

Spatial and temporal scales of landscape structure affect the biodiversity-landscape relationship across ecologically distinct species groups

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This document is the accepted manuscript version of the following article:

Pan, Y., Hersperger, A. M., Kienast, F., Liao, Z., Ge, G., & Nobis, M. P. (2022). Spatial and temporal scales of landscape structure affect the biodiversity-landscape relationship across ecologically distinct species groups. *Landscape Ecology*, 27, 2311-2325.
<https://doi.org/10.1007/s10980-022-01477-x>

Abstract

Context

The effects of landscape structure on biodiversity may change with the spatial and temporal scale at which landscape structure is measured. Identifying the spatial extent and temporal scale at which the biodiversity-landscape relationship is strongest (i.e., the scale of effect) is important to better understand the effect of landscape structure.

Objectives

The spatial and temporal scale of effect is analyzed to identify whether it differs in ecologically distinct species groups. How species richness-landscape relationship changes with spatial and temporal scales is tested.

Methods

Based on 98 survey plots (1 km²) of vascular plants on the Swiss Plateau, we analyzed the relationships between species richness of different species groups and landscape predictors at different spatial extents (1 km², 4 km², 16 km², 36 km²) and time periods (past landscapes - 1985, 1997, 2009 and the current landscape 2018).

Results

The spatial scale of effect was 1 km for most species groups, while the temporal scale of effect differed among species groups. The strength of the species richness-landscape relationship generally decreased with increased spatial extents, while it changed little across temporal scales.

Conclusions

Although our study only considered changes in landscape structure over the last c. 30 years, ecologically distinct species groups revealed differences in the temporal scale of effect including a rapid response of neophytes linked to ongoing biological invasions. However, the variation in the species richness-landscape relationship was greater when changing spatial extent than time. We highlight that studying the relationship between landscape structure and biodiversity should consider not only space but also time, and different responses of ecologically distinct species groups.

Keywords: landscape composition; landscape configuration; modelling; species richness; spatial scale; vascular plants; Swiss Plateau.

Introduction

Human-induced land use change is a primary driver of changes in biodiversity in terrestrial ecosystems (Chapin III et al. 2000; Sala et al. 2000; Haines-Young 2009). The effects of human modified landscapes on biodiversity have been widely explored in recent decades (Fahrig 2003; Duflot et al. 2017; Martin et al. 2019; Lami et al. 2021). However, the spatial and temporal scales at which biodiversity-landscape relationships are studied may profoundly influence the outcomes (Turner 1989). Specifically, effect size, statistical significance, the direction of effect (positive or negative), and the relative importance of different landscape predictors can vary in analyses at different scales of the biodiversity measure (Holland et al. 2004; Smith et al. 2011; Piano et al. 2020; Semper-Pascual et al. 2021). In addition, important biodiversity-landscape relationships can be missed, or conclusions can be biased if landscape structure is not measured at the scale at which it has the strongest effect (i.e., scale of effect) (Jackson and Fahrig 2015).

The “scale of effect” is usually referring to spatial context (Jackson and Fahrig 2012). However, the scale can refer not only to space but also to time. In this study, the spatial and temporal scale of effect are used to express the spatial extent or time period at which the biodiversity response to landscape is strongest. Nowadays, a growing number of studies have assessed the spatial scale of effect on different organisms and even processes, but few studies evaluate the temporal scale of effect (Adriaens et al. 2006; Semper-Pascual et al. 2021). Jackson and Fahrig (2015) summarized ranges of spatial scale of effect for different organisms (e.g., amphibians, bats, and birds) that are evaluated from 71 studies. Semper-Pascual et al. (2021) evaluated the temporal scale of effect for birds and mammals by using a time series of woodland maps for each year between 1985 and 2016 in a subtropical/tropical dry forest in South America.

Although our understanding of the spatial scale of effect has increased, the spatial scale at which landscape structure should be assessed is hardly known (Galán-Acedo et al. 2018). The spatial scale of effect may differ among species, ecological responses (e.g., species richness, species abundance) and landscape predictors (Miguet et al. 2016), and thus, no single spatial scale is generally suitable to detect the strongest relationships between landscape structure and biodiversity (Levin 1992). Usually, the spatial scale of effect is unknown for the relationship between landscape predictors and biodiversity measures in advance. One way to detect the spatial scale of effect is to estimate the biodiversity-landscape relationship at multiple scales, e.g., by creating multiple buffers around the plots on which the biodiversity response (e.g., species richness) is surveyed (Pautasso 2007; Moraga et al. 2019; Fourcade et al. 2021). However, it has been argued that most multiscale studies do not measure landscape structure at the appropriate scale due to the limited ranges of scales used (Jackson and Fahrig 2015).

Compared to spatial scale, studies on the temporal scale of effect are rare because of the lack of time-series data on landscape structures and biodiversity (Kuussaari et al. 2009; Lira et al. 2019; Semper-Pascual et al. 2021). Species do not always react to landscape change immediately and may persist for decades even if the habitat requirements for a species long-term persistence are no longer met, resulting in time lag effects (Kuussaari et al. 2009; Jackson and Sax 2010). In a similar manner, biological invasions may exhibit a time lag between the initial introduction, establishment, and final spread, leading to an invasion debt (Essl et al. 2011; Duncan 2021). Although an increasing number of scientists emphasize the importance of the temporal scale, we still know little about the time lag effects of landscape changes (Lindborg and Eriksson 2004; Le Provost et al. 2020; Semper-Pascual et al. 2021). At present, some studies support time lag effects on biodiversity-landscape relationships (Vellend et al. 2006; Helm et al. 2006; Krauss et al. 2010), while others do not (Adriaens et al. 2006; Öster et al. 2007). Those studies that support the extinction debt usually find that past landscape structure explains current biodiversity better

than the current landscape. Estimated time lags vary from 5 to 570 years, and the total time required to pay off the debt might be even longer in some cases (Figueiredo et al. 2019).

