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Assessing the Synergistic Effects of Land Use and Climate Change on Terrestrial Biodiversity: Are Generalists Always the Winners?

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Abstract

Purpose of Review There is increasing evidence that land use and land cover (LULC) change interacts with climate change to shape biodiversity dynamics. The prevailing hypothesis suggests that generalist species have an advantage in novel climatic and land cover conditions, while specialists are expected to be more sensitive to both stressors (generalization hypothesis). Some posit, however, that specialization is key to success in the face of combined climate and LULC change (specialization hypothesis). The goal of this review is to examine recent evidence for the generalization and specialization hypotheses.

Recent Findings Recent findings at population, species, and community levels provide initial support for the generalization hypothesis—i.e., that wide niche breadths are advantageous in the face of the combined threats of climate and LULC change. Evidence for the specialization hypothesis, however, also exists. Variation among studies in terms of their geographic context, spatial and temporal extent, environmental conditions, taxonomic scope, and metrics used to quantify niche breadth is a likely factor underlying the contradictory evidence for the generalization and specialization hypotheses.

Summary Recent research suggests that generalist species are likely able to withstand greater changes brought about by climate and LULC change than specialist species because they persist in environmental conditions that are typically further away from their thermal or resource limits. However, to fully understand factors driving species' vulnerability to interaction of climate and LULC change, future work should adopt standardized descriptions of niche breadth, retain consistent taxonomic scope whenever possible, and provide increased replication across different geographic contexts.

Keywords Climate change · Generalists · Land cover change · Land use change · Specialists

Introduction

In times of increasing anthropogenic pressure on many ecosystems and the resulting global biodiversity loss on par with Earth's past mass extinctions [1], understanding the main drivers of biodiversity change is a pressing issue. Land use and land cover (LULC) change is currently the largest contributor to global biodiversity change, but climate change is emerging as an increasingly important factor in shaping biodiversity dynamics and is predicted to exceed the impacts of LULC change over the next several decades [2]. Ecological responses to climate change have not been uniform across populations, species, and communities, and there is increasing evidence that LULC change interacts with anthropogenic climate change to shape biodiversity across organizational levels [3, 4, 5•]. Despite this recognition, impacts of LULC change and climate change on biodiversity are often considered independently of one another, and projections of future states of biodiversity rarely account for synergies between both factors. Understanding the interplay between these two processes will be critical to understanding and predicting changes to biodiversity as the climate crisis and habitat loss continue to unfold.

Climate change increases both average and maximum temperatures and shifts precipitation patterns

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heterogeneously at a global scale [6]. Species might respond to changing climatic patterns in a variety of ways, through shifts in geographic ranges [7, 8], changes to phenological [9], ecological, or morphological [10, 11] traits through either phenotypic plasticity or adaptation, or local extinctions [7]. Land use and land cover change encompasses a number of different processes (e.g., agricultural conversion, habitat fragmentation, urbanization), which typically lead to thermal landscape modification through increases in direct solar exposure and evaporation rates, alongside structural changes associated with direct habitat conversion (e.g., loss of tree cover) [12, 13]. As such, LULC change has the potential to exert similar selective pressures on populations and species to those of climate change [5•]. Together, both processes are likely to only benefit individuals and species that are able to tolerate physical and thermal landscape modification, potentially leading to increased community homogenization at a regional scale [5•, 14].

The specific traits or characteristics of species that might make them more or less susceptible to the combined threat of LULC change and climate change (Fig. 1A) have not yet been fully elucidated. One prevailing hypothesis is that niche generalization is paramount to tolerating the synergistic effects of LULC and climate change (hereafter, generalization hypothesis; [15–17]). The generalization hypothesis suggests that individuals, populations, or species with wide niche breadths have an advantage in novel climatic conditions by being broadly tolerant of environmental changes [18], while those with narrow niche breadths are typically expected to be more sensitive to climate change because they are often near their upper climatic limit ([18, 19]; Fig. 1B). In other words, the same amount of change in climatic conditions, both in terms of its mean and variability, is expected to exert a stronger negative effect on individuals, populations, or species with narrow niche breadths than on those with wide ones. Note that in the context of climate change, niche breadth is often defined as a range of thermal tolerance (thermal niche breadth) even though other climatic factors (e.g., precipitation) are equally important components of the climatic niche.

