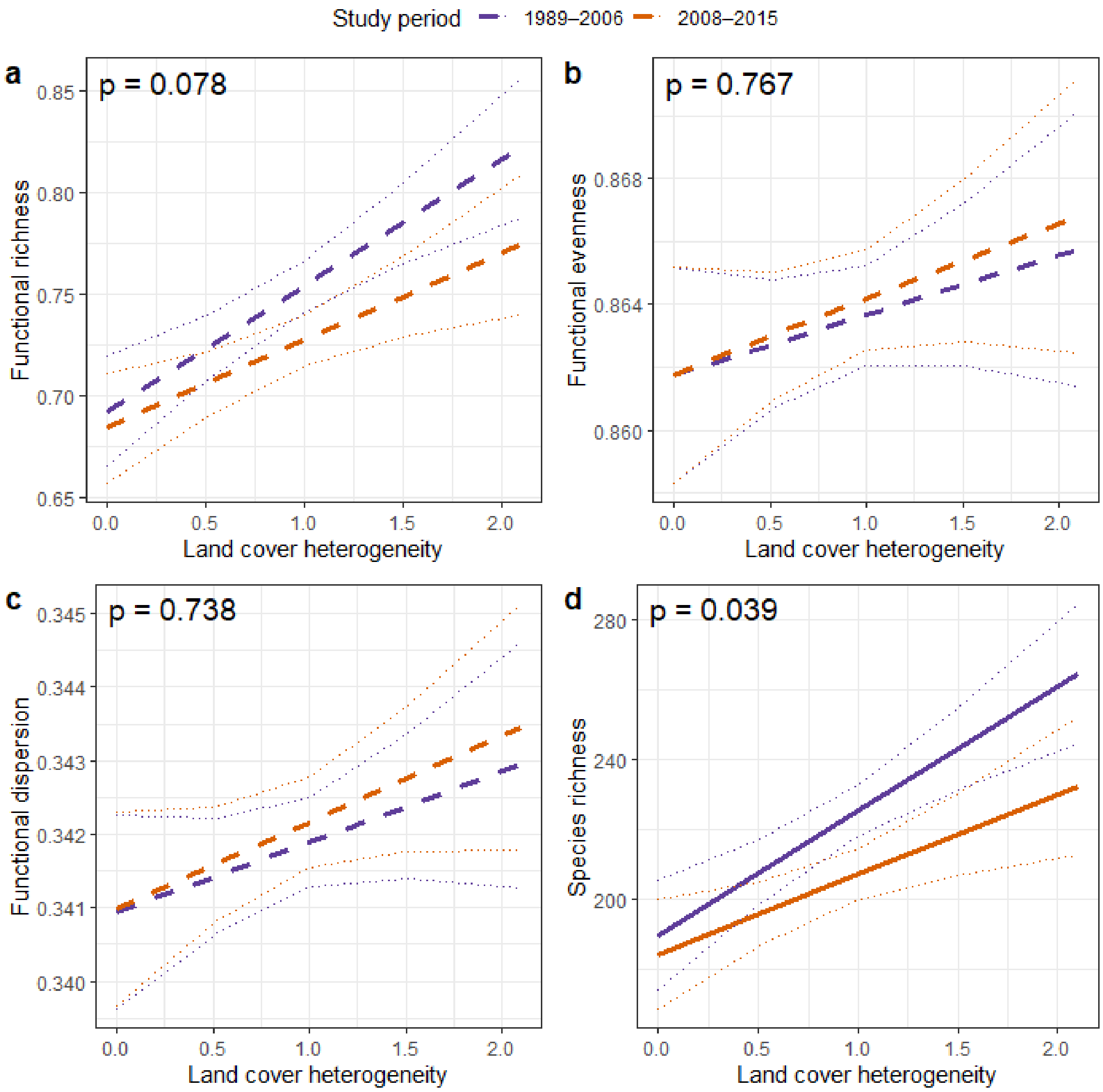

Figure 4. Interactive effect of Land cover heterogeneity and Study period on floral resource plant species' diversity measured as Functional richness (panel a), Functional evenness (panel b), Functional dispersion (panel c), and Species richness (panel d) based on linear mixed effect models (Table 2). The significant interaction effect is indicated with a continuous line, and non-significant effects are indicated with dashed lines.

