Check for updates

Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

PERSPECTIVE OPEN ACCESS

Interacting Effects of Climate and Land Use on Biodiversity: A Guide to What They Are and Why They Matter

Matilda Arnell[1] | Andrew J. Suggitt[2] | Laura H. Antão[3] | Rob Cooke[4] | Andrea Cristiano[5] | Cristina Ganuza[6] | Phillipa K. Gillingham[7] | Blaise Martay[8] | Teresa Montràs-Janer[9] | Hedvig Nenzén[10] | Tim Newbold[11] | Charlotte L. Outhwaite[12] | Jessica J. Williams[13] | Alistair G. Auffret[10]

[1]Department of Ecology, Environment and Plant Sciences Stockholm University, Stockholm, Sweden and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden | [2]Department of Geography and Environmental Sciences, Northumbria University, Newcastle Upon Tyne, UK | [3]Research Centre for Ecological Change, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland and Department of Biology, University of Turku, Turku, Finland | [4]UK Centre for Ecology & Hydrology, Wallingford, UK | [5]Department of Geography and Environmental Sciences, Northumbria University, Newcastle Upon Tyne, NE1 8ST, United Kingdom and Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza University of Rome, Rome, Italy | [6]Department of Animal Ecology and Tropical Biology, Biocenter, Julius-Maximilians-Universität Würzburg, Würzburg, Germany | [7]School of Life and Environmental Sciences, Bournemouth University, Poole, UK | [8]British Trust for Ornithology, Thetford, UK | [9]Greensway AB, Uppsala, Sweden | [10]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden | [11]Centre for Biodiversity and Environment Research, University College London, London, UK | [12]Centre for Biodiversity & Environment Research, University College London, Gower Street, London, United Kingdom and Institute of Zoology, Zoological Society of London, London, UK | [13]Department of Life Sciences, Imperial College London, Berkshire, UK

Correspondence: Alistair G. Auffret (alistair.auffret@slu.se)

Received: 17 February 2026 | **Revised:** 23 September 2026 | **Accepted:** 16 October 2026

Handling Editor: Michele Di Musciano

Keywords: additive | antagonistic | biodiversity | climate change | conservation | habitat destruction | habitat dynamics | land-use change | multiple stressors | statistical interactions

ABSTRACT

Problem: Climate and land-use change are two key drivers of biodiversity change. Their widespread effects on species and communities have prompted fears that interactions between the two drivers could cause severe biodiversity loss. As the literature on this subject expands rapidly, variation in methodological choices and the terminology used to describe results, combined with context-dependent or individualistic responses across taxa and systems, hinders our ability to systematically evaluate how species and communities are affected by the interacting effects of climate and land-use change.

Clarification: We provide guidance for investigating climate-land-use interactions, following clear definitions and including recent examples from natural and semi-natural systems. We highlight how variation in methodologies, language inconsistencies, data limitations, and the inherent variation among populations and species can affect the analysis of climate-land-use interactions. Importantly, we demonstrate how failing to consider interactive effects can negatively impact the outcomes of conservation interventions designed to protect biodiversity.

Communicating Climate-Land-Use Interactions: We provide a roadmap to guide future work, highlighting important considerations for understanding and communicating climate-land-use interactions relevant for both policy and conservation. Outlining how different factors can complicate our understanding of interactive effects is a key step towards the accurate detection, interpretation and communication of the effects of climate and land-use change on biodiversity in a rapidly-changing world.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

1 | Introduction

Climate and land-use change are two of the most prominent drivers of biodiversity change, leading to range shifts, population declines, and increased extinction risk (Newbold et al. 2015; Spooner et al. 2018; IPBES 2019). The broad scale and increasing magnitude of these drivers makes them a key threat to meeting global targets to halt biodiversity loss (IPBES 2019; WWF 2024). Where changes in land use (or land cover, see Box 1) result in biodiversity loss through habitat loss or degradation (Drakare et al. 2006; Fahrig 2013; Chase et al. 2020), climate change may lead to parts of a species' range becoming more or less suitable due to the direct or indirect effects of warmer temperatures, altered precipitation patterns, and increased frequency and intensity of extreme weather events (Johansson et al. 2020; Antão et al. 2022). When both climate and land-use changes act simultaneously, their combined effects might be expected to result in larger impacts (positive or negative) on species or populations than if either of the changes had occurred individually (Figure 1A). However, changes in biodiversity due to climate and land-use changes can also be larger or smaller than would be expected from a simple combination of their individual effects (Figure 1B), that is, climate and land-use change can interact to affect biodiversity.

The prevalence of concurrent changes in climate and land use, and their potential to negatively affect biodiversity, is an issue that has been regularly investigated during recent decades. Earlier reviews discussed the potential problem of interactive effects and some potential mechanisms (Dale 1997; de Chazal and Rounsevell 2009; Oliver and Morecroft 2014), while later work has argued that we should look beyond the classification of interactions and onto the risk that they pose to biodiversity (Schulte to Bühne et al. 2021). Concurrently, research has also highlighted how the effects of a combination of different ecosystem stressors can be more than, less than, or equal to their individual effects (e.g., Piggott et al. 2015; Burgess et al. 2021). Such frameworks could broadly include climate and land-use change as stressors, but much of the existing literature is related to experimental aquatic systems, where stressors are often factors that can be added in a controlled manner (e.g., Orr et al. 2020).

Unlike experimental systems, where comparisons of individual and combined effects are relatively straightforward, the rapidly-expanding literature aiming to quantify the effects of climate and land use on biodiversity in natural and semi-natural systems is based on heterogeneous data collected across large temporal and geographical gradients (e.g., Hudson et al. 2017; Dornelas et al. 2025). These gradients—usually across continuous variables of climate and/or land use—combined with other issues with such data biases (Boyd et al. 2023), make it challenging to understand and communicate their interactive effects on biodiversity using the same framework that has been proposed for other environmental stressors (Piggott et al. 2015; Burgess et al. 2021). Importantly, studies that rely on these kinds of data have so far been unable to reach a consensus regarding the extent to which species and communities are affected by the interacting effects of climate and land-use change. As an example, high-profile research investigating the species richness of insect assemblages have reported interactions resulting in both larger (Outhwaite et al. 2022) and smaller (Montràs-Janer et al. 2024) impacts than would be expected from their individual effects, whilst another did not detect interactive effects at all (Uhler et al. 2021). There are several potential reasons behind these contrasting findings, including differences in how individuals, populations, species and communities respond to

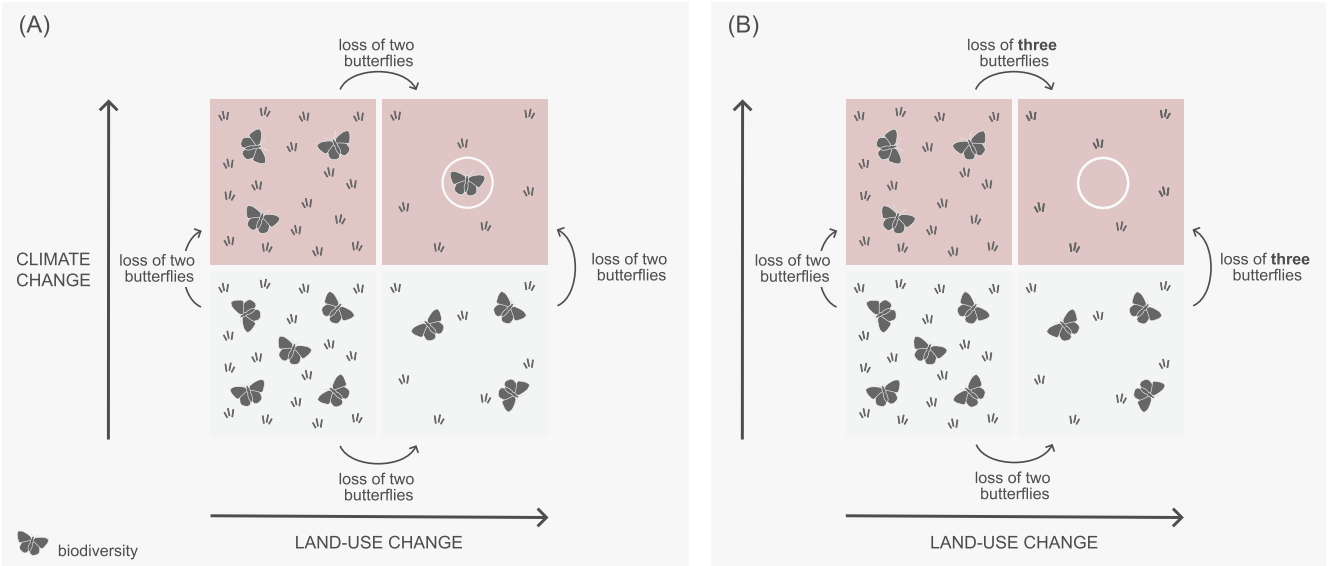


FIGURE 1 | A simple example of additive and interactive effects of climate and land-use change on biodiversity. Climate and land-use changes can both have detrimental effects on biodiversity (represented here by butterfly symbols). The bottom left square in each panel shows initial conditions, while changes in either climate or land use can reduce biodiversity (from five to three individuals). When both changes occur simultaneously (top right square), the effect on biodiversity is worse than if only one had occurred. In panel A, the combined effect equals the sum of the effect of climate and land use: Five initial butterflies minus the loss of two butterflies to climate and two to land use. In panel B, the combined effects are worse, with the simultaneous effect of climate and land use being stronger than the sum of their individual effects—an interactive effect. Note that interactions between climate and land use can also result in less biodiversity loss than expected (not shown).

