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The shifting balance between habitat and climate drivers of boreal biodiversity across space and taxa

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Abstract

Changes in land use and climate pose major threats to biodiversity[1–5]. However, variation in species responses to climate and land use across space, time, and taxa remains poorly understood[3,6–10], hindering our ability to predict and mitigate biodiversity change. Here, we evaluate the relative importance of concurrent changes in climate and land use in driving the occurrence and abundance patterns of 503 terrestrial animal species of various taxa over 20 years in Finland. Habitat composition proved to be the main driver of biodiversity patterns but how much and with what uncertainty it explained species distributions depended highly on the context. Specifically, habitat was the dominant driver for butterflies, birds, and small mammals, while habitat and climate were equally important for large mammals and moths. Additionally, species patterns between biogeographical regions were mainly explained by climate, while habitat was the main driver within regions. Traits, such as, body size, pace of life, habitat and diet specialization modulated the relative importance of both drivers' impacts. Climate and habitat impact on most species were also partially correlated, highlighting the tight connection between the drivers. Our findings emphasize that land use is a major force in shaping terrestrial biodiversity, while highlighting its tight connection with climate. Considering functional and spatial contexts is thus essential for building effective management and conservation strategies for biodiversity under rampant global change.

Main document

Main:

Biodiversity is undergoing widespread change driven by interacting anthropogenic pressures[11–13], with serious implications for ecosystem resilience[1,4,11–13]. Climate and land use change are among the most pervasive threats to biodiversity[2,3,14,15], both directly and through their influence on other drivers of change[7,16,17]. Yet, the interplay between climate and land use impacts on species occurrence and abundance remains poorly understood, partly due to the limited availability of high-resolution data across broad spatial and temporal scales and across taxonomic groups[3,6,10,18]. Disentangling the interplay between these two key drivers of biodiversity change has direct implications for policy and management. Still, their simultaneous impacts raise both methodological and conceptual challenges[3,7–9], including how to incorporate variability over space and time and how to evaluate context dependencies. Species' traits can additionally modulate their sensitivity to environmental drivers, and thus shape species' responses to climate and habitat change[19–21]. These aspects are often neglected when evaluating biodiversity changes[22].

Here, we evaluate the impacts of habitat and climate in shaping occurrence and abundance patterns in 503 animal species, including birds, large mammals, small mammals, butterflies, and moths across a ~ 1,100 km latitudinal gradient in Finland. Leveraging over 3 million records from over 20 years (1999–2019) and extending a Bayesian joint species distribution model (JSDM[23]) to include conditional

variance partitioning[24] (see *Methods*), we quantify the relative and shared importance of habitat composition and climate across five species groups, as well as their spatial (between and within biogeographical regions) and functional context-dependence (Fig. 1). As a result, we provide fundamental insights into how the impacts of climate and habitat on species occurrence and abundance vary across space and functional groups, improving the accuracy of biodiversity evaluation and supporting evidence-based strategies to halt biodiversity loss[25].

Habitat explains most of the variation in the occurrence and abundance patterns

Overall, we expected climate to play a major role in explaining biodiversity patterns due to Finland's extensive latitudinal gradient, while the relative importance of both climate and habitat drivers to vary between taxa[9,12].

However, the effects of climate – annual mean temperature, cumulative precipitation and number of snow days – came out secondary, and the relative impact of habitat vs. climate varied substantially across taxa. Variability in habitat composition – quantified as the percent cover of the main habitat types (urban, crops, forest, semi natural – herbaceous – pastures (SHP), and wetland) around a site – explained the largest proportion of variability in both species' occurrence and abundance across all taxa. This driver was followed by climate and landscape configuration – a combination of habitat fragmentation and diversity around a site (Fig. 2a and 2b).

Nonetheless, the relative importance of habitat and climate varied both between and within taxa (Fig. 2). For instance, climate and landscape configuration were equally important for butterflies while climate and habitat composition had similar importance for moths and large mammals (Fig. 2a and 2b). Moths and large mammals also showed the highest variability between species in the relative importance of habitat and climate (Fig. 2c and 2d). Furthermore, moths were the only group for which climate was more important than habitat in explaining variability in abundance (40% of species; Fig. 2b, Supplementary Figure S3.4a & b). Despite habitat composition being the most important driver for 25–80% of species across taxa, for many species there was no single dominant driver, highlighting the combined importance of habitat and climate (Supplementary Figure S3.4a & b).

The importance of drivers varies with the spatial context

We hypothesized that the relative importance of habitat and climate would vary across biogeographical space[12,26,27]. We also predicted that climate would have a greater relative importance at higher latitudes, given the harsher and faster-changing climatic conditions in Northern Finland[28] compared to the more heterogeneous and fragmented landscapes in the south[29]. While not all taxa displayed latitudinal patterns, the relative importance of climate and habitat drivers varied between and within biogeographical regions. These patterns were overall similar for occurrence and abundance, with the latter showing higher within-taxon variability (Fig. 3 and supplementary Figure S3.1). For butterflies and large mammals, the relative importance of climate was greater at higher latitudes, while for birds it decreased with latitude, as matched by an increasing importance of habitat composition (Fig. 3 and

supplementary Figure S3.1). For butterflies, the importance of habitat composition increased towards the south, while for small mammals and large mammals the relative importance of landscape configuration increased towards the north. Finally, there was no clear latitudinal pattern for moths (Fig. 3 and Supplementary Figure S3.1).

Differences in species occurrence and abundance patterns between regions were mostly explained by climate, except for small mammals (Fig. 3 and supplementary figure S3.1). In contrast, habitat composition emerged as the dominant driver within regions for all taxa except moths, for whom climate and habitat were equally important in explaining species patterns. Again, the proportion of species for which a single driver explained most of the variation differed by taxa and regions (Supplementary Figure S3.5). Our findings emphasize the importance of context-dependence, given how species are differently affected by habitat composition, landscape configuration and climate within regions.

The importance of drivers varies with the functional group

Given the diversity of the focal species groups life history, we expected different responses to climate and land use to be partly attributable to species traits. In particular, body size, life history pace, and the level of specialization are expected to modulate the importance of habitat and climate on species occurrence and abundance[16,30]. Based on the literature, we expected larger, more dispersive species to be less impacted by habitat composition and landscape configuration (i.e. fragmentation), while smaller species respond more strongly to variation in both habitat and climate[31]. Similarly, species with a faster pace of life (i.e., species with short generation length or high fecundity) were expected to be less impacted by variation in both habitat and climate than those with a slower pace of life[21]. Finally, we anticipated that specialists (narrow habitat or diet breadth) vary more strongly with habitat composition than generalists[19,30] (see *Methods, Table M1 for details on the traits used*). Matching these expectations, for all taxa except butterflies, climate showed greater effects on slower pace of life species (Fig. 4 – abundance and supplementary figure S3 - occurrence). However, birds, butterflies, and moths showed no differences between generalists and specialists, nor between small and large species (Fig. 4 – abundance and supplementary figure S3 - occurrence). Conversely, for both small and large mammals' groups climate was more important for small-sized species, while habitat composition was relatively more important for larger species (Fig. 4 and supplementary figure S3). For small mammals, climate had a higher relative importance and habitat a lower relative importance for generalist species, while large mammals showed the opposite pattern (Fig. 4 and supplementary figure S3).