Although past research has increased our understanding of the effects of landscape composition (i.e., the proportion of land covers) and configuration (i.e., the spatial arrangement of land covers) at multiple scales on biodiversity, three knowledge gaps remain. First, most studies have focused on either spatial scales or temporal scales separately, while few have focused on both. Assessments of the effect of landscape structure on biodiversity may be inaccurate if they only consider either the spatial or the temporal scale, since landscape patterns and processes are reflected by both (Gillson 2009). Second, many studies have focused on a single land cover (Cousins et al. 2015), such as a forest (Redon et al. 2014; Haddad et al. 2015) or grassland (Helm et al. 2006; Reitalu et al. 2012), although landscapes are generally composed of various land covers and tend to form complex mosaic landscapes with natural, seminatural, and anthropogenic habitats. A focus on a single land cover increases the possibility of overestimating or underestimating the importance of landscape structure. Third, many studies analyze a single species or the total species richness of a given taxon (Miller et al. 2015; Duan et al. 2019). The effects of landscape structure, however, may vary between ecologically distinct species groups (e.g., groups that differ in dispersal ability or lifespan), and the spatial and temporal scales of effect may differ for different species groups (Holland et al. 2004; Kuussaari et al. 2009; Schleicher et al. 2011; Martin et al. 2019). Although traits can provide a mechanistic approach for evaluating the relationship between ecological responses and landscape structure, our current understanding of the role of species traits on how these relationships vary among spatial and temporal scales is still limited (Suárez-Castro et al. 2018).

Here, we evaluate the potential role of landscape structure in explaining vascular plant species richness at multiple spatial and temporal scales to address the following questions. (1) What is the spatial and temporal scale of effect for the species richness-landscape relationship, i.e., at which spatial and temporal scales are the species richness-landscape relationships strongest? (2) How do the species richness-landscape relationships of ecologically different species groups vary across different spatial and temporal scales? To address these questions, we considered different species groups of vascular plants according to their origin/invasion history, degree of specialization, dispersal ability and lifespan.

Methods

Study area

The study was carried out on the Swiss Plateau (Fig. 1), which is located between the Alps and the Jura Mountains. With an area of approximately 11,200 km², it is the largest biogeographic region in Switzerland. The Swiss Plateau has an elevation range from 246 to 1285 m (Swisstopo 2010), an annual mean temperature of 5.9-11.6 °C, and an annual precipitation of 713-1995 mm (www.chelsa-climate.org). The most important land covers are agricultural areas (48% of the region), wooded areas (24%) and urban areas (17%) (BFS GEOSTAT 2013/18). In recent decades, this region has undergone strong land use changes due to increasing urban sprawl and transportation-infrastructure development (Schwick et al. 2018). It is now the most fragmented region among the five biogeographic regions (Jaeger et al. 2008). Switzerland experienced large biodiversity losses since 1900. Furthermore, in the Swiss Plateau, as in Switzerland as a whole, the ongoing loss of endangered species and habitats could not be stopped despite a slight increase in the average number of vascular plants and butterflies from 2005 to 2015 (Lachat et al. 2010; FOEN 2017).

Biodiversity data

We used occurrence data of vascular plants from the Swiss Biodiversity Monitoring program (BDM, Weber et al. 2004). These data were derived from 105 plots at the landscape scale (1×1 km), which were regularly distributed in the study area (Fig. 1a). Species were recorded during the survey period from 2014-2018 using a standardized assessment approach on each 1 km^2 plot (Plattner et al. 2004). Specifically, species were recorded within 2.5 m on both sides of a 2500 m transect, starting directly at the side of the road, sidewalk or trail. The same transect length and survey area was covered in all plots. Transects within each 1 km^2 landscape were selected by experts to represent different types of land covers (Plattner et al. 2004; Weber et al. 2004; BDM Coordination Office 2014). The transect sampling method does not enable to record the total number of species in each survey plot, but the recorded number of species is closely correlated with the total number (Weber et al. 2004; BDM Coordination Office 2014). Such sampling can be used to analyze “within-habitat-mosaic-diversity” of landscapes (Weber et al. 2004; BDM Coordination Office 2014). For each plot, we calculated the species richness of ecologically defined species groups related to the species’ origin/invasion history (natives, archaeophytes, neophytes), degree of specialization (specialists, generalists), dispersal ability (high, low) and lifespan (annuals, perennials). Thus, we have nine species groups in total (Supplementary Table S1, Table S2). Instead of determining the species’ specialization based on habitat affinity (e.g., grassland or forest specialists), we used a broad definition using the values and range of several ecological indicators (i.e., temperature, light, moisture, humus, soil aeration, continentality, soil pH and nutrients) where the species occur (Landolt et al. 2010). Specifically, a specialist is a species with extreme values or narrow ranges of ecological indicators (Concepción et al. 2016, Table A.2).

Landscape data

We calculated predictors of current species richness related to past and current landscapes based on ‘Swiss Land Use Statistics’ with a 100-m resolution for 1985 (BFS GEOSTAT 1979/85), 1997 (BFS GEOSTAT 1992/97), 2009 (BFS GEOSTAT 2004/09) and 2018 (BFS GEOSTAT 2013/18). In addition to the original BDM plot extent (1×1 km), three square buffers (2×2 , 4×4 , 6×6 km) around the center of each plot were created for the assessment of the landscape structure (Fig. 1b). Thus, we have explanatory variables for four spatial extents as well as four periods in time. Plots near the border of Switzerland whose 6×6 km buffer had less than 90% of the area within the national boundary were excluded from further analyses, resulting in 98 plots remaining. Selecting spatial extents is challenging because there are no consistent reference standards due to different sample areas and taxonomic groups in different studies (Jackson and Fahrig 2015). We chose the spatial extents following a previous study with data from the same monitoring program (Concepción et al. 2015).

