

RESEARCH ARTICLE

Disentangling effects of climate and land use on biodiversity and ecosystem services—A multi-scale experimental design

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Abstract

1. Climate and land-use change are key drivers of environmental degradation in the Anthropocene, but too little is known about their interactive effects on biodiversity and ecosystem services. Long-term data on biodiversity trends are currently lacking. Furthermore, previous ecological studies have rarely considered climate and land use in a joint design, did not achieve variable independence or lost statistical power by not covering the full range of environmental gradients.
2. Here, we introduce a multi-scale space-for-time study design to disentangle effects of climate and land use on biodiversity and ecosystem services. The site selection approach coupled extensive GIS-based exploration (i.e. using a Geographic information system) and correlation heatmaps with a crossed and nested design covering regional, landscape and local scales. Its implementation in Bavaria (Germany) resulted in a set of study plots that maximise the potential range and independence of environmental variables at different spatial scales.
3. Stratifying the state of Bavaria into five climate zones (reference period 1981–2010) and three prevailing land-use types, that is, near-natural, agriculture and

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urban, resulted in 60 study regions (5.8×5.8 km quadrants) covering a mean annual temperature gradient of $5.6\text{--}9.8^\circ\text{C}$ and a spatial extent of $\sim 310 \times 310$ km. Within these regions, we nested 180 study plots located in contrasting local land-use types, that is, forests, grasslands, arable land or settlement (local climate gradient $4.5\text{--}10^\circ\text{C}$). This approach achieved low correlations between climate and land use (proportional cover) at the regional and landscape scale with $|r \leq 0.33|$ and $|r \leq 0.29|$ respectively. Furthermore, using correlation heatmaps for local plot selection reduced potentially confounding relationships between landscape composition and configuration for plots located in forests, arable land and settlements.

4. The suggested design expands upon previous research in covering a significant range of environmental gradients and including a diversity of dominant land-use types at different scales within different climatic contexts. It allows independent assessment of the relative contribution of multi-scale climate and land use on biodiversity and ecosystem services. Understanding potential interdependencies among global change drivers is essential to develop effective restoration and mitigation strategies against biodiversity decline, especially in expectation of future climatic changes. Importantly, this study also provides a baseline for long-term ecological monitoring programs.

KEYWORDS

biodiversity, climate change, ecosystem functioning, insect monitoring, land use, space-for-time approach, spatial scales, study design

1 | INTRODUCTION

Human actions are threatening the interdependent yet fragile balance of the biosphere, with far-reaching consequences for the diversity of plants (Brummitt et al., 2015) and animals (Dirzo et al., 2014). As biodiversity contributes a wealth of ecological services, cascading effects and reassembly of communities jeopardise human well-being and biosphere's resilience against current and future disturbance (Chaplin-Kramer et al., 2019; Mori et al., 2018). Many of the services, such as food provisioning, decomposition or maintenance of soil fertility, rely on biotic interactions potentially sensitive to global change. This is especially true for regulating services provided by the highly diverse class of insects: pollination and pest regulation, both shown to strongly affect food production (Dainese et al., 2019; Duffy et al., 2017). Reported losses of insect biomass and abundances across Europe and the globe are therefore particularly worrisome (Hallmann et al., 2017; Seibold et al., 2019; Wagner, 2020). Yet the full cross-taxon magnitude of declines and the relative contributions of man-made drivers remain poorly understood.

One of the greatest threats to biodiversity is land-use change, the transformation of terrestrial ecosystems for infrastructure, human settlements and the production of crops, animals and timber (Newbold et al., 2015). Landscape simplification, urbanisation, deforestation and agricultural intensification alter environmental conditions and the

availability of habitats and resources, but also the structure of entire landscapes, that is, their composition (amount of different habitat types) and configuration (spatial arrangement and patch size of habitats, commonly assessed as 'edge density'). Both variables are often highly correlated (Fahrig et al., 2011) and might interact in nonlinear ways (Martin et al., 2019; Redlich et al., 2018), while attempts to disentangle them by reducing the parameter space may lower the statistical power of study designs (Figure 1). Concurrently, land-use effects on biodiversity and ecosystem services depend on spatial scaling, the degree of specialisation and movement capability of taxa and ecological processes considered (Piano et al., 2020; Wiens, 1989), with important implications for population dynamics, the diversity of fungi, plants and animals, and in consequence for ecosystem functions and services (Díaz et al., 2019; Foley et al., 2005; Newbold et al., 2015). While macroecological processes such as environmental filtering determine regional species pools, species diversity and population abundances at smaller spatial scales relate to multi-habitat use, dispersal ability, resource availability and trophic interactions. For instance, large-scale urbanisation reassembles terrestrial and aquatic invertebrate communities (Piano et al., 2020), but local conversion from natural habitat to cropland reduces species abundances and the multitrophic functional biodiversity in agroecosystems (Provost et al., 2020) with flow-on effects for pollination, pest regulation and crop productivity (Dainese et al., 2019).

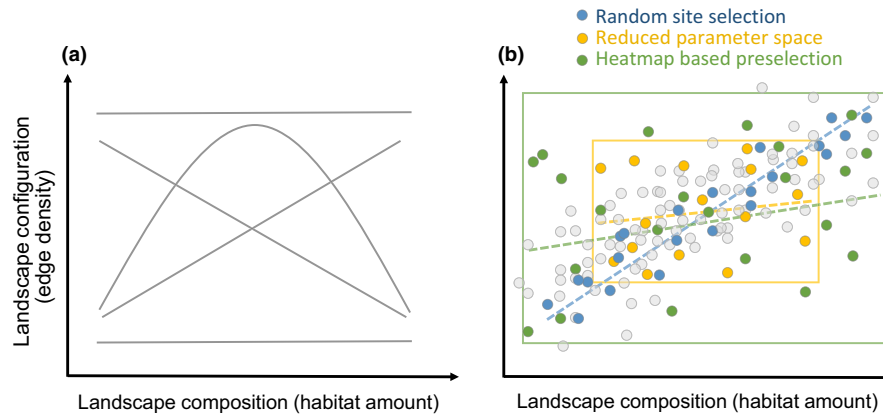


FIGURE 1 Disentangling effects of landscape composition and configuration in large-scale ecological studies. Relationship between variables can be positive, negative, nonlinear or independent, depending on habitat amount, habitat type and region (a). Random selection of study plots regularly results in significant correlations between variables (blue points, b), while posterior exclusion of plots reduces correlations but also the covered parameter space (yellow rectangle and points, b). A priori knowledge of potential correlations and targeted selection of study plots using heatmaps reduces correlations and increases the parameter space (green rectangle and points). Dashed trend lines in blue, yellow and green in (b) indicate the expected change of landscape variable correlations depending on the site selection approach

Climate is another major driver of biodiversity. Long-term data on species distributions along latitudinal and elevational climatic gradients demonstrate significant poleward and upward shifts of species' ranges driven by global warming (Parmesan, 2006). In the future, extinction risks across all animal taxa—but particularly ectothermic organisms such as insects—may further increase with accelerating climate change (Urban, 2015; Warren et al., 2018). Similarly, plant community richness is likely to decrease in temperate climates, where the range of thermal tolerances in regional species pools is narrow (Harrison, 2020). Both for animals and plants, the risk of extinction and the potential to expand their geographic range in response to climate change largely depend on species-specific traits such as the climatic tolerance and the capacity to disperse and colonise new habitats (Estrada et al., 2016). As a consequence, individual species' traits and the resulting ratio between climate change winners and losers drive the overall impact of climate change on biodiversity and the restructuring of communities.

