

Highlights

- Context-dependency in species responses to habitat change can be explained by processes occurring at macroecological scales, such as distance to geographic range edges, climatic suitability, and evolutionary history of disturbance events.
- Further exploring how multiple stressors at different scales interact will lead to a better understanding of the strength and direction of anthropogenic impacts on biodiversity.
- In the same way that edge effects impact biodiversity in patches with more convoluted shapes, range edge effects may also drive higher sensitivity to habitat change in species with more complex range shape.
- Using a cross-scale approach will lead to more accurate predictions of biodiversity change with habitat transformation and more effective conservation strategies.

The macroecology of landscape ecology

Cristina Banks-Leite^{1,2*}, Matthew G. Betts³, Robert M. Ewers^{1,2}, C. David L. Orme^{1,2}, Alex Pigot⁴

1 - Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK

2 - The Georgina Mace Centre for the Living Planet, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK

3 - Forest Biodiversity Research Network, Dept. of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, 97331

4 - Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, Gower Street, London, WC1E 6BT

*corresponding author email: c.banks@imperial.ac.uk

Twitter handle: [@crisbanksleite](https://twitter.com/crisbanksleite), [@MattBetts11](https://twitter.com/MattBetts11), [@alex_pigot](https://twitter.com/alex_pigot)

Abstract

One of landscape ecology's main goals is to unveil how biodiversity is impacted by habitat transformation. However, the discipline suffers from significant context-dependency in observed spatial and temporal trends, hindering progress towards understanding the mechanisms driving species declines and preventing the development of accurate estimates of future biodiversity change. Here, we discuss recent evidence that populations' and species' responses to habitat change at the landscape scale are modulated by factors and processes occurring at macroecological scales, such as historical disturbance rates, distance to geographic range edges, and climatic suitability. We suggest that placing landscape ecology studies within a macroecological lens will help explain seemingly inconsistent results, and will ultimately create better predictive models to help mitigate the biodiversity crisis.

Keywords: biodiversity models, centre-periphery hypothesis, extinction-filter hypothesis, drivers of biodiversity loss, physiological tolerance hypothesis

The case for a bird's eye view of landscape ecology

One of ecology's main goals is to identify generalities in patterns of interactions among living organisms and the environment. So far, very few robust rules have been identified and instead, a multitude of exceptions, context-dependencies, and methodological issues are invoked to explain contrasting results [1]. This phenomenon is particularly common within **landscape ecology** (see Glossary) — a sub-discipline that has taken on the urgent task of assessing and predicting the impacts of human-driven habitat change on biodiversity. Here, we suggest that by viewing landscape ecology from a large-scale perspective, we can obtain such sought-after generalities and better understand the processes driving species' responses to environmental change.

Broadly speaking, **macroecology** and landscape ecology share the common goal of investigating spatial patterns in biodiversity and the processes underlying these patterns [2] (Box 1). These disciplines also have a core focus on spatial scale, with macroecology concerned with generally larger spatial and temporal scales than landscape ecology [3,4]. Although parallels between the two disciplines have recently begun to emerge [2,5], they have mostly evolved independently and are almost entirely conducted separately [2].

Here, we discuss how and why populations' and species' responses to habitat change are modulated by processes operating at macroecological scales [6–8]. We propose approaches that could lead to the discovery of improved ways to predict species sensitivity to environmental change and to solutions to mitigate biodiversity loss.

Landscape ecology fails to make general predictions

To paraphrase Lawton's famous quote "Community Ecology is a mess" [9] - Landscape Ecology is also a bit of a mess. As we approach 50 years of studying habitat fragmentation [10–12], we cannot agree on how to best measure habitat loss and fragmentation [13,14] or

the relative importance of these variables [15–17]. Furthermore, there is a vast number of competing, non-mutually exclusive hypotheses to explain biodiversity responses to habitat change [18]. To complicate matters further, quantitative predictions of species' responses to habitat change are usually quite variable and irreproducible across studies and regions [2] (Fig. 1). There are two fundamental issues at the heart of this pervasive context-dependency — the inter- and intraspecific variability in species' and populations' responses to **habitat transformation** [19].