Discussion

Using 26 years of monitoring data from southern Sweden, we observed a clear decline in the number of pollinator-relevant species as well as a tendency of decline in functional richness of floral resource species. Notably, the loss of species richness was most prominent in heterogeneous landscapes, which are particularly important for the conservation of pollinating insects (Eckerter et al., 2022; Zanini et al., 2024). A simultaneous lack of change in functional evenness and dispersion over time likely indicates some degree of functional resilience in plant communities. This information can be applied to assess to what extent floral resource resilience buffers land use effects on pollinators.

Spatial variation in floral resource diversity

Within each survey period, we observed large variation in both taxonomic and functional diversity across the study landscapes. Some landscapes harbored rich and varied floral trait communities, while others supported only a few plant species with limited trait diversity. For insect pollinators, this spatial variation has important implications: areas with high functional diversity likely offer a broader array of floral resources, for example in terms of flower color, shape, symmetry, flowering time, and nectar rewards, supporting a wider range of pollinator species and functional groups (Fornoff et al., 2017). In contrast, landscapes with low functional diversity may act as functional "deserts", offering fewer options and potentially excluding specialized pollinators.

Temporal change in floral resource diversity

In line with previous studies using the same monitoring data (Tyler et al., 2018, 2020), we observed that species richness declined over time. Here, we also found that the loss of species diversity brought with it a marginally significant decline in functional richness. A nearly significant decline in functional richness suggests that fewer unique trait combinations are present, meaning contemporary plant communities comprise less variation in floral traits than plant communities surveyed during the first period. This could reduce the adaptive capacity of ecosystems, making them more vulnerable to environmental change and less able to support a diverse pollinator community (Dawson et al., 2011).

While the majority of the landscapes showed declines in diversity, some experienced increases (similarly to patterns observed by Abrahamczyk et al., 2022). It has previously been shown that the species that increase the most in the area are escapes from cultivation (Tyler et al., 2020) and in line with this, the increases in species richness and functional diversity occurred in the southern part of the study region, which is dominated by agriculture (Appendix S2, Figure S1). This pattern may also reflect the influence of various agri-environmental schemes implemented in Sweden during the study period (e.g. EU regulation 658/96 on compensatory payments for crop producers), such as set asides, buffer zones, and unsprayed field margins, with potentially positive effects on habitat availability for wild plants in areas dominated by arable land (Hald, 1999; Primdahl et al., 2003).

The sensitivity analysis showed that landscapes with an initially high floral resource diversity experienced stronger declines in both taxonomic and functional measures. Although this may be interpreted to challenge the prevailing diversity-stability hypothesis (Loreau et al., 2001), this pattern is more likely associated with the fact that a bulk of common habitat generalists are resistant towards land use and climate changes, also mirrored in the increasing global dominance of ecological generalists (Clavel et al., 2011). As a consequence, the areas exhibiting high species richness, initially and later, are also those where we expect the highest number of species that are more sensitive to environmental changes.

Effects of land cover heterogeneity on floral resource diversity

As expected, heterogeneity in the land cover composition was a strong predictor of the overall level of floral diversity (Table 2), such that landscapes with higher land cover heterogeneity, i.e. higher diversity of land cover types, tended to harbor higher overall levels of functional and taxonomic diversity, regardless of the diversity measure. This aligns with the idea that structurally complex environments offer a wider array of ecological niches, microclimates, and dispersal corridors, supporting a more stable and resilient plant community (Ammann et al., 2024; Cavigliasso et al., 2022). However, we note that the positive effect of land cover heterogeneity on functional evenness and functional dispersion was not statistically significant, indicating that heterogeneity is not significantly causing any loss of species with rare or extreme trait value combinations.

Heterogeneity also had an impact on the change in functional diversity over time, where the greatest decline occurred in the most heterogeneous landscapes (Figure 4). Although we did not model land cover change directly, this process likely underlies some of the observed declines in floral diversity. Low land cover heterogeneity is associated with the plains in southeastern Scania, which are dominated by arable land, whereas high landscape heterogeneity is associated with the central and northern parts of the region, where forest and semi-natural grasslands are more common than on the plains. Previous declines in plant species richness have shown that these are often linked to semi-natural grasslands (Tyler et al., 2020). These habitats are traditionally managed through grazing or mowing, practices that help maintain plant diversity (Tälle et al., 2016). However, a long-term trend of reduction in such management has led to an increase in forest cover (Auffret & Thomas, 2019), particularly spruce forests, both through plantation and natural succession, and existing forests have become denser and darker with less ground vegetation (Hedwall & Brunet, 2016).