The shared impacts of environmental drivers

Environmental drivers often vary simultaneously and can either suppress or reinforce each other's impact on individual species[24] and biodiversity[7,9] – i.e. the impact of drivers on species distribution can be correlated with either opposite or the same direction, respectively. Independent effects between habitat and climate occurred for less than 15% of species, while correlated effects between drivers or

between drivers and random effects were common (Fig. 5 and Supplementary Figure S3.6 and S3.7; see *Methods* and [24]). Climate and habitat composition both suppressed and reinforced each other's impacts on species occurrences and abundances, while landscape configuration mostly suppressed the impact of the other drivers (Fig. 5). Specifically, we observed suppressing effects between climate, habitat composition and landscape configuration for birds (36% of species), large mammals (29%), small mammals (63%), moths (68%) and butterflies (52%), and reinforcing effects for ~ 20–52% of small mammals species (Fig. 5). Fully confounded impacts (see Fig. 1) were observed mostly between climate and landscape configuration (45% of all taxa) or between landscape configuration and habitat composition (34%).

A large proportion of taxa also displayed shared impacts (suppressing or reinforcing) between either habitat composition or climate and spatiotemporal random effects (Supplementary Figure S3.6 and S3.7), indicating that there are also other drivers of biodiversity that correlate with climate and habitat. These results demonstrate that while drivers have unique impacts on biodiversity, they seldom operate independently and highlight the tight connection between environmental drivers and their potential joint impact on species occurrences and abundances[7,8].

Discussion

While climate change has taken centre stage in current assessments of biodiversity change, our analyses reveal a complex interplay between climate and habitat composition in shaping spatiotemporal patterns of terrestrial biodiversity in Finland over the past 20 years. Habitat composition emerges as the dominant driver overall, though climate plays a significant role for some taxa, especially in terms of species-specific abundances. The relative influence of these drivers varies along the 1,100 km latitudinal gradient of Finland, with spatial context, taxonomic group, and life-history traits as key modulators. While both habitat and climate are established drivers of biodiversity change, our findings underscore their varying effects in different geographic and taxonomic contexts. Our results also unveil substantial variability in species responses to climate and habitat drivers within taxa — variation that is often obscured by averaging in models and assessments, and thus commonly overlooked [24,32]. These results reinforce the message that there is no universal response to these drivers[3,6,12,27].

Overall, species occurrences and abundances were largely explained by their surrounding habitat – but through our detailed analyses, we revealed nuances in the relative importance of impacts across taxa and space. Large mammals and moths showed the largest variation among species in the relative importance of climate and habitat. Such variation can be attributed to the diversity of species included among large mammals (moose, Eurasian otter, red squirrel, etc.), and among the vast number of moth species included in our study (*Eupithecia* weighs 5 mg while *Catocala* weighs 900 mg). However, we detected no similar variation among birds, despite their large variation in body size (e.g. capercaillie versus goldcrest). The large latitudinal gradient in climatic conditions, as well as higher climatic stochasticity towards northern Finland[33], translate into an increased importance of climate compared to

habitat composition at higher latitudes for mammals, moths and butterflies – whereas birds showed the opposite trends. This differential response observed in birds is consistent with the reported effects of local land use changes on shifts in birds' ranges and abundances, such as farmland intensification in the south of Finland[34].

Our comparison of responses across taxa highlights the complexity of terrestrial animal species' responses to environmental changes[3,27,35,36] even within functional groups[30,37,38]. Ectotherm species are often assumed to be more sensitive to climate change than endotherms[39], but their observed responses to environmental change are in fact non-uniform. Indeed, moths are a highly diverse group with species characterised by widely differing life cycles[40], and butterflies have been found to respond to multiple drivers at different scales[20,41]. In our analyses, we found that moth occurrences and abundances were largely explained by climate, while butterflies showed the highest sensitivity to landscape configuration among all taxa. Such sensitivity was detected in particular for abundance, a finding in line with past studies[42]. We also note that the scale resolution of the study can lead to different conclusions i.e. at coarse scale, climate was found to be the main driver of ¾ of Finnish butterfly species[43]. Thus, nuances —related to scale and resolution and context-dependency exist when considering taxa-specific impacts of habitat or climate for subsets of the whole community[26]. For instance, there was little difference among functional groups of butterflies and moths, except that species with a faster pace of life tended to be less sensitive to climate variability. Hence, it remains challenging to associate specific traits with responses to environmental change for Lepidoptera[44–46].

Although endotherms have been suggested to be overall less sensitive to climate change than ectotherms[38,47], mammals' responses to climate change are poorly known[36]. We found that large mammals were more affected by climate than birds, which responded strongly to habitat composition. These differences may be explained by functional traits such as migratory behaviour[29] or range size[30]. Consistent with previous findings[30], we showed that larger mammals were less sensitive to climate variability than smaller mammals, while we found little differences for other taxa. In addition, both bird and mammal species with a faster pace of life tended to be less sensitive to climate variability. Other studies focusing on dynamic situations such as altitudinal abundance[48] and latitudinal range shifts[49] have suggested that smaller bird species are more sensitive to temperature change in Fennoscandia. These studies hint that more taxa specific functional trait like migratory behaviour could help pinpoint better species sensitivity to global changes.

Support for the interplay between climate, habitat composition, and landscape configuration was detected for a large proportion of the studied species. This shared importance between two covarying drivers arises when a species responds to both[24]. We found that the effects of climate and habitat composition could either suppress (impact in opposite directions) or reinforce (impact in the same direction) each other. The interplay between climate and other drivers could hint at buffering effects[26]. Meanwhile, landscape configuration mostly suppressed the effects of the other drivers. This points to a

complex interplay between impacts of local habitat and the surrounding landscape[50], highlighting how their impacts on biodiversity cannot be easily disentangled.

Evaluating biodiversity change and its variability in response to climate and habitat impacts remains a major challenge, constrained by long-standing data limitations and analytical challenges[7,8,22]. Due to lack of data and/or mismatches in the spatial and temporal resolution between ecological and environmental datasets, many studies rely on space-for-time substitution[51], coarser distributional data[3,6,10], or are restricted to individual or few drivers[27,52]. Leveraging several high-quality and high-resolution monitoring datasets allowed us to analyse variation in species responses simultaneously for a broad range of taxa and both over a long period (20 years) and a large spatial extent. Our expanded framework enabled us to capture key variation in the relative importance of the drivers of species responses across taxa, biogeographic regions, and functional groups. Importantly, climate and habitat vary and interact at different spatial and temporal scales[43,53]. Including both drivers into our analysis allowed us to confirm that climate mainly drives coarse and latitudinal biodiversity variation in species distributions[43,54], while local conditions in habitat composition and landscape configuration better explain responses within regions and between taxa. Climate and habitat are not, however, the only defining factors for biodiversity. Further factors are at play as indicated by substantial variation attributed to the random effects of site and year included in our models. These unexplained effects are likely to be partly due to demographic and environmental stochasticity, as well as interspecific interactions inherent in ecological patterns and processes. Nonetheless, they can also represent a connection between or biased sampling along the environmental drivers[42] (e.g. mountain tundra is only found in the northernmost areas and mires are also more common in the north) or direct human impacts (e.g. exploitation of resources, pollution, invasive species)[2,14,18]. Notably, we have an imperfect ability to capture habitat and climatic drivers using Corine land cover data and climatic variables that represent coarse approximations of conditions experienced by species.

Overall, our results contribute to ongoing efforts to disentangle the effects of habitat and climate change on species[3,6,7,22], providing valuable insights into how, where and why these drivers may be important. Our results also highlight strong context dependency that should be considered when assessing species' sensitivity to climate and habitat change. Specifically, our breakdown of patterns over spatial gradients[33] and functional contexts[16,38] provides greater understanding of how species are impacted by both climate and habitat, which in turn affects how entire communities are responding to global change. Our findings suggest that current habitat and landscape remain more important drivers of biodiversity patterns than is climate. This can be turned into positive news for conservation action, since we can directly impact decisions affecting land use nationally which are easier compared to the multinational decisions determining the future of climate change. However, to arrive at effective actions, we must account for context-dependence. What this implies is that the same change and action will have different consequences in different places, at different times. As land use decisions are typically done on a local level, it is crucial to determine the factors with the highest impact on biodiversity in the given target region – an urgent goal that our findings contribute to address.