The amount of each land cover (e.g., wooded area, urban area) within an area is a common measurement of composition, and landscape fragmentation is a common measurement of configuration (Martin and Fahrig 2012; Hadley et al. 2014). To characterize landscape structure, we calculated thus the amount of wooded area, amount of urban area and landscape fragmentation. We did not consider agricultural areas due to their high multicollinearity with wooded and urban areas. Wooded area and urban area were calculated as the amount of their respective land cover within the 1, 4, 16, 36 km^2 squares. We calculated landscape fragmentation as the effective mesh size index (m_{eff}) (Jaeger 2000). The fragmentation geometries for calculating m_{eff} included impervious buildings and infrastructures in urban and peri-urban areas, rivers and lakes in unproductive areas, roads at least 3 m wide, and railways (see Supplementary Table S2 and TextS1 for more details).

Climate covariates

Studies about the impact of land use and land use change on biodiversity often ignore climate (De Chazal and Rounsevell 2009). Since annual mean temperature and annual precipitation are important environmental factors of plant species richness in Switzerland (Wohlgemuth et al. 2008), we analyzed the species-landscape relationship along with general climate covariates of annual precipitation and annual mean temperature, which were accessed from the CHELSA portal (www.chelsa-climate.org; data averaged for the period from 1979-2013) (Karger et al. 2017). For climate, we did not consider different spatial or temporal scales and used zonal statistics to extract the mean value of annual precipitation and annual mean temperature within the 1×1 km plots of the biodiversity assessment.

Statistical analyses

The effects of landscape predictors on biodiversity were analyzed at multiple spatiotemporal scales in a modeling framework with the species richness of the nine species groups as a response. First, we tested the goodness-of-fit (deviance explained, D^2) of generalized linear models (GLMs) that included (1) the two climate predictors only, (2) all spatiotemporal combinations of the three landscape predictors, or (3) both predictor types, i.e., landscape predictors with all scale combinations and the two climate covariates. For further analyses, we used all models that included both the climate and landscape predictors. Our study area belongs to a single biogeographic region with relatively homogeneous topography and soil properties at the landscape scale where land use often becomes the dominant factor (Wohlgemuth et al. 2008), thus we did not include topography and soil properties into the model. In addition, terrain and soil properties are dependent on land use and would add unwanted multicollinearity to the model.

We considered all combinations of all landscape predictors at all scales in multivariate models because landscapes are complex systems, and this complexity arises from the dependencies or dynamic interactions of heterogeneous components within the systems across space and time (Newman et al. 2019). Given three landscape predictors at four temporal and four spatial scales, there were $4^3 \times 4^3 = 4,096$ possible scale combinations (model parametrizations) for each species group. For all nine species groups, the total number of models was 36,864. GLMs were fitted with quasi-Poisson distributions and linear predictor terms, and all predictors were standardized to a mean of 0 and a standard deviation of 1. The Pearson's correlation coefficient was lower than 0.7 among different landscape predictors (Supplementary Fig. S1), and the variance inflation factor (VIF) of each predictor in each model was lower than 5 in all 36,864 models (Supplementary Fig. S2). The spatial autocorrelation (Moran's I test) of residuals was tested for all models.

To compare the species richness-landscape relationship for the large number of different spatial and temporal scale combinations, we grouped models with the same temporal or spatial scale (hereinafter referred to as models with a fixed scale). For instance, in models with a fixed spatial scale, all predictors had the same spatial scale but varied in their temporal scale. Thus, we have fixed spatial scales of 1 km, 2 km, 4 km and 6 km and fixed temporal scales of 1985, 1997, 2009, and 2018. The Kruskal–Wallis test (R function *kruskal.test*) was used to evaluate whether changing the fixed spatial scale or temporal scale significantly affected the model performance, i.e., the amount of deviance explained (D^2). Wilcoxon tests were used for post hoc tests (R function *pairwise.wilcox.test*). The coefficient of variation (ratio of the standard deviation to the mean) of D^2 at fixed spatial and fixed temporal scales was used to compare the variation of D^2 when changing the spatial extent or time scale. Standard coefficients in each fixed spatial and fixed temporal scale model were used to compare the strength and direction of the effect of each landscape predictor and their relative importance.

All data management and analyses were conducted using R 4.0.3 (Core and Team 2020) and ArcGIS 10.7.1.

Results

Currently (assessed from BFS GEOSTAT 2013/18), the mean proportion of wooded area is 28% within 1×1 km plots and 2×2 km plots, 27% within 4×4 km plots and 6×6 km plots, and the mean proportion of urban area is 16% within the four spatial extents. The mean m_{eff} is 0.43, 1.04, 1.78, 2.08 km² within 1×1 , 2×2 , 4×4 , 6×6 km plots, respectively. Over the last few decades, the urban areas increased and m_{eff} decreased in most analyzed landscapes within the four spatial extents, while the wooded areas remained consistent on the Swiss Plateau (Fig. S3). For example, the mean proportion of urban area has increased from 12% to 16%, and the mean m_{eff} decreased from 0.51 km² to 0.43 km² within 1×1 km plots from 1985 to 2018, showing an increase in urban sprawl and landscape fragmentation. Moreover, Moran's I coefficient of residuals for all models that included climate and landscape predictors ranged from -0.13 to 0.20 and were in the very majority not significant (Supplementary Fig. S4). The results also showed that on the Swiss Plateau, landscape predictors explained plant species richness better than climate predictors (Fig. 2).

In the analysis with the fixed spatial scales, in general, the models with the landscape predictors measured at 1 km performed best, and the explained deviance dropped rapidly with increasing spatial extent of the buffer (Fig. 3). That is, the spatial scale of effect is 1 km. The only exceptions were for low dispersal species, where models performed best at the 2 km spatial extent (Fig. 3g). For all species groups, except neophytes (Fig. 3c), the model with the maximum D^2 value was a combination of different spatial scales (Fig. 3). The median D^2 value for models with not fixed spatial scale were higher than the median D^2 value for models with fixed spatial scale only when fixed scale was 4 km or 6 km (Fig. 4).