It is now well established that there is a large interspecific variation in responses to habitat transformation [20,21], as some species are negatively affected while others are positively affected (Fig. 1a). Functional traits have been suggested as a promising avenue to identify the species at risk of extinction, based on the assumption that **response traits** drive species' responses to environmental changes [22]. However, recent studies challenge the current use of response traits [23,24]. For instance, Hatfield *et al.* [23] found a low transferability of response traits between similar datasets obtained from the same region, results which highlight the correlative nature of such analyses and the dangers of interpreting their outcomes as causal effects.

However, the equally large intraspecific variation in populations' responses to habitat transformation goes largely unaccounted for (Fig. 1b). The few studies that have assessed intraspecific variability have found that different populations of the same species are often not affected in the same way [7,25–28]. And this is a major obstacle for landscape ecology's ability to predict the numbers and identities of species at risk of extinction.

Macroecology to the rescue

It is generally acknowledged that regional processes can influence local patterns [29]. For instance, species pools at regional scales influence local alpha diversity (Box 1) and species

with small geographic ranges are more sensitive to habitat loss [30,31]. Recent studies applying macroecological theory and concepts to explain the idiosyncratic populations' and species' responses to habitat transformation have shown that there exists the potential to go much further.

One example is the centre-periphery hypothesis, which postulates that demographic performance and genetic variation decrease from the centre to the edge of a species' geographic range [32,33]. Orme *et al.* [7] found support for this hypothesis by showing that bird occupancy declines near the range edge. These authors also showed that, *within the same species*, some populations respond negatively to habitat loss, while others are not affected or even respond positively (Fig. 1b). Crucially, this intraspecific variability in population responses to habitat loss is spatially structured. Populations further than ~800 km from the range edge were positively affected by habitat loss, while near the range edge populations were negatively affected (Box 1).

The extinction-filter hypothesis postulates that areas that have experienced disturbance over extended periods of time host communities that are more resilient to present-day habitat transformation [34]. Betts *et al.* [6] provide evidence that indeed species occurring in areas disturbed by historical glaciation, fire, storms and deforestation are less strongly affected by habitat fragmentation than species occurring in more stable areas. Betts *et al.* [6] also showed that historical disturbances were more common at higher latitudes and suggested that this is the reason why tropical species tended to be more strongly impacted by habitat fragmentation than temperate species (Fig. 1a).

Finally, the physiological tolerance hypothesis postulates that species' bioclimatic envelopes dictate large-scale patterns of diversity [35–37]. Williams and Newbold [8] showed that species are more negatively affected by land use in areas near their climatic tolerances. Interestingly, Williams and Newbold [8] also found that tropical species are more strongly

affected by the interaction of proximity to thermal limits and habitat change than temperate species (Fig. 1c).

Together, these studies highlight the complexity of ecological systems; not only do species, regions and biomes respond differently to habitat transformation, but populations within a single species can also respond in contrasting ways (Fig. 1). However, these studies also provide hope that we can explain this seemingly insurmountable variation. In fact, these studies provide preliminary evidence that this variation is strongly structured in space and time. The challenge now lies in uncovering general rules that govern which aspects of context matter, why, and in which directions.

Why macroecological processes may drive sensitivity to habitat transformation.

The studies from Orme *et al.* [7], Betts *et al.* [6], and Williams and Newbold [8] offer the tantalising prospect that we can derive general rules governing local biodiversity responses to habitat transformation. Yet they simultaneously raise almost as many questions as they answer. Here, we explore how these macroecological theories could explain the variation in populations' and species' responses to habitat transformation.

Centre-periphery hypothesis - **Range edge effects** can be driven by multiple drivers, including bioclimatic suitability, dispersal and interspecific interactions, all of which are likely to have a detrimental effect on populations at the range edge. The results obtained by Williams and Newbold [8] provide evidence that climatic suitability could indeed be a major driver behind the increased population sensitivity to habitat transformation at range edges [7]. However, dispersal and biotic interactions can still play a significant role. Populations at range edges receive immigrants from fewer directions than those at the centre, potentially reducing population sizes (i.e. weaker **mass effects**) and making these locations less resilient to habitat transformation. Additionally, trophic interactions and interspecific

competition vary across species' ranges [38–40], and different populations distributed across a species' range will interact with different species of predators, pathogens and/or competitors. Thus, populations at the range edge may be under higher stress from interspecific interactions and climate, and habitat transformation would further amplify these stressful conditions.