Declarations

Author contributions:

E.G., L.A., A.S, M. J., M.S., T.R., A.-L.L, and J.V.. conceived the ideas and designed the methodology; J. H., H. H., O. H., E. K., M. K., A. Le., A. Li., H. P., P. S., I-M.H. and J.P. collected the data; E.G. analysed the data; E.G. and J.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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References

1. IPBES. Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://zenodo.org/records/6417333 (2019) doi:10.5281/zenodo.6417333.
2. Jaureguiberry, P. et al. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. **8**, eabm9982 (2022).
3. Montràs-Janer, T. et al. Anthropogenic climate and land-use change drive short- and long-term biodiversity shifts across taxa. Nat. Ecol. Evol. **8**, 739–751 (2024).
4. Pereira, H. M. et al. Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. Science **384**, 458–465 (2024).
5. Brodie, J. F. & Watson, J. E. M. Human responses to climate change will likely determine the fate of biodiversity. Proc. Natl. Acad. Sci. **120**, e2205512120 (2023).
6. Suggitt, A. J. et al. Linking climate warming and land conversion to species’ range changes across Great Britain. Nat. Commun. **14**, 6759 (2023).
7. Mantyka-Pringle, C. S., Martin, T. G. & Rhodes, J. R. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Change Biol. **18**, 1239–1252 (2012).

8. Côté, I. M., Darling, E. S. & Brown, C. J. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B Biol. Sci. **283**, 20152592 (2016).
9. Santos, M. et al. The role of land use and land cover change in climate change vulnerability assessments of biodiversity: a systematic review. Landsc. Ecol. **36**, 3367–3382 (2021).
10. Neff, F. et al. Different roles of concurring climate and regional land-use changes in past 40 years' insect trends. Nat. Commun. **13**, 7611 (2022).
11. Auliz-Ortiz, D. M. et al. Underlying and proximate drivers of biodiversity changes in Mesoamerican biosphere reserves. Proc. Natl. Acad. Sci. **121**, e2305944121 (2024).
12. Pilotto, F. et al. Meta-analysis of multidecadal biodiversity trends in Europe. Nat. Commun. **11**, 3486 (2020).
13. Van Klink, R. et al. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science **368**, 417–420 (2020).
14. Pereira, H. M., Navarro, L. M. & Martins, I. S. Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources vol. 37 25–50 (2012).
15. Caro, T., Rowe, Z., Berger, J., Wholey, P. & Dobson, A. An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. Conserv. Lett. **15**, e12868 (2022).
16. Urban, M. C. et al. Improving the forecast for biodiversity under climate change. Science **353**, aad8466 (2016).
17. Newbold, T. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proc. R. Soc. B Biol. Sci. **285**, 20180792 (2018).
18. Mazor, T. et al. Global mismatch of policy and research on drivers of biodiversity loss. Nat. Ecol. Evol. **2**, 1071–1074 (2018).
19. Pacifici, M. et al. Species' traits influenced their response to recent climate change. Nat. Clim. Change **7**, 205–208 (2017).
20. Riva, F., Barbero, F., Balletto, E. & Bonelli, S. Combining environmental niche models, multi-grain analyses, and species traits identifies pervasive effects of land use on butterfly biodiversity across Italy. Glob. Change Biol. **29**, 1715–1728 (2023).
21. Albaladejo-Robles, G., Böhm, M. & Newbold, T. Species life-history strategies affect population responses to temperature and land-cover changes. Glob. Change Biol. **29**, 97–109 (2023).
22. Boennec, M., Dakos, V. & Devictor, V. Sources of confusion in global biodiversity trends. Oikos (2023).
23. Ovaskainen, O. & Abrego, N. Joint Species Distribution Modelling: With Applications in R. (Cambridge University Press, 2020).
24. Schulz, T., Saastamoinen, M. & Vanhatalo, J. Model-based variance partitioning for statistical ecology. Ecol. Monogr. **95**, e1646 (2025).
25. /4. Kunming-Montreal Global Biodiversity Framework.

26. Guilbault, E. et al. Strong context dependence in the relative importance of climate and habitat on nation-wide macro-moth community changes. J. Anim. Ecol. **94**, 1948–1961 (2025).
27. Antão, L. H. et al. Climate change reshuffles northern species within their niches. Nat. Clim. Change **12**, 587–592 (2022).
28. Aalto, J. et al. High-resolution analysis of observed thermal growing season variability over northern Europe. Clim. Dyn. **58**, 1477–1493 (2022).
29. Howard, C. et al. Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds. Divers. Distrib. **26**, 1442–1455 (2020).
30. Etard, A. & Newbold, T. Species-level correlates of land-use responses and climate-change sensitivity in terrestrial vertebrates. Conserv. Biol. **38**, e14208 (2023).
31. Hof, C. Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change. J. Exp. Biol. **224**, jeb238352 (2021).
32. Fischer, M. M. Quantifying the uncertainty of variance partitioning estimates of ecological datasets. Environ. Ecol. Stat. **26**, 351–366 (2019).
33. Aalto, J., Lehtonen, I., Pirinen, P., Aapala, K. & Heikkinen, R. K. Bioclimate change across the protected area network of Finland. Sci. Total Environ. **893**, 164782 (2023).
34. Lehikoinen, A., Johnston, A. & Massimino, D. Climate and land use changes: similarity in range and abundance changes of birds in Finland and Great Britain. Ornis Fenn. **98**, 1–15 (2021).
35. Martay, B. et al. Impacts of climate change on national biodiversity population trends. Ecography **40**, 1139–1151 (2017).
36. Paniw, M. et al. The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis. J. Anim. Ecol. **90**, 1398–1407 (2021).
37. Hällfors, M. et al. Recent range shifts of moths, butterflies, and birds are driven by the breadth of their climatic niche. Evol. Lett. https://doi.org/10.1093/evlett/qrad004 (2023) doi:10.1093/evlett/qrad004.
38. Newbold, T. et al. Global effects of land use on biodiversity differ among functional groups. Funct. Ecol. **34**, 684–693 (2020).
39. Paaijmans, K. P. et al. Temperature variation makes ectotherms more sensitive to climate change. Glob. Change Biol. **19**, 2373–2380 (2013).
40. Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S. & Woiwod, I. P. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biol. Conserv. **132**, 279–291 (2006).
41. Sunde, J. et al. Century-long butterfly range expansions in northern Europe depend on climate, land use and species traits. Commun. Biol. **6**, 1–14 (2023).
42. Heikkinen, R. K., Luoto, M., Kuussaari, M. & Pöyry, J. New insights into butterfly–environment relationships using partitioning methods. Proc. R. Soc. B Biol. Sci. **272**, 2203–2210 (2005).