In the analysis with fixed temporal scales, we found differences in the temporal scale of effect among species groups (Fig. 4). Neophytes and high dispersal species responded better to contemporary landscape predictors than to past landscape conditions (Figs. 4c, 4f). Species with a low dispersal ability responded best to landscape predictors at intermediate temporal scales, i.e., with a delay of 9-21 years (Fig. 4g). The landscape structure measured in 1985 showed the lowest effect on species richness (median D^2), and this effect was significant for all species groups but natives and perennials (Figs. 4b-h). For natives and perennials there was no significant difference among all fixed temporal scales (Figs. 4a, i). The models with the maximum D^2 values for natives, neophytes, generalists, high dispersal species, and annuals were the models with the fixed temporal scale of 2018, the current temporal scale (Figs. 4a, c, e, f, h). In addition, D^2 values at fixed temporal scales showed a significantly higher variation than D^2 values at fixed spatial scales (Fig. 3, Fig. 4; Fig. S5).

The standard regression coefficients of landscape predictors varied between different spatial extents and species groups (Fig. S6). Absolute values of regression coefficients tend to decline at larger fixed spatial scales, especially for predictors with high relative importance, such as wooded areas or m_{eff} (Fig. S6). In contrast, for fixed temporal scales, the coefficients of landscape and climatic covariates showed higher variability at a given scale, but only minor differences between fixed temporal scales among all species groups (Fig. S7).

Discussion

This study focuses on how ecologically distinct species groups respond to landscape structure at multiple spatial and temporal scales, which has been an important topic of debate among landscape ecologists (Levin 1992; Wu and Hobbs 2002). In contrast to studies with strong climatic gradients (Wohlgemuth et al. 2008; Peters et al. 2019),

our research showed that landscape structure plays a more important role than climate for biodiversity in mosaic landscapes of our lowland study region.

Biodiversity-landscape relationships across temporal scales

The temporal scale of effect differed for species groups according to their origin/invasion history, dispersal ability and lifespan. Neophytes tended to respond strongest to the current landscape structure, while natives and archaeophytes did not, suggesting that neophytes respond to landscape change faster. In addition, several studies have shown that neophytes are positively affected by the presence and the amount of urban area (Deuschewitz et al. 2003; Nobis et al. 2009; Concepción et al. 2016; Čeplová et al. 2017). This species group seems to be the most directly affected by highly dynamic landscape change due to urban sprawl. Although there are time lags for species from introduction to establishment in a new landscape (Richardson et al. 2000), this response of already established neophytes seems to rapidly track urban sprawl and related anthropogenic disturbances. Longer-term survival in the soil seedbank may contribute to a delayed response of archaeophytes to landscape changes (Brunzel et al. 2009; Le Provost et al. 2020). High dispersal species responded to the current landscape structure the most strongly, while low dispersal species showed a 9-21 year time lag. This means that low dispersal species are likely to show a longer time lag than high dispersal species when responding to changes in landscape structure. Because many low dispersal species show long generation times (75% are perennial in our study), many low dispersal species might be able to survive and cope with the local habitat for many years, while high dispersal species might be more likely to vanish from unsuitable local habitats (Krauss et al. 2010; Löffler et al. 2020).

Perennials are expected to pay off their extinction debt slower than annuals (Lindborg 2007). However, the perennials were almost equally explained by past and current landscape structure, as well as natives (85% are perennials), showing the absence of a clear time lag response in our study. One possible explanation is that the analyzed temporal scale of c. 30 years may not be long enough to detect a time lag response for these species' groups. This is supported by studies that found that current plant species diversity is still influenced by the past landscape structure more than five decades ago (Lindborg and Eriksson 2004; Helm et al. 2006; Aggemyr and Cousins 2012).

Species with different degrees of specialization were not detected to differ in their temporal response. Both specialists and generalists showed a similar 0-21 year time lag. The existing literature is contradictory in this respect. Some researchers showed that the current species richness of both specialists and generalists were showed time lag response (Löffler et al. 2020). This is consistent with our findings. However, someone stated that the time lag response is only for habitat specialists (Helm et al. 2006; Krauss et al. 2010; Soga and Koike 2013), and some did not find the time lag response for neither specialists nor generalists (Adriaens et al. 2006). One reason for the contradicting results might be different conditions in habitat since the specialists in these studies are defined according to their habitat, which means their occurrence strictly depends on the habitat. For the studies mentioned above, the habitat patches are well connected in the study that found time lag response (Löffler et al. 2020), while the habitats are highly fragmented in the study that found no evidence for time lag response (Adriaens et al. 2006). In addition, the individual longevity of species might also play an important role in combination with specialization. As it has been shown that long-lived specialists show a delayed response, but not short-lived specialists (Krauss et al. 2010). Since in our study, specialists are defined by environmental preferences like temperature, moisture, and light conditions, this means specialists and generalists here show more diverse life-history traits including life span. Overall, however, the proportion of long-lived species (perennials) among specialists and generalists is very

similar (76% and 88%, respectively), which may mask the differences in time lag response between specialists and generalists.

In addition to different species groups, historical contingency could be another important factor that affects the time lag (Hendershot et al. 2020). The historical contingency, refers to the effect of historical events (e.g., disturbances, landscape change) on ecosystems (Brudvig 2011; Fukami 2015). The relationship between current species richness and past or contemporary habitat patterns depends on the existing habitat area and the magnitude of land cover changes (Cousins 2009; Kolk et al. 2017). In many studies on extinction debt, the habitat area severely declined (Lindborg and Eriksson 2004; Helm et al. 2006). However, forested areas in the lowlands of Switzerland were relatively stable over the past 150 years (Loran et al. 2016). This stable status of wooded area may explain the minor change in D^2 value and the regression coefficients of landscape predictors among different temporal scales.