Specific land-use types may prevent climate-induced range shifts and accelerate extinctions (Fox et al., 2014; Peters et al., 2019), especially in case of less mobile specialists (Fourcade et al., 2021; Warren et al., 2001). Alternatively, (in)vertebrate communities in anthropogenic land-use types may shift towards drought- and warming-tolerant species (Williams & Newbold, 2020). Understanding the independent and combined impact of land-use and climate change on biodiversity, community composition and ecosystem services is needed to predict future changes and allow for management strategies that mitigate further losses. However, <10% of available studies analyse combinations of both drivers (Rillig et al., 2019), and commonly observed correlations make it difficult to disentangle individual effects (Peters et al., 2019). First, land use is driven by current and historic demographic and political settings, environmental conditions (e.g. soil characteristics) and climatic parameters, often causing geographic clustering of land-use types (Dale, 1997).

Second, land-use change may feed back to the atmosphere and alter regional climate including water availability by precipitation (Laux et al., 2017; Williams & Newbold, 2020). Furthermore, as long-term data on climate, land use and biodiversity are currently lacking, recently established monitoring schemes will not deliver sufficient data in the near future and time-series analysis may be prone to biases (Didham et al., 2020).

Here, we report on a step-by-step protocol (Figure 2) for a comprehensive study design that systematically combines full gradients of climate and land use at various spatial scales to investigate interacting effects on biodiversity of a wide range of primarily terrestrial taxa. This method was developed within the framework of a large-scale interdisciplinary climate research project (LandKlif, www.landklif.biozentrum.uni-wuerzburg.de). The stratified, nested design used intensive GIS-based exploration of potential study regions and a new site-selection approach based on heatmaps to reduce potential pitfalls of ecological studies on effects of land-use and climate: (a) non-independence of climate and land-use variables, and correlations among land-use related composition and configuration variables; (b) restrictions in gradient range or the number of spatial scales considered (i.e. reduction of parameter space); and (c) lacking monitoring data for biodiversity and ecosystem services. The described method can be useful for similar multi-scale research programs and long-term ecosystem monitoring, but will also allow for predictions of potential interactive impacts of climate and land use in a space-for-time approach.

2 | MATERIALS AND METHODS

2.1 | Study area

The three-step study design (Figure 2) was implemented in 2019 in Bavaria, Southern Germany. With an area of around 70,000 km² and

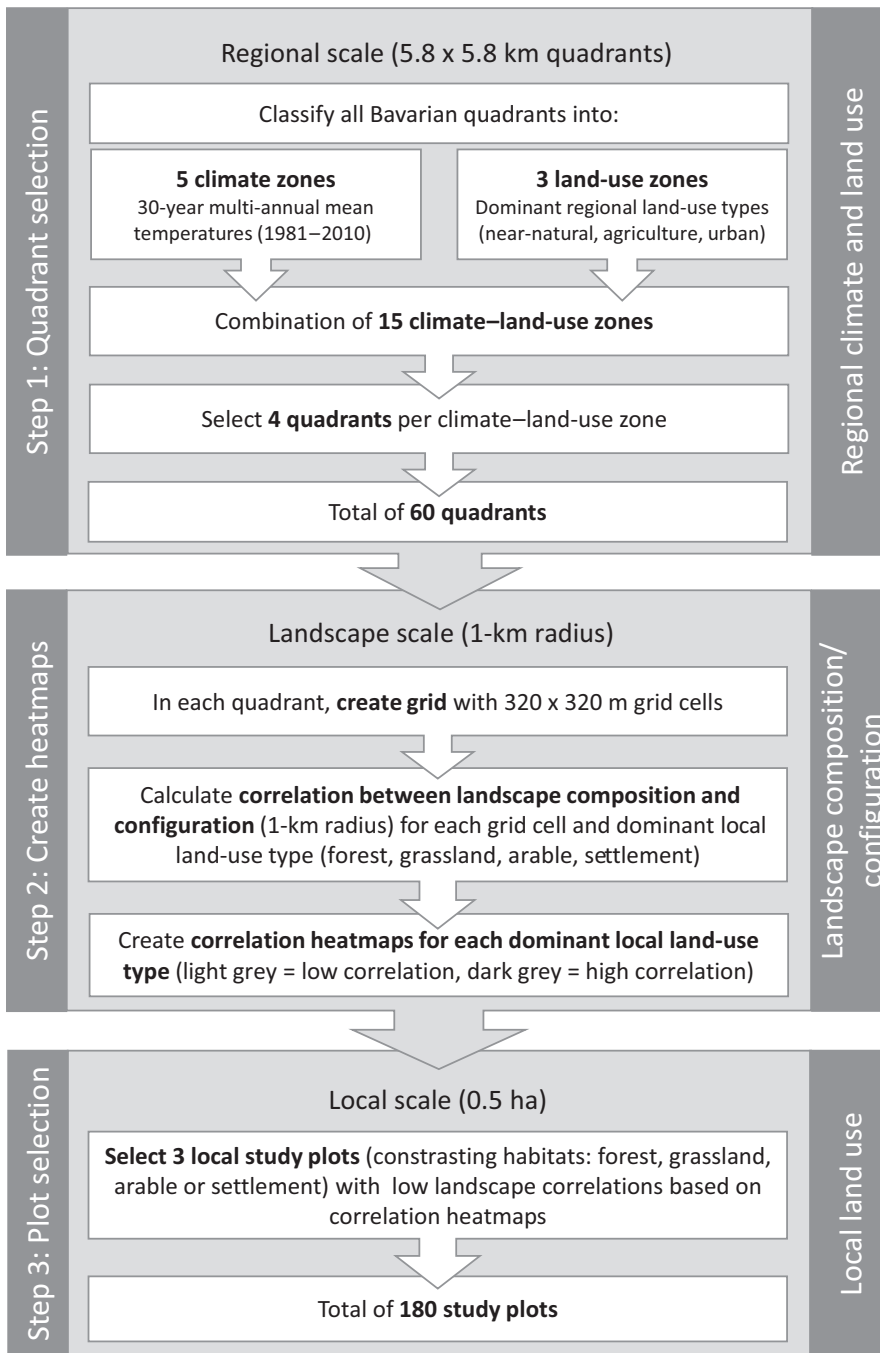


FIGURE 2 General overview of three-step plot selection process, exemplified by a large-scale interdisciplinary climate research project in Bavaria, Germany. Step 1: Selection of 60 study quadrants (i.e. study regions) based on 15 climate–land-use combinations. Step 2: Creation of heatmaps to disentangle landscape composition and configuration variables in 1-km radius. Step 3: Based on heatmaps, selection of final 180 study plots in contrasting local land-use types