Land use and land cover change is likely to compound these climate change effects. Open habitats, such as ones resulting from conversion of forest to agricultural cover, are largely characterized by more variable micro-climates [20, 21••]. As per the thermal adaptation hypothesis [19, 22–26], thermally variable environments typically comprise species with wider thermal niches than less variable or aseasonal environments. It is thus reasonable to expect that climate and LULC change will synergistically lead to increased prevalence of generalization in communities exposed to both processes. Some studies of LULC and climate change, however, have found evidence for the relative success of specialist species over generalists [27, 28•] or for a combination of responses [29•]. Others have therefore argued, that

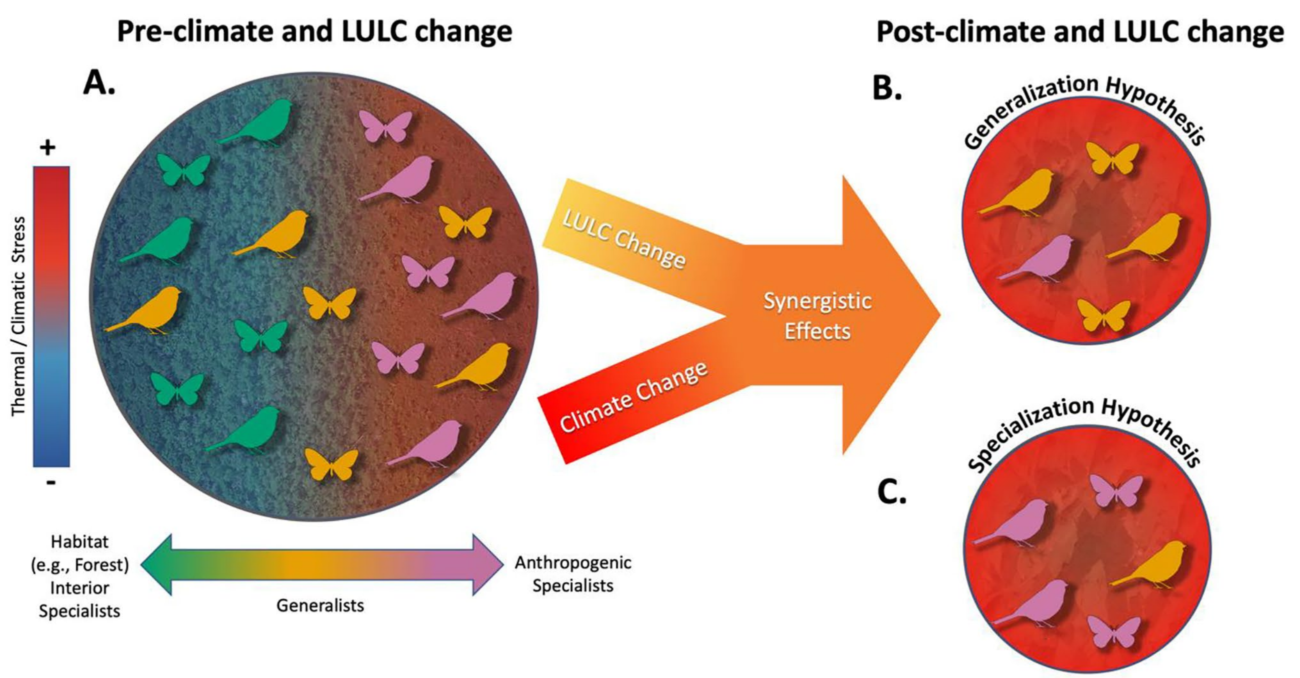

Fig. 1 Communities along environmental and thermal gradients are comprised of habitat interior specialists, generalists, and anthropogenic specialists (**A**). Combined land use and land cover (LULC) and climate change might lead to communities characterized by either relative dominance of generalist (**B**) or anthropogenic specialist (**C**) individuals or species. Species silhouettes were taken from PhyloPic (PhyloPic-Free Silhouette Images of Life Forms) and colorized

it is particular types of specialization—i.e., open habitat, often anthropogenic, specialists with narrow niche breadths but higher thermal margins—that are key to success in the face of combined climate and land cover change (hereafter, specialization hypothesis; [28•]) (Fig. 1C).

Here, we outline the evidence for the generalization and specialization hypotheses (Table 1). Our review is not based on an exhaustive or systematic literature review nor is it a formal meta-analysis. Rather, we simply highlight select latest research examples in support of each hypothesis and discuss potential confounding factors that might be contributing to any contrasting evidence.