Biodiversity-landscape relationships across spatial scales

The spatial scale at which species richness was best predicted by landscape predictors was 1 km in our study, i.e., the spatial extent to which species occurrences were surveyed. Although many studies showed that the relationship between landscape structure and the ecological response was strongest at the smallest or largest spatial scale, the true scale of effect is often either smaller than the smallest or larger than the largest spatial scale investigated (Jackson and Fahrig 2015). This suggests our true scale of effect may be smaller than 1 km spatial extent. However, in contrast to usual surveys at the habitat level, our biodiversity survey is based on a unique 1 km² assessment at the landscape scale (see methods). This means species richness, as the biodiversity response, represents a habitat and landscape mosaic rather than distinct species communities of specific habitats affected by the surrounding landscape. This spatial extent is within the potential dispersal distance for many plant species and is also used as the spatial scale at which the landscape structure is measured for biodiversity-landscape relationships in other studies (Adriaens et al. 2006; Krauss et al. 2010; Cousins and Vanhoenacker 2011; Kolk and Naaf 2015; Auffret et al. 2018).

Species traits such as the specialization degree, lifespan and dispersal ability are often considered important factors influencing the spatial scale of effect (Thornton and Fletcher Jr 2014; Miguët et al. 2016). However, we found that the spatial scale of effect did not differ with specialization degree or lifespan. In a conceptual paper, Miguët et al. (2016) suggested that whether the spatial scale of effect for specialists is larger or smaller than for generalists depends on their dispersal ability. However, studies found inconsistent differences in dispersal ability for specialists and generalists (Bonte et al. 2003; Martin 2015; Miguët et al. 2016), and we are not aware of any empirical studies that found a relationship between the scale of effect and specialization for plants. In our study, most specialists (84% of specialists) and most generalists (84% of generalists) were high dispersal species. Thus, according to Miguët et al. (2016), we expect a similar scale of effect for both species groups, which we can confirm with our findings. In addition, among the predictions of Miguët et al. (2016), they also hypothesized that species with higher reproductive rates tend to have a smaller spatial scale of effect. Annuals are usually r-strategists while perennials tend to be more K-strategists (Whigham and Simpson 1978; Aarssen 2000; Bonser 2013; Gliessman 2014). Accordingly, the spatial scale of effect for annuals should be smaller than that for perennials. However, our study did not provide evidence for such a hypothesis. A meta-analysis evaluating the spatial scale of effect among different studies also did not find support for this relationship (Jackson and Fahrig 2015). Although an empirical study on beetles (Kallio 2014) and a simulation study (Jackson and Fahrig 2012) did support this prediction, Miguët et al. (2016) state that this may in part be driven by dispersal ability rather than by the direct influence of

reproductive rate because reproductive rate may be negatively correlated with dispersal ability. Our study also fails to support this prediction because most annuals (68%) and most perennials (71%) are high dispersal species. Therefore, although such species traits are often considered important factors influencing the spatial scale of effect, there is little support for these predictions in our study.

Surprisingly, the spatial scale of effect for low dispersal species was larger than that for high dispersal species. This is contrary to previous predictions that hypothesize that the scale of effect increases with the dispersal ability of the species (Miguet et al. 2016). However, no empirical evidence was found to support this (Avon et al. 2015; Miguet et al. 2016; San-José et al. 2019). For example, San-José et al. (2019) found that the mean spatial scale of effect for landscape structure for species with local-, wind-, and animal-dispersed seeds did not differ significantly. There is limited knowledge to explain how dispersal ability affects the spatial scale of effect of landscape structures in empirical studies, partly because the dispersal ability of species is difficult to quantify (Miguet et al. 2016). In addition, Avon et al. (2015) discussed that both spatial and temporal effects are linked together, and the greater the spatial extent is, the greater the past landscape is captured and the more the current species diversity can be explained. In our study, low dispersal species showed a 9-21 year time lag and a 2 km scale effect, while high dispersal species responded best to the current landscape and at the 1 km scale. A different interaction of landscape history and spatial scale may be one aspect to explain why the spatial scale of effect is larger for low dispersal species than for high dispersal species in our study.

There is a lively debate about whether the predictors should be estimated individually at their spatial scale of effect (“multi-scale” models) or at a common scale (“single-scale” models) when there are multiple landscape predictors. (Graf et al. 2005; Martin and Fahrig 2012). Besides the analyses using fixed scales (“single-scale” for the fixed temporal or spatial scale), we considered all combinations of all landscape predictors at all scales (“multi-scale”) in our models too. Our approach is similar to Boscolo and Metzger (2009) who also considered all combinations of spatial scales of landscape predictor for bird incidence. Our approach allows us to compare and decide whether we should focus on multiple scales or a single scale when assessing the effect of landscape structure on species diversity. According to our results, the median D^2 of the models with no fixed spatial scale (i.e., multi-scale) was not greater than the median D^2 of the models at the spatial scale of effect (i.e., fixed 1 km). From this perspective, if the multi-scale models do not perform better than the single-scale models, assessing how landscape structure affects species diversity at multiple scales is unnecessary because a single scale would greatly simplify.

Limitations

There are limitations in our study that must be addressed. First, although the results may indicate that changing the spatial extent affects the species-landscape relationship more than changing the temporal scale, the relative importance of spatial and temporal scales may change if the range of scales changes. It should be noted that the comparison between the spatial and temporal scales is based on 1-2 km intervals within a 6 km extent and on c.10-year intervals within a 30-year period. Due to the lack of long time-series of past land use data, we were not able to test the effects at longer temporal scales. Second, we could not test the interactions of spatial and temporal scales because the low number of replications for testing interactions (four fixed spatial scales \times four fixed temporal scales \times nine species groups). Third, although we detected time lag in the responses of some species groups, the proportion of the present-day species richness in the study area that will potentially decrease or increase in the future due to the time lag effects remains unknown. This is linked to the different methods used in time lag studies. One of most widely used approaches is the one used in our study, which is called “past habitat” approach, i.e., detection of time lag responses by comparing the predictive power of past and current landscape structures. Other

approaches are called the “stable habitat” approach and the “past communities” approach, respectively (Ridding et al. 2021). The former quantifies the difference between predicted (predicted by using the species-landscape relationship in stable habitats) and observed species richness in unstable habitat. The latter compares the observed current species richness with predictions based on the past species richness-landscape relationships. Such approaches are better capable of calculating the magnitude of the extinction debt (Ridding et al. 2021).