13 mil. inhabitants, it is the largest and second most populous state of Germany (Bayerisches Landesamt für Statistik, 2020). The land use of Bavaria is dominated by human influences, but also comprises less intensively used near- or semi-natural areas. While 7% constitute urban areas and 53% agricultural land or managed grassland, the remaining 40% are covered by (mostly managed) forests, nature protection areas and other near-natural habitats (CORINE, 2012). Bavaria's size and heterogeneity of climate and anthropogenic influences makes it a suitable pilot region for studying and disentangling effects of climate and land use in temperate regions and at the regional, landscape and local scale.

2.1.1 | Step 1—Selection of study regions ('quadrants') based on climate and land-use zones

At the regional scale, a stratified sampling approach ensured complete coverage of climate and land-use gradients and largely uncorrelated, orthogonal parameter combinations of both (Figure 2). Regions were hereby defined as existing 5.8 x 5.8 km quadrants, which build the cells of a spatial grid covering the whole of Bavaria ('TK25' topographical map established in 1868, scale 1:25,000). The scale of the TK25 mapping system is large enough to assess effects of climate and accommodate three spatially independent study plots

(see below), while maximising regional climate and land-use contrasts. Additionally, historic land use maps and floristic and faunistic inventories allow to evaluate changes over time.

To select potential climate–land-use combinations, quadrants were first classified into five climatic zones (<7.5, 7.5–8, 8–8.5, 8.5–9 and >9°C) based on 30-year mean air temperature data (1-km² resolution) averaged for each quadrant (climatological reference period 1981–2010, Deutscher Wetterdienst, 2020). We further categorised each quadrant as one of three dominant regional land-use types based on proportional land use (CORINE, 2012; Table S1): near-natural quadrants (>85% near-natural vegetation with a minimum of 50% forest), agricultural quadrants (>40% arable land and managed grassland) and urban quadrants (>14% housing, industry and traffic infrastructure). Due to the long history of anthropogenic land use, pristine native habitats are very rare in Bavaria (<2%). Forests—mostly managed but permanent habitats—can therefore be considered as less disturbed than agricultural land with high pesticide pressure or urban areas with high levels of sealing. Accordingly, we merged forests, woodlands, nature protection areas and semi-natural habitats (mostly calcareous grasslands and wetlands) in the category ‘near-natural’, and made sure a sufficient amount of forest (>50%) was present in each ‘near-natural’ quadrant. Cut-off values for land use and climate were chosen to (a) maximise climatic differences and the contrast among land-use types, with anthropogenic impact ranging from low (near-natural) to very high (urban); (b) achieve equal intervals and a similar number of quadrants within each category; and (c) obtain enough quadrants in each class to realise an even distribution and meet logistic requirements (e.g. reduce travelling time, avoid no-fly zones for UAVs where aerial assessments were planned). Based on these prerequisites, we selected

four quadrants of each of the 15 climate–land-use combinations (60 quadrants, i.e. study regions, Figures 2 and 3).

2.1.2 | Step 2—Create heatmaps to reduce correlations among landscape variables

Within each of the 60 quadrants, we aimed to investigate the impact of local land use and interactive effects of landscape-scale land use (composition and configuration) on biodiversity and ecosystem services. The landscape scale was hereby defined as 1-km radius around local study plots, as this scale was shown to have ecological relevance for arthropods (Bosem Baillod et al., 2017; Holzschuh et al., 2016; Thies et al., 2003). As the strength of correlations among landscape variables depends on the location of local study plots, we implemented a novel heatmap approach with a priori knowledge of potential relationships (Figure 1). These correlation heatmaps—created for four dominant contrasting local land-use types identified within our quadrants—served as systematic criterion for local study plot selection by identifying potential sites with the lowest possible correlation between landscape composition and configuration (Figure 2).

The procedure to create these heatmaps involved the following steps: (1) Within each quadrant and starting 1 km away from the quadrant edge, we created a grid of 320 m resolution (resolution of the underlying CORINE data (2012), Figure 4a). We calculated four landscape composition variables (proportional cover of four local land-use types: forest, grassland, arable land, settlement) and one configuration variable (edge density, i.e. length of edges between all habitat types on a per unit area, m/ha) for a 1-km radius buffer