43. Luoto, M., Heikkinen, R. K., Pöyry, J. & Saarinen, K. Determinants of the biogeographical distribution of butterflies in boreal regions. J. Biogeogr. **33**, 1764–1778 (2006).
44. Hällfors, M. et al. Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera. Ecol. Lett. **24**, 1619–1632 (2021).
45. Beissinger, S. R. & Riddell, E. A. Why Are Species' Traits Weak Predictors of Range Shifts? Annu. Rev. Ecol. Evol. Syst. **52**, 47–66 (2021).
46. Hill, G. M., Kawahara, A. Y., Daniels, J. C., Bateman, C. C. & Scheffers, B. R. Climate change effects on animal ecology: butterflies and moths as a case study. Biol. Rev. **96**, 2113–2126 (2021).
47. Khaliq, I., Hof, C., Prinzinger, R., Böhning-Gaese, K. & Pfenninger, M. Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proc. R. Soc. B Biol. Sci. **281**, 20141097 (2014).
48. Couet, J. et al. Short-lived species move uphill faster under climate change. Oecologia **198**, 877–888 (2022).
49. Välimäki, K., Lindén, A. & Lehikoinen, A. Velocity of density shifts in Finnish landbird species depends on their migration ecology and body mass. Oecologia **181**, 313–321 (2016).
50. Didham, R. K., Kapos, V. & Ewers, R. M. Rethinking the conceptual foundations of habitat fragmentation research. Oikos **121**, 161–170 (2012).
51. Lovell, R. S. L., Collins, S., Martin, S. H., Pigot, A. L. & Phillimore, A. B. Space-for-time substitutions in climate change ecology and evolution. Biol. Rev. **98**, 2243–2270 (2023).
52. Yazdanian, M. et al. Ecological and life-history traits predict temporal trends in biomass of boreal moths. Insect Conserv. Divers. **n/a**, 1–16 (2023).
53. Opdam, P. & Wascher, D. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol. Conserv. **117**, 285–297 (2004).
54. Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. **37**, 637–669 (2006).

Material and Methods

Monitoring data

We investigated the main drivers of spatiotemporal variation in Finnish species occurrences and abundances using high quality monitoring data for birds, butterflies, moths, large mammals, and small mammals using over 3 million records across 907 sites in Finland covering 20 years (1999-2019). Each dataset was extracted from a different monitoring program and focused on different group of species. For example, the Lepidoptera and mammalian groups came from distinct monitoring schemes, namely butterflies vs. moths and large mammals vs. small mammals. Thus, we analyse each dataset and occurrences/abundances separately. We summarize below the main aspects of the monitoring programs; more information can be found in[1] and references therein.

Birds

Bird surveys are run every year on previously established transects across Finland but not all transects are sampled every year[2]. Each sampling occasion consists of bird counts along a 3 to 6 km transect during the census period. The census period happens when bird singing activity is at its seasonal peak and when the weather is dry, but the exact dates vary with the latitude. The census period in Southern Finland starts in early June (1st to 20th), whereas that in the northernmost Finland starts later (10th to 30th). Data are curated by the Finnish Museum of National History. Sampling effort is defined by the transect length.

Butterflies

Butterfly monitoring surveys focus on agricultural landscapes and are coordinated by the Finnish Environment Institute (SYKE)[3]. Each year, weekly transect counts of butterflies are made by volunteers at least seven times during May–August. Sampling effort is a function of the transect length.

Moths

Moth surveys are coordinated by the Finnish Environment Institute (SYKE) and run by the National Moth Monitoring scheme (Nocturna)[4]. Each year, 'Jalas' light traps were sampled weekly at the same location from early spring to late autumn. The length of the sampling period is typically longer in the south than in the north, but it is set to cover the entire moth activity season across the latitudinal gradient of Finland.

Large mammals

Large mammal surveys (wildlife triangles) were established by the Natural Resources Institute Finland (Luke) and carried out by volunteers (mainly hunters)[5,6]. Each year during the winter period, snow tracks of crossing mammals over approximately 12 km perimeter triangle-shaped transects are counted. The sampling effort is a function of transect length and duration (days) over which tracks have accumulated between pre-count (or snowfall) and the actual count.

Small mammals

Small mammal monitoring surveys are carried out by the Natural Resources Institute Finland (Luke)[7]. Trapping of voles is conducted in spring (mid-April to mid-June) and autumn (mid-August to mid-October). Sampling effort is measured as the number of traps set in each trapping session multiplied by the number of nights the traps have been set for.

Study design and data preparation

We focus our analyses on data from 1999 to 2019 to match the timeline among all taxa and with the availability of high-resolution land cover data. Moreover, given the substantial number of sites and to have manageable computational running times, we used stratified sampling to subsample representative

sites in time and space for birds and mammals. Finally, we retained species with at least 40 observations in this period in our models; thus, rare species were omitted to prevent model overfitting. Overall, these criteria resulted in the following data:

- For *birds*: the dataset included 99 species across 845 sampling occasions. The species belonged to the families Alaudidae (N=1), Anatidae (N=4), Apodidae (N=1), Bombycillidae (N=1), Certhiidae (N=2), Charadriidae (N=2), Columbidae (N=2), Corvidae (N=6), Cuculidae (N=1), Falconidae (N=1), Fringillidae (N=12), Gaviidae (N=2), Gruidae (N=1), Hirundinidae (N=2), Laniidae (N=1), Motacillidae (N=4), Muscicapidae (N=5), Paridae (N=6), Passeridae (N=2), Phasianidae (N=5), Phylloscopidae (N=3), Picidae (N=4), Prunellidae (N=1), Rallidae (N=3), Regulidae (N=1), Scolopacidae (N=9), Stercorariidae (N=1), Sturnidae (N=1), Sylviidae (N=7), Turdidae (N=7),
- For *large mammals*: the dataset included 15 species across 2132 sampling occasions. The species belonged to the families Canidae (N=3), Cervidae (N=3), Felidae (N=1), Leporidae (N=2), Mustelidae (N=5), Sciuridae (N=1).
- For *small mammals*: the dataset included 10 species across 803 sampling occasions. All species belong to the following families: Cricetidae (N=4), Muridae (N=1) and Soricidae (N=3).
- For *butterflies*: the dataset included 57 species across 922 sampling occasions. All species belong to the following families: Hesperiidae (N=5), Lycaenidae (N=16), Nymphalidae (N=26), Papilionidae (N=1) and Pieridae (N=9).
- For *moths*: the dataset included 319 species across 1080 sampling occasions. All species are "macromoths" from the following families: Drepanidae (N=8), Endromidae (N=1), Erebidae (N=33), Geometridae (N=132), Lasiocampidae (N=3), Noctuidae (N=123), Nolidae (N=3), Notodontidae (N=12), Sphingidae (N=4).

Environmental variables

Climatic data

We extracted climatic variables at the site level for each year from the Finnish Meteorological Institute[8]. From the 10 × 10 km gridded daily climatology dataset, we calculated the annual mean temperature, cumulative annual precipitation, and the number of days of snow cover at each sampled site.

Habitat data

To characterise the landscape around the sampling sites, we calculated 1) habitat composition as the proportions of various habitat types and 2) landscape configuration as the level of fragmentation and habitat diversity of all habitat types within a buffer around each sampling site (Figure M1). We used the CORINE land cover (CLC) database[9] for the years 2000, 2006, 2012 and 2018. We converted CLC data to a pixel resolution of 20 × 20 meters using the R package terra[10] and reclassified each pixel into one of five broad aggregated habitat categories: urban, crops, forest, semi natural – herbaceous – pastures (SHP), and wetland (for the relation to original CORINE© classes, see Supplementary Table S1.1).

Species samples were matched to habitat information from the closest year available (CLC year 2000 was used for sampling years- 1999 to 2003, etc.). After this classification, we calculated the following habitat features over 500 m, 1 km, 2 km, 4 km and 6 km buffers around the sampling sites (Extended Data Figure 1, Supplementary Table S1.2):

1. Habitat composition: Proportions of the five habitat types (urban, crops, forest, SHP, and wetland).

2. Landscape configuration:

- Overall landscape fragmentation of all original CLC categories calculated by the FracCV index using the R package landscapemetrics[11,12].