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

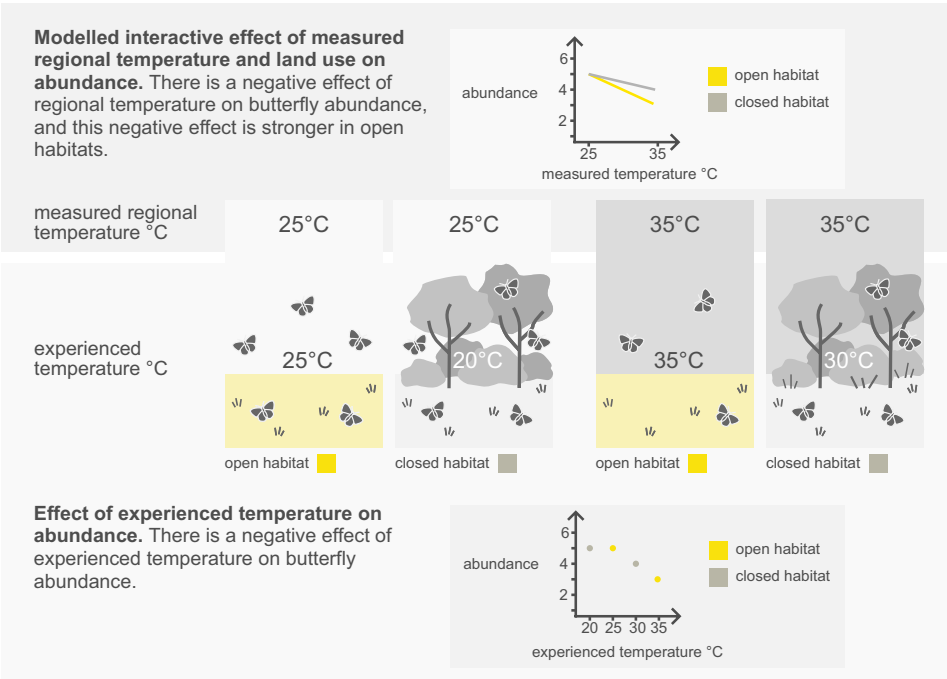


FIGURE 2 | Example showing how climate and land use can interact to affect biodiversity, and how modelled statistical interactions can arise due to the scale at which variables are measured. In closed habitats, vegetation buffers local (experienced) temperature, creating a cooler microclimate, hence the butterfly experiences cooler conditions than temperatures measured at the regional scale. Butterfly abundance responds to experienced temperature (points on lower panel), generating an interaction between regional temperature and habitat (open vs. closed) when modelled statistically (fitted lines on upper panel), with stronger negative effects of warming observed in the open habitats.

environmental pressures, variation in these responses in time or in space, as well as in the methods and data used to investigate potential interactions.

As research on the effects of climate and land-use change on biodiversity continues to expand across taxa, spatio-temporal scales and biodiversity metrics, any attempt to synthesise and apply these findings will depend on a common understanding regarding how climate-land-use interactions are described, investigated and interpreted. Using recent examples, we describe ways in which climate and land use can interact to affect biodiversity, and how methodological choices and terminology can impact whether or not interactions are detected. We provide a roadmap for understanding and communicating climate-land-use interactions, giving urgently needed guidance when navigating this important topic, given that failing to detect and effectively communicate climate-land-use interactions can have serious impacts for conservation and policy.

2 | Defining and Interpreting Interactions

Climate-land-use interactions arise when a change in a climate variable affects the biodiversity response to a land-use variable for a given population or community, and vice versa. For instance, denser canopy cover can buffer local temperatures within forests relative to regional temperatures, resulting in cooler daytime temperatures. This variation in local microclimate can allow the persistence of cool-adapted plant species below canopies, despite regional temperatures becoming unfavourably high due to climate warming (Greiser et al. 2020; Zellweger et al. 2020; Samira Geres et al. 2025). In these circumstances, we cannot predict the effect of regional temperatures on biod without knowing the canopy cover. For warm-adapted species, increasing temperatures may change a species' preferred habitat, for example allowing butterflies to lay eggs in denser patches of vegetation that would previously have been too cold (Davies et al. 2006). By failing to observe and quantify such interactions, we risk misinterpreting and misattributing observed population or community trends (Figure 2).

The term 'interaction' is used with different definitions and in different contexts throughout the scientific literature (Box 1). We focus on *statistical* interactions, since assessing the presence, direction, and strength of interactions between drivers in ecological systems usually involves fitting statistical models. Specifically, we discuss interactions between variables of climate and land use, but the principles apply to any interaction between two drivers of biodiversity change. Statistical interactions can arise through different ecological mechanisms, directly or indirectly driving a biodiversity response. In the example above, describing how canopy cover buffers local temperatures, the mechanism is a direct effect of local temperature on cold-adapted species, but in practice, this pattern would be detected by a statistical interaction when modelling the effect of variation in regional temperature and canopy cover (Figure 2).

Interactions are clearly important to consider and model in ecology. However, when a species responds to both climate and land-use variables, and the effect of, for example, temperature is constant for all land-use values, the modelled effects are additive, and not interactive (Figures 1A and 3A). Interactive effects between two variables occur when the effect of each variable is not constant across the measured interval of the other variable

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

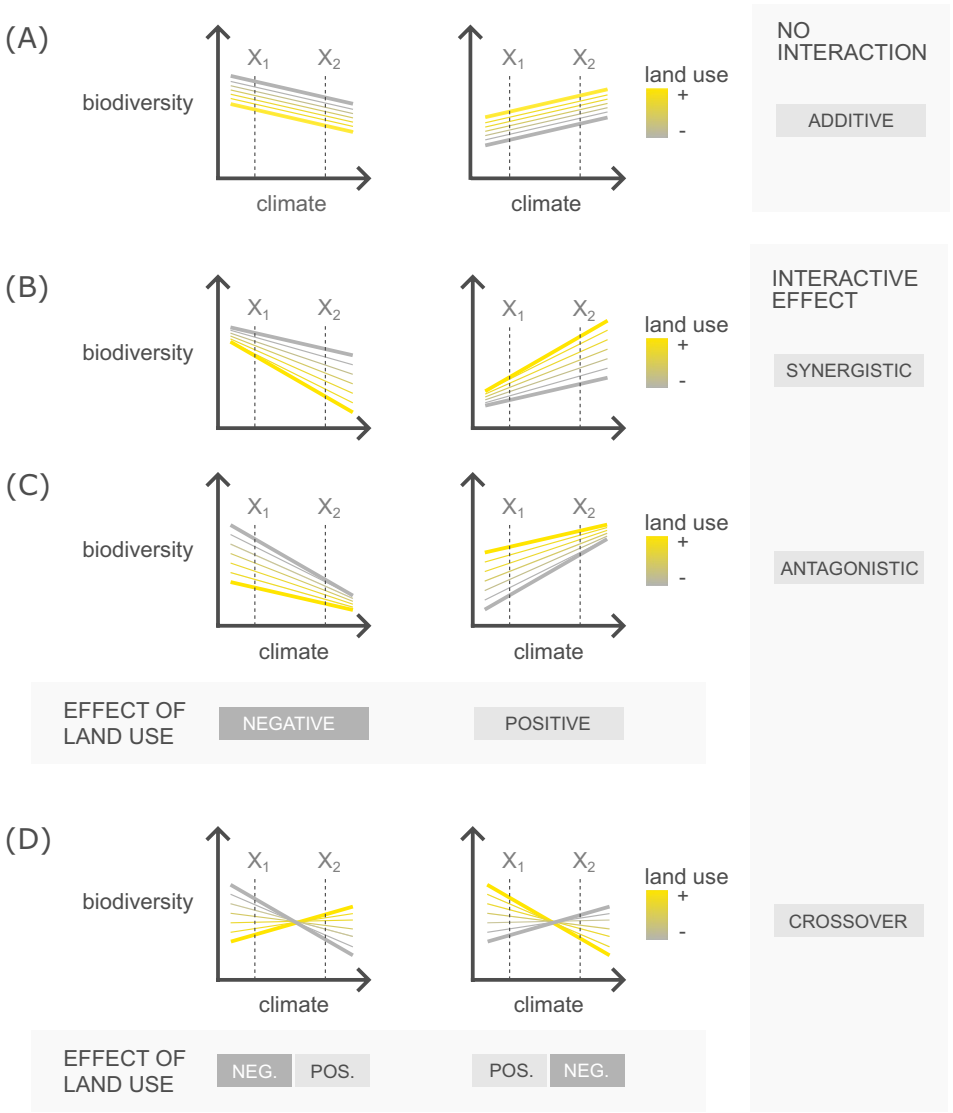


FIGURE 3 | Additive and interactive effects of climate and land use on biodiversity. Overview of potential (modelled) effects of climate and land-use variables (continuous scales, for example temperature and proportion of arable land) on a biodiversity response variable, for example, number of individuals or number of species. The plots allow us to see the direction of effects of both predictor variables, as well as the moderating effect of each predictor variable on the other. The slopes show the effect of climate at a given value of land use, while at any point on the *x*-axis, the direction of the colour gradient indicates the effect of land use; for example, comparing x_1 and x_2 shows how the value of the land-use variable modifies the effect of the climate variable. (A) additive effects, where the effect of land use is constant for all climate values; (B) synergistic interactions, where higher values of the climate variable make the effect of land use stronger, that is, the difference in effect between lower and higher land-use values increases with higher climate values; (C) antagonistic interactions, where higher values of the climate variable make the effect of land use less strong, that is, the difference in effect between lower and higher land-use values decreases with higher climate values; and (D) crossover interactions, where the effect of the climate variable switches sign according to the value of the land-use variable within the climate variable's measured range. In the left panels in A, B and C the effects of climate and land use are both negative, while in the panels to the right, both effects are positive. In the left panel in D, the effect of land use switches from negative to positive, while in the right panel, the effect of land use switches from positive to negative.