Importantly, the effects of such changes may be delayed, and the current floral resource diversity patterns may reflect land cover changes that took place well before the first study period. For example, an abandoned semi-natural grassland can harbor grassland species for decades despite the eventual local extinction, a symptom of extinction debt (Cousins & Vanhoenacker, 2011; Johansson et al., 2011). The continued conservation and restoration of semi-natural grassland will be essential in counteracting these trends. The role of land cover heterogeneity also highlights the importance of landscape-scale management. Even if individual habitat types become degraded, a mosaic of different land cover types may buffer against total diversity loss by providing complementary resources across space and time.

Implications for pollinators and conservation

The diversity of floral traits in a landscape directly affects the availability and accessibility of resources for insect pollinators. Greater trait diversity translates to a higher variety of floral shapes, colors, and phenologies, which then attract and sustain pollinator species with varying foraging strategies and morphologies. Therefore, a decline in functional diversity of floral resources can lead to mismatches between plants and their pollinators, disrupting mutualistic networks and potentially reducing plant reproductive success and pollinator population viability (Bascompte & Scheffer, 2023).

Improving pollinator habitat quality is an alternative conservation strategy in agricultural landscapes where adequate habitat already exists (Fijen et al., 2025). Based on our results, heterogeneous landscapes are most vulnerable to decline in functional diversity and that actions to conserve floral trait diversity may be most efficient in these landscapes, where functional and species richness are still high. This likely includes maintaining active management of semi-natural grasslands, and other species rich landscape elements that contribute to landscape heterogeneity. Restoration can also be applied in landscapes that have lost some of their previous heterogeneity, for example, if semi-natural grasslands have been abandoned and begun transitioning into forest, restoration actions can have a large impact on the landscape diversity.

Limitations and future directions

Despite the comprehensive trait and occurrence data, our datasets and study design have limitations. First, estimates of flowering duration may overstate the length of the flowering period, as they are based on full months rather than more precise intervals. Several species, although recorded flowering across multiple months, likely exhibit strong seasonal peaks. Second, our trait data may not fully capture recent shifts in phenology due to climate change that causes spring- and early summer-flowering species to now flower 2–3 weeks earlier than in past decades (Menzel et al., 2020). Third, our dataset excludes non-native species that could have contributed to local increases in floral trait diversity in some landscapes over time. Fourth, using two discrete time periods rather than continuous monitoring likely results in conservative estimates of diversity change, as the approach misses any short-term dynamics. Finally, additional traits could also be considered. For example, the relative positioning of the stamen and stigma is crucial for optimizing pollination, as it determines the efficiency of pollen receipt and removal during plant–pollinator interactions (Opedal, 2018). A valuable next step would be to explore which specific floral traits contribute most to functional diversity and its change over time. This would help clarify which aspects of floral resources are most sensitive to environmental pressures and most critical for conserving pollinators and the pollination service.

Conclusions

We found that functional diversity of floral traits in insect-pollinated plants in southern Sweden has been more stable over time than species richness, though both show overall declines. Landscapes with greater land cover heterogeneity are key to maintaining floral resource diversity but also have more to lose when species decline. Given the tight link between floral traits and pollinator communities, our findings underline the need for targeted conservation strategies to safeguard both plant and pollinator diversity in the face of continued environmental change and land use intensification. Despite the clear importance of floral traits for plant reproductive success, functional diversity rarely includes floral traits in their measure of functional diversity. Additionally, because these traits are tightly linked to plant-pollinator interactions, spatiotemporal variation in the functional diversity of floral resources studied here can have huge implications for ecosystem functioning, i.e. pollination. Work should therefore be done on including these traits when assessing functional diversity.

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Appendix S1 Supplementary methods

Landscape heterogeneity moderates temporal changes in floral resource diversity

Elena Albertsen, Lina Herbertsson, Oskar Löfgren, Torbjörn Tyler, Emma-Liina Marjakangas

Detailed description of the plant trait compilation process.

Following the design by Stefanaki et al. (2015), we extracted plant trait data from multiple data sources (databases, descriptions in standard floras) and based on personal knowledge. Trait data were originally extracted for another project (Stefanaki unpublished). Trait data (for native species only) were extracted from databases and floras. We obtained life-form, pollen vector and asexual reproduction traits from BioFlor, Ecoflora, and LEDA databases (Fitter & Peat 1994, Klotz et al. 2002, Kleyer et al. 2008) using TR8 R package (Bocci 2015). We obtained floral shape, flower color, flower symmetry, corolla segmentation, and functional reproductive unit from standard floras (Lid & Lid 2005; Mossberg & Stenberg 2014, luontoportti.fi) and personal knowledge (mostly TT) of the species. Estimates of nectar and pollen production were obtained from Tyler et al. (2021); data on onset of flowering in southern Sweden was obtained from the same source and then combined with estimates of the length of the flowering period based on own (TT) personal knowledge to produce data on flowering seasonality.