Conclusion

In conclusion, we highlight that over a medium timespan, such as 30 years, the relationship between landscape structure and species richness was more variable when changing the assessed spatial extent compared with changing the temporal scale. However, compared with spatial scales, different species groups exhibit more significant differences when exploring the strongest temporal scale at which they respond to landscape structure. Our findings emphasize that if the landscape structure is not measured at the appropriate spatial and temporal scales, the importance of biodiversity-landscape relationships can be underestimated and misinterpreted. In addition, the quick response of neophytes to landscape change demonstrates that biological invasions are likely to increase further, especially with ongoing urban sprawl. Last but not least, understanding the spatial and temporal scales of effect of landscape structure on biodiversity is a challenging issue and has not been fully addressed. Meanwhile, these challenges can be viewed as an opportunity to better understand the biodiversity-landscape relationship. Therefore, future studies should focus on the integration of the different approaches in assessing the spatial and temporal scales of effect, as well as the interaction effect of spatial scale and temporal scale on the biodiversity-landscape relationship.

Acknowledgement

The authors are grateful to the Federal Office for the Environment (FOEN) and the Swiss Biodiversity Monitoring Program (BDM) for providing the vascular plant monitoring data, and Swiss Federal Statistical Office (FSO) for providing the land use data. We gratefully acknowledge to Jonathan Cole for help with the calculation of the effective mesh size. We also gratefully acknowledge financial support from China Scholarship Council. The authors would like to thank two reviewers for their detailed and constructive comments. They were very helpful in improving the manuscript.

Declarations

Funding: YP holds a research grant from the China Scholarship Council (CSC).

Conflicts of interest/Competing interests: The authors declare no conflict of interest.

Ethics approval: Not applicable.

Consent to participate: The authors consent the participation of the study.

Consent for publication: The authors consent the publication of the study.

Availability of data and material: It is not allowed to share the biodiversity monitoring data.

Code availability: Not applicable.

Authors' contributions: YP and MN conceived the idea. YP and FK performed the landscape analysis. YP, MN, and ZL performed statistical analysis. YP drafted the manuscript. YP, AH, and MN revised the manuscript. FK, ZL and GG commented on the manuscript.

Figure captions

Fig. 1 Map of study area within Switzerland. (a) Spatial distribution of the 98 survey plots in the Swiss Plateau. Land use types (100-m resolution) were represented in the estimated spatial extents (i.e., 1×1 , 2×2 , 4×4 , 6×6 km). (b) Landscape predictors were measured at multiple spatial extents. The vascular plants were surveyed along transects of 2500 m length and 5 m width within each focal square (i.e., the smallest spatial extent).

Fig. 2 Amount of explained deviance (D^2) in the models including landscape structure and/or climate for predicting species richness. Besides the single D^2 value of the climate-only model, the mean value (the vertical green and blue bars) and range (the vertical black lines) of D^2 are shown for the models with landscape predictors and models with both landscape and climate predictors.

Fig. 3 Explained deviance D^2 of models with fixed spatial scales in comparison to all models of all remaining spatiotemporal scale combinations (36,864 models in total). Box plots show the median, 25% and 75% quartiles and 1.5 interquartile range; outliers are indicated by circles. The best model (red dot) and its corresponding temporal scales (18 = 2018, 09 = 2009, 97 = 1997, 85 = 1985) and spatial scales (1 km, 2 km, 4 km, 6 km) of each predictor are shown above the box plots (W = wooded area, U = urban area, M = effective mesh size). Climatic covariates are not shown in the formula. The results of the global Kruskal–Wallis test and the pairwise Wilcoxon tests among fixed spatial scales are shown in each plot of the nine species groups (a-i). Asterisks (ns = $p > 0.1$; (*) = $0.05 < p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$) refer to comparisons among different fixed spatial scales.

Fig. 4 Explained deviance D^2 of models with fixed temporal scales in comparison to all models of all remaining spatiotemporal scale combinations (36,864 models in total). Box plots show the median, 25% and 75% quartiles and 1.5 interquartile range; outliers are indicated by circles. The best model (red dot) and its corresponding temporal scales (18 = 2018, 09 = 2009, 97 = 1997, 85 = 1985) and spatial scales (1 km, 2 km, 4 km, 6 km) of each predictor are shown above the box plots (W = wooded area, U = urban area, M = effective mesh size). Climatic covariates were not shown in the formula. The results of the global Kruskal–Wallis test and the pairwise Wilcoxon tests among fixed temporal scales are shown in each plot of the nine species groups (a-i). Asterisks (ns = $p > 0.1$; (*) = $0.05 < p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$) refer to comparisons among different fixed temporal scales.

