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Opinion

Improving Predictions of Climate Change–Land Use Change Interactions

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Climate change and land use change often interact, altering biodiversity in unexpected ways. Research into climate change–land use change (CC–LUC) interactions has so far focused on quantifying biodiversity outcomes, rather than identifying the underlying ecological mechanisms, making it difficult to predict interactions and design appropriate conservation responses. We propose a risk-based framework to further our understanding of CC–LUC interactions. By identifying the factors driving the exposure and vulnerability of biodiversity to land use change, and then examining how these factors are altered by climate change (or vice versa), this framework will allow the effects of different interaction mechanisms to be compared across geographic and ecological contexts, supporting efforts to reduce biodiversity loss from interacting stressors.

Highlights

Climate change–land use change (CC–LUC) interactions have a wide range of effects on biodiversity.

Current research focuses on classifying interaction types by identifying unexpected biodiversity outcomes under combined climate change and land use change.

The mechanisms underpinning these interactions are often overlooked, limiting our ability to predict biodiversity change and inform conservation responses.

The concept of risk focuses attention on how climate change alters the exposure, sensitivity, and adaptive capacity of biodiversity in the face of land use change (and vice versa).

Risk frameworks can improve our understanding of CC–LUC interaction mechanisms, offering a method for identifying species and ecosystems at risk from these interactions, as well as for targeting conservation responses.

Predicting Biodiversity Change When Stressors Interact

Climate change and land use change are two major drivers of biodiversity change [1–3]. Predicting the effects of climate change and land use change on biodiversity is necessary to inform effective conservation strategies and ultimately safeguard biodiversity and the benefits that humans derive from it [4]. The impacts of both drivers on species and ecosystems have been extensively studied in the past, mostly separately from each other [5], and are relatively well understood. However, there is a rapidly growing body of evidence showing that climate change and land use change do not always affect biodiversity independently from each other, meaning that climate change alters the impact of land use change on biodiversity, and vice versa [6]. It is these combined effects, or so-called climate change–land use change (CC–LUC) interactions, that are comparatively less well understood.

Most research into CC–LUC interactions has focused on identifying situations in which the combined impact of climate change and land use change could have dramatic negative effects on species or ecosystems [7]. For instance, land use change often reduces habitat availability and landscape connectivity, thereby reducing carrying capacity and dispersal between neighbouring populations, and increasing their sensitivity to extreme events. Specifically, populations fragmented or isolated by land use change are at a higher risk of decline and extinction as extreme climatic events become more frequent due to climate change (Figure 1) [8]. However, since climate change does not always exacerbate the effects of land use change on biodiversity and vice versa [9,10], it is equally important to predict neutral or positive, as well as negative, outcomes to help improve targeting of management and policy interventions.

Climate change and land use change, and their interactions, operate across different scales, posing challenges to effective conservation planning, resourcing, and management. At the regional to global level, accounting for CC–LUC interactions could change conservation prioritisation hierarchies of ecosystems and species [11], highlighting the need to identify species and ecosystems at the highest risk of adverse outcomes from CC–LUC interactions. At the site level, CC–LUC

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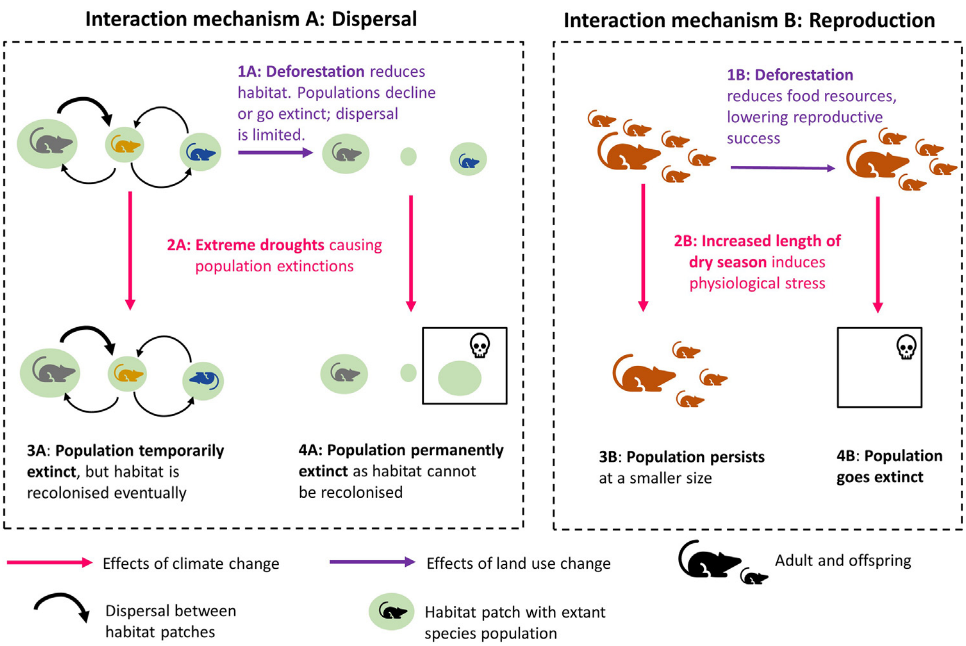