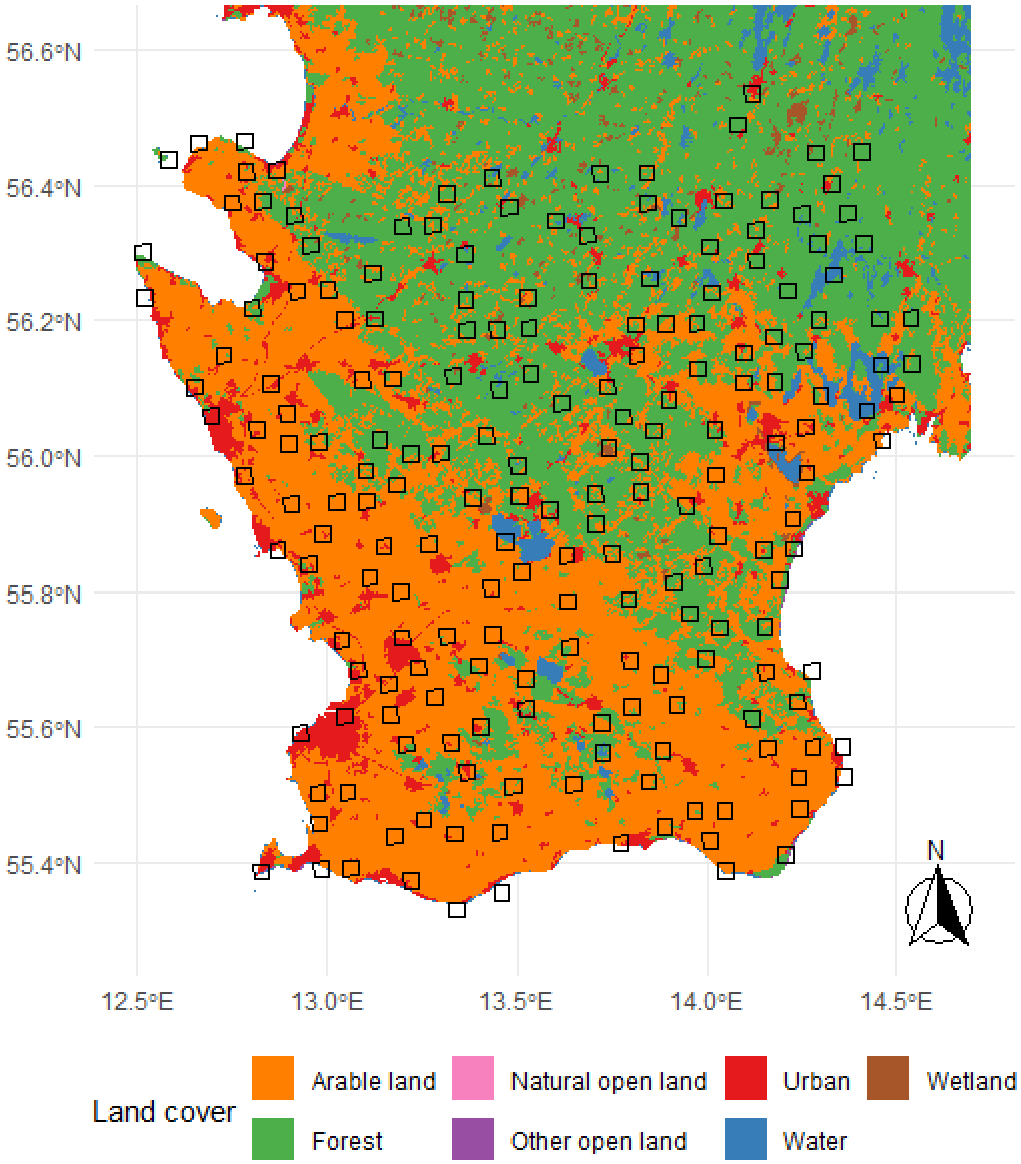

Figure S1. Map of land use in the study area in 2000. Original CORINE categories have been merged to obtain the broader categories illustrated on the map (colors indicate different categories). The black squares indicate the Millora quadrants.