Support for the Generalization Hypothesis

Evidence for the generalization hypothesis is perhaps most apparent in population level studies where thermal niche breadth is explicitly measured. For a number of taxonomic groups, wider thermal breadths have been found in populations of open, fragmentated, or otherwise more exposed habitats. For example, thermal tolerance limits of populations of a Central African butterfly *Bicyclus dorothea* in a mosaic of woody or herbaceous savanna—a thermally variable boundary ecotone—were wider than thermal breadths of populations found in more thermally stable tropical forests [21••]. Likewise, populations of black-capped chickadees (*Poecille atricapillus*) showed differences in thermogenic capacity, wherein individuals from fragmented landscapes were characterized by slightly higher thermal capacity and lower metabolic costs, resulting in higher absolute aerobic scope than populations of contiguous forests [30]. These results suggest that selection in environments that undergo human modifications such as land cover change and habitat fragmentation indeed favors individuals that have wider thermal niches.

Species with generalist habitat strategies have also been shown to benefit from the synergistic effects of climate and LULC change. For instance, tropical butterfly communities saw decreases in the proportion of narrow-range and forest-associated species when habitat was modified and temperatures increased [21••, 31]. Given that species with smaller geographic ranges often have narrower niche margins compared to species with large geographic ranges ([32], but see [33, 34]), species that benefited the most from climate change and land cover conversion were likely those with generalist strategies. Bonebrake et al. (2016) further demonstrated, through projections, that warming and habitat fragmentation exert similar pressures with respect to community composition and together lead to an increased proportion of widespread—i.e., presumably characterized by wide niche breadths—species [31]. Platts et al. (2019) showed that generalist invertebrate species expanded their ranges more than specialist invertebrates, and those range shifts were mediated by the amount of species-specific habitat availability at the leading edge of the range expansion. One caveat is, however, that species with smaller geographic ranges tend to have lower probabilities of persistence in the face of environmental disturbance (e.g., [35]), regardless of their niche breadth. Disentangling the vulnerability of restricted-range species from the vulnerability of specialized species remains challenging.

Community level studies provide further support for the generalization hypothesis. Communities with a greater proportion of species near their upper temperature limit saw stronger declines in species richness as a result of

Table 1 Evidence for generalist and specialist hypotheses given by the studies cited in this review. Study number is consistent with the in-text citation

Study	Author(s)	Hypothesis supported	Spatial extent	Biome	Ectotherm/endotherm	Taxa	Biological level
[21••]	Dongmo et al. (2021)	Generalist	Cameroon	Tropical	Ecto	Butterflies	Population
[30]	Latimer et al. (2018)	Generalist	County (Wisconsin)	Temperate	Endo	Birds	Population
[31]	Bonebrake et al. (2016)	Generalist	Vietnam, National Park	Tropical	Ecto	Butterflies	Species/community
[3]	Platts et al. (2019)	Generalist	Great Britain	Temperate	Ecto	Invertebrates	Species
[4]	Jarzyna et al. (2015)	Generalist	State (New York)	Temperate	Endo	Birds	Community
N/A	Jarzyna et al. (unpublished)	Generalist	State (New York)	Temperate	Endo	Birds	Community
[29•]	Mimet et al. (2019)	Both	Continental USA	Temperate	Endo	Birds	Species/community
[35]	Prince et al. (2015)	Specialist	France	Temperate	Endo	Birds	Species/community
[36]	Reino et al. (2018)	Specialist	Iberian Peninsula	Temperate	Edno	Birds	Species/community
[28•]	Fishkoff et al. (2019)	Specialist	Dominican Republic	Tropical	Ecto	Lizards	Species/community
[27]	Fishkoff et al. (2015)	Specialist	Costa Rica	Tropical	Ecto	Amphibians/reptiles	Species/community

combined climate and land cover change. Jarzyna et al. [4] found weaker associations between avian community change and climate change in highly fragmented landscapes, which they attributed to the fact that habitat generalists with wide thermal breadths—and thus potentially greater tolerance for changing climatic conditions—tend to be more common in fragmentated than contiguous habitats. A follow-up study further showed that generalist birds showed lower change in their distributions than birds with more specialized habitat associations (Jarzyna, unpublished data). In human-dominated areas, decreased temperature stability resulted in, on average, less specialized avian communities and increased biotic homogenization [29•]. This combined evidence from population, species and community level studies suggests that individuals and species with wider niches might indeed be at an advantage in the face of the synergistically acting climate and LULC change.