Figure 1. Multiple Mechanisms Drive Climate Change–Land Use Change Interactions. In this example, a combination of climate change and land use change drives population extinction in both scenarios, but interaction mechanisms differ. In scenario A (left panel), deforestation reduces habitat availability (green patches), reducing the size of three hypothetical populations and, in some cases, leading to their extinction. Dispersal between these populations is also reduced (1A). Climate change may also drive population declines, for example, by increasing the frequency of extreme droughts (2A). In absence of deforestation, these declines may be reversed by dispersal and recolonisation (inverted rodent icon, 3A). However, in conjunction with deforestation, recolonisation of habitat patches is impossible, leading to local extinction of some populations (skull icon; 4A). In scenario B (right panel), habitat clearance reduces availability of food resources, leading to lower reproductive success (fewer offspring), and therefore population decline, in a hypothetical population (1B). Climate change may also reduce reproductive rates in this population, for instance by increasing aridity, inducing physiological stress (2B). Habitat clearance again mediates the effect of climate change on the population: in its absence the population declines in size, but persists (3B), whereas climate change in conjunction with habitat clearance leads to population collapse and local extinction (4B).

interactions could affect which biodiversity management options have the greatest effectiveness [12]. Understanding the potential impacts of CC–LUC interactions on biodiversity will therefore provide critical information to guide effective conservation interventions and to mitigate against the impacts of anthropogenic global change at local and regional levels [13].

Despite substantial progress in our understanding of interactions between climate change and global change stressors [14], including decades of research into CC–LUC interactions, we currently have little ability to predict when and where these interactions are going to happen, and how they are likely to affect biodiversity [7]. Predicting CC–LUC interactions is challenging because climate change, land use change and biodiversity are all multidimensional concepts [15–17], resulting in a high number of possible interactions. For instance, climate change can entail changes in average temperature, shifts in season, or a change in the frequency of extreme events, which may interact with a multitude of land use change effects, ranging in intensity from land conversion such as deforestation to more subtle changes in land management (e.g., altering fertiliser regimes). As a result, predicting the presence, type, and magnitude of CC–LUC interactions by looking at each potential driver combination in turn is unlikely to provide comprehensive insights into the effects of multiple drivers and their interactions. Additionally, CC–LUC interactions are likely to be shaped by interspecific interactions and trophic cascades [18,19]. This is further complicated by the fact that biodiversity responses at different organisational scales (e.g., individual behaviour, population size, and species composition) can play out over different timescales, and that CC–LUC interactions can change over time [20].

To address the challenges in predicting and managing CC–LUC interactions, we (i) summarise recent research into CC–LUC interactions; (ii) demonstrate the need to expand this research, which is currently focused on quantifying biodiversity outcomes, by focusing on the mechanisms underpinning these interactions; and finally (iii) propose a risk-based framework as a way to efficiently identify key mechanisms governing the outcome of CC–LUC interactions in different ecological contexts.

CC–LUC Interactions: Current State of Play

What We Know so Far

To identify the main gaps in our understanding of CC–LUC interactions, we collated a representative sample of peer-reviewed studies (including empirical studies, meta-analyses, and reviews) that explicitly discuss or quantify an interaction between climate change and land use change in the context of their effects on terrestrial and freshwater biodiversity (see supplemental information online for methodology). We excluded the marine realm since land use change does not directly affect large parts of the oceans. We did not consider studies which only show that climate change alters the rate of land use change, or vice versa [6]. Although such studies identify situations in which biodiversity is affected by combined climate and land use change (and that there is thus a chance for CC–LUC interactions to occur), they do not directly consider how the impacts of climate change on biodiversity are altered by land use change (and vice versa).