Extinction-filter hypothesis - This hypothesis can be explained in two ways - sensitive species in intensively disturbed areas have either already been driven extinct, or they have adapted over time to become less sensitive. If historical disturbances have led species to extinction, it was likely that species with smaller ranges were the ones that went extinct. This is because small-ranged species have higher sensitivity to habitat change [30,41] and large-range species are more likely to have had ranges that encompassed refugia and other areas not impacted by the disturbance. We reanalysed the data from Betts *et al.* [6] and found a weak but positive correlation between the occurrence of natural disturbances and range size ($r = 0.21$), which provides some support to this mechanism. Alternatively, species that have become less sensitive through time are also likely to have adapted to deal with a larger range of habitats and, specifically, a larger range of abiotic conditions and disturbances [41,42], thereby conferring higher resilience to anthropogenic changes [8,27]. In support of this hypothesis, Betts *et al.* [6] found that dampening effects of frequent historical disturbance on fragmentation sensitivity remained even after statistically accounting for distance to range edges.

Physiological tolerance hypothesis - The fact that climate suitability, distance to range edge, and habitat transformation are all able to reduce population sizes, fitness and gene flow in similar ways [32,38,43,44], suggests that the strength and direction of populations' and species' responses to habitat transformation could be driven by the interaction among natural and anthropogenic stressors [45,46]. Two or more simultaneous stressors can have strong, negative additive or synergistic impacts on species or ecosystems [45]. Such interaction among stressors would explain why populations located near thermal limits (or

range edge) are strongly impacted by habitat transformation [7,8]. It is less clear why populations in thermal optimal habitats (or range core) are less impacted or even benefit from habitat transformation [7,8]. There is evidence that when two stressors occur at very different magnitudes, the combined effect may be either less than additive (i.e. antagonistic) or in the opposite direction than expected (i.e., reversed outcomes) [45]. Indeed, Jacob *et al.* [47] showed that while thermal specialists choose optimal habitats, generalists selectively choose suboptimal habitats to avoid competition with specialists, and such a mechanism could explain the observation of positive effects of habitat transformation for some populations. The study of how multiple stressors affect species persistence is a growing area of ecology [48,49] and can help us explain and better predict biodiversity responses to habitat transformation.

New avenues to predict variation in sensitivity to environmental change

Evidence that species' responses to habitat change are simultaneously shaped by processes at landscape and macroecological scales opens new avenues for improving our ability to understand present patterns and predict future trends. Here, we propose key knowledge gaps, along with our predictions of the likely answers, in an attempt to stimulate further discussion and research.

Variable range edge effects - A number of studies have now shown that abiotic conditions are the main factors delimiting species' cold range edges, while biotic interactions are more important at warm-edges [38,50], thus it is possible that the **magnitude** and **extent** of range edge effects will vary between poleward and equatorward-facing range edges. Additionally, range edges can also be soft or hard [51]. Soft range edges are driven by gradual changes in abiotic and biotic factors, and often coincide with a species' niche limit (Fig. 2a) [51,52]. Hard range edges, on the other hand, usually occur along coastlines or steep elevational gradients (Fig. 2a), where abiotic and biotic conditions – and therefore niche limits – only

change at the range edge and beyond [51]. Although mass effects are equally important in soft and hard range edges, hard range edges should not present novel competitors or lower climatic suitability [51]. For this reason, Orme *et al.* [7] deliberately excluded hard edges from their analysis, and only measured distance from soft range edges to test how population responses to habitat loss varied across the species' range. We hypothesise that range edge effects are only pronounced at soft range edges, leading to the prediction that two species with similar range sizes but with different lengths of hard or soft edges would have ranges that differ in their proportions of core-edge area. Because populations are less sensitive to habitat transformation within the range core [7], these differences could help explain why two species with similar range sizes can face different levels of threat (Fig. 2a,b).

Range shape - If range-edge effects are ubiquitous across taxa, then we predict that the shape or perimeter-area ratio of a species' range may be a better indicator of species vulnerability than range size alone. In the same way that patch edge effects have been shown to drive patch area and shape effects [53–55], we hypothesise that, for any two species with similar range size, species with less compact distributions or complex range edges could be more negatively impacted by habitat transformation because most populations of those species will be closer to range edges (Fig. 2c).