Support for the Specialization Hypothesis

Evidence in support of specialization hypothesis appears scanter but can be found at both the species and community levels. Bird species with affinities for open and human-modified habitats (i.e., open habitat specialists) were on average more tolerant of current and future predicted climate and LULC change than generalist species [36, 37•]. Bird habitat specialists also showed stronger range expansions than generalists which tended to retract their ranges under climate change scenarios [37•]. In the tropics, warm-climate lowland specialist species of lizards were better able to utilize deforested high elevation regions than thermal generalists [28•], suggesting that upper thermal tolerance rather than thermal range is adaptive in anthropogenic settings. Admittedly, however, Frishkoff et al. (2019) focused on land use and land cover change only and did not consider the effects of climate change per se, though previous studies of herpetological communities in Costa Rica that included temperature measurements in an experimental setting also found that thermal tolerance was higher for species thriving in deforested areas [27]. Across 50 years of breeding bird surveys, prevalence of specialization increased over time in mountainous regions and high-altitude deserts that are typically characterized by dry, low-intensity land-use, and historically low climate velocity, in contrast to wetter, more productive, and higher-intensity land use regions, where trends toward generalization were more apparent [29•].

Why the Discrepancy?

Can we reconcile findings supporting the specialization hypothesis with the evidence for the generalization hypothesis? These disparate findings might result from a number of factors, including variation in the geographic location, spatial and temporal variation, environmental conditions, taxonomic scope, and ways in which niche breadth is calculated.

Geographic Factors

Thermal adaptation hypothesis posits that thermally variable environments tend to comprise species with wider thermal niches than less variable, aseasonal environments. Given a strong latitudinal and, to a lesser extent, elevational gradient in environmental variability (particularly with respect to temperature; [38]), it is expected that tropical communities are comprised of individuals and species with narrower niche margins than communities in high latitude regions. This increase in specialization toward low-latitude regions has been demonstrated for a number of taxonomic groups at both population- and species-level ([39–43]; but see [38, 44]), suggestive of disproportionate sensitivity of tropical diversity to the combined threats of LULC and climate change [45]. Indeed, tropical biodiversity has shown strongest biodiversity loss [45] and range shifts [46] as a result of combined pressures of climate and land cover change, potentially providing an indirect support for the generalization hypothesis. The studies presented in this review, however, do not show any discernible latitudinal gradient, with only a handful carried out in subtropical or tropical regions. Moreover, studies cited here show both support for [4, 21••, 30, 31] and repudiation of [28•, 36, 37•] the generalization hypotheses regardless of the latitudinal position of the study location. A formal meta-analysis and/or a more exhaustive literature review are needed, however, to demonstrate whether latitude is the underlying factor leading to the contrasting support for the generalization hypothesis.

Spatiotemporal Variation in Niche Breadth

Evidence suggests that populations of the same species across the species' range differ from one another in terms of their phenotypic and/or genotypic characteristics [47–49], which might affect their response to environmental variation and change [50]. For example, intraspecific trait differences mediated the effects of warming on a benthic grazer community [51]. Likewise, the availability of resources shows clear temporal variability that results in many animals changing their habitat, foraging, and dietary preferences across time [52] and potentially leading to seasonal variation in generalization. For example, some resident birds that typically forage arboreally in the breeding season become frequent ground foragers outside of the breeding season presumably because of increased prey availability near the ground [53]. Failure to capture the entire range of environmental and resource conditions a species experiences throughout its geographic range and across its life cycle might mischaracterize its niche and affect the conclusions in respect to the generalization versus specialization hypotheses.