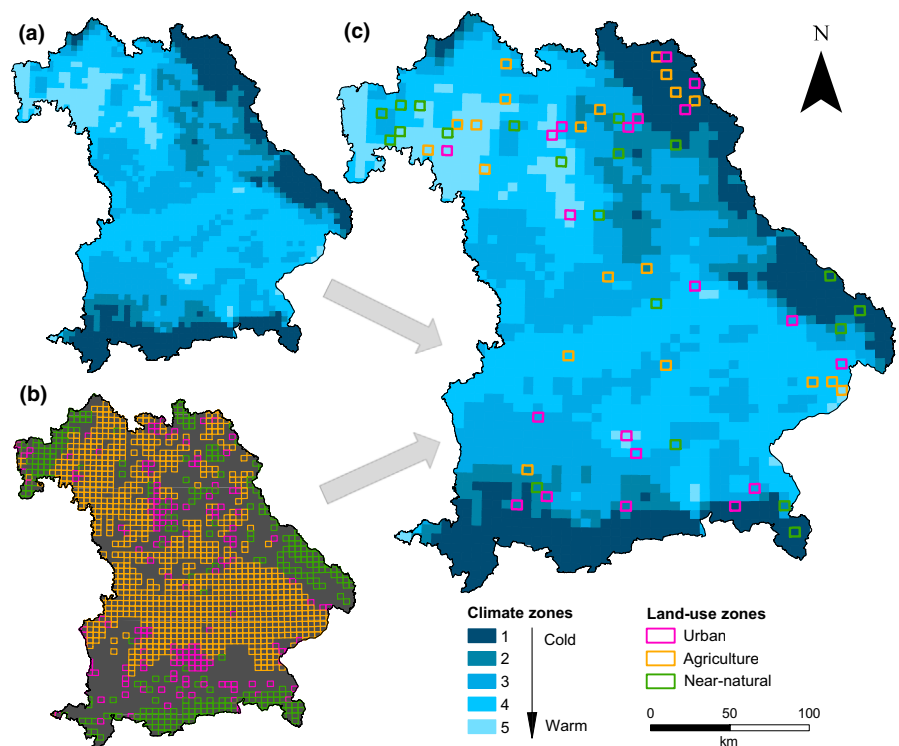


FIGURE 3 Implementation of a full-factorial, stratified design crossing regional climate and land use in Bavaria, Southern Germany. Climate zones (a) were based on 30-year (1981–2010) mean air temperatures in each quadrant (1: <7.5°C, 2: 7.5–8°C, 3: 8–8.5°C, 4: 8.5–9°C, 5: >9°C). For land use (b), we distinguished between near-natural quadrants (>85% near-natural vegetation with a minimum of 50% forest), agricultural quadrants (>40% arable land and managed grassland), and urban quadrants (>14% housing, industry and traffic infrastructure). The final 60 quadrants (i.e. study regions, c) covered 15 climate–land-use combinations with four replicates each

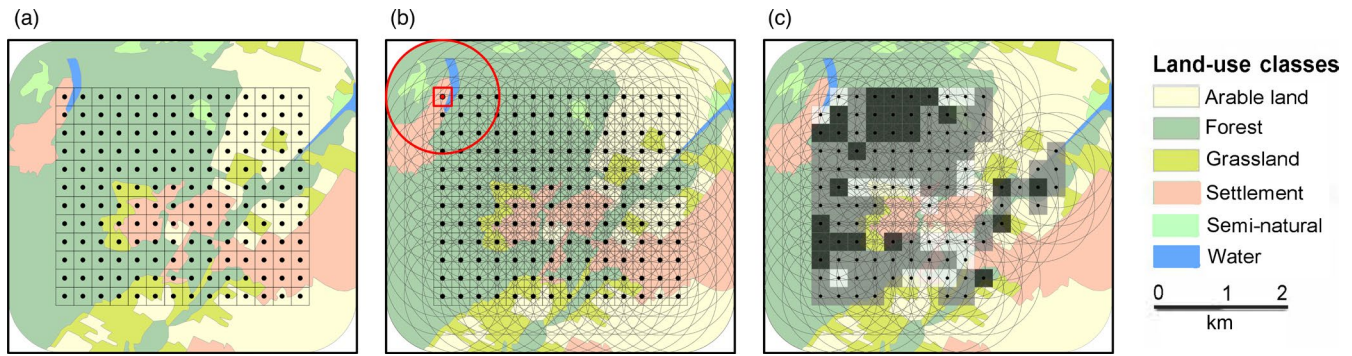


FIGURE 4 Process of deriving correlation heatmaps for each dominant land-use type to guide the selection of local study plots. Colours of polygons represent different land-use types (see classification in Table S1). Create a fishnet (a) of 320 m resolution inside each of 60 study quadrants (i.e. study regions). Calculate landscape composition and configuration within a 1-km radius around the centre of each 320 × 320 m grid cell (b). Select grid cells dominated by the respective land-use type (here forest, dark green) and create land-use specific heatmaps of mean correlations between landscape composition and configuration based on 10,000 random selections of grid cells across all quadrants (c). Shades of grey in heatmaps indicate levels of the predicted degree of correlation (light = high correlation, dark = low correlation) if the respective grid was chosen

around the centre of each 320 × 320 m grid cell (Figure 4b). Edge density was selected, because previous studies highlight its relevance for spillover and resource complementarity for biodiversity and ecosystem services (e.g. Martin et al., 2019). The next steps, here exemplified for forest, were repeated for each local land-use type. (2) We selected all grid cells (Figure 4c) with a proportional forest cover of >20% (to accommodate a 0.5-ha study plot and a 3 × 30 m experimental area) and >5% forest in the surrounding 1-km radius buffer (to ensure a minimum amount of forest was present in the surrounding landscape). (3) Of these forest grid cells and associated landscape buffers, we randomly chose one in each of the 60 study quadrants—if existent (quadrants without forest grids were excluded)—and calculated the overall Pearson's r correlation coefficient between the surrounding landscape composition (here forest cover) and configuration (edge density) based on the random plot selection. (4) This random selection and calculation was repeated 10,000 times. (5) For each forest grid cell i we then calculated the average Pearson's \bar{r}_i coefficient across all the random combinations of points in which this cell was included:

$$\bar{r}_i = \frac{\sum_{j=1}^n r_{ij}}{n},$$

where r_{ij} is the j th Pearson's r coefficient resulting from random selection of that specific forest dominated grid cell i , and n is the number of times that grid cell i was included in one of the 10,000 random selections of points. And (6) in a last step and considering all forest grid cells in our 60 quadrants, we used natural breaks (Jenks natural breaks algorithm implemented in ArcMap v10.4) to classify the range of mean correlations into three categories to create the correlation heatmap for the local land-use type forest (Figure 4c). By repeating the steps described in (2–6) for all land-use types (forest, grassland, arable land, settlement), we derived a set of four heatmaps for each of the 60 quadrants. During the local plot selection process (Step 3), these heatmaps helped to reduce correlations of landscape composition and

configuration around plots with specific land-use types (e.g. only forest plots), but also across all study plots.

2.1.3 | Step 3—Selection of local study plots

Within each quadrant, we aimed to establish local study plots of 0.5 ha size within contrasting land-use types (Figure 2). Although six main local land-use types had been identified during the heatmap process, two were neglected due to irrelevance for the project's scope (water) or as not available in sufficient quantity (semi-natural). Of the four dominant types (forest, grassland, arable land or settlement) not all were present in each quadrant. Therefore, we focused on three of the four dominant types per quadrant by considering availability (if only three types present) or regional dominance (three types with highest proportional cover) and contrast (whenever proportional cover of two land-use types was similar). We then used the respective heatmaps to preferentially place study plots in grid cells that had low predicted correlation values for the specific land-use type. We aimed to maximise the representativeness of land-use types by making predefined choices in plot selection: broadleaf was favoured over coniferous forests, intensive over extensive grasslands, conventional arable fields over organic or perennial fields and urban over rural settlements. To account for additional differences within habitats, we assessed local plant communities after plot establishment (vegetation surveys on seven subplots with a total of 10 m² in 2019 and during transect walks in 200-m radius of sites in 2020). We also recorded local microclimatic variables (hourly measurements of temperature and humidity in 1.2 m height using thermologgers) to complement our long-term macroclimatic data, allow for across-scale comparisons and assess the potential of specific land-use types to mitigate climate change impacts by creating microclimatic refugia. Further decision rules for plot selection included land-owner permission, >2 km between plots, >50 m away from roads,

water bodies and other land-use types, protection from vandalism and good accessibility. Nested within our large-scale factorial design, the resulting 180 plots allowed us to assess the influence of local land use on biodiversity and ecosystem services, while minimising correlations between landscape composition and configuration and accounting for microclimatic and structural differences.