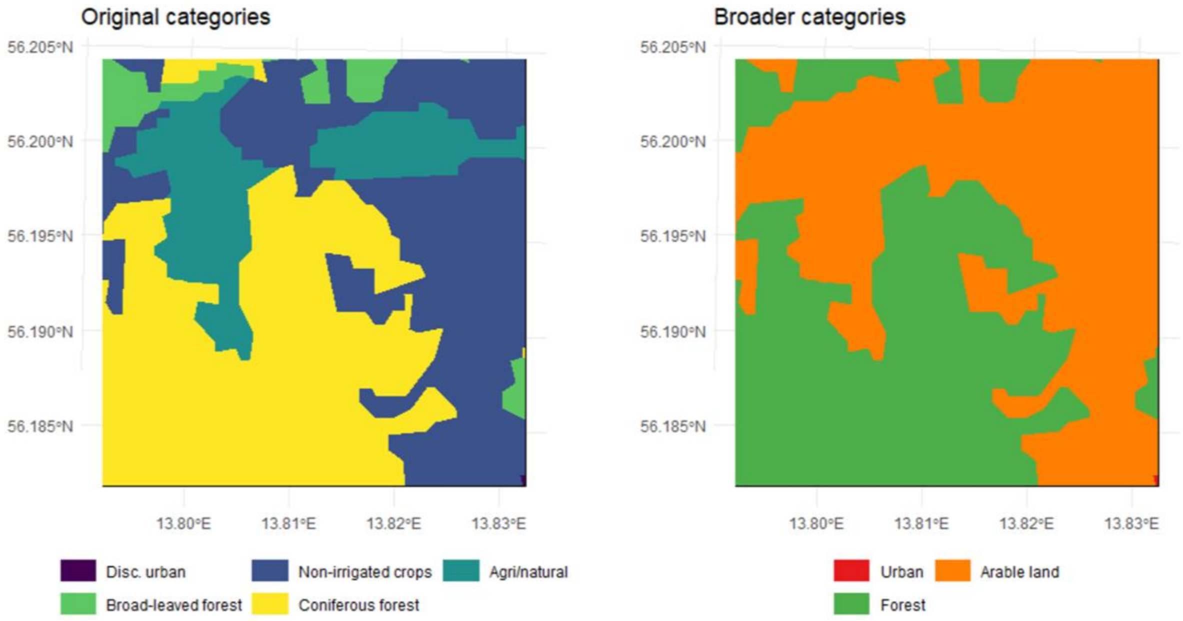

Figure S2. Example of one landscape land cover categories in the original CORINE dataset (left) and after grouping into broader categories (right).

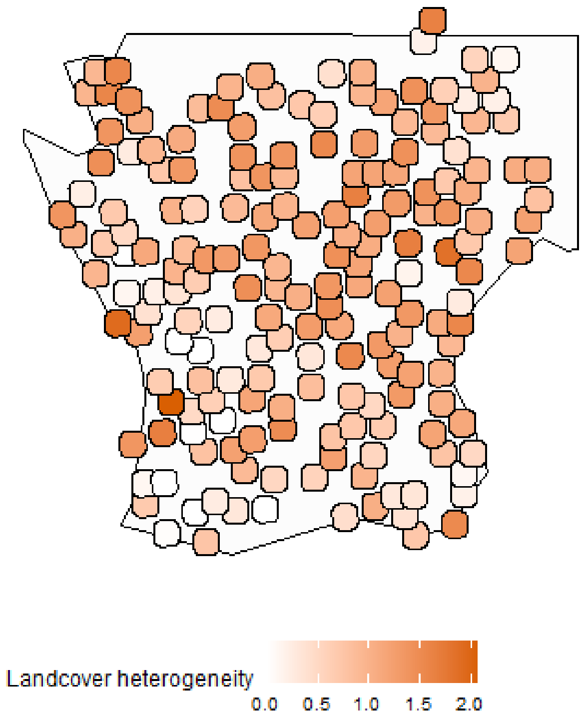

Figure S3. Landcover heterogeneity (measured as Shannon diversity index among all CORINE (version 2000) landcover categories) across the study area in southern Sweden.

Table S1. Reclassification of CORINE land cover classes into broader categories.