Habitat Heterogeneity and Microclimatic Conditions

Microclimatic conditions play an important role in populations or species' abilities to persist in the face of changing climate. Specifically, habitat and topographic heterogeneity create thermal refugia that buffer the individuals and populations from the effects of thermal stress [54]. In England, high levels of microclimatic heterogeneity, resulting primarily from topographic variation, benefited species negatively impacted by climate change and reduced the risk of extirpation due to climate change by 22% and 9% for plant and insect species, respectively [55••]. Others have also demonstrated that topographic heterogeneity increased the resilience of the biota to climate change impacts across regional [56] and global [57] scales. Can topographic variability explain the contradictory findings regarding the generalization and specialization hypotheses? Mimet et al. (2019) found support for the specialization hypothesis in their study on North American breeding birds, but only in regions characterized by low climate velocity, such as highly topographically varied mountainous regions [58]. Likewise, Frishkoff et al. [28•] provided support for the specialization hypothesis in highly topographically heterogeneous region of Dominican Republic and showed that the effects of habitat loss are less severe in high elevations. Topographic heterogeneity and the resulting microclimatic variation might thus play an important role in how specialists and generalists respond to the synergistic effects of climate and LULC change. However, LULC change has historically been more pronounced in low elevation and topographically homogenous regions, which hinders our ability to control for topographic and microclimatic variation in studies of LULC and climate change effects on biodiversity and thus arrive at any generalities.

Taxonomic Scope

The differences in thermal physiology between ectotherms and endotherms affect how species interact with and are constrained by their environment. This suggests that global change might have different consequences for ectotherms than for endotherms [59], including its impact across the specialization-generalization spectrum. Despite this expectation, however, we do not find any discernible differences between responses of ectotherms and endotherms to the synergistic effect of LULC and climate change. A formal meta-analysis that focuses on the ectotherm-endotherm comparison, particularly in the context of the gradient of specialization to generalization, is warranted.

Furthermore, the placement of a species (or, alternatively, individuals) along the specialization-generalization gradient is most often determined by comparing niche breadths among species within a given taxonomic group. As a consequence, a species might in principle be categorized both as a specialist and a generalist depending on the taxonomic range of a given study. The taxonomic scope of the study thus has the potential to affect the conclusions in respect to the generalization versus specialization hypotheses. For example, Princé et al. [36] and Reino et al. [37•] found specialist species to be less adversely affected by combined climate and LULC change than generalist species (i.e., support for the specialization hypothesis), but their taxonomic scopes were restricted to species of farmland habitats. As argued earlier, open and anthropogenic environments are often characterized by more variable microclimatic conditions and might thus comprise individuals or species with wider thermal niches. Should the taxonomic scopes of both studies be extended to include species of forested habitats—i.e., those with presumably on average narrower niche breadths—the conclusions might have instead pointed toward the generalization hypothesis, as seen in the case of Jarzyna et al. [4]. We thus find it plausible that the discrepancies in the taxonomic scopes among the studies cited in this review are a crucial factor underlying the differences in support for either of the hypotheses. Going forward, studies conducted in the same geographic region should consider a consistent taxonomic scope as vital to understanding factors driving species' vulnerability to the combined threats of climate and LULC change.

Niche

The last, and perhaps most crucial, factor in identifying the characteristics of individuals and species that make them vulnerable to the combined threats of climate and LULC change is the description of the niche and its breadth. First, for the majority of examples presented in this review, niche breadths are derived from descriptors of realized rather than fundamental niches, even though abiotic favors and competition for resources can affect the observed niche characteristics and thus the level of generalization (e.g., [60, 61]). Second, niche is an n-dimensional object [18, 62] whose breadth can only be approximated if its description is limited to its one or two components (axes). Despite this multi-dimensionality of a niche, in the context of the synergistic effects of climate and LULC change, niche breadth is often defined either as a range of thermal tolerance (e.g., [21••, 31]) or as habitat affinity (e.g., [29•, 36, 37•]). While thermal and habitat niche breadths are often correlated with one another [63], this is not necessarily always the case due to evolutionary cost–benefit trade-offs between the ability to tolerate a wide range of climatic conditions and exploiting a particular set of resources in an efficient manner [64]. Likewise, other axes of the climatic niche might be particularly relevant to quantifying the responses to LULC and climate change. For terrestrial species, precipitation is an important niche component that determines resource availability and has shown a close association with certain land uses [45, 65]. Finally, the resolution at which niche breadth is measured in the studies cited in this review varies from continuous measurements (e.g., [3, 21••, 29•]) to binary characterizations of specialization or generalization [36, 37•]. Ignoring trait resolution can have profound implications for the ability to detect ecological processes [66] and might affect the conclusions drawn regarding the specialization versus generalization hypothesis. Indeed, both Princé et al. [36] and Reino et al. [37•]—two studies that found support for the specialization hypothesis—used binary depictions of niche breadth (i.e., specialist versus generalist) in contrast to studies that have provided evidence for the generalization hypothesis. To provide unequivocal evidence for the prevalence of generalization hypothesis, future work should adopt standardized descriptions of niche breadth both in terms of the niche axes as well as the resolution at which niche width is measured.