2.2 | Assessing efficiency of study design

We assessed the efficiency of our stratified selection and heatmap approach by (a) region (5.8×5.8 km): calculating Pearson's r correlation coefficients between regional climate and the proportion of our regional dominant land-use types near-natural, agriculture and urban; and (b) landscape (1-km radius): assessing relationships between local climate and the proportion of our dominant local land-use types forest, grassland, arable land and settlement. We also visually compared final correlation values between landscape composition and configuration with histograms of potential correlations resulting from 10,000 random selections.

The proportion of land-use types (region, landscape) and landscape composition and configuration variables were calculated in ArcGIS pro v2.2.0 and ArcMap v10.4 using CORINE data (2012). Climate data for regions and landscapes (mean air temperatures and associated precipitation amounts) were calculated using Esri ASCII grid raster files with 1×1 km resolution (Deutscher Wetterdienst, 2020) by averaging pixel values within each 5.8×5.8 km quadrant and 1-km buffer around selected study plots, respectively. Although the land-use and climate variables presented here for the quadrant and 1-km scale were the basis for establishing our design, we also calculated these metrics at smaller and larger scales for different subprojects and depending on the biodiversity and ecosystem services under consideration (not shown). All Pearson's r coefficients were calculated in R v4.0.2.

3 | RESULTS

3.1 | Implementation of the experimental design

Our design and selection process (Figure 2) allowed us to minimise the correlations between climate, land use and landscape metrics at multiple scales and resulted in an approximately even distribution of 60 quadrants (i.e. study regions) across Bavaria (Figure 3).

The regions stretched across extensive environmental gradients of temperature, precipitation and elevation, while covering large land-use gradients (Table 1). Regional land use (proportion of near-natural, agriculture and urban habitat) showed low correlations with regional mean temperatures (Figure 5a–c) and precipitation ($|r| < 0.3$), Figure S1a–c).

For each quadrant, the heatmap procedure yielded four heatmaps (one each for the local land-use types forest, grassland, arable land and settlement), which were used to identify potential study

plots within dominant local land-use types (Figure 6b–d). After ground-truthing of sites and gaining permission of landowners, three final plots were chosen per quadrant (Figure 6e), yielding 179 of 180 expected study plots (Figure 6a). One study plot was discarded as landowner permission was denied. Forest ($n = 55$) was the most selected local land-use type, followed by grassland ($n = 46$), arable land ($n = 43$) and settlement ($n = 35$).

On the landscape scale in 1-km radius around our study, the use of heatmaps during the site selection process helped us to achieve extensive, mostly uncorrelated spatial gradients of climate and land use (Table 1). Correlations of landscape-scale temperature and precipitation with composition variables (Figure 4d–g, Figure S1D–G) were low, as were correlations of both climate variables with edge density (temperature $r = -0.17$, precipitation $r = 0.07$). The correlation between precipitation and temperature was moderately negative across plots ($r = -0.51$), yet the microclimatic variables temperature and humidity, which were assessed throughout the study season, showed a low positive relationship ($r = 0.32$).

Compared to potential correlations based on the random selection of study plots (histograms of 10,000 random selections, Figure 7), the heatmap approach resulted in lower actual correlations (blue lines, Figure 7) between landscape composition and configuration in 1-km radius around study plots if plots were located in forest, arable land and settlements (Figure 7a,c,d). Only for grassland, the final correlation was positive and higher than predicted (Figure 7b). Taking all study plots independent of the local land-use type into account, this pattern was even stronger, with correlations between the proportion of habitats and edge density being very low for forest (Pearson's $r = -0.31$), arable land ($r = 0.09$) and settlement ($r = -0.08$), yet high for grassland ($r = 0.51$) (red line, Figure 7, Figure S2). Correlations among composition variables ranged from $r = -0.13$ (settlement and grassland) to -0.55 (arable land and forest).

This multi-scale GIS-supported study design is suited to disentangle climate and land-use effects on general and functional biodiversity and plant- or animal-based ecosystem services. In LandKlif, numerous add-on studies assess these relationships using a range of observational, empirical, modelling and survey data collected on different spatial scales (Table 2). The diversity of studies will allow us to investigate trade-offs between different measures of biodiversity and ecosystem services.

4 | DISCUSSION

Studies assessing the combined effects of land use and climate on biodiversity and ecosystem services commonly struggle with non-independence of climate and land-use variables, restrictions in gradient range or scale and insufficient long-term datasets. Here, we present the protocol for a large-scale experimental design that aims to overcome these issues. While our basic design follows the selection principles for multi-scale landscape studies outlined in previous papers (Fahrig et al., 2011; Gillespie et al., 2017; Pasher et al., 2013), the use of a novel, automated heatmap approach and the inclusion of

TABLE 1 Summary statistics and description of climate and land-use variables on local, landscape and regional scale

		Variable	Description	Range	Mean \pm SD
Region (5.8 \times 5.8 km)					
Climate		Temperature	30-year (1981–2010) mean air temperature	5.6–9.8°C	8.2 \pm 0.8°C
		Precipitation	30-year (1981–2010) mean precipitation	614–1,820 mm	939 \pm 263 mm
		Elevation	Elevation averaged at resolution of 1 arc-second (SRTM, 2020)	228–915 m	477 \pm 161 m
Land use		Near-natural	Proportion near-natural including forest	0.8 to 97.1%	40 \pm 27.7%
		Agriculture	Proportion agriculture (arable + grassland)	0.3%–91.0%	44.7 \pm 24.9%
		Urban	Proportion urban (housing, industry + traffic)	0%–97.2%	14.7 \pm 21.1%
Landscape (1-km radius)					
Climate		Temperature	30-year (1981–2010) mean air temperature	4.5–10°C	8.2 \pm 0.8°C
		Precipitation	30-year (1981–2010) mean precipitation	590–1,987 mm	928 \pm 249 mm
		Elevation	Elevation averaged at resolution of 1 arc-second (SRTM, 2020)	168–1,122 m	489 \pm 167 m
Land use	Composition	Forest	Proportion forest	0%–100%	37.9 \pm 32.3%
		Grassland	Proportion grassland	0%–80.2%	15.7 \pm 17.1%
		Arable Land	Proportion arable land	0%–99.4%	28.7 \pm 29.2%
		Settlement	Proportion settlement	0%–100%	16.1 \pm 25.8%
	Configuration	Edge density	Edge density (length of edges between all habitat types on a per unit area)	0–66.0 m/ha	28.1 \pm 13.8 m/ha
Study plot (0.5 ha)					
(Micro)climate		Temperature	Average temperature on study plots between April and September 2019	13.7–19°C	16.9 \pm 1.0°C
		Humidity	Average relative humidity on study plots between April and September 2019	62.3%–82.2%	70.2 \pm 4.1%
Land use		Local land-use type	Three out of four dominant habitat types (forest, grassland, arable land, settlement)—categorical variable	NA	NA

independent climatic gradients sets this design apart, both as baseline and space-for-time study.