- Diversity of habitat types of all original CLC categories estimated with the number of distinct habitat types within the buffer.

Trait information

To evaluate whether groups of species within the taxa studied display similar patterns of driver importance, we gathered information on traits that may relate to species' ability to adapt to changes in their environment (Extended data Table 1). We selected traits reflecting species' ability to move[13,14], their habitat or diet preferences (specialists versus generalists)[15,16] and life history (pace)[17]. The wing and body size measures were the only continuous traits; thus, we categorized them to obtain groups of similar size species. All other traits were categorical and grouped into two levels to simplify the conditional variance partitioning analysis.

Joint species distribution modelling

To evaluate the relative effects of different drivers, we fitted a hierarchical joint species distribution model to either annual species occurrence or abundance data for each taxon using the R package Hmsc[18]. We used a probit model for species presence-absence and a lognormal Poisson model for species abundance observations[19]. We included as fixed effects climatic and habitat covariates, as well as sampling effort on a log scale measured at each site according to the monitoring scheme for the focal taxon (see *Monitoring scheme and species data*). The following covariates were added to the model with a second order polynomial term to allow for a unimodal response: annual mean temperature, cumulative annual precipitation, number of days of snow cover, and proportion of the different land cover categories. The remaining covariates (landscape fragmentation and diversity, effort) were modelled as simple linear terms. Finally, to account for any additional variation not measured by our environmental variables, we included site, year, and biogeographical region as random effects. We pooled the two southernmost biogeographical regions in Finland (hemiboreal and south boreal) to obtain 3 regions: south boreal (SB), middle boreal (MB) and north boreal (NB) (Figure 1). To facilitate the analysis of our large datasets in a spatially explicit context, we constructed the site random effect as a spatially structured random effect using the Gaussian Predictive Process approach[20].

We performed posterior sampling using four Markov Chain Monte Carlo (MCMC) chains, each collecting 250 samples, yielding a total of 1,000 samples. We used a thinning interval of 1000 and excluded the first 125,000 iterations as burn-in, only sampling the subsequent 250,000 iterations per chain.

We ran Hmsc models for three consecutive purposes: (1) evaluating the sensitivity of results on the buffer size on a subset of the data, (2) evaluating the sensitivity of variance partitioning results to grouping of variables, and (3) final model on the full datasets.

1. Given that species may respond to drivers at various scales, we fitted Hmsc models with 5 buffer sizes (500 m, 1 km, 2 km, 4 km, 6 km) for the habitat and landscape information (see *Habitat data*). We randomly selected 5 years and 100 sites for each taxon dataset and ran models with all covariates using the above-mentioned buffer sizes. For small mammals, we included all available sites. We compared cross-validated Tjur R^2 values across buffer sizes for each taxon and chose the buffer size with the highest Tjur R^2 for the final analyses (step 3 below). For each model, the MCMC convergence was assessed by visual evaluation of the sample chains and with the potential scale reduction factor for the beta parameters[21]. Results are shown in Supplementary S2.A.

2. Given that our groups of environmental drivers included different numbers of variables, we evaluated how sensitive fractions of explained variance attributed to climate vs habitat were to the number of covariates within each of these groups (i.e. climate vs habitat drivers). Thus, we compared the models run in (1) at the chosen buffer size to two other models: a model where habitat drivers were summarized via three PCA axes to match the number of climate covariates, and a model where some habitat categories' proportions were combined to match the number of climate covariates (forest cover was grouped with the cover of other (semi)natural vegetation types and urban land cover was merged with crop cover). See Supplementary 2.B for these results.

3. Once we had selected the best performing buffer size (highest mean Tjur R^2) for each taxon, we ran the models with the chosen buffer size for the full datasets (Supplementary S2.A). We repeated the performance measure analyses (cross-validation, convergence assessment) in addition to calculating AUC and Tjur R^2 as measures of model fit and discriminatory power.

Quantifying the relationship between drivers and species occurrences and abundances using variance and covariance partitioning

To quantify the relative importance of each group of drivers of change, we partitioned the variability in the linear predictor among the three drivers (climate, habitat composition and landscape configuration). Variance partitioning[22] is widely used to evaluate the relative contributions of multiple drivers in explaining species distribution patterns[21–24]. In our context, it measures the impact of environmental variability on variability in species' occurrences and abundances through space and time. To answer our questions regarding spatial and functional context dependency in the importance of the drivers, we also

calculated conditional variance partitioning[22,25] between/within sites grouped by biogeographical regions and between/within species grouped by traits.

The marginal variance partition is the sum of the unique (i.e., variability that does not correlate with other drivers) and shared (i.e., variability that correlates with other drivers) contributions of the drivers to the variability in species occurrence and abundance[22] (Figure 1C). To disentangle them into the three groups of environmental variables (i.e., climatic variables, habitat composition and landscape configuration), and into random effects, we followed the procedure from Schulz et al. (2025; Table 2) for all species that expressed larger than 1% correlation between any two groups of drivers i.e. linear terms (otherwise the drivers were assumed to have independent effects only). We also calculated the partial variance partition (the unique explained variance of a driver[22]) to assess whether the shared contributions amplify or suppress the variability in species occurrence and abundance[22]. Such shared contributions arise from covariation among two drivers that simultaneously impact a species' occurrence or abundance. All variance partition measures were weighted by Tjur R^2 (occurrence model) or R^2 (abundance model) to account for the overall explained variability in species occurrences and (log) abundances.

References:

1. Antão, L. H. *et al.* Climate change reshuffles northern species within their niches. *Nat. Clim. Change* **12**, 587–592 (2022).

2. Virkkala, R. & Lehikoinen, A. Patterns of climate-induced density shifts of species: Poleward shifts faster in northern boreal birds than in southern birds. *Glob. Change Biol.* **20**, 2995–3003 (2014).

3. Heliölä, J., Huikkonen, I.-M. & Kuussaari, M. Maatalousympäristön päiväperhosseuranta 1999–2021. (2022).

4. Leinonen, R., Pöyry, J., Söderman, G. & Tuominen-Roto, L. Suomen yöperhosyhteisöt muutoksessa—valtakunnallisen yöperhosseurannan keskeisiä tuloksia 1993–2012. *Baptria* **42**, 74–92 (2017).

5. Helle, P., Ikonen, K. & Kantola, A. Wildlife monitoring in Finland: online information for game administration, hunters, and the wider public. *Can. J. For. Res.* **46**, 1491–1496 (2016).

6. Lindén, H. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finn Game Res* **49**, 4–11 (1996).

7. Korpela, K. *et al.* Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Glob. Change Biol.* **19**, 697–710 (2013).

8. FMI. Finnish Meterological Institute. https://en.ilmatieteenlaitos.fi/seasons-in-finland (2022).

9. Feranec, J. Project CORINE Land Cover. *Eur. Landsc. Dyn. CORINE Land Cover Data* 9–14 (2016).

10. Hijmans, R. J. terra: Spatial Data Analysis. *R Package Version 13-22* https://CRAN.R-project.org/package=terra (2021).

11. Hesselbarth, M. H., Sciaini, M., With, K. A., Wiegand, K. & Nowosad, J. landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography* **42**, 1648–1657 (2019).

12. Wang, X., Blanchet, F. G. & Koper, N. Measuring habitat fragmentation: an evaluation of landscape pattern metrics. *Methods Ecol. Evol.* **5**, 634–646 (2014).