We considered 69 studies focusing on the combined effects of climate change and land use change on biodiversity (see supplemental information online for a complete list). These studies addressed numerous features of biodiversity, including the distribution of individual species [21,22], species abundance [23], response to disturbance dynamics [24], species diversity [25,26], or ecosystem composition and processes [27,28]. Across these studies, we found two predominant empirical approaches to investigating CC–LUC interactions. First, some analyses compared biodiversity outcomes between scenarios of no climate and land use change, either climate or land use change, and combined climate and land use change [29–31]. Second, other analyses tested a dose–response relationship between climate, land use, an interaction term, and biodiversity variables using a statistical model [32–34]. Only eight of the empirical studies directly investigated interaction mechanisms (Table 1) [9,35–41]. However, all 11 reviews retrieved by our literature search explicitly discussed mechanisms through which climate change could alter the impact of land use change on biodiversity, and vice versa (Table 1).

Studies of CC–LUC interactions are drawn from different research fields with an emphasis on either climate, land use, or biodiversity science, and thus would benefit from a shared, unifying framework to interpret and extract general patterns from the results. Previous attempts to provide such a framework – based on studies of interactions between different stressors (including, but not limited to, climate change and land use change) – have focused on classifying interactions based on how realised outcomes differ from expected outcomes; that is, those occurring in the absence of an interaction [42–44]. These classifications tend to distinguish between: (i) independent effects (cases where climate change does not change the effect of land use change on biodiversity, or vice versa); (ii) antagonistic effects (cases where climate change reduces the strength of the effect that land use change has on biodiversity, or vice versa); and (iii) synergistic effects (cases in which climate change increases the strength of the effect of land use change on biodiversity). Sometimes, a so-

Table 1. Overview of Known or Hypothesised CC–LUC Interaction Mechanisms

Interaction mechanism[a]	Description	Refs
Microclimate refugia	Land use change alters the structure of the vegetation canopy and the litter layer, as well as drainage patterns, and thus can create microclimates that either accentuate or reduce sensitivity to climate change.	[8,33,36,37,63]
Disturbance responses	Climate change reduces the resistance and/or resilience of ecosystems to disturbance caused by land use change (e.g., by delaying recovery from habitat disturbance), and vice versa, thereby increasing risk.	[8,64,65[b]]
Range shifts	Land use change can hinder adaptive range shifts, including access to climate refugia, reducing the habitat available to a species affected by climate change. Conversely, climate change can prevent the expansion of species into habitat that land use change has made suitable (e.g., due to forest clearance or abandonment of cultivation).	[8,9,41,66–70]
Natural selection	Land use change can reduce local effective population size or gene flow, potentially reducing or counteracting selection for genotypes that increase fitness under climate change, and thus reducing adaptive capacity. Conversely, climate change can lead to genetic homogenisation of populations, potentially reducing their capacity to adapt to new ecological conditions caused by land use change.	[71[b],72[b]]
Genetic constraints	Coadaptation to climate change and land use change could be difficult because of antagonistic pleiotropy (i.e., the same genes confer high fitness under climate change but low fitness under land use change, or vice versa), or epistasis (i.e., genetic interdependence) of traits conferring high fitness in the presence of one driver but low fitness in the presence of another. This mechanism reduces the capacity of a population to adapt to either stressor in the presence of the other.	[8,73[b]]
Metapopulation dynamics	Land use change can lower the size of habitat patches and increase the effective distance between them. Thus, species populations may decline or disappear within patches, and incur reduced connectivity or genetic transfer between patches (e.g., by constraints on dispersal of individuals or propagules), increasing the sensitivity of metapopulations to climate change.	[4,8,66–68,74–77]
Community filtering	Species can be cotolerant or cosensitive to climate change and land use change, suggesting that the sensitivity of communities to subsequent climate change depends on whether they have already been 'filtered' by land use change, and vice versa.	[38,39,78,79]
Portfolio effect	Land use change can increase sensitivity of species communities to climate change by decreasing species richness and functional diversity. This is because such declines decrease the so-called portfolio effect whereby apparent high redundancy provides greater insurance or resilience in the face of climate change.	[40]
Antagonistic interaction	Antagonistic species (e.g., predator, pathogen, dominant competitor) can benefit from changes to habitat associated with land use change, increasing sensitivity to climate change for associated species (e.g., prey, host, subordinate competitor). Similarly, the risk of disease can be elevated by climate change (especially warming temperatures), reducing the resilience of populations to land use change.	[32,35,80,81[b]]
Mutualistic interaction	Climate change can disrupt mutualistic interactions by driving asymmetric range shifts or asynchronous phenology, for example, between plants and their pollinators, thereby reducing population size and theoretically increasing sensitivity to land use change. Similarly, land use change can theoretically fragment populations of codependent mutualists and increase their sensitivity to phenological mismatches or other effects of climate change.	[82[b],83[b]]
Community rearrangement	A species community can adapt to climate change by shifting community trait distributions to match the new climatic conditions. Land use change could decrease the capacity of communities to adapt by limiting the arrival of new species whose traits match the new climatic conditions.	[84[b]]