First, the crossed and nested design resulted in relatively weak correlations between climate and land use at the regional ($|r| < 0.33$) and landscape scale ($|r| < 0.29$). The design also decoupled regional climate and land-use effects from the influence of small-scale land use due to the selection of three of four dominant local land-use types (forest, grassland, arable land or settlements) within our 60 quadrants (i.e. study regions). Regarding landscape composition and configuration in a 1-km radius around study plots, the heatmap approach lowered correlations compared to average potential correlations for specific local land-use types (blue lines, Figure 7), but these benefits were not that substantial in absolute terms (i.e. correlations for selected plots quite close to peak of distribution for random selection). However, there are three points to consider: (a) these actual correlations were based on a subset of plots (specific local land-use types), and were much lower for forest, arable land and settlement if calculated across all study plots (red lines, Figure 7), which is the gradient range primarily used for analysis in our project; (b) reducing landscape correlations may be difficult for land-use types such as forest, where patches generally occur clustered, causing higher negative correlations with edge density than for settlements or arable

land. For grassland, correlations seem to be generally low, yet increased during the selection process, possibly due to inherent correlations among land-use types and nonlinear relationships between grassland amount and edge density in the landscape; and (c) in our project, complex private ownership structures, logistic and other constraints (e.g. transportation costs, time constraints, accessibility and permissions) prevented us from selecting combinations of study plots closer to $r = 0$. Our method is situated halfway between two extremes: the blind selection of study plots that may inherently cause strong landscape correlations or requires the reduction in parameter space (see Figure 1) and choosing the best available random selection of plots during the process of creating heatmaps. Accordingly, the chance of moving towards low landscape correlations ultimately depends on the gradient range and land-use type considered and methodological, logistical and ownership constraints that may be lower in other studies.

Second, we increased the coverage of spatial scales and land-use types, thereby maximising the number of explanatory factors that can be analysed in parallel. Concurrently, our method of 'a priori' employing long-term climate data and extensive GIS-based exploration of potential study plots enabled us to cover independent, large climatic and land-use gradients. For landscape composition

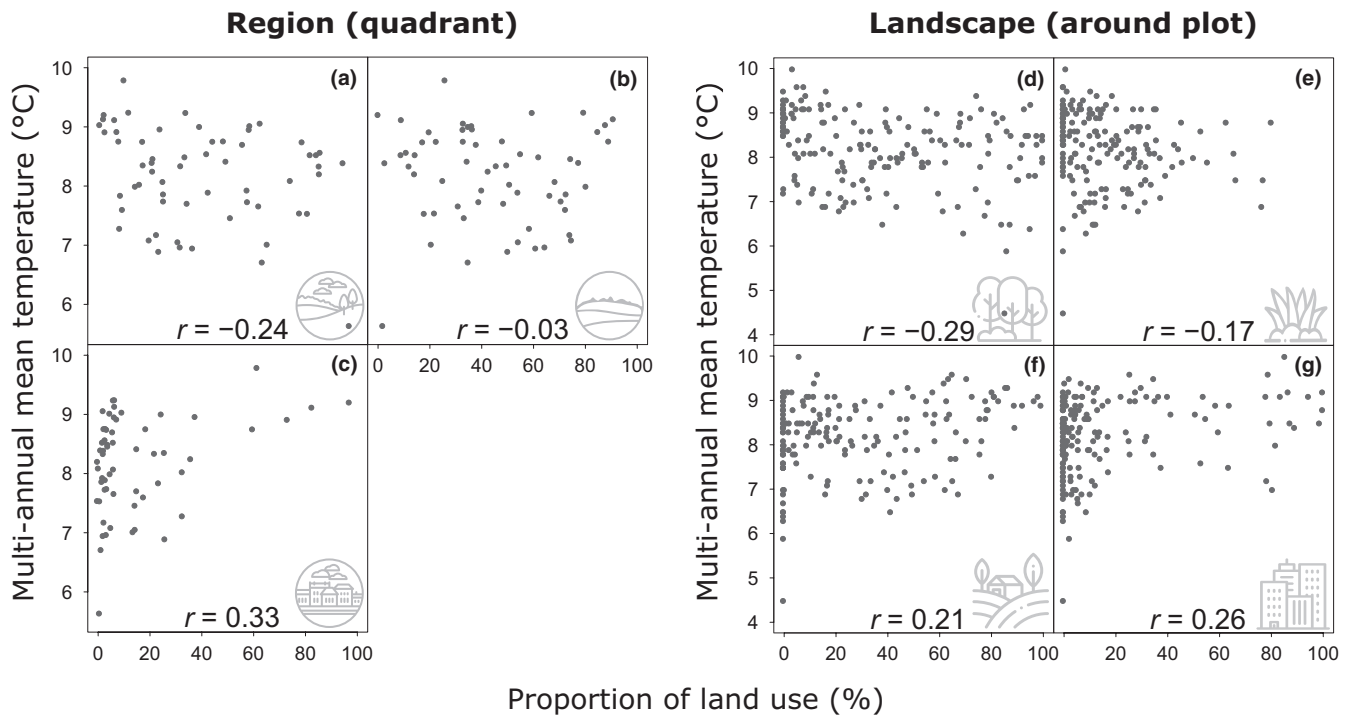


FIGURE 5 Relationships between 30-year mean temperatures (1981–2010) and proportional land cover (composition) for the regional land-use types near-natural (a), agriculture (b) and urban (c), and for the landscape-scale land-use types forest (d), grassland (e), arable land (f) and settlement (g). Pearson's r coefficients based on 60 quadrants (5.8×5.8 km study regions, a–c) and 179 (out of expected 180) study plots (1-km radius around local study plots, d–g)