13. Hof, C. Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change. *J. Exp. Biol.* **224**, jeb238352 (2021).

14. Valtonen, A. *et al.* Long-term species loss and homogenization of moth communities in Central Europe. *J. Anim. Ecol.* **86**, 730–738 (2017).

15. Etard, A. & Newbold, T. Species-level correlates of land-use responses and climate-change sensitivity in terrestrial vertebrates. *Conserv. Biol.* **38**, e14208 (2023).

16. Pacifici, M. *et al.* Species' traits influenced their response to recent climate change. *Nat. Clim. Change* **7**, 205–208 (2017).

17. Albaladejo-Robles, G., Böhm, M. & Newbold, T. Species life-history strategies affect population responses to temperature and land-cover changes. *Glob. Change Biol.* **29**, 97–109 (2023).

18. Tikhonov, G. *et al.* Joint species distribution modelling with the R-package Hmsc. *Methods Ecol. Evol.* **11**, 442–447 (2020).

19. Ovaskainen, O. *et al.* How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.* **20**, 561–576 (2017).

20. Tikhonov, G. *et al.* Computationally efficient joint species distribution modeling of big spatial data. *Ecology* **101**, e02929 (2020).

21. Ovaskainen, O. & Abrego, N. *Joint Species Distribution Modelling: With Applications in R*. (Cambridge University Press, 2020).

22. Schulz, T., Saastamoinen, M. & Vanhatalo, J. Model-based variance partitioning for statistical ecology. *Ecol. Monogr.* **95**, e1646 (2025).

23. Legendre, P., Borcard, D. & Peres-Neto, P. R. Analyzing Beta Diversity: Partitioning the Spatial Variation of Community Composition Data. *Ecol. Monogr.* **75**, 435–450 (2005).

24. Heikkinen, R. K., Luoto, M., Kuussaari, M. & Pöyry, J. New insights into butterfly–environment relationships using partitioning methods. *Proc. R. Soc. B Biol. Sci.* **272**, 2203–2210 (2005).

25. Guilbault, E. *et al.* Strong context dependence in the relative importance of climate and habitat on nation-wide macro-moth community changes. *J. Anim. Ecol.* **94**, 1948–1961 (2025)

Figures

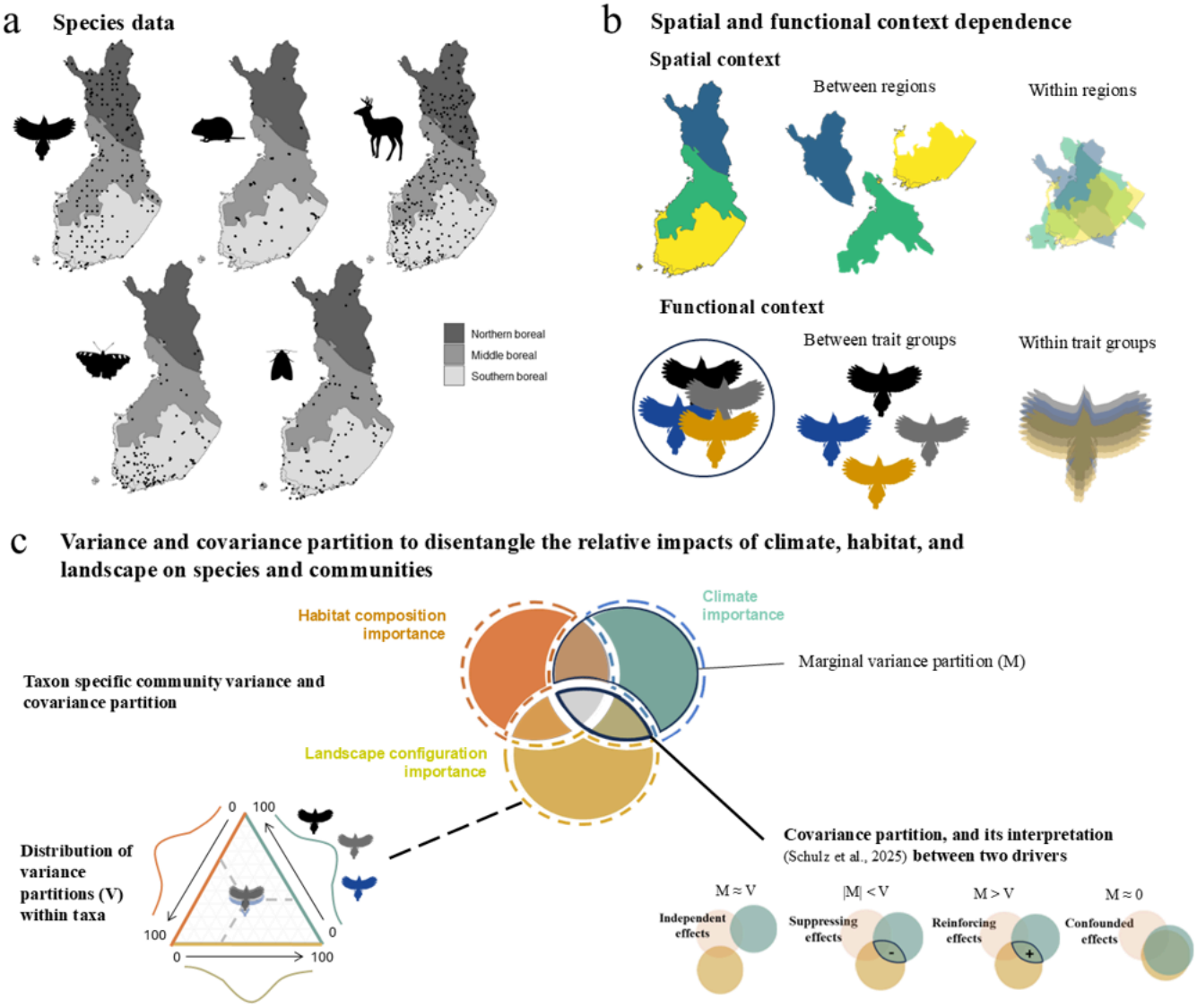

Figure 1

Conceptual framework. *Spatial distribution of sampling sites per taxon (a), different spatial and functional contexts considered in the analyses (b), and conceptual scheme of the variance partition framework (c). Habitat composition, landscape configuration and climate group of drivers are detailed in Environmental variables (Methods).*