[a]Examples are given of mechanisms by which climate change can alter the sensitivity of biodiversity to land use change, or its capacity to adapt to land use change (and vice versa).
[b]Indicates references not captured by the systematic literature search.

called dominance effect is included whereby climate change reduces the effect of land use change to zero, or vice versa [45,46], although dominance effects are more commonly framed as an alternative null model describing an independent effect [47,48].

Issues with the Current Approach

The current approach to researching CC–LUC interactions makes it difficult to synthesise insights from empirical studies that can predict the prevalence and effect of CC–LUC interactions. One reason for this is that there is no standard approach to formally define interaction types: what may be termed, for example, synergy by one study may not be considered an interaction at all, or an antagonistic interaction, by another [7]. To overcome this challenge, however, it is not enough to develop a consensus on how interactions are classified based on the difference between expected and observed outcomes. What outcomes are expected always depends on the chosen null model; that is, the expected biodiversity outcome if no CC–LUC interaction occurs. This means that the choice of null model affects whether an interaction is classified as independent, antagonistic, or synergistic. Often, however, null models are not explicitly chosen but imposed by the choice of statistical methods. As a result, there are now efforts to standardise null model choice in stressor interaction research to account for known differences in the mechanisms driving the effects of single stressors on biodiversity [48] and thus to enable direct comparison of results and the synthesis of insights across studies.

However, standardising the way we measure and classify outcomes of CC–LUC interactions is by itself insufficient for the development of predictive power. For this, we need an improvement in our understanding of the mechanisms underlying CC–LUC interactions. Since climate change, land use change, and biodiversity each have multiple dimensions, interactions that are classified as synergistic (or antagonistic or independent, respectively) are likely to include cases from many different geographic and ecological contexts, which may not be directly comparable. For instance, change in species richness, abundance or interactions due to habitat loss may depend on climate change, but how it depends on climate change varies between biomes and taxonomic groups [49]. The type, strength and direction of CC–LUC interactions is therefore shaped by a range of different biological or ecological processes (Figure 1 and Table 1) – put differently, the surprising outcomes that characterise CC–LUC interactions likely result from different mechanisms, depending on geographic and ecological context.

Using Risk-Based Frameworks to Predict Interactions

The mechanistic pathways by which climate change and land use change interact are best identified using a framework based on risk, as this can improve our ability to predict the outcomes of CC–LUC interactions on biodiversity. Risk is the likelihood of an adverse outcome resulting from an external hazard, and can be conceptualised as a function of the exposure to this hazard, as well as the intrinsic vulnerability of any particular entity to it [50,51], where vulnerability is determined by sensitivity and adaptive capacity [52]. In a biodiversity context, species, communities, or ecosystems with high exposure and high vulnerability are at a higher risk of an adverse outcome than other species, communities, or ecosystems (Figure 2) [53]. Overall risk can be estimated by: (i) identifying indicators for each risk component (exposure, sensitivity, adaptive capacity) [54], so that each indicator represents a process that affects the risk of an adverse outcome, then (ii) deriving an overall risk estimate, typically by combining scores from different risk components either qualitatively [55] or quantitatively [56].