Intraspecific variability in functional traits - We expect that variation in population-level responses to habitat transformation across species' ranges may be driven by intraspecific variation in both response and **effect traits**. There is some evidence for geographically structured intraspecific variation: for example, the European ground beetle *Carabus hortensis* is larger near its range edge [56], and the dietary niche breadth of moths varies consistently with distance to range edge [39]. Thus, rather than using species-averaged functional traits to predict sensitivity to habitat changes, we suggest the focus should shift to examining population-level traits, how these vary across environmental gradients, and the extent to which that spatial variation of intraspecific traits might then drive intraspecific variation in local responses to habitat transformation.

Geographic variation in disturbance history - The only test to date of the extinction-filter hypothesis to explain sensitivity to habitat fragmentation used coarse metrics of historical disturbance; Betts *et al.* [6] used only presence or absence of stand-replacing disturbance, and treated equally very different types of disturbance: fires, hurricanes, glaciation, and historical anthropogenic disturbance. We expect that as more biodiversity datasets, and more reliable metrics of disturbance become available [57], we will be able to delve deeper and gain an improved understanding of how extinction filters operate. For instance, does *time since most recent glaciation*, or the *return interval* of stand-replacing fire explain species sensitivity more effectively than simply the presence or absence of these disturbances? We also expect that disturbance-associated extinction filters may also operate, and be discernible, at finer (regional) scales [57].

Concluding remarks

We argue that the messy and idiosyncratic ecological trends within landscape ecology might be tidied up if we look at processes occurring at larger temporal and spatial scales (see also Outstanding Questions). Few ecological trends are more important than species' responses to habitat transformation, and recent research is showing that we cannot understand what drives these trends if research continues to be siloed into artificially restricted sets of spatial scales. Integrating theories from macroecology into landscape ecology brings the potential to rapidly improve our understanding of the drivers of species loss, ultimately leading to more reliable guidelines of where to best allocate resources for conservation and restoration.

Acknowledgments

We thank Prof. Anya Jones and Malavika Saji for help with figures. CBL was funded by NE/S011811/1. We thank the CALE Lab for providing inspiration through preliminary results and insightful discussions.

Glossary

Effect traits – an individuals' behavioural, physiological and morphological traits that are associated with the species' functions in the ecosystem.

Extent of range edge effects - Refers to how far the range edge effects extends into the geographic range, either as an absolute distance or relative to the width of the geographic range.

Habitat transformation - Refers to all habitat changes including habitat loss, habitat fragmentation and habitat degradation. Term used prominently in the Millennium Ecosystem Assessment of 2005 as one of the direct drivers of biodiversity loss.

Landscape ecology – a sub-field of ecology concerned with the reciprocal interactions between spatial patterns and ecological processes at a range of spatial scales. The appropriate spatial scale to quantify the influence of landscape on biodiversity is generally conceptualised in terms of the particular species, communities, or ecological processes of interest.

Macroecology - a sub-field of ecology concerned with large spatial and/or temporal scales, focusing on using statistical models to identify emergent properties in species traits (e.g. body size), geographic ranges, local abundance and diversity to understand the general ecological and evolutionary forces that influence these patterns.

Magnitude of range edge effects - Refers to the strength or the impact that range edge effects may have on populations located near the edge of their geographic range.

Mass effects – process which maintains populations that are not self-sustaining in isolation through dispersal of individuals from nearby populations.

Range edge effect - Populations located at their species' geographic range edges are often smaller, more isolated and more negatively affected by habitat transformation than populations located at the range core.

Response traits – an individuals' behavioural, physiological and morphological traits that determine the species' responses to environmental change.

Box 1 – Integrating macroecology with landscape ecology

The use of species' geographic ranges (Fig. IA) is central to macroecology, and many studies superimpose maps of multiple species' ranges (Fig. IF) to estimate large-scale patterns in species richness, threat and endemism [58,59]. Landscape ecologists also make observations of species presence or abundance (crosses, Fig. IE) and estimate landscape metrics in the surrounding regions (circular buffers, Fig. IE). These data can then be modelled to extrapolate the probability of incidence across the wider landscape (Fig. ID). Incidence models from different species can again be superimposed to estimate community patterns across the region (Fig. IH, 64).