Broad category	CORINE codes	CORINE descriptions
Urban	111–142	Continuous and discontinuous urban fabric; industrial/commercial units; transport networks; port areas; airports; green urban areas; sport and leisure facilities
Arable land	211–244	Non-irrigated and irrigated arable land; rice fields; vineyards; fruit trees and berry plantations; olive groves; pastures; complex cultivation patterns; agro-forestry areas
Forest	311–313, 324	Broad-leaved, coniferous, and mixed forest; transitional woodland/shrub
(Semi-)natural open land	321–323	Natural grassland; moors and heathland; sclerophyllous vegetation
Other open land	331–335	Beaches, dunes, sands; bare rocks; sparsely vegetated areas; burnt areas; glaciers and perpetual snow
Wetland	411–423	Inland marshes; peat bogs; salt marshes; salines; intertidal flats
Water	511–523	Water courses; water bodies; coastal lagoons; estuaries; sea

Table S2. Correlations among functional diversity measures across all landscapes in study period 1.

	Functional richness	Functional evenness	Functional dispersion	Species richness
Functional richness				
Functional evenness	-0.41			
Functional dispersion	0.60	-0.09		
Species richness	0.93	-0.52	0.44	

Table S3. Correlations among functional diversity measures across all landscapes in study period 2.

	Functional richness	Functional evenness	Functional dispersion	Species richness
Functional richness				
Functional evenness	-0.40			
Functional dispersion	0.52	0.09		
Species richness	0.93	-0.52	0.35	

Landscape heterogeneity moderates temporal changes in floral resource diversity

Elena Albertsen, Lina Herbertsson, Oskar Löfgren, Torbjörn Tyler, Emma-Liina Marjakangas

Appendix S2. Supplementary results

Table S1. Changes in occurrence of floral traits in flowering plant communities in landscapes across southern Sweden over time. For categorical traits, occurrence is measured as frequency of species in each trait category in landscapes in each study period. For continuous traits (flowering onset, flowering duration, nectar production), occurrence is measured as the mean of species' trait values in landscapes in each study period. The change in traits is calculated both as the absolute change (difference in frequency or mean between the first and the second study period) and as proportional change (difference in frequency or mean between the first and the second study period in relation to the frequency in the first study period). For definitions of traits and trait categories, see Table 1 in the main text.

Trait	Trait category	Frequency/ mean in Period 1	Frequency/ mean in Period 2	Change (absolute)	Change (proportional)
Flowering seasonality	Spring species	7118	6722	-396	-0.056
Flowering seasonality	Not spring species	33955	31270	-2685	-0.079
Flowering seasonality	Summer species	26840	24630	-2210	-0.082
Flowering seasonality	Not summer species	14233	13362	-871	-0.061
Flowering seasonality	Autumn species	21323	19762	-1561	-0.073
Flowering seasonality	Not autumn species	19750	18230	-1520	-0.077
Flower shape	Bell	1887	1857	-30	-0.016
Flower shape	Brush	1687	1540	-147	-0.087
Flower shape	Disk	10687	9978	-709	-0.066
Flower shape	Disk-tube	7779	7085	-694	-0.089
Flower shape	Funnel	3486	3366	-120	-0.034
Flower shape	Flag	3274	3051	-223	-0.068
Flower shape	Gullet	4170	3817	-353	-0.085
Flower shape	Head	6793	6190	-603	-0.089
Flower shape	Lip	336	250	-86	-0.256

Flower shape	Tube	935	827	-108	-0.116
Flower shape	Trap	39	31	-8	-0.205
Flower depth	High-depth	3589	3305	-284	-0.079
Flower depth	Medium-depth	9154	8311	-843	-0.092
Flower depth	Low-depth	28330	26376	-1954	-0.069
Flower symmetry	Bilateral	10160	9335	-825	-0.081
Flower symmetry	Radial	30913	28657	-2256	-0.073
Corolla segmentation	Choripetaly	21973	20492	-1481	-0.067
Corolla segmentation	Semichoripetaly	16412	15025	-1387	-0.085
Corolla segmentation	Sympetaly	2688	2475	-213	-0.079
Reproductive unit	Cylindrical	9808	8967	-841	-0.086
Reproductive unit	Flat/spherical	12864	11910	-954	-0.074
Reproductive unit	Single flowers	18401	17115	-1286	-0.070
Flower color	Blue	4401	4057	-344	-0.078
Flower color	Green	1574	1556	-18	-0.011
Flower color	Violet / purple / pink / red / brown / rose / lilac / magenta	11816	10905	-911	-0.077
Flower color	White	11475	10674	-801	-0.070
Flower color	Yellow/cream	11807	10800	-1007	-0.085
Flower size	Large	16311	15170	-1141	-0.070
Flower size	Medium	14709	13557	-1152	-0.078
Flower size	Small	10053	9265	-788	-0.078
Onset of flowering	-	7.437	7.422	-0.015	-0.002
Flowering duration	-	5.428	5.418	-0.01	-0.002
Nectar production	-	4.013	4.023	0.009	0.002