Conclusions

Recent research provides fairly strong support that individuals and species with wider niche breadths have an advantage in the face of the combined threats of climate and land use and land cover change. This is likely because the environmental conditions in which most generalists persist are typically further away from their thermal or resource limits, allowing them to withstand greater changes brought about by climate and LULC change. Still, evidence to the contrary also exists. These discrepancies among studies, however, can be mostly reconciled by considering the data-based and methodological decisions, and specifically the disparities in the taxonomic scope and ways in which niche breadth is quantified among the different studies. Future attempts to examine how land use and land cover change and climate change interact to impact biodiversity worldwide would strongly benefit from standardization of the methodological protocol.

Author Contribution Both authors devised the manuscript idea and wrote the manuscript.

Compliance with Ethical Standards

Conflict of Interest The authors declare no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

References

Papers of particular interest, published recently, have been highlighted as:
• Of importance
•• Of major importance

1. Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, et al. Has the Earth's sixth mass extinction already arrived? Nature Nature Publishing Group. 2011;471:51–7.
2. Newbold T. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proc Royal Soc B: Biolog Sci. 2018;285.
3. Platts PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, et al. Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. Scientific Reports. Springer US. 2019;9:1–10.
4. Jarzyna MA, Porter WF, Maurer BA, Zuckerberg B, Finley AO. Landscape fragmentation affects responses of avian communities to climate change. Change Biology. 2015;21:2942–53.
5.• Newbold T, Adams GL, Robles GA, Boakes EH, Ferreira GB, Chapman ASA, et al. Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. Emerg Top Life Sci. 2019;3:207–19. **This review outlines theoretical reasons for biotic homogenization due to synergistic effects of climate change and land use change.**
6. Climate Change IPCC. The Physical Science Basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge Univ Press. 2021;2021:F0003–F0003.
7. Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, et al. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science. 2017;355.
8. Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, et al. Species better track climate warming in the oceans than on land. Nat Ecol Evol. 2020;4:1044–59.
9. Zimova M, Willard DE, Winger BM, Weeks BC. Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. J Anim Ecol. 2021;90:2348–61.
10. Weeks BC, Willard DE, Zimova M, Ellis AA, Witynski ML, Hennen M, et al. Shared morphological consequences of global warming in North American migratory birds. Ecol Lett. 2020;23:316–25.
11. Jirinec V, Burner RC, Amaral BR, Bierregaard RO, Fernández-Arellano G, Hernández-Palma A, et al. Morphological consequences of climate change for resident birds in intact Amazonian rainforest. Sci Adv. 2021;7.
12. Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-römermann M, et al. Forest microclimate dynamics drive plant responses to warming. Science. 2020;368:772–5.