(Duncan and Kefford 2021; Spake et al. 2023; Figures 1B and 3B). In this case, we cannot know the effect of one variable (plotted on the x-axis) without also knowing the value of the second variable. Interactive effects can be classed as 'synergistic', 'antagonistic' or 'crossover'. The term 'synergistic' means that the effect of the second variable is stronger at higher values of the first (*x*-axis) variable, that is, the difference in effect between low and high values of the second variable increases along the measured interval of the first variable (Figure 3B). The term 'antagonistic' means that the effect of the second variable is less strong at higher values of the first variable, that is, the difference in effect between low and high values of the second variable decreases along the measured interval of the first variable (Figure 3C). The term 'crossover' means that the effect of the second variable changes from positive to negative (*or vice versa*) within the measured range of the value of the first variable (Figure 3D), changing from antagonistic to synergistic.

Examples of all the above categories of interactions between climate and land-use variables have been detected. An example of a synergistic effect includes the positive effect of climate warming on insect species richness in primary vegetation, with

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

BOX 1 | Glossary of terms.

Additive effect: When the modelled effect of one variable is constant for all values of a second variable (Figures 1A and 3A).

Climate: Climate is defined by the World Meteorological Organisation as the average weather conditions at a specific location over long time periods, ranging from months to millions of years (WMO 2025). Climate change is defined as changes in the state of the climate that persist for an extended period, typically decades or longer, although the standard period used to determine climate change is 30 years (WMO 2025). Given these definitions, climate and climate change can be described and detected over shorter time periods than 30 years, which is common throughout the ecological literature. Here, we use the collective term 'climate variable' to describe variables such as temperature and precipitation while acknowledging that they can be used to describe both weather and climate, depending on the time frame.

Crossover effect: When the modelled effect of one variable on the response 'switches sign' across the measured interval of the other (Figure 3D). This can also be referred to as a 'crossed', 'qualitative' or 'reversal' effect, or as a 'non-removable' interaction. Non-removable refers to the fact that interactions that involve a change of sign (e.g., from positive to negative) are not affected by transformations of the response variable (Spake et al. 2023).

Interaction (linguistic and ecological): The linguistic definition of the word interaction is *reciprocal action*. In the scientific literature, the term has been applied to myriad phenomena, including interactions between individuals or species (species interactions, biotic interactions, trophic and non-trophic interactions, etc.) and the effect of one environmental variable on another, such as the effect of increased frequency of drought events on the degradation of forest habitats.

Interaction (statistical): A statistical interaction is when the effect of one variable depends on the value of another variable (VanderWeele and Knol 2014), that is, the response is *context dependent*. Note that this effect is an interaction between the measured variables, which can be either directly or indirectly related to the ecological mechanisms driving the biodiversity response.

Land cover and land use: Land cover refers to the observed cover of the land, while land use refers to how land is used by humans. These terms are often used interchangeably, with land use tending to be inferred from observed land cover. At the same time, the same broad category of land cover (e.g., agriculture) can have a variety of land uses (e.g., arable vs. pastoral). We consider both to be relevant in terms of interactions with climate variables change, but use the term land use throughout, as it is more common in the ecological literature.

Synergy and antagonism (linguistic and ecological): The linguistic definition of synergy is something that is *mutually reinforcing*, while antagonism is *mutual resistance*. For example, when used to describe *ecological symbiotic interactions*, the words synergy and antagonism can refer to mutualistic and parasitic interactions, respectively. As such, the words are primarily used to describe the *direction* of the interaction, that is, positive or negative effects on an organism's fitness.

Synergistic and antagonistic interactions (statistical): In statistics, the terms synergistic and antagonistic refer to the *strength* of the effect. A synergistic interaction is when higher values of one variable make the effect of the other stronger, *independent of the direction of the effect* (Figure 3B). An antagonistic interaction occurs when higher values of one variable make the effect of the other less strong (Figure 3C). Depending on the direction of effects, synergistic effects have been described as amplifying, magnifying or concordant (used for both positive or negative effects) or as compounding (mostly used for negative effects). Antagonistic effects can be described as opposing, mitigating, buffering or dampening. The words synergistic and antagonistic, as well as their synonyms, have also been used elsewhere to refer to additive effects alone (e.g., 'synergistic' where both effects are positive, even if there is no statistical interaction).

negative effects of agriculture on richness becoming stronger at higher temperatures (Outhwaite et al. 2022). Increases in canopy cover have decreased the effect of warming on community shifts in European forest understorey plant communities (Zellweger et al. 2020), demonstrating an antagonistic interaction. A crossover effect has been shown in stream-breeding amphibians in tropical forests, whose abundance was relatively high in areas of primary vegetation where maximum temperatures were also high, while in agricultural areas, abundances were lowest in sites with the highest maximum temperatures (Murray et al. 2021). Importantly, the synergistic and antagonistic terminology does not refer to the direction of the individual drivers, only to their interactive effect. That is, the difference between the effect of a climate variable on biodiversity at higher compared to lower values of a land-use variable can be larger (synergistic effect, Figure 3B) or smaller (antagonistic effect, Figure 3C), independently of the direction of the individual effects.

Ambiguities in terminology can obscure the interpretation of climate-land-use interactions on biodiversity. Several additional terms have been used to describe additive and interactive effects of climate and land-use change on biodiversity (Box 1). For example, 'compounding effect' has been used to describe a synergistic interaction (Forister et al. 2010; Auffret and Svenning 2022), but linguistically could equally refer to an additive effect. However, it is not only language that can affect our understanding of climate-land-use interactions. Different methodological approaches can influence the detection or strength of interaction effects, including model structure, numerical scaling and

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

potential correlations and transformations of the predictor and response variables. Such statistical matters are well-described elsewhere (Schielzeth 2010; Duncan and Kefford 2021; Spake et al. 2023), but perhaps most importantly for the interpretation and communication of climate-land-use interactions is the so-called symmetrical nature of statistical interactions (Spake et al. 2023). This symmetry means that if the effect of a climate variable is not constant across the measured land-use interval, then also the inverse is true: the effect of the land-use variable will not be constant across the climate interval. Understanding this property of climate-land-use interactions, as well as the different ways in which statistical interactions are described, will help the effective interpretation and communication of research in the field.

3 | Climate-Land-Use Interactions Across Species and Assemblages

3.1 | Variation in Responses Between Species

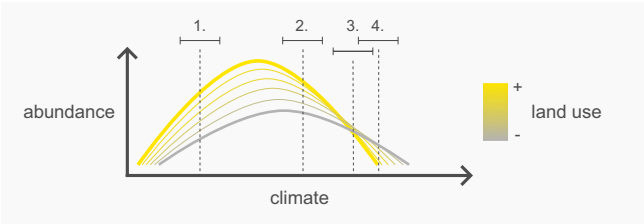
Different species require specific conditions to survive and thrive (Grinnell 1917; Hutchinson 1957). When the environment changes, some species will benefit, some will suffer, and some will be unaffected. As such, studies at the species level show a range of responses to climate variables (Lynn et al. 2021; Antão et al. 2022), land-use variables (Negret et al. 2021) or both (Beissinger et al. 2023; Suggitt et al. 2023), while the results of studies undertaken at the community level (e.g., considering species richness) often show high levels of variation (Blowes et al. 2024; Montràs-Janer et al. 2024). In addition to exhibiting different responses (positive, negative or neutral) to climate and land-use change, different species or organism groups can vary in whether they respond additively or interactively to these drivers (Murray et al. 2021; Latimer and Zuckerberg 2021; Auffret and Svenning 2022; Lauck et al. 2023). For example, occupancy change of plants, butterflies and moths in Great Britain responded additively to climate warming and land conversion at the group level (with persistence positively associated with both variables), while birds showed an antagonistic interaction (the positive effect of one variable becoming less strong at higher values of the other; Suggitt et al. 2023). At the individual species level, the study revealed that there was substantial variation in the direction of responses to climate and land use, and in fact species were found to be just as likely to respond additively as interactively. The mechanisms underlying species-level variation in responses to climate and land use range from physiological tolerance limits of temperature (Moore et al. 2023), to life-history traits associated with vulnerability to environmental change (Hof 2021). For instance, taxa that are more mobile and/or have shorter life spans often respond faster to environmental change (Figueiredo et al. 2019). Further examples of species groups exhibiting different relationships with climate and land use include findings that cup-nesting birds in the United States showed lower nesting success in agricultural areas with highest maximum temperatures compared to those nesting in cavities, potentially due to the former types of nest being more exposed (Lauck et al. 2023). On the other hand, reproductive mode determined the extent to which maximum temperatures and agricultural land uses affected local abundances of tropical amphibian species (Murray et al. 2021). Finally, range shifts in Swedish plant species in response to climate warming were more pronounced in warm than cool-associated generalist species, while grassland specialist species declined regardless of their thermal affinity (Auffret and Svenning 2022).