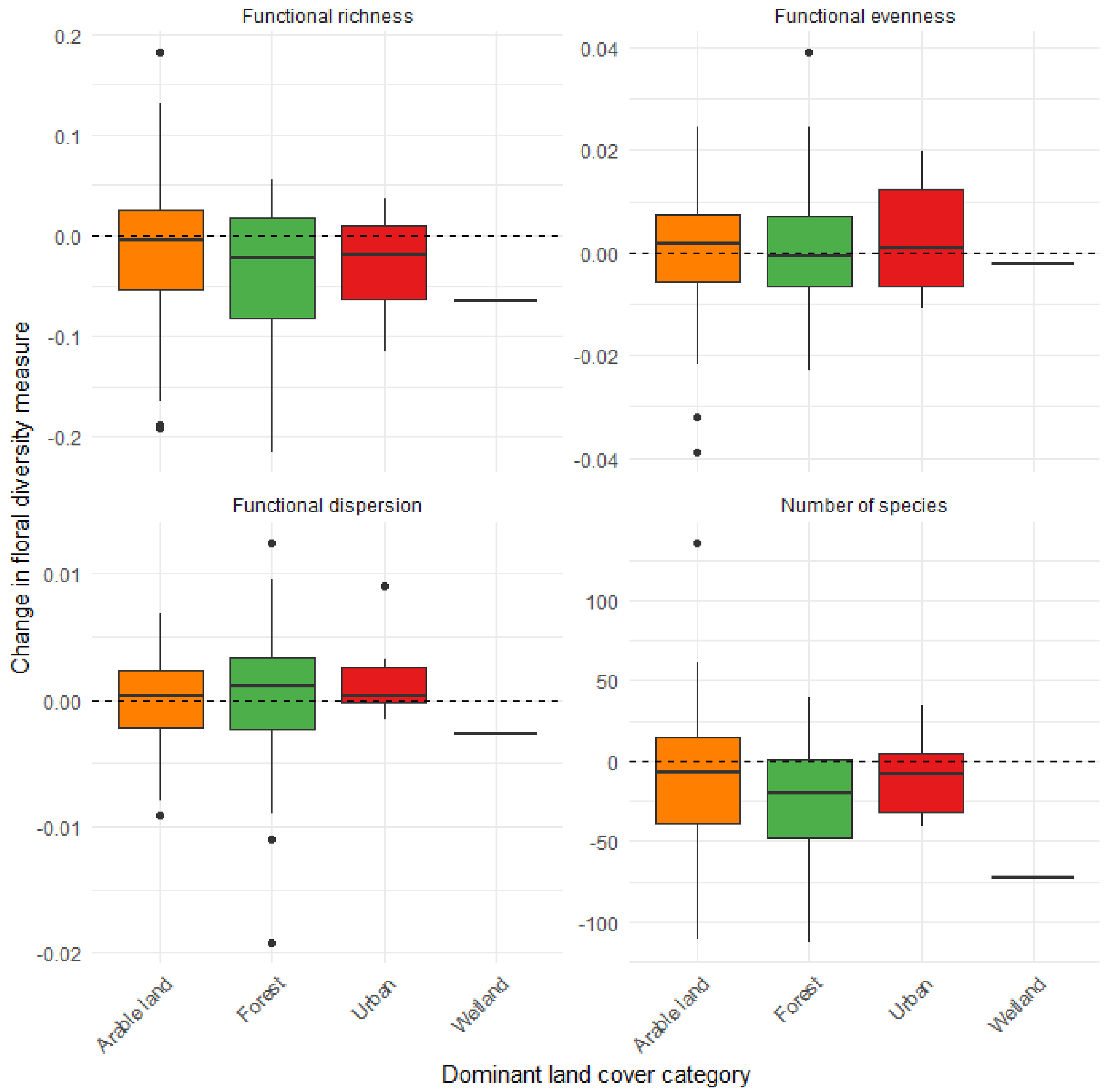

Figure S1. Changes in floral diversity measures across dominant land cover types in southern Sweden between study periods. Boxplots show the variation in four metrics: functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), and number of species (N species). Each landscape (n = 185) was assigned a dominant land cover category based on the highest proportional cover among arable land, forest, urban, and wetland in CORINE land cover data from year 2000. The horizontal dashed line at zero indicates no change. Colors correspond to dominant land cover types. Note the uneven distribution of number of landscapes in different dominant land cover categories.