13. Nowakowski AJ, Watling JI, Thompson ME, Brusch GA, Catenazzi A, Whitfield SM, et al. Thermal biology mediates responses of amphibians and reptiles to habitat modification. Ecol Lett. 2018;21:345–55.
14. Karp DS, Frishkoff LO, Echeverri A, Zook J, Juárez P, Chan KMA. Agriculture erases climate-driven β-diversity in Neotropical bird communities. Glob Change Biol. 2018;24:338–49.
15. Lurgi M, López BC, Montoya JM. Novel communities from climate change. Philosophical Transactions of the Royal Society B: Biological Sciences. 2012;367:2913–22.
16. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional homogenization? Front Ecol Environ. 2011;9:222–8.
17. Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A. Rise of the generalists: evidence for climate driven homogenization in avian communities. Glob Ecol Biogeogr. 2012;21:568–78.
18. Kelly A. Carscadden, Nancy C. Emery, Carlos A. Arnillas, Marc W. Cadotte, Michelle E. Afkhami, Dominique Gravel, Stuart W. Livingstone and JJW. Niche breadth: causes and consequences for ecology, evolution, and conservation. Quart Rev Biol. 2020;95:179–214.
19. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, et al. Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci USA. 2008;105:6668–72.
20. Kark S. Effects of ecotones on biodiversity. Reference Module in Life Sciences. 2017;1–7.
21.•• Dongmo MAK, Hanna R, Smith TB, Fiaboe KKM, Fomena A, Bonebrake TC. Local adaptation in thermal tolerance for a tropical butterfly across ecotone and rainforest habitats. Biol Open. 2021;10. **This paper demonstrates wider thermal niches in ecotone habitats through laboratory testing of niche breadth.**
22. Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Glob Change Biol. 2015;21:1092–102.
23. Kellermann V, Overgaard J, Hoffmann AA, Fljøgaard C, Svenning JC, Loeschcke V. Upper thermal limits of drosophila are linked to species distributions and strongly constrained phylogenetically. Proc Natl Acad Sci USA. 2012;109:16228–33.
24. Sunday JM, Bates AE, Dulvy NK. Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B: Biological Sciences. 2011;278:1823–30.
25. Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Pérez HJÁ, et al. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B: Biological Sciences. 2009;276:1939–48.
26. Chown SL, Addo-Bediako A, Gaston KJ. Physiological variation in insects: large-scale patterns and their implications. Comparative Biochemistry and Physiology - B Biochemistry and Molecular Biology. 2002;131:587–602.
27. Frishkoff LO, Hadly EA, Daily GC. Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. Glob Change Biol. 2015;21:3901–16.
28.• Frishkoff LO, Gabot E, Sandler G, Marte C, Mahler DL. Elevation shapes the reassembly of Anthropocene lizard communities. Nat Ecol Evol. Springer US; 2019;3:638–46. **This paper provides evidence for the specialization hypothesis and an articulation for its adoption over the generalization hypothesis.**
29.• Mimet A, Buitenwerf R, Sandel B, Svenning JC, Normand S. Recent global changes have decoupled species richness from specialization patterns in North American birds. Glob Ecol Biogeogr. 2019;28:1621–35. **This paper measures avian specialization and species richness over large spatial scale and reveals different patterns of specialization across different regions.**
30. Latimer CE, Cooper SJ, Karasov WH, Zuckerberg B. Does habitat fragmentation promote climate-resilient phenotypes? Oikos. 2018;127:1069–80.
31. Bonebrake TC, Pickett EJ, Tsang TPN, Tak CY, Vu MQ, Vu L Van. Warming threat compounds habitat degradation impacts on a tropical butterfly community in Vietnam. Global Ecology and Conservation. Elsevier B. V. 2016;8:203–11.
32. Slatyer RA, Hirst M, Sexton JP. Niche breadth predicts geographical range size: a general ecological pattern. Ecol Lett. 2013;16:1104–14.
33. Cardillo M, Dinnage R, McAlister W. The relationship between environmental niche breadth and geographic range size across plant species. J Biogeogr. 2019;46:97–109.
34. Moore TE, Bagchi R, Aiello-Lammens ME, Schlichting CD. Spatial autocorrelation inflates niche breadth–range size relationships. Glob Ecol Biogeogr. 2018;27:1426–36.
35. Staude IR, Navarro LM, Pereira HM. Range size predicts the risk of local extinction from habitat loss. Glob Ecol Biogeogr. 2020;29:16–25.
36. Princé K, Lorrillière R, Barbet-Massin M, Léger F, Jiguet F. Forecasting the effects of land use scenarios on farmland birds reveal a potential mitigation of climate change impacts. PLoS ONE. 2015;10:1–25.
37.• Reino L, Triviño M, Beja P, Araújo MB, Figueira R, Segurado P. Modelling landscape constraints on farmland bird species range shifts under climate change. Science of the Total Environment. Elsevier B.V. 2018;625:1596–605. **This paper models climate induced range shifts of specialist and generalist farmland birds across different landcover regimes and provides support for the specialization hypothesis.**
38. Vázquez DP, Stevens RD. The latitudinal gradient in niche breadth: concepts and evidence. Am Nat. 2004;164:0–19.
39. Araüjo MS, Costa-Pereira R. Latitudinal gradients in intraspecific ecological diversity. Biol Let. 2013;9:6–10.
40. Salisbury CL, Seddon N, Cooney CR, Tobias JA. The latitudinal gradient in dispersal constraints: Ecological specialisation drives diversification in tropical birds. Ecol Lett. 2012;15:847–55.
41. Saupe EE, Myers CE, Peterson AT, Soberón J, Singarayer J, Valdes P, et al. Non-random latitudinal gradients in range size and niche breadth predicted by spatial patterns of climate. Glob Ecol Biogeogr. 2019;28:928–42.
42. Cerezer FO, de Azevedo RA, Nascimento MAS, Franklin E, de Morais JW, de Sales DC. Latitudinal gradient of termite diversity indicates higher diversification and narrower thermal niches in the tropics. Glob Ecol Biogeogr. 2020;29:1967–77.
43. Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, et al. The global distribution of diet breadth in insect herbivores. Proc Natl Acad Sci USA. 2015;112:442–7.
44. Cirtwill AR, Stouffer DB, Romanuk TN. Latitudinal gradients in biotic niche breadth vary across ecosystem types. Proc Royal Soc B: Biolog Sci. 2015;282.
45. Williams JJ, Newbold T. Local climatic changes affect biodiversity responses to land use: a review. Divers Distrib. 2020;26:76–92.
46. Guo F, Lenoir J, Bonebrake TC. Land-use change interacts with climate to determine elevational species redistribution. Nat Commun. Springer US; 2018;9:1–7.
47. Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett. 2015;18:1406–19.
48. Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, et al. Why intraspecific trait variation matters in community ecology. Trends in Evolution and Ecology. 2011;26:183–92.
49. Forsman A, Polic D, Sunde J, Betzholtz PE, Franzén M. Variable colour patterns indicate multidimensional, intraspecific trait variation and ecological generalization in moths. Ecography (Cop). 2020;43:823–33.