Risk-based frameworks have previously been used to identify the risk of single stressors such as climate change on species [53,57], and have been adapted to include observed outcomes of interactions between two stressors [58]. Building on this work, we propose a novel application of

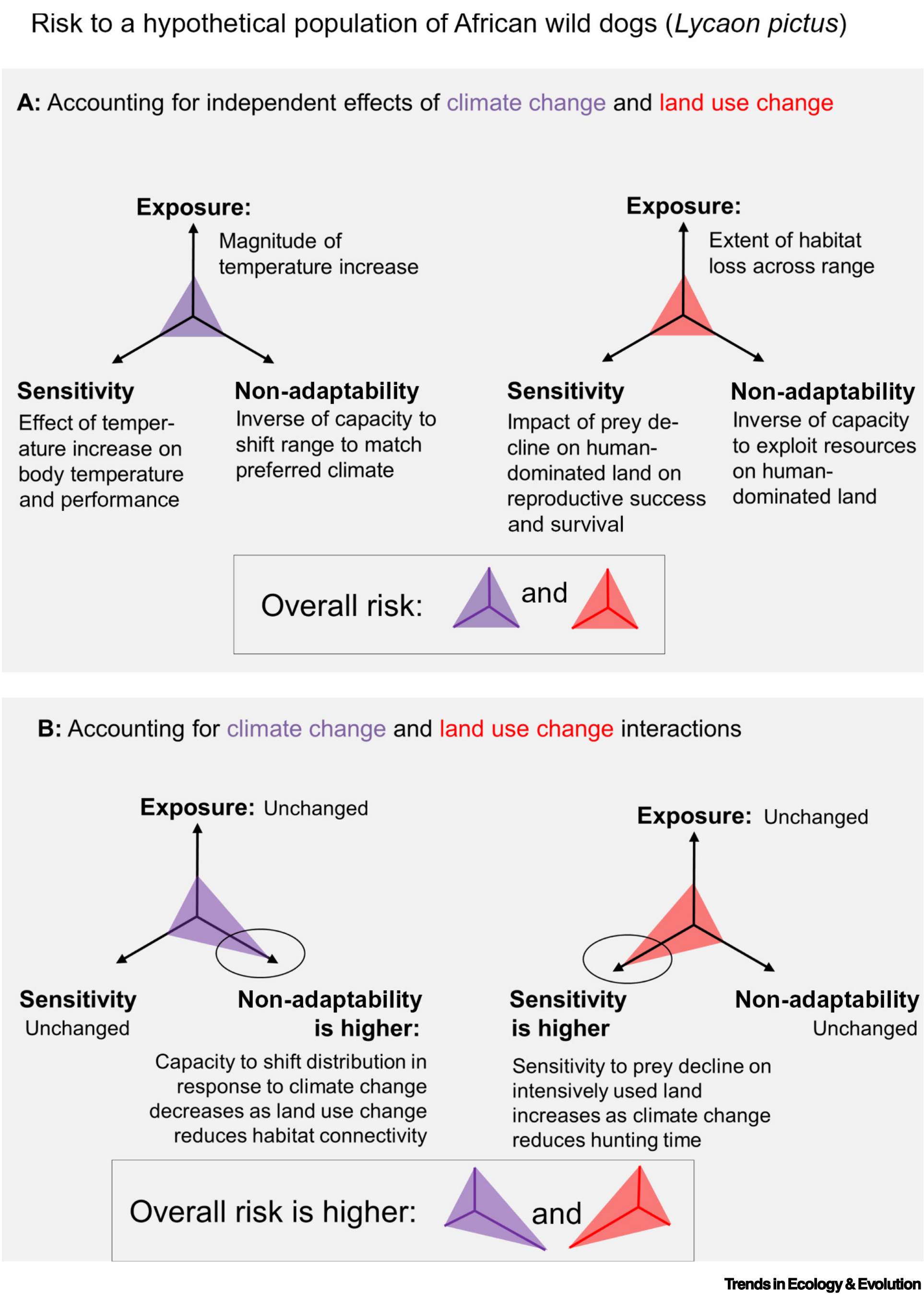

Figure 2. Using the Concept of Risk to Conceptualise Interactions between Biodiversity Stressors. These diagrams illustrate the approach as applied to a hypothetical African wild dog (*Lycaon pictus*) population. The risk of biodiversity change in response to a single stressor is determined by different risk components; the overall risk increases as each component increases. These components are exposure to a hazard (the rate or magnitude of the stressor that biodiversity experiences), and vulnerability of biodiversity to this hazard, which is determined by sensitivity (the magnitude of the biodiversity response to a unit of a given stressor), and adaptive capacity (the capacity of biodiversity to undergo changes in response to a hazard that allow it to persist). Following [62], we use non-adaptability, that is, the inverse of adaptive capacity, to visualise this relationship, so that increases along this axis represent increases in overall risk. Each risk component represents an en-