Both approaches are flawed. The macroecological approach (Fig. IA, F) assumes that species occurs with equal probability throughout their extent of occurrence, which they do not [6, 38]. The landscape approach (Fig. ID, H) captures that variation, but neglects the limits to species' distributions. Using distance from a species' range edge (Fig. IB) and relevant landscape metrics as predictors of occupancy (Fig. ID) simultaneously prevent the model from predicting occupancy outside range boundaries and allow occupancy to vary within the range (Fig. IC). Superimposing incidence models (Fig. IC) provides an integrated estimate of species richness (Fig. IG).

There are several advantages to using an integrated approach. First, it correctly takes into account that a species has to be in its range *and* in its habitat needs to be present. Second, the integrated approach corrects the over-prediction of species richness obtained by both macroecology and landscape ecology approaches (Fig. IF,H have warmer colours than Fig. IG). Third, studies using an integrated approach have shown that the effects of habitat change on biodiversity can vary even within a biome as a function of the proportion of species in the community that are near their range edge [7]. Finally, because the integrated approach provides more accurate predictions on local species richness, it can provide more reliable targets for conservation interventions [7].

Figure I – Merging macroecology and landscape ecology approaches. Panels A, B and F on the left represent a purely macroecological approach, panels D, E and H on the right represent a purely landscape ecology approach, while the integrated approach is represented in the middle panels (C, G). Content of panels A-E are presented above the boxes, and contents of panels F-H are presented below the boxes. Black arrows indicate naïve approach, and red arrows indicate integrated approach. See Box 1 text for advantages of integrated approach.

Figure legends

Figure 1 - Context-dependency in landscape ecology. Trends of how species respond to habitat transformation may differ across biomes with different levels of historical disturbance (A), across populations within a single species' geographic range (B), and across populations and species located in regions with different climatic suitability (C). Panels A, B and C summarise some of the results obtained by Betts *et al.* [6], Orme *et al.* [7] and Williams and Newbold [8] respectively, illustrating how the effects of habitat transformation on species incidence (or abundance) are highly context-dependent.

Figure 2. Predicting how variation in geographic ranges influence local species responses to habitat transformation. A species with a hard range edge along the coastline (A) will have a larger core area (dark blue) and therefore be less sensitive to habitat transformation than a species with a similar shape and size of range, but in which the range border (lighter blue to white) is entirely "soft" (B). Similarly, a species with an elongated range may be more sensitive to habitat transformation than another species with a compact range of similar size (C). Dark blue represents areas with low magnitude of range edge effects, where populations have high occupancy and weak responses to habitat transformation. Lighter colours illustrate areas with higher magnitude of range edge effects.

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Outstanding questions

- *Does intraspecific variation in functional traits also impact species' roles in the ecosystem?*

Some studies have shown that individuals tend to be larger or have different diets near the range edge, traits which are associated with species' responses to habitat transformation as well as their roles in the ecosystem. Thus, it is possible that intraspecific variation in functional traits could lead to different populations of the same species having different roles in the ecosystem.

- *Are mass effects driving range edge effects?* It has been long hypothesised that sink populations in fragmented landscapes may be subsidised by nearby source populations in more contiguous habitat, and for reasons of geometry alone, range edges will have reduced amounts of contributing source habitat in the surrounding region. Mass effects are expected to be equally important at both soft and hard boundaries, so determining whether range edge effects are stronger at soft boundaries provides an easy test of this question.

- *Given a similar range size, do species with discontinuous ranges respond more strongly to habitat transformation than those with one single continuous range?* Species with discontinuous ranges are already expected to be at higher risk of extinction given reduced dispersal between populations. Additionally, populations in discontinuous ranges may also respond more negatively to habitat transformation, simply because a large proportion of the population will be near the range edge, thereby amplifying their risk of extinction.

- *How do climate-driven range shifts impact the way populations are affected by habitat transformation?* Species ranges will shift in location, size and shape as climate change progresses. However, it is still unclear whether range edge effects from novel range edges will impose similar constraints as current range edges.