That species may differ in their responses to the combined pressures of climate and land-use variables is perhaps not surprising. Aggregating individual responses into community-level biodiversity metrics can mask this variation (Cazalis 2022), while synthesising species-level responses across large spatial scales will often produce results that exhibit neither clear positive nor negative effects on the assemblage as a whole. Results based on different metrics, aggregation and scales can generate disagreement among studies (Boënnec et al. 2024) and cause issues when communicating with policymakers. It is therefore important to highlight that among-species variation in responses to climate and land-use variables means that assemblage-level studies might not always show strong directional responses to climate and land-use change.

3.2 | Variation in Responses Within Species

In addition to different species responding differently to land use, climate and their interactions, individuals and populations of the same species can show differential responses across climate and land-use gradients (Figure 4). This can arise when variation in land use modulates local climate, causing species to respond differently to one driver depending on the status of the other (Williams et al. 2022). For example, the level of canopy shading can moderate individual species' responses to climate along altitudinal temperature gradients (Samira Geres et al. 2025), while a change in climate at a single location can alter species' habitat preferences (Davies et al. 2006; Anthes et al. 2008; Box 2).

While populations of a species can respond differently to climate and land-use variables along environmental gradients,



climate range	effect of climate	effect of land use	interactive effect
1.	POSITIVE	POSITIVE	SYNERGISTIC
2.	NEGATIVE	POSITIVE	ANTAGONISTIC
3.	NEGATIVE	POS. NEG.	CROSSOVER
4.	NEGATIVE	NEGATIVE	SYNERGISTIC

FIGURE 4 | Variation in the response of a species across gradients of climate and land use. The climate gradient could for example represent temperature at a single location over time, or different temperatures experienced across a species range. At different values of the climate and land-use variables, a species' interactive response to these two variables can differ (points 1–4). A measured response to climate and land use can therefore depend on which part of the curve is being sampled.

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

BOX 2 | Within-species responses to climate and land use.



The butterfly *Hamearis lucina*. Image from the public domain, licence: CC0 1.0.

The butterfly *Hamearis lucina* was until the early 20th century found in open deciduous woodland in the UK (Frohawk 1934). As traditional management ceased, deciduous woodlands became more densely vegetated, resulting in population declines and local extinction of *H. lucina* and its *Primula* host plants. However, the abandonment and woody encroachment of calcareous grassland resulted in shaded slopes that were suitable for the host plants and the butterfly (Anthes et al. 2008; Turner et al. 2009). As climate warming can accelerate this encroachment (Buitenwerf et al. 2018) and *H. lucina* responds positively to temperature change (Anthes et al. 2008), prevailing land-use changes and climate change could result in increased occupancy and population size (Figure 4, climate range position 1). However, if temperatures continue to increase, more open habitats may become too dry for the host plants, and butterfly populations could be expected to decline. This interaction can be described as antagonistic: the positive effect of openness becomes less strong as temperatures increase (Figure 4, climate range position 2). As the climate continues to warm, ambient temperatures may exceed *H. lucina's* optimum at existing sites, especially in more open areas (Bladon et al. 2020). These habitats would offer fewer cool microclimatic refuges, potentially leading to lower butterfly abundances, while forest-dominated regions that contain more shaded and moist areas could support higher abundances. The interactive effects in this scenario are "crossover", as the effect of openness changes from positive to negative as temperature increases (Figure 4, climate range position 3). In the future, the use of calcareous grasslands may no longer be an option for *H. lucina*, as the species may become restricted to the few forest openings still available locally, and where increasing temperatures and conservation efforts to reduce grassland encroachment could result in greater butterfly declines than would be expected from either change alone (Figure 4, climate range position 4).

many species also exhibit intraspecific trait variation across their geographic ranges, which can influence their responses to environmental change. Characteristics that have been shown to vary along gradients of climate and/or land use include body size (Liker et al. 2008; Henry et al. 2023), the timing of life cycle events (Menzel et al. 2020), thermal tolerance (Howells et al. 2012), reproduction and dispersal ability (Schroeder et al. 2021). These characteristics are directly and indirectly linked to population persistence, and therefore this intraspecific variation could result in different types of climate-land-use interactions depending on where along these gradients a study is being conducted.

To fully understand a species' response to climate-land-use interactions, we would therefore need to study the full range of environmental gradients (e.g., multiple points across the climate variable range in Figure 4), while also understanding the potential role of intraspecific trait and behavioural variation. Any empirical model fitted to data from one place or time is unlikely to capture the full range of species' responses, and will likely lead to contradicting results when compared to other studies of the same species from another place or time. Just as empirical models should never be used to predict responses outside the range of the training data, we must be mindful of the climate and land-use contexts of a specific study when interpreting its findings.

4 | Implications of Data, Metrics and Scale

It is clear that differing responses both between and within species can make it difficult to make general statements about the effects of climate and land use on biodiversity. The choices or availability of both biological and environmental data are also critical. These choices, in addition to the spatial and temporal coverage and resolution of the data being analysed, are another source of variation affecting the quantification of biodiversity change and its attribution to changes in climate and land use.

4.1 | Variation in Biodiversity Metrics

Observations of species can be used to calculate hundreds of metrics aiming to represent biodiversity (Burgess et al. 2024). At the species level, responses to climate and land-use variables

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

are typically determined by changes in abundance (Northrup et al. 2019; Whitehorn et al. 2022; Neff et al. 2022), occupancy (Soroye et al. 2020; Ramesh et al. 2022) or colonisation-extinction dynamics (Howard et al. 2023; Suggitt et al. 2023). These measures can exhibit different responses to the same pressures, including both the detection of change, and any attribution to climate and land use (Uhler et al. 2021). For example, when subject to an environmental change, a species might show a decline in abundance across a number of sites in a study area (a negative response), but a metric related to occupancy might show no change or even a positive response if there are few or no local extinctions, and/or small populations establish in new locations.

There are also many metrics that can be used to describe ecological assemblages. Species richness, despite an ongoing debate over its utility (Valdez et al. 2023), is still among the most common ways to measure biodiversity and estimate the effects of climate and land-use change (Antão et al. 2020; Keck et al. 2025). A more powerful approach to attribute biodiversity change to climate, land use and their interactions is to use metrics that focus on species' traits (e.g., habitat specialists; Warren et al. 2021; Neff et al. 2022) or are related to the environmental pressures being investigated (e.g., the relative abundances of warm- and cold-adapted species; Fadrique et al. 2018; Zellweger et al. 2020). In cases where classical measures such as species richness and total abundance show no directional trend, analysing such group-wise responses will increase our understanding of the types of species that are more likely to be negatively affected by climate-land-use interactions (Sweeney and Jarzyna 2022).

4.2 | Variation in Research Data: 'State' and 'Flux'

One major way in which analysed data might affect how climate and land-use variables are found to affect biodiversity is related to the spatio-temporal scale of the data being used to explain biodiversity change. Climate, land-use and biodiversity variables can be categorised in terms of what we refer to as 'state' and 'flux'. 'State' refers to a measured value at a particular point in time (or averaging period), while 'flux' describes changes in variables over a particular time period (quantified for example in absolute or percentage terms). For example, space-for-time substitution analyses relate climate and land-use variables to biodiversity data at one point in time across an environmental gradient (i.e., using spatial gradients as proxies for temporal trends; Peters et al. 2019; Ganuza et al. 2022; McKeon et al. 2023). In such cases, it is the 'state' of climate and land use that are analysed. Alternatively, sourcing biodiversity and environmental data from a specific location (or set of locations) over time allows researchers to examine temporal trends explicitly, that is, examining the effect of 'flux' in both climate and land use (Marta et al. 2021; Neff et al. 2022; Montràs-Janer et al. 2024).

It is also common for a combination of state and flux variables to be analysed within a single study. For example, when historical land-use data are unavailable, temporal biodiversity responses (flux) to climate change (flux) can be compared across areas with contrasting land use (state; Fourcade et al. 2021; Comte et al. 2021; Nowakowski et al. 2023). Other variations include assessing biodiversity (state) response to past climate change (flux) across a space-for-time gradient of land use (state; Outhwaite et al. 2022), while both past and contemporary climate and land-use data (both state and flux) have been used to explain present patterns of biodiversity (state; Haddou et al. 2022). While all of the above approaches can be valid, care must be taken in the interpretation and communication of climate-land-use interactions arising from studies that use differing combinations of state and flux. For example, observed differences in the estimated effect of habitat destruction (flux) between two or more climatic regions (state) may not be comparable to observed differences in the estimated effect of habitat destruction (flux) between two or more regions experiencing different rates of climate change (flux; Lovell et al. 2023).