50. Moran EV, Hartig F, Bell DM. Intraspecific trait variation across scales: implications for understanding global change responses. Glob Change Biol. 2016;22:137–50.
51. Salo T, Mattila J, Eklöf J. Long-term warming affects ecosystem functioning through species turnover and intraspecific trait variation. Oikos. 2020;129:283–95.
52. Zuckerberg B, Fink D, La Sorte FA, Hochachka WM, Kelling S. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. Divers Distrib. 2016;22:717–30.
53. Cale P. Temporal changes in the foraging behaviour of insectivorous birds in a sclerophyll forest in tasmania. Emu. 1994;94:116–26.
54. Muñoz-Sáez A, Choe H, Boynton RM, Elsen PR, Thorne JH. Climate exposure shows high risk and few climate refugia for Chilean native vegetation. Sci Total Env. 2021;785.
55.•• Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, et al. Extinction risk from climate change is reduced by microclimatic buffering. Nature Climate Change. Springer US. 2018;8:713–7. **This paper illustrates the importance of topographic microclimates to act as climate change refugia.**
56. Virkkala R, Aalto J, Heikkinen RK, Rajasärkkä A, Kuusela S, Leikola N, Luoto M. Can topographic variation in climate buffer against climate change-induced population declines in northern forest birds. Diversity. 2020;12.
57. Lawrence A, Hoffmann S, Beierkuhnlein C. Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change. Global Ecology and Conservation. The Authors. 2021;25:e01445.
58. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. The velocity of climate change. Nature Nature Publishing Group. 2009;462:1052–5.
59. Buckley LB, Hurlbert AH, Jetz W. Broad-scale ecological implications of ectothermy and endothermy in changing environments. Glob Ecol Biogeogr. 2012;21:873–85.
60. Martin PR, Martin TE. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology. 2001;82:189–206.
61. Martin PR, Martin TE. Behavioral interactions between coexisting species: song playback experiments with wood warblers. Ecology. 2001;82:207–18.
62. Hutchinson GE. Concluding remarks. Cold Spring Harb Symp Quant Biol. 1957;22:415–27.
63. Barnagaud JY, Devictor V, Jiguet F, Barbet-Massin M, Viol I, Archaux F. Relating habitat and climatic niches in birds. PLoS ONE. 2012;7:1–10.
64. Futuyma DJ, Moreno G. The evolution of ecological specialization. Annu Rev Ecol Evol Syst. 1988;19:207–33.
65. Frishkoff LO, Karp DS, Flanders JR, Zook J, Hadly EA, Daily GC, et al. Climate change and habitat conversion favour the same species. Ecol Lett. 2016;19:1081–90.
66. Kohli BA, Jarzyna MA. Pitfalls of ignoring trait resolution when drawing conclusions about ecological processes. Glob Ecol Biogeogr. 2021;30:1139–52.