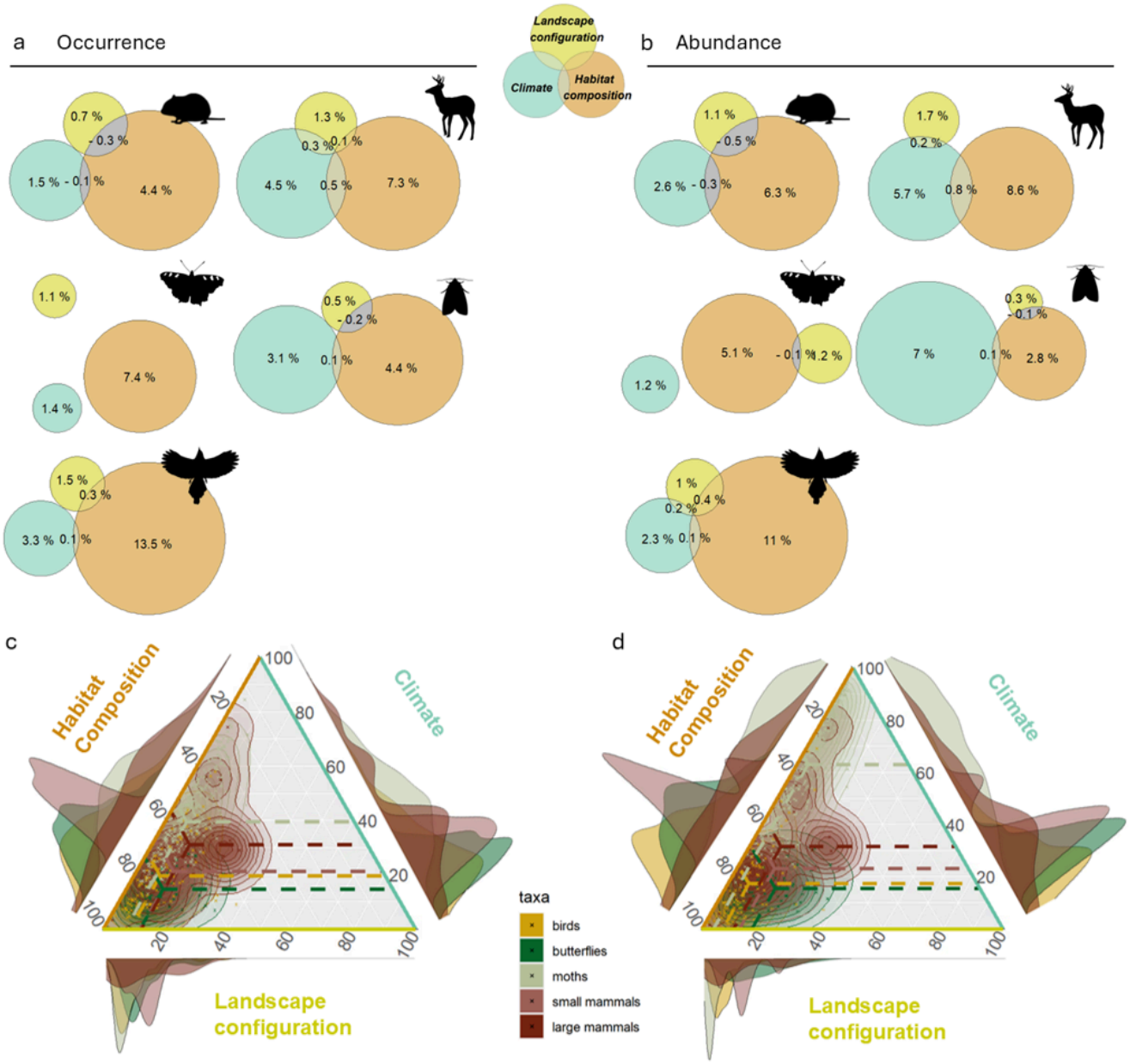

Figure 2

Habitat explains most of the variation in Finnish species occurrences and abundances. *The Venn diagrams at the top show the average variance and covariance partition across species in each taxon for occurrence (a) and abundance (b) patterns. The diagrams indicate the proportion of variance explained by each driver (i.e., habitat composition, landscape configuration or climate, represented by different colours) on a scale of 0–100%. The covariance partitions (i.e. the intersection between colours) show the proportion of explained variance shared between two drivers. Ternplots at the bottom show the distribution in variance partition values between the three drivers (normalized to sum to 100) among species in each taxon (colours) for occurrence (C) and abundance (D) patterns; the kernel densities represent the joint values, while the density plots outside the triangles show the marginal values for each driver.*

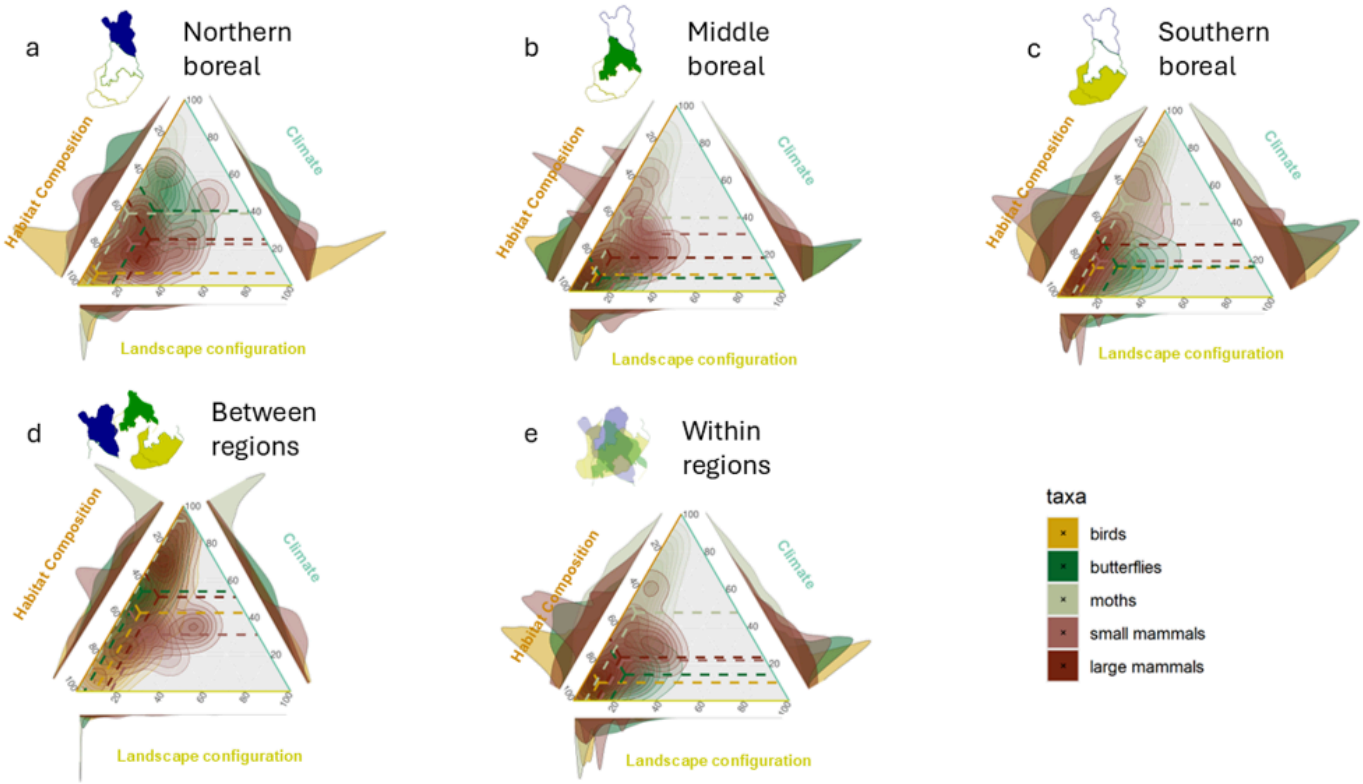

Figure 3

Conditional, within- and between-regions relative variance partition for abundance data. *Ternplots show the distribution in relative variance partition between the three drivers (sum to 100) among species in each taxon (colours); the kernel densities represent the joint values, while the density plots outside the triangles show the marginal values for each driver. Each subplot shows the relative variance partition for each biogeographical region (A, B & C), between (D) and within (E) regions.*