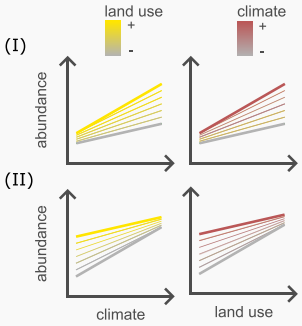
4.3 | The Effect of Temporal Resolution and Spatial Scale

The values of both climate and land-use variables, and their modelled effects on biodiversity will depend on the length of time and the spatial grain over which those data have been collected. This is especially critical for climate variables, which can represent for example minimum, maximum, or mean values for different times of the year, or metrics aiming to quantify extreme events (Suggitt et al. 2017). When studying flux in climate variables, that is, climate *change*, it is good practice to use long data series (decades) and to clearly state the time period used to assess the trends. When measuring state, values from each location on the gradient should represent averages of values collected over long time periods. For meaningful climate-land-use interactions to be detected, studies should ideally span large enough gradients in the chosen climate and land-use variables (Box 2; Müller et al. 2015). However, long-term and large-scale historical land-use data are rarely available digitally, while difficulties in predicting future land use mean that it is rarely included in projections of climate-driven species distribution shifts (Frans and Liu 2024).

Spatial resolution of both biological and environmental data can introduce further variation in detected outcomes. For example, species-area relationships are non-linear, and coarser spatial resolutions make the threshold for local extinction higher, and the threshold for colonisation lower (Kuczynski et al. 2023). This makes comparison or synthesis of results difficult when studies aggregate data at a range of scales, from local field sites (Zellweger et al. 2020), through grid squares (Marta et al. 2021; Suggitt et al. 2023), to counties and regions (Neff et al. 2022). In terms of climate, species and communities respond strongly to local microclimatic variables, reflecting the conditions that organisms directly experience over their lifespans (Zellweger et al. 2020; Maclean and Early 2023; König et al. 2024). One example where differences in the spatial scale of climate variables can affect the detection of interactions is related to the effects of temperature and canopy cover on cold-adapted species (Figure 2). For land use, measured variables become more similar at larger spatial scales (at least within bioregions and ecoregions; Turner et al. 1989), which potentially affects the strength of any relationship with biodiversity and can reduce the gradient being studied, with implications for the detection of interactions.

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

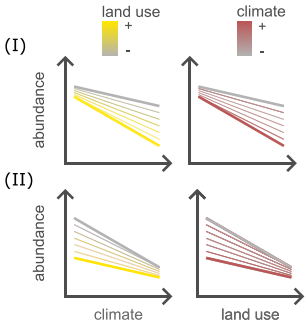
(A) Direction of effects. climate: **POSITIVE**, land use: **POSITIVE**



Example. The wall bedstraw *Galium parisiense* is a plant that is found on disturbed ground (positive effect of land-use change) and whose expansion in Britain could be related to climate warming (positive effect of climate change). A synergistic interaction (I) would entail that disturbances are increasing the rate of climate-related colonisations. An antagonistic interaction (II) could occur if this competition-sensitive species was unable to fill its potential in warm, disturbed habitats due to the arrival of other, more competitive species.

Implications. Species responding well to both climate and land-use change are not usually considered in terms of conservation actions, but synergistic responses (I) could mean that non-native or even native species become unexpectedly successful, to the detriment of more sensitive species.

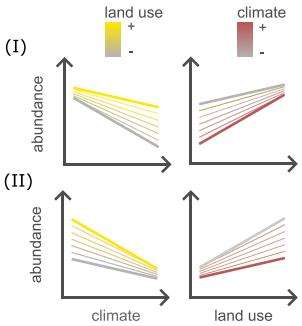
(B) Direction of effects. climate: **NEGATIVE**, land use: **NEGATIVE**



Example. The capercaillie *Tetrao urogallus* is a forest specialist bird species (negative effect of land-use change) that has exhibited lower breeding success in Britain, believed to be linked to a mismatch between egg laying dates and changes in spring phenology of food plants and insect larvae (negative effect of climate change). If the climate-associated population declines were stronger in areas with declining forest cover, it would indicate a synergistic effect (I). That the negative effect of climate change would be stronger in undisturbed habitats (II), resulting in an antagonistic effect, is not a likely scenario for this species.

Implications. Ongoing climate change means that effects of area-based conservation are unlikely to be enough to halt population declines. Antagonistic effects (II) may give extra (but not unlimited) time to implement conservation and policy actions.

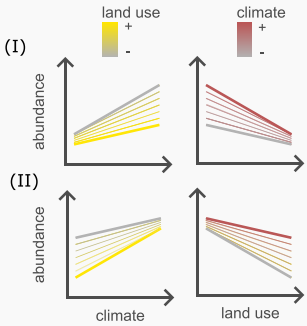
(C) Direction of effects. climate: **NEGATIVE**, land use: **POSITIVE**



Example. The large white *Pieris brassicae* is a generalist butterfly, successful in agricultural and urban landscapes (positive effect of land-use change), but sensitive to increased frequency and magnitude of drought (negative effect of climate change). If the negative effect of drought was less severe in areas with more gardens and allotments (high urbanization; I), this would indicate a synergistic effect of human land use and climate change. On the other hand, if the effects of drought were especially strong in urban landscapes (II), then this would be evidence of an antagonistic effect.

Implications. For common species that respond negatively to climate change and positively to land-use change, synergistic effects (I) where the effect of climate change is stronger in less-disturbed habitats, can result in unexpectedly strong declines at regional levels.

(D) Direction of effects. climate: **POSITIVE**, land use: **NEGATIVE**



Example. The hazel dormouse *Muscardinus avellanarius* has its northern range margin in Britain, and is associated with traditionally-managed semi-open woodland which are in decline (negative effect of land-use change). Increasing population trends have been linked to increasing spring to autumn temperatures (positive effect of climate change). Synergistic effects (I) could arise if the positive effects of climate warming were higher in traditionally-managed habitats. Antagonistic effects (II) could arise if the warming climate allowed populations to persist in unsuitable habitats.

Implications. For species that respond positively to climate change but negatively to land-use change, synergistic effects (I) mean that climate warming would increase the positive effects of habitat restoration, but the positive effects of previous actions could be overestimated if the effect of climate is not considered. Antagonistic effects (II) would mean that habitat restoration might not have as strong an impact as expected.

FIGURE 5 | Climate-land-use interactions and their consequences for conservation. We show eight potential responses to climate (red) and land-use change (yellow) that could be generated by a statistical model: Positive or negative response to climate × positive or negative response to land use × interactive effects, divided into four panels (A–D). Each section has four sub-panels showing example interaction plots (synergistic: Where the effect of land-use change is stronger at higher values of climate change; or antagonistic: Where the effect of land-use change is less strong at high values of climate change). Sub-panels for each scenario (I or II) plot the effect of both climate and land use moderated by the other variable, illustrating the symmetrical nature of interactions. In (C and D), this shows how the same model can produce results that can be described as either synergistic or antagonistic, depending on the driver plotted on the x-axis. We then give an example of a species shown to exhibit specific responses to climate and land use, and the implications of statistical interactions for both that species and conservation in general. References for examples: (A) Stroh et al. (2023); (B) Moss et al. (2001) and Balmer et al. (2014); (C) Oliver et al. (2015) (D) Goodwin et al. (2018) and Crawley et al. (2020).