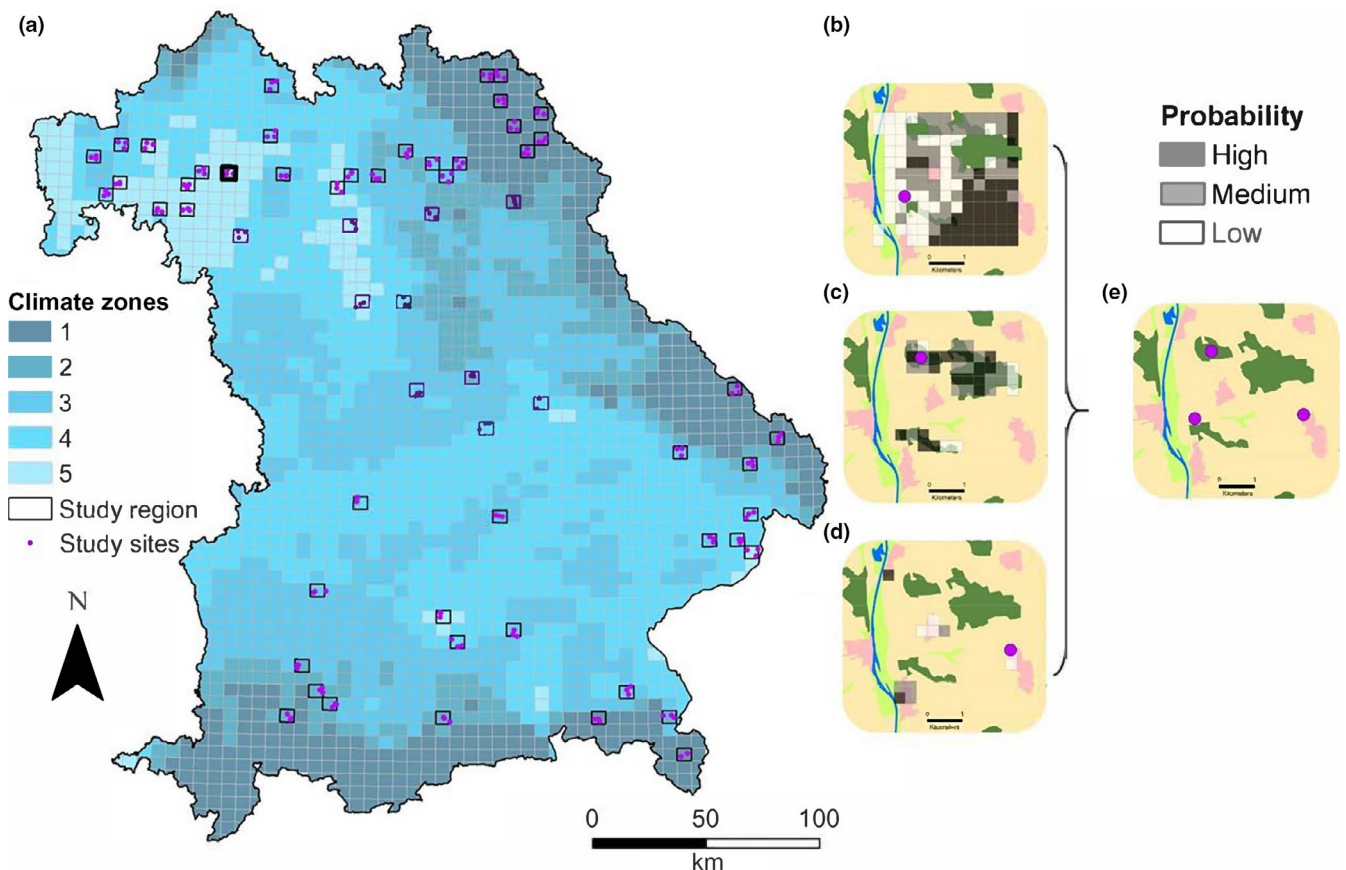


FIGURE 6 Map of all 179 (out of expected 180) study plots in 60 study regions (a) and example of heatmaps for three dominant local land-use types (arable land (b), forest (c), and settlement (d)) used for the final selection of study plots (e). Shades of grey in heatmaps indicate levels of the predicted degree of correlation (light = high correlation, dark = low correlation) if the respective grid was chosen

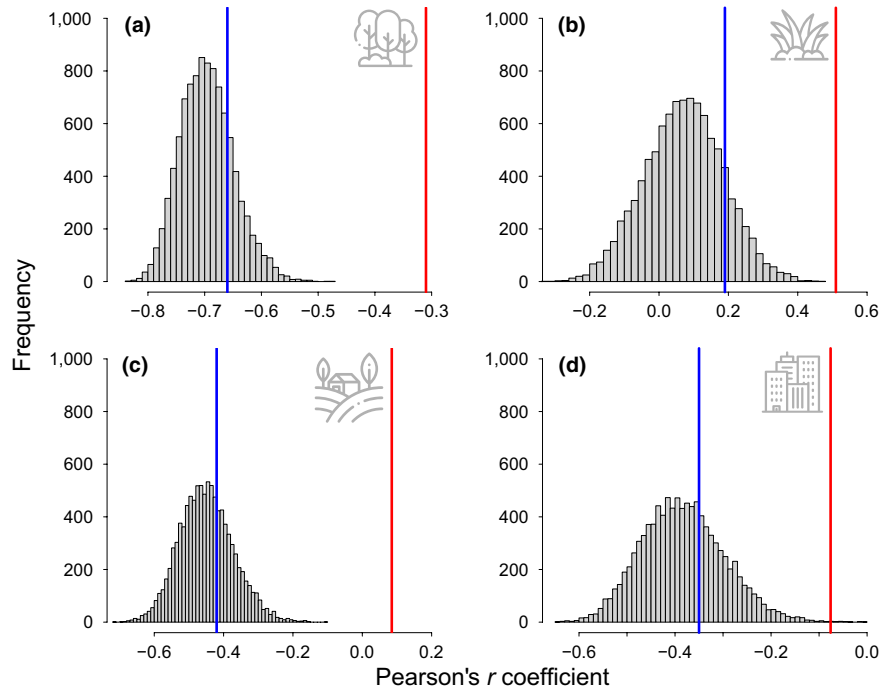


FIGURE 7 Potential and actual Pearson's r correlations between landscape composition (proportional cover of land-use types) and configuration (edge density) in 1-km radius around study plots. Histograms (grey bars) show range of potential correlations resulting from 10,000 random selections of grid cells (i.e. potential study plots, cf. 'heatmap procedure'). Compared to those, actual correlations (blue lines) between edge density and the proportion of forest ($n = 55$; a), arable land ($n = 43$; c) and settlement ($n = 35$; d) were lower than expected for the final selection of plots if only considering plots within the same land-use type as at the landscape scale (e.g. only forest plots for a). For grassland plots, the actual correlation between grassland proportion and edge density was higher than expected ($n = 46$; b). Red lines show actual correlations among edge density and land-use specific composition variables across all selected study plots, independent of local habitat type ($n = 179$)

and configuration of the full set of 179 final study plots, our data highlight the natural, unimodal relationship between these variables, which is most pronounced for forest cover and grows weaker from grassland to arable land and settlement, with peaks between 40% and 60% land cover (Appendix S2). This implies that studies covering narrow landscape gradients between 0%–50% and 50%–100% may observe contrasting positive or negative correlations between these landscape variables, respectively, while studies focussed on intermediate landscape gradients are most likely to reduce the correlation between variables and differentiate between individual effects, which may be impossible at the extreme ends of the spectrum.