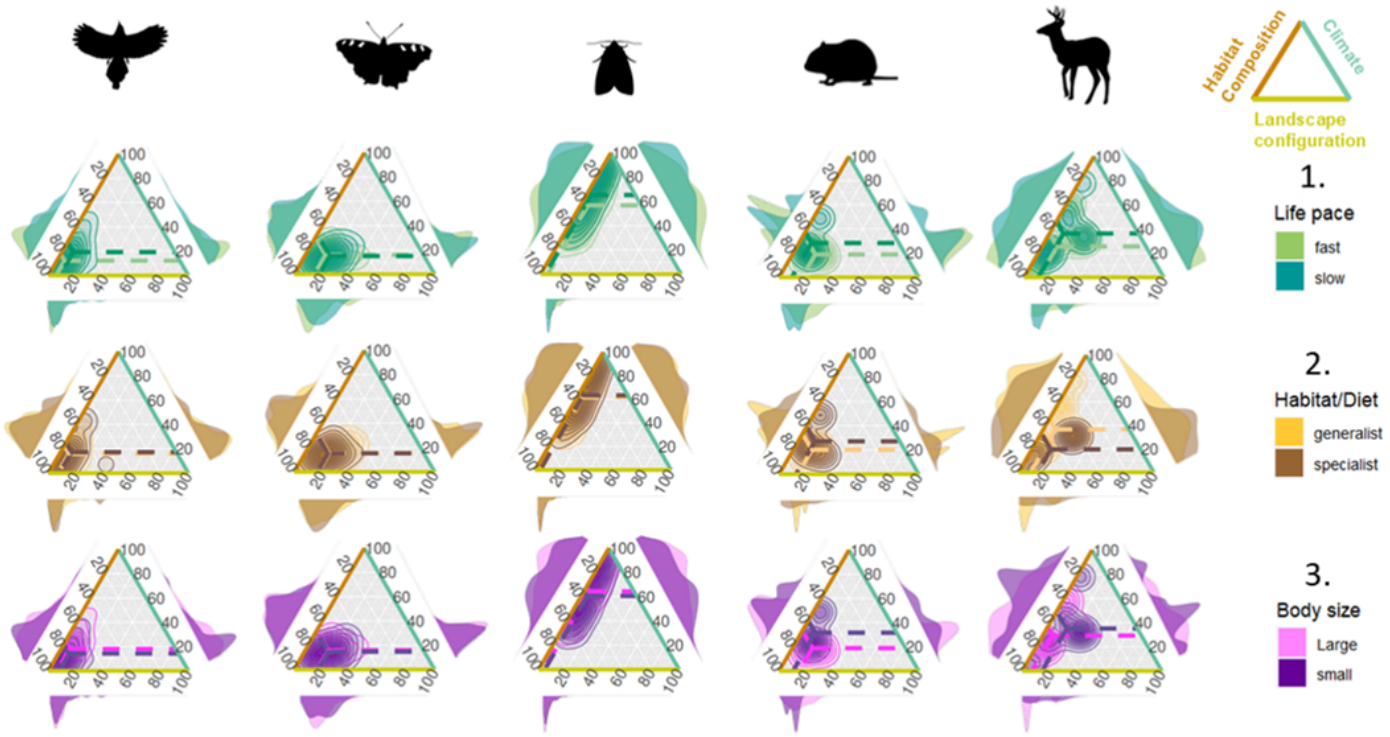

Figure 4

Trait-based relative variance partition summaries for abundance data. *Ternplots show the distribution in relative variance partition between the three drivers (sum to 100) among species in each taxon (colours); the kernel densities represent the joint values, while the density plots outside the triangles show the marginal values for each driver. Each column represents a taxon and each row a trait: 1. Life history pace (slow versus fast), 2. habitat/diet specialization (specialist versus generalist) and 3. Body size (small vs large), represented by different colours.*

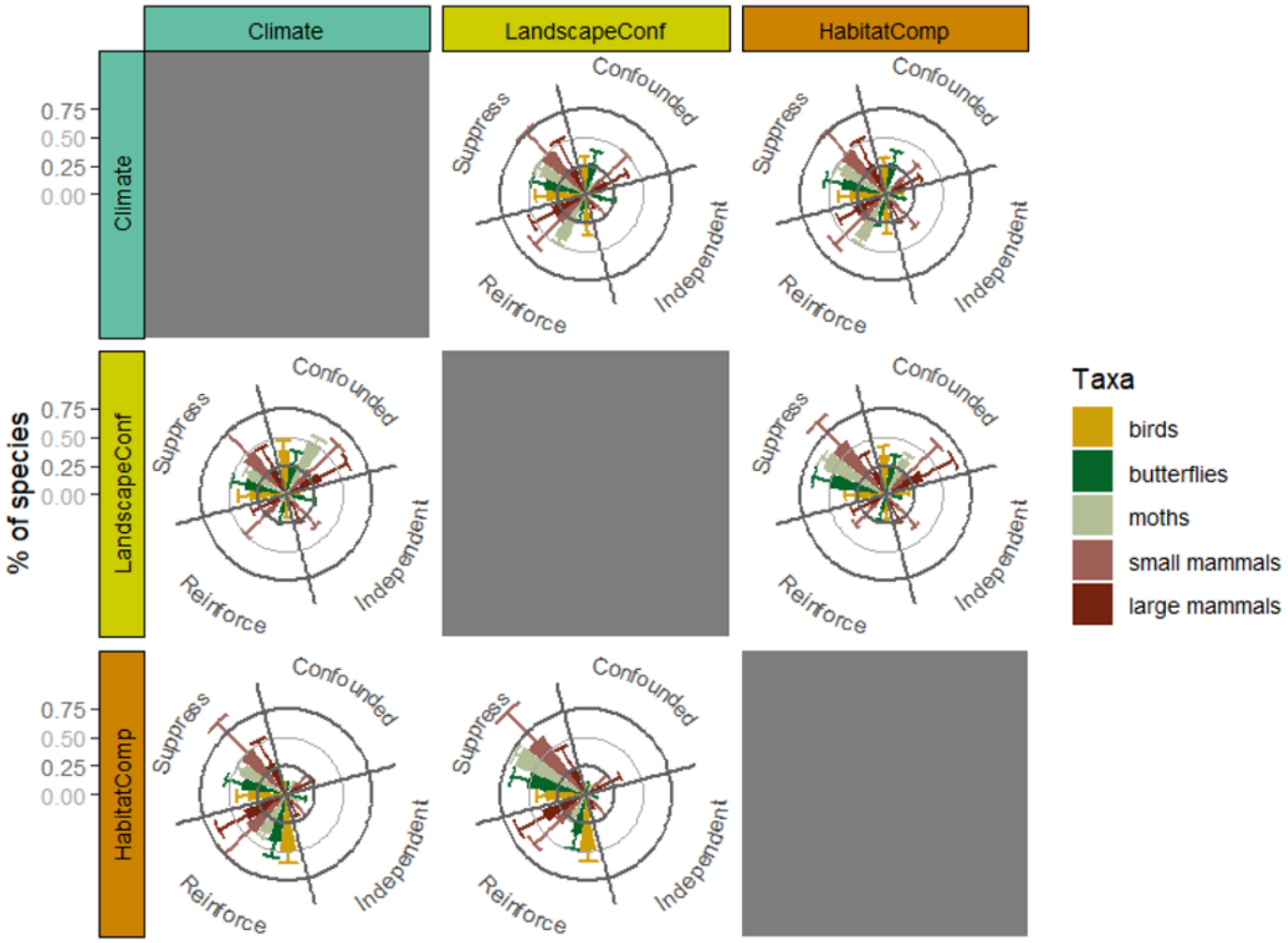

Figure 5

Proportion of species expressing independent variation along the focal (rows) environmental driver or suppressing, reinforcing, or confounded joint impact between the focal and another (columns) environmental driver in their abundance. *Each panel displays one pairwise covariance partition (posterior mean with a bar and the 95% credible interval with error whiskers).*

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ExtendedFig1.tif
- ExtendedTable1.tif
- Supplementarymaterial.docx