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

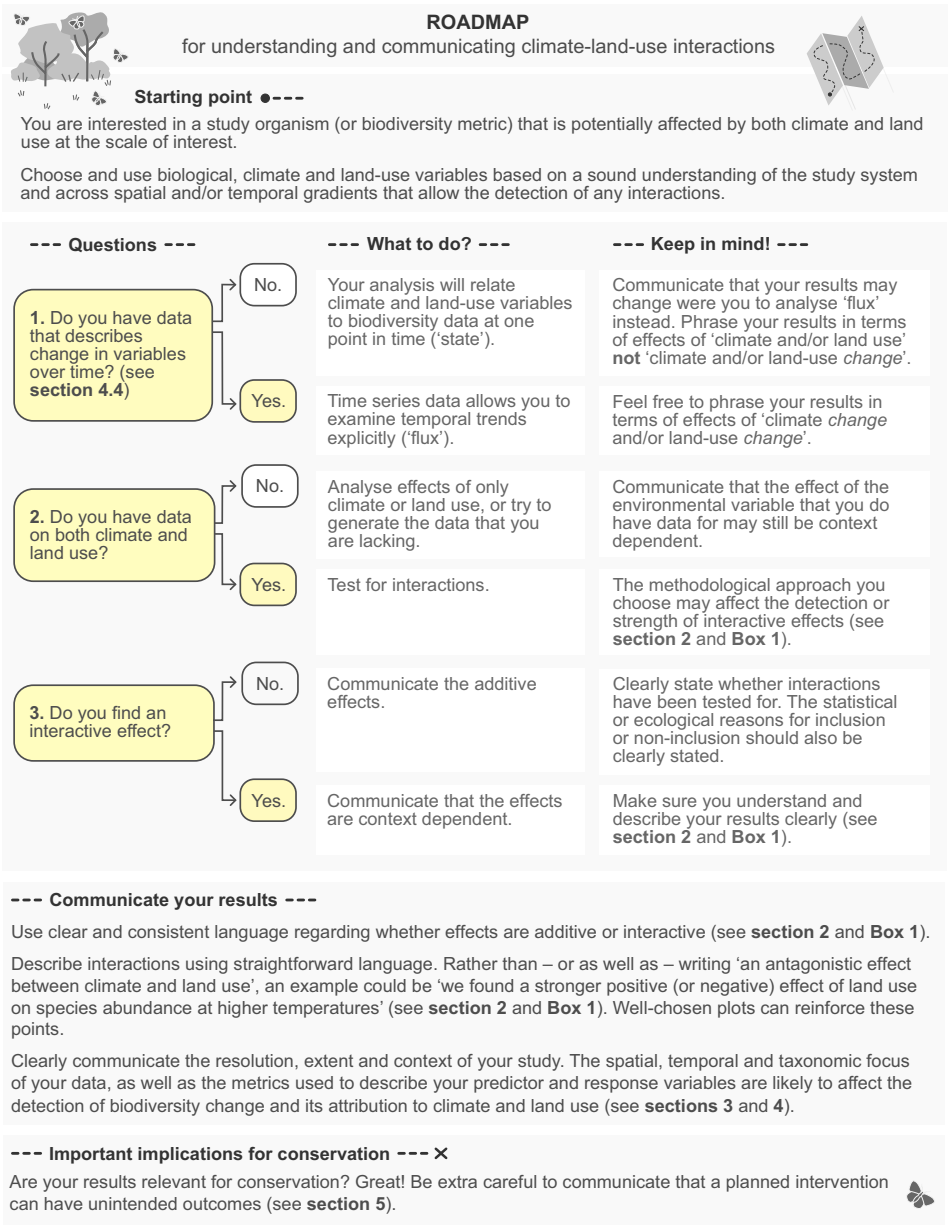


FIGURE 6 | A roadmap for understanding and communicating climate-land-use interactions. The roadmap guides researchers from study design and data selection, via testing for statistical interactions, to the clear communication of additive or interactive effects. Key decisions, methodological considerations, and potential sources of misinterpretation are highlighted at each step.

5 | Importance of Climate-Land-Use Interactions for Conservation

The potential confusion caused by the multitude of biological and environmental variables that could be included in an analysis could make it tempting not to look for statistical interactions at all, as this would produce simpler messages for conservationists, land managers and policymakers (Côté et al. 2016). However, there are risks associated with failing to detect these interactions, because if present, they mean that we cannot predict the effect of one driver without knowing the value of the other. This can have real-world consequences for biodiversity conservation and policy (Figure 5) because it would mean that future projections of species distributions could be incorrect, and that subsequent conservation actions are insufficient, unsuitable, or even maladaptive or detrimental.

Failing to detect synergistic interactions means that we would underestimate the effect of overall environmental change on a species or community. This can mean that the situation could be worse than expected, and that stronger actions are likely needed to conserve current levels of biodiversity. For example, forecasts of mammal species' responses to environmental change in southeast Asia show that the negative effect of predicted oil palm expansion is expected to be stronger at higher compared to lower scenarios of climate warming (Brodie 2016). Synergistic interactions between climate and land-use changes will often mean that efforts to conserve populations need to look beyond the protection and restoration of habitat to also facilitate species' adaptation to climate change. Where conservation actions are in place, synergistic interactions can also result in an overestimation of the effect of the action. A species' positive response to habitat restoration could be enhanced (including a switch from

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

negligible to positive effects) by climate change, which if undetected could mean that the intervention is not transferable to areas with differing climatic conditions.

Antagonistic interactions can also result in under- and overestimation of change that can be damaging for conservation. Most strikingly, climate change could mean that land-based conservation actions are less (or in-) effective at preserving biodiversity (Müller et al. 2015; Riddell et al. 2021). Butterflies associated with open and semi-open habitats are expected to benefit from grassland conservation and restoration, while high-intensity management can reduce positive effects if the vegetation becomes too short to effectively buffer adverse extreme temperatures (Rytteri et al. 2021; Jones et al. 2024). As temperatures increase, this antagonistic interaction could potentially crossover to a synergistic negative effect of management, whereby targeted management of hotter/drier habitats could ultimately become detrimental to extant butterfly populations (see also Box 2).

6 | A Roadmap for Understanding and Communicating Climate-Land-Use Interactions

Studying biodiversity in a rapidly changing world is not an easy task (Boënnec et al. 2024). Although climate-land-use interactions have been shown to exacerbate biodiversity losses in particular taxa or regional contexts, there is as yet no emerging consensus on how they affect overall levels of biodiversity. Here, our aim was to describe climate-land-use interactions in a digestible way, and to explain how and why studies that may appear similar in their design can generate widely divergent results. As we have highlighted above, variation in species' responses to environmental change, in combination with data availability and specific research aims and methods, will result in a near-infinite number of ways that the same broad question can be addressed and analysed. Rather than providing detailed instructions on how to model interactions, we therefore offer a roadmap for understanding and communicating climate-land-use interactions (Figure 6). In doing so, we hope to encourage a wider acceptance of the inherent complexity in studying, analysing and interpreting interactive effects of climate and land use. We emphasise that clear communication of methods and results, together with a sound understanding of context-dependence, are critical for reaching consensus in this rapidly growing research field. Our roadmap provides a guide to alleviate some of the difficulties that researchers, practitioners and policymakers face when tasked to understand differences in results caused by this inherent variation and context-dependence. Most importantly, we stress that failing to understand and detect climate-land-use interactions may prove detrimental to the species we are trying to conserve. As this field continues to develop, we hope that a better understanding of the effects of climate and land use on biodiversity will generate conservation-relevant knowledge that will ultimately help to bend the curve of biodiversity loss.

Acknowledgements

Many thanks to the Oscar and Lili Lamm Memorial Foundation for their help in forming this working group. Grants from the Swedish Research Councils Formas (Grants 2023-00435 to A.G.A. and M.A.; 2023-02457 to A.G.A., R.C., B.M. and A.J.S.; 2023-01658 to H.N. and A.G.A.) and VR (2020-04276 to A.G.A., B.M. and A.J.S.) supported this study. A.J.S. and T.N. are funded by the UKRI Natural Environment Research Council (UKRI1262). L.H.A. acknowledges funding from the Research Council of Finland (grants 340280 and 361416/372215). C.L.O. was supported by funding from Research England and by UK Natural Environment Research Council grant NE/V006533/1; C.G. was funded by the Bavarian Ministry of Science and Arts grant to Bavarian Climate Research Network (bayklif), project LandKlif. Many thanks to two anonymous reviewers for their helpful comments and feedback.

Funding

This work was supported by Svenska Forskningsrådet Formas, 2023-00435, 2023-02457, 2023-01658. Vetenskapsrådet, 2020-04276. UK Research and Innovation, UKRI1262. Academy of Finland, 340280, 361416/372215. Natural Environment Research Council, NE/V006533/1. Bayerisches Staatsministerium für Wissenschaft und Kunst, LandKlif.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

References

Antão, L. H., A. E. Bates, S. A. Blowes, et al. 2020. "Temperature-Related Biodiversity Change Across Temperate Marine and Terrestrial Systems." *Nature Ecology & Evolution* 4: 927–933.

Antão, L. H., B. Weigel, G. Strona, et al. 2022. "Climate Change Reshuffles Northern Species Within Their Niches." *Nature Climate Change* 12: 587–592.

Anthes, N., T. Fartmann, and G. Hermann. 2008. "The Duke of Burgundy Butterfly and Its Dukedom: Larval Niche Variation in Hamearis Lucina Across Central Europe." *Journal of Insect Conservation* 12: 3–14.

Auffret, A. G., and J.-C. Svenning. 2022. "Climate Warming Has Compounded Plant Responses to Habitat Conversion in Northern Europe." *Nature Communications* 13: 7818.

Balmer, D., S. Gillings, B. Caffrey, B. Swann, I. Downie, and R. Fuller. 2014. *Bird Atlas 2007–11: The Breeding and Wintering Birds of Britain and Ireland*. HarperCollins UK.

Beissinger, S. R., S. A. MacLean, K. J. Iknayan, and P. de Valpine. 2023. "Concordant and Opposing Effects of Climate and Land-Use Change on Avian Assemblages in California's Most Transformed Landscapes." *Science Advances* 9: eabn0250.

Bladon, A. J., M. Lewis, E. K. Bladon, et al. 2020. "How Butterflies Keep Their Cool: Physical and Ecological Traits Influence Thermoregulatory Ability and Population Trends." *Journal of Animal Ecology* 89: 2440–2450.

Blowes, S. A., B. McGill, V. Brambilla, et al. 2024. "Synthesis Reveals Approximately Balanced Biotic Differentiation and Homogenization." *Science Advances* 10: eadj9395.

Boënnec, M., V. Dakos, and V. Devictor. 2024. "Sources of Confusion in Global Biodiversity Trends." *Oikos* 2024: e10732.

Boyd, R. J., G. D. Powney, and O. L. Pescott. 2023. "We Need to Talk About Nonprobability Samples." *Trends in Ecology & Evolution* 38: 521–531.

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Brodie, J. F. 2016. "Synergistic Effects of Climate Change and Agricultural Land Use on Mammals." *Frontiers in Ecology and the Environment* 14: 20–26.