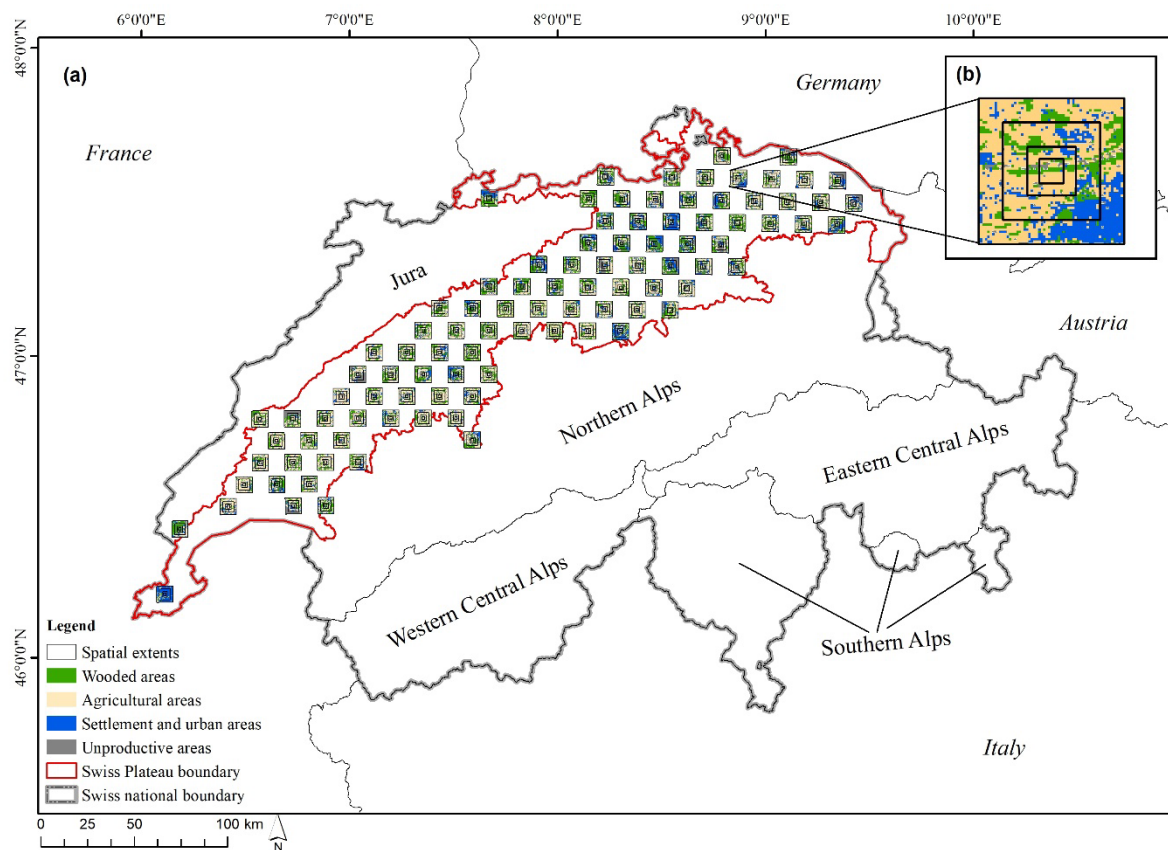


Fig. 1

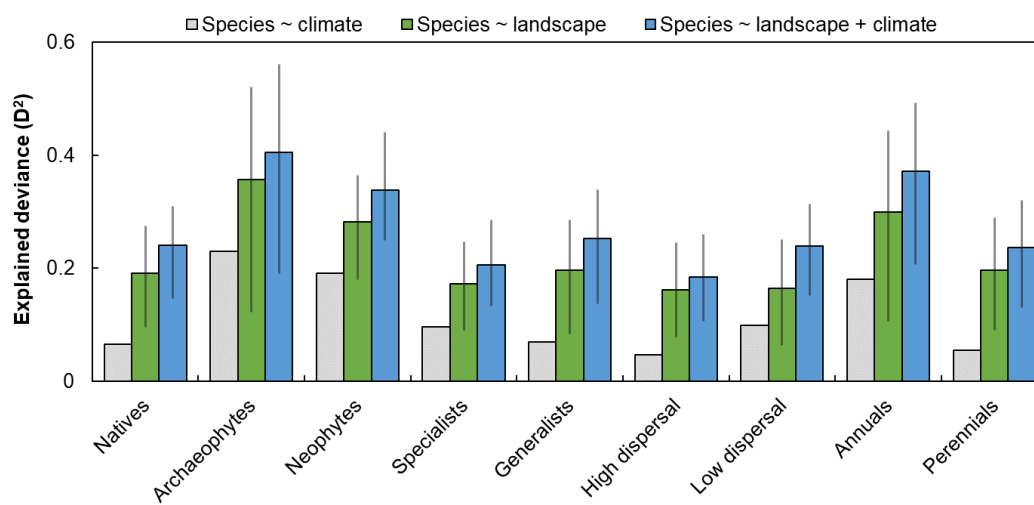


Fig. 2

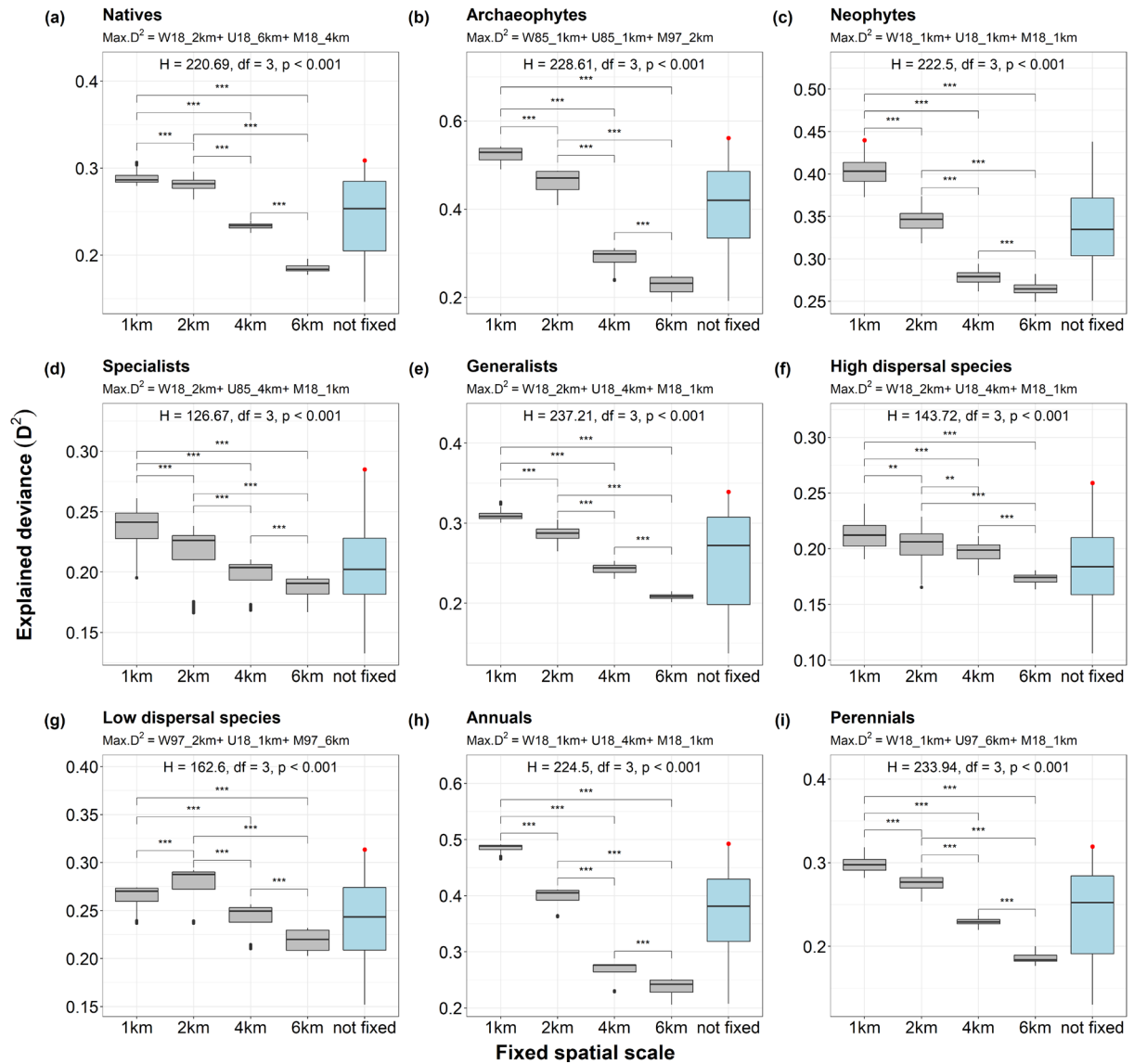