Finally, our extensive on-field assessments within this experimental framework will fill existing knowledge gaps about biodiversity trends across taxa, relationships between above- and below-ground arthropods and the microbial diversity of decomposer communities. For instance, the current design allowed us to detect contrasting responses of total flying insect biomass and richness to land use and climate (Uhler et al., 2021). Yet the proposed method can also easily be extended to include higher resolution land-use types or detailed landscape structures ecologically relevant for specific target organisms. We can also assess potential trade-offs among ecosystem service provisioning and current and predicted interactive effects of climate and land use on biodiversity–ecosystem functioning relationships. In this context, the implemented space-for-time approach

has crucial advantages over time series. Recently established long-term biodiversity monitoring schemes will not yield meaningful results before several decades, which may be too late considering the current speed of global change. Furthermore, long-term climatic change often goes hand in hand with land-use change, making it difficult to disentangle individual effects (Dale, 1997). In addition, issues such as shifting baselines or phenologies, bias in site selection and detection may cause misleading results in time-series analysis (Didham et al., 2020). Other methods, such as large-scale, manipulative climate–land-use experiments following the idea of BACI designs (Before-After-Control-Impact studies, Christie et al., 2019) are highly interesting but almost impossible to implement. While large-scale factorial experiments can be used to cancel out environmental noise that may override ecosystem responses to global change (Schädler et al., 2019), implementation costs are high and the required block set-up on relatively small spatial scales is unsuitable for assessing effects on mobile organisms such as pollinators or mammals.

Space-for-time approaches also have limitations. For instance, other drivers of biodiversity, such as anthropogenic pressure or altered biotic interactions, may mask the response to climate, especially if only small spatial scales (a few kilometres or less) with small climatic differences are considered (Blois et al., 2013). Similarly, time-lags in the response of biodiversity to either climate or land

TABLE 2 Example for assessments of biodiversity (yellow), ecosystem services (green) and socio-economic/management information ('other', blue) in the LandKlif project used to investigate relationships with climate and land use. Observational and empirical data were collected on up to 179 study plots in 2019 and 2020 and complemented with modelling approaches and stakeholder surveys. Extended categorisation of ecosystem services based on TEEB (2010) and Rabe et al. (2016)

	Group/service	Detail	Scale
Biodiversity	Plants	Plant/Pollen diversity and phenology	Plot
	Microbes	Soil/decomposer microbial diversity	Plot
	Arthropods	Total biomass and richness of flying and crawling arthropods; functional abundance and richness of arthropod decomposers, pollinators, trap-nesting Hymenoptera, pests and predators	Plot
	Vertebrates	Diversity and density of game	Plot/Bavaria
Ecosystem services	Pest regulation*	Predation and parasitism rate, herbivory	Plot
	Decomposition*	Decomposition of deadwood, carrion and dung	Plot
	Pollination	Seed set (yield); pollination services; flower resource availability	Plot/Region
	Food	Crop biomass and yield, game	Plot/Region
	Raw materials	Timber stock; vegetation biomass; Normalised Difference Vegetation Index (NDVI)	Plot/Bavaria
	Maintenance of soil fertility	Soil fertility (soil organic carbon and nutrient content)	Plot
	Erosion prevention	Wind/water erosion prevention (e.g. vegetation cover)	Region
	Regulation of water flows	Groundwater recharge	
	(Micro)Climate regulation	Net productivity; carbon storage	Plot/Bavaria
	Moderation of extreme events	Flood control (soil infiltration, vegetation cover, topography)	Region
Water treatment	Water quality regulation (nitrogen and phosphorus retention)	Region	
Other	Stakeholder preferences	Preferences for ecosystem services	Region
	Stakeholder perceptions	Climate change perceptions	Region
	Landowner management	Management of land and crop fields used for experiments	Plot

*Additional ecosystem services assessed.

use may reduce the accuracy of space-for-time studies compared to long-term time series (Banet & Trexler, 2013). In contrast, data obtained from spatial observations were shown to overestimate phenology responses to temperature compared to long-term phenological data (Jochner et al., 2013). Still, space-for-time substitutions based on the largest possible climatic gradient are a useful and fast alternative to gain important, policy-relevant insights into the interactive effects of climate and land-use change on biodiversity and ecosystem services. They also complement long-term studies by highlighting more general patterns. By utilising the full parameter space of the climatic and landscape variables assessed here (Figure 1), we enhanced the validity of space-for-time substitutions related to climate change (Blois et al., 2013). We further reduced the chance of observing misleading findings in cases where non-monotonic relationships cause contradictory relationships between environmental variables and biodiversity if only a narrow variable range is used (Eigenbrod et al., 2011).

5 | CONCLUSIONS

Our multi-scale study protocol expands on previous designs which addressed local gradients in climate and land use (Peters et al., 2019)

or gradients in landscape structure in multiple regions (Gillespie et al., 2017; Holzschuh et al., 2016). It allows to evaluate scale-dependent and interactive effects of current climate and land-use gradients on biodiversity and ecosystem services, thereby highlighting landscape management schemes with the potential to mitigate adverse effects of climate change. Similarly, the assessment of a large diversity of ecosystem responses identifies high-risk groups and trade-offs between different aspects of biodiversity and ecosystem services, as well as land-use types and scales particularly prone to face negative climate change impacts. The observed relationships can then be used to parameterise and validate climate-land-use models, which help to predict long-term responses to climate change. Furthermore, our design provides valuable baseline data to assess the effectiveness of future restoration measures at local, landscape and regional scales. We believe that this approach of an objective, multi-scale site selection across large regions deserves consideration in the implementation of national and European long-term ecosystem monitoring schemes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

S.R., J.Z., J.M., T.H. and I.S.-D. conceived the ideas and designed the methodology; J.Z. and C.K.-F. collected the data; S.R. and J.Z. analysed the data; S.R., J.Z. and I.S.-D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and R code are available at Dryad Digital Repository <https://doi.org/10.5061/dryad.np5hqbzv1> (Redlich et al., 2021).

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