Buitenwerf, R., B. Sandel, S. Normand, A. Mimet, and J.-C. Svenning. 2018. "Land Surface Greening Suggests Vigorous Woody Regrowth Throughout European Semi-Natural Vegetation." *Global Change Biology* 24: 5789–5801.

Burgess, B. J., D. Purves, G. Mace, and D. J. Murrell. 2021. "Classifying Ecosystem Stressor Interactions: Theory Highlights the Data Limitations of the Additive Null Model and the Difficulty in Revealing Ecological Surprises." *Global Change Biology* 27: 3052–3065.

Burgess, N. D., N. Ali, J. Bedford, et al. 2024. "Global Metrics for Terrestrial Biodiversity." *Annual Review of Environment and Resources* 49: 673–709.

Cazalis, V. 2022. "Species Richness Response to Human Pressure Hides Important Assemblage Transformations." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2107361119.

Chase, J. M., S. A. Blowes, T. M. Knight, K. Gerstner, and F. May. 2020. "Ecosystem Decay Exacerbates Biodiversity Loss With Habitat Loss." *Nature* 584: 238–243.

Comte, L., J. D. Olden, P. A. Tedesco, A. Ruhi, and X. Giam. 2021. "Climate and Land-Use Changes Interact to Drive Long-Term Reorganization of Riverine Fish Communities Globally." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2011639118.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. "Interactions Among Ecosystem Stressors and Their Importance in Conservation." *Proceedings of the Royal Society B: Biological Sciences* 283: 20152592.

Crawley, D., F. Coomber, L. Kubasiewicz, et al. 2020. *Atlas of the Mammals of Great Britain and Northern Ireland*. Pelagic Publishing Ltd.

Dale, V. H. 1997. "The Relationship Between Land-Use Change and Climate Change." *Ecological Applications* 7: 753–769.

Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. "Changing Habitat Associations of a Thermally Constrained Species, the Silver-Spotted Skipper Butterfly, in Response to Climate Warming." *Journal of Animal Ecology* 75: 247–256.

de Chazal, J., and M. D. A. Rounsevell. 2009. "Land-Use and Climate Change Within Assessments of Biodiversity Change: A Review." *Global Environmental Change* 19: 306–315.

Dornelas, M., L. H. Antão, A. E. Bates, et al. 2025. "BioTIME 2.0: Expanding and Improving a Database of Biodiversity Time Series." *Global Ecology and Biogeography* 34: e70003.

Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. "The Imprint of the Geographical, Evolutionary and Ecological Context on Species–Area Relationships." *Ecology Letters* 9: 215–227.

Duncan, R. P., and B. J. Kefford. 2021. "Interactions in Statistical Models: Three Things to Know." *Methods in Ecology and Evolution* 12: 2287–2297.

Fadrique, B., S. Báez, Á. Duque, et al. 2018. "Widespread but Heterogeneous Responses of Andean Forests to Climate Change." *Nature* 564: 207–212.

Fahrig, L. 2013. "Rethinking Patch Size and Isolation Effects: The Habitat Amount Hypothesis." *Journal of Biogeography* 40: 1649–1663.

Figueiredo, L., J. Krauss, I. Steffan-Dewenter, and J. Sarmento Cabral. 2019. "Understanding Extinction Debts: Spatio–Temporal Scales, Mechanisms and a Roadmap for Future Research." *Ecography* 42: 1973–1990.

Forister, M. L., Z. Gompert, C. C. Nice, G. W. Forister, and J. A. Fordyce. 2010. "Ant Association Facilitates the Evolution of Diet Breadth in a Lycaenid Butterfly." *Proceedings of the Royal Society B: Biological Sciences* 278: 1539–1547.

Fourcade, Y., M. F. WallisDeVries, M. Kuussaari, C. A. M. van Swaay, J. Heliölä, and E. Öckinger. 2021. "Habitat Amount and Distribution Modify Community Dynamics Under Climate Change." *Ecology Letters* 24: 950–957.

Frans, V. F., and J. Liu. 2024. "Gaps and Opportunities in Modelling Human Influence on Species Distributions in the Anthropocene." *Nature Ecology & Evolution* 8: 1365–1377.

Frohawk, F. W. 1934. *The Complete Book of British Butterflies*. Ward, Lock & Co.

Ganuza, C., S. Redlich, J. Uhler, et al. 2022. "Interactive Effects of Climate and Land Use on Pollinator Diversity Differ Among Taxa and Scales." *Science Advances* 8: eabm9359.

Goodwin, C. E. D., A. J. Suggitt, J. Bennie, et al. 2018. "Climate, Landscape, Habitat, and Woodland Management Associations With Hazel Dormouse *Muscardinus avellanarius* Population Status." *Mammal Review* 48: 209–223.

Greiser, C., J. Ehrlén, E. Meineri, and K. Hylander. 2020. "Hiding From the Climate: Characterizing Microrefugia for Boreal Forest Understory Species." *Global Change Biology* 26: 471–483.

Grinnell, J. 1917. "The Niche-Relationships of the California Thrasher." *Auk* 34: 427–433.

Haddou, Y., R. Mancy, J. Matthiopoulos, S. Spatharis, and D. M. Dominoni. 2022. "Widespread Extinction Debts and Colonization Credits in United States Breeding Bird Communities." *Nature Ecology & Evolution* 6: 324–331.

Henry, E., L. Santini, M. A. J. Huijbregts, and A. Benítez-López. 2023. "Unveiling the Environmental Drivers of Intraspecific Body Size Variation in Terrestrial Vertebrates." *Global Ecology and Biogeography* 32: 267–280.

Hof, C. 2021. "Towards More Integration of Physiology, Dispersal and Land-Use Change to Understand the Responses of Species to Climate Change." *Journal of Experimental Biology* 224: jeb238352.

Howard, C., E.-L. Marjakangas, A. Morán-Ordóñez, et al. 2023. "Local Colonisations and Extinctions of European Birds Are Poorly Explained by Changes in Climate Suitability." *Nature Communications* 14: 4304.

Howells, E. J., V. H. Beltran, N. W. Larsen, L. K. Bay, B. L. Willis, and M. J. H. van Oppen. 2012. "Coral Thermal Tolerance Shaped by Local Adaptation of Photosymbionts." *Nature Climate Change* 2: 116–120.

Hudson, L. N., T. Newbold, S. Contu, et al. 2017. "The Database of the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) Project." *Ecology and Evolution* 7: 145–188.

Hutchinson, G. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.

IPBES. 2019. *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by E. S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo. IPBES secretariat.

Johansson, V., O. Kindvall, J. Askling, and M. Franzén. 2020. "Extreme Weather Affects Colonization–Extinction Dynamics and the Persistence of a Threatened Butterfly." *Journal of Applied Ecology* 57: 1068–1077.

Jones, R., R. Wilson, I. Maclean, and N. Bourn. 2024. "Habitat Management Interventions for a Specialist Mid- Successional Grassland Butterfly, the Lulworth Skipper." *Journal of Insect Conservation* 29: 2.

Keck, F., T. Peller, R. Alther, et al. 2025. "The Global Human Impact on Biodiversity." *Nature* 641: 395–400.

14668238, 2026, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

König, S., J. Krauss, A. Classen, et al. 2024. "Micro- and Macroclimate Interactively Shape Diversity, Niches and Traits of Orthoptera Communities Along Elevational Gradients." *Diversity and Distributions* 30: e13810.

Kuczynski, L., V. J. Ontiveros, and H. Hillebrand. 2023. "Biodiversity Time Series Are Biased Towards Increasing Species Richness in Changing Environments." *Nature Ecology & Evolution* 7: 994–1001.

Latimer, C. E., and B. Zuckerberg. 2021. "Habitat Loss and Thermal Tolerances Influence the Sensitivity of Resident Bird Populations to Winter Weather at Regional Scales." *Journal of Animal Ecology* 90: 317–329.

Lauck, K. S., A. Ke, E. M. Olimpi, et al. 2023. "Agriculture and Hot Temperatures Interactively Erode the Nest Success of Habitat Generalist Birds Across the United States." *Science* 382: 290–294.

Liker, A., Z. Papp, V. Bókony, and Á. Z. Lendvai. 2008. "Lean Birds in the City: Body Size and Condition of House Sparrows Along the Urbanization Gradient." *Journal of Animal Ecology* 77: 789–795.

Lovell, R. S. L., S. Collins, S. H. Martin, A. L. Pigot, and A. B. Phillimore. 2023. "Space-For-Time Substitutions in Climate Change Ecology and Evolution." *Biological Reviews* 98: 2243–2270.

Lynn, J. S., K. Klanderud, R. J. Telford, D. E. Goldberg, and V. Vandvik. 2021. "Macroecological Context Predicts Species' Responses to Climate Warming." *Global Change Biology* 27: 2088–2101.

Maclean, I. M. D., and R. Early. 2023. "Macroclimate Data Overestimate Range Shifts of Plants in Response to Climate Change." *Nature Climate Change* 13: 484–490.

Marta, S., M. Brunetti, R. Manenti, A. Provenzale, and G. F. Ficetola. 2021. "Climate and Land-Use Changes Drive Biodiversity Turnover in Arthropod Assemblages Over 150 Years." *Nature Ecology & Evolution* 5: 1291–1300.