Fig. 3

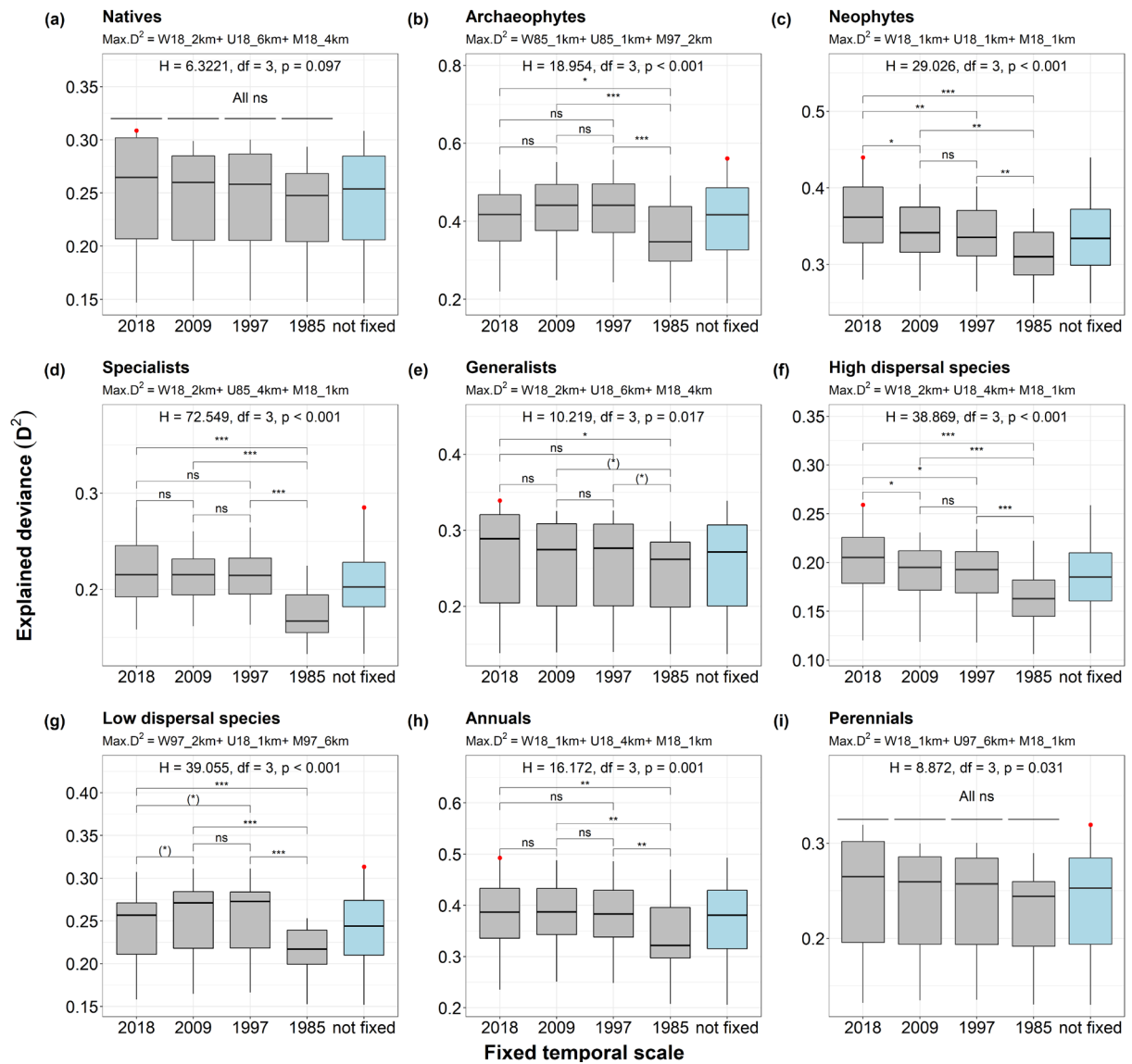


Fig. 4

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