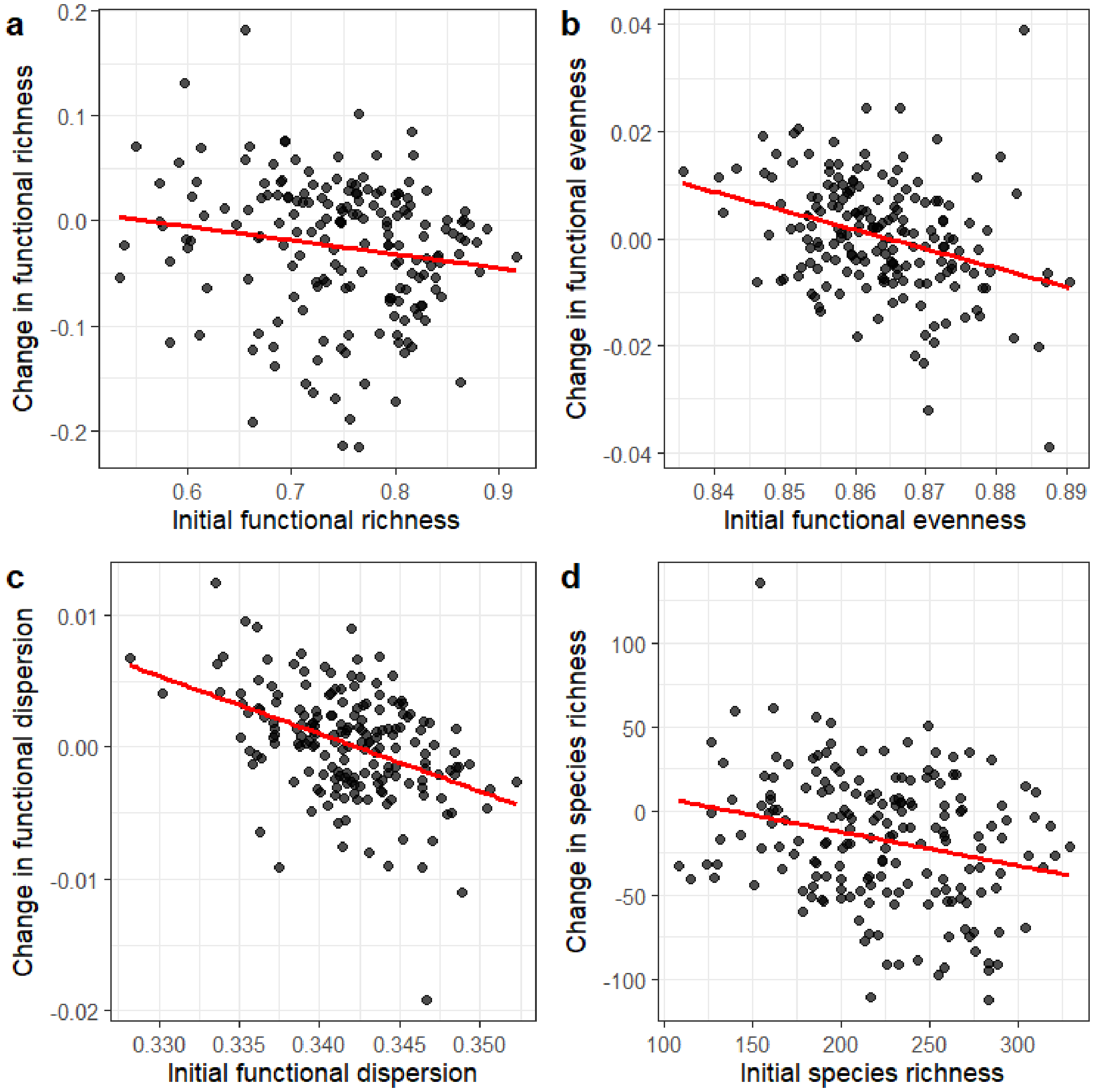

Figure S2. Relationships between initial values (Period 1) and subsequent changes of four floral resource diversity metrics across landscapes in Southern Sweden (N = 185). Each panel shows a scatterplot with a fitted linear regression line for: (a) functional richness (FRic), (b) functional evenness (FEve), (c) functional dispersion (FDis), and (d) species richness (Nsp). Points represent individual landscape (grid cell) observations.