McKeon, C. M., R. Kelly, L. Börger, A. De Palma, and Y. M. Buckley. 2023. "Human Land Use Is Comparable to Climate as a Driver of Global Plant Occurrence and Abundance Across Life Forms." *Global Ecology and Biogeography* 32: 1618–1631.

Menzel, A., Y. Yuan, M. Matiu, et al. 2020. "Climate Change Fingerprints in Recent European Plant Phenology." *Global Change Biology* 26: 2599–2612.

Montràs-Janer, T., A. J. Suggitt, R. Fox, et al. 2024. "Anthropogenic Climate and Land-Use Change Drive Short- and Long-Term Biodiversity Shifts Across Taxa." *Nature Ecology & Evolution* 8: 739–751.

Moore, N. A., I. Morales-Castilla, A. L. Hargreaves, et al. 2023. "Temperate Species Underfill Their Tropical Thermal Potentials on Land." *Nature Ecology & Evolution* 7: 1993–2003.

Moss, R., J. Oswald, and D. Baines. 2001. "Climate Change and Breeding Success: Decline of the Capercaillie in Scotland." *Journal of Animal Ecology* 70: 47–61.

Müller, J., H. Brustel, A. Brin, et al. 2015. "Increasing Temperature May Compensate for Lower Amounts of Dead Wood in Driving Richness of Saproxylic Beetles." *Ecography* 38: 499–509.

Murray, A. H., A. J. Nowakowski, and L. O. Frishkoff. 2021. "Climate and Land-Use Change Severity Alter Trait-Based Responses to Habitat Conversion." *Global Ecology and Biogeography* 30: 598–610.

Neff, F., F. Korner-Nievergelt, E. Rey, et al. 2022. "Different Roles of Concurring Climate and Regional Land-Use Changes in Past 40 Years' Insect Trends." *Nature Communications* 13: 7611.

Negret, P. J., M. Maron, R. A. Fuller, H. P. Possingham, J. E. M. Watson, and J. S. Simmonds. 2021. "Deforestation and Bird Habitat Loss in Colombia." *Biological Conservation* 257: 109044.

Newbold, T., L. N. Hudson, S. L. L. Hill, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520: 45–50.

Northrup, J. M., J. W. Rivers, Z. Yang, and M. G. Betts. 2019. "Synergistic Effects of Climate and Land-Use Change Influence Broad-Scale Avian Population Declines." *Global Change Biology* 25: 1561–1575.

Nowakowski, A. J., J. I. Watling, A. Murray, et al. 2023. "Protected Areas Slow Declines Unevenly Across the Tetrapod Tree of Life." *Nature* 622: 101–106.

Oliver, T. H., H. H. Marshall, M. D. Morecroft, T. Brereton, C. Prudhomme, and C. Huntingford. 2015. "Interacting Effects of Climate Change and Habitat Fragmentation on Drought-Sensitive Butterflies." *Nature Climate Change* 5: 941–945.

Oliver, T. H., and M. D. Morecroft. 2014. "Interactions Between Climate Change and Land Use Change on Biodiversity: Attribution Problems, Risks, and Opportunities." *WIREs Climate Change* 5: 317–335.

Orr, J. A., R. D. Vinebrooke, M. C. Jackson, et al. 2020. "Towards a Unified Study of Multiple Stressors: Divisions and Common Goals Across Research Disciplines." *Proceedings of the Royal Society B: Biological Sciences* 287: 1926.

Outhwaite, C. L., P. McCann, and T. Newbold. 2022. "Agriculture and Climate Change Are Reshaping Insect Biodiversity Worldwide." *Nature* 605: 97–102.

Peters, M. K., A. Hemp, T. Appelhans, et al. 2019. "Climate–Land-Use Interactions Shape Tropical Mountain Biodiversity and Ecosystem Functions." *Nature* 568: 88–92.

Piggott, J. J., C. R. Townsend, and C. D. Matthaei. 2015. "Reconceptualizing Synergism and Antagonism Among Multiple Stressors." *Ecology and Evolution* 5: 1538–1547.

Ramesh, V., P. R. Gupte, M. W. Tingley, V. V. Robin, and R. DeFries. 2022. "Using Citizen Science to Parse Climatic and Land Cover Influences on Bird Occupancy in a Tropical Biodiversity Hotspot." *Ecography* 2022: e06075.

Riddell, E. A., K. J. Iknayan, L. Hargrove, et al. 2021. "Exposure to Climate Change Drives Stability or Collapse of Desert Mammal and Bird Communities." *Science* 371: 633–636.

Rytteri, S., M. Kuussaari, and M. Saastamoinen. 2021. "Microclimatic Variability Buffers Butterfly Populations Against Increased Mortality Caused by Phenological Asynchrony Between Larvae and Their Host Plants." *Oikos* 130: 753–765.

Samira Geres, L., N. Blüthgen, J. Müller, L. Seifert, S. Seibold, and C. Bässler. 2025. "To the Top or Into the Dark? Relationships Between Elevational and Canopy Cover Distribution Shifts in Mountain Forests." *Ecography* 2025: e07449.

Schielzeth, H. 2010. "Simple Means to Improve the Interpretability of Regression Coefficients." *Methods in Ecology and Evolution* 1: 103–113.

Schroeder, H., H. Grab, A. Kessler, and K. Poveda. 2021. "Human-Mediated Land Use Change Drives Intraspecific Plant Trait Variation." *Frontiers in Plant Science* 11: 592881.

Schulte to Bühne, H., J. A. Tobias, S. M. Durant, and N. Pettorelli. 2021. "Improving Predictions of Climate Change–Land Use Change Interactions." *Trends in Ecology & Evolution* 36: 29–38.

Soroye, P., T. Newbold, and J. Kerr. 2020. "Climate Change Contributes to Widespread Declines Among Bumble Bees Across Continents." *Science* 367: 685–688.

Spake, R., D. E. Bowler, C. T. Callaghan, et al. 2023. "Understanding 'It Depends' in Ecology: A Guide to Hypothesising, Visualising and Interpreting Statistical Interactions." *Biological Reviews of the Cambridge Philosophical Society* 98: 983–1002.

Spooner, F. E. B., R. G. Pearson, and R. Freeman. 2018. "Rapid Warming Is Associated With Population Decline Among Terrestrial Birds and Mammals Globally." *Global Change Biology* 24: 4521–4531.

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Stroh, P. A., K. J. Walker, T. A. Humphrey, O. L. Pescott, and R. J. Burkmar. 2023. *Plant Atlas 2020: Mapping Changes in the Distribution of the British and Irish Flora*. Princeton University Press.

Suggitt, A. J., P. J. Platts, I. M. Barata, et al. 2017. "Conducting Robust Ecological Analyses With Climate Data." *Oikos* 126: 1533–1541.

Suggitt, A. J., C. J. Wheatley, P. Aucott, et al. 2023. "Linking Climate Warming and Land Conversion to Species' Range Changes Across Great Britain." *Nature Communications* 14: 6759.

Sweeney, C. P., and M. A. Jarzyna. 2022. "Assessing the Synergistic Effects of Land Use and Climate Change on Terrestrial Biodiversity: Are Generalists Always the Winners?" *Current Landscape Ecology Reports* 7: 41–48.

Turner, E. C., H. M. V. Granroth, H. R. Johnson, et al. 2009. "Habitat Preference and Dispersal of the Duke of Burgundy Butterfly (Hamearis Lucina) on an Abandoned Chalk Quarry in Bedfordshire, UK." *Journal of Insect Conservation* 13: 475–486.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne. 1989. "Effects of Changing Spatial Scale on the Analysis of Landscape Pattern." *Landscape Ecology* 3: 153–162.

Uhler, J., S. Redlich, J. Zhang, et al. 2021. "Relationship of Insect Biomass and Richness With Land Use Along a Climate Gradient." *Nature Communications* 12: 5946.

Valdez, J. W., C. T. Callaghan, J. Junker, A. Purvis, S. L. L. Hill, and H. M. Pereira. 2023. "The Undetectability of Global Biodiversity Trends Using Local Species Richness." *Ecography* 2023: e06604.

VanderWeele, T. J., and M. J. Knol. 2014. "A Tutorial on Interaction." *Epidemiological Methods* 3: 33–72.

Warren, M. S., D. Maes, C. A. M. van Swaay, et al. 2021. "The Decline of Butterflies in Europe: Problems, Significance, and Possible Solutions." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2002551117.

Whitehorn, P. R., B. Seo, R. F. Comont, M. Rounsevell, and C. Brown. 2022. "The Effects of Climate and Land Use on British Bumblebees: Findings From a Decade of Citizen-Science Observations." *Journal of Applied Ecology* 59: 1837–1851.

Williams, J. J., R. Freeman, F. Spooner, and T. Newbold. 2022. "Vertebrate Population Trends Are Influenced by Interactions Between Land Use, Climatic Position, Habitat Loss and Climate Change." *Global Change Biology* 28: 797–815.

WMO. 2025. *Climate*. World Meteorological Organization. https://wmo.int/topics/climate.

WWF. 2024. *Living Planet Report 2024—A System in Peril*. WWF.

Zellweger, F., P. De Frenne, J. Lenoir, et al. 2020. "Forest Microclimate Dynamics Drive Plant Responses to Warming." *Science* 368: 772–775.

14668238, 2026, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70322 by UK Centre For Ecology & Hydrology, Wiley Online Library on [06/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License