(Figure legend continued at the bottom of the next page.)

risk frameworks that identifies the mechanisms driving such interactions, and incorporates them into the assessment. Specifically, candidate interaction mechanisms are systematically identified (and then tested) by asking how climate change could alter the exposure and vulnerability of a species, community, or ecosystem to land use change; that is, how climate change can affect the components that determine risk of an adverse outcome in response to land use change, and vice versa (Figure 2).

To illustrate this, consider risks from CC–LUC interactions to populations of a large predator, such as African wild dogs (*Lycaon pictus*). This species declines in anthropogenically modified landscapes due to reduced prey populations. Climate change (specifically increased temperatures) is predicted to increase sensitivity of wild dogs to land use intensification by restricting the number of hours they can hunt [59]. Such time restrictions around hunting compound the risk from reduced prey availability, and thus increase the overall risk posed by land use change to this population. CC–LUC interactions could also affect adaptive capacity. For instance, a species' ability to adapt to climate change by shifting its range can be impeded by habitat fragmentation, increasing the overall risk posed by climate change (Figure 2). These mechanisms, which relate to changes in intrinsic vulnerability (sensitivity and adaptive capacity), correspond to what Didham *et al.* [6] term 'modification effects', that is, true CC–LUC interactions (Table 1).

The risk framework approach we propose can also explicitly account for the direct effects of climate change and land use change on each other via effects on exposure, which need to be considered to estimate the overall impact on biodiversity. For instance, if the exposure of an ecosystem to climate change is determined by the magnitude of rainfall change, then land use change in the form of large-scale deforestation, which affects regional rainfall patterns, could increase the exposure of this particular ecosystem to climate change. Such interaction mechanisms correspond to the 'chain effects' of Didham *et al.* [6].

To account for CC–LUC interaction mechanisms within this framework, it is necessary to identify risk components (exposure, sensitivity, and adaptive capacity) with regard to both climate change and land use change, as well as suitable risk indicators to estimate each component. Potential indicators may be drawn from existing frameworks and databases that identify and quantify threats to biodiversity, such as the International Union for Conservation of Nature (IUCN) Red List of Species or Ecosystems (http://www.iucnredlist.org) and existing climate change or land use change risk assessments [57,60,61]. Once risk components are known, candidate interaction mechanisms can be identified based on known sets of possible interaction mechanisms (Table 1) as well as local and expert knowledge. Which of these interaction mechanisms affect biodiversity in a given context can then be tested empirically. Interaction mechanisms that are shown to have important effects on overall risk levels to biodiversity can subsequently be integrated into risk assessments, either by modifying risk scores, or by including interaction mechanisms in quantitative risk models.

An important aspect of our risk framework is that it can be applied to any dimension of biodiversity, such as genetic diversity or community composition. Indeed, the process explicitly considers

vironmental, biological or ecological process that shapes biodiversity. If different stressors do not interact, the risk from a given stressor is independent from the presence of another (A). Stressor interactions can be conceptualised as mechanisms by which a second stressor alters processes that affect each risk component (B). In this example, land use change decreases the African wild dogs' ability to adapt to climate change by limiting range shifts, and climate change increases their sensitivity to land use change by limiting the time available to hunt prey, which are already depleted owing to land use change. The interaction of these effects increases overall risk from global change.

all ways by which climate change may impact biodiversity's response to land use change, as well as the ways by which land use change may impact biodiversity's response to climate change, to ensure that the largest range of potential CC–LUC interaction mechanisms are identified (Table 1). The scope and flexibility of our framework can thus be harnessed to provide conservation decision makers with context-specific information about all interaction mechanisms posing risks to all aspects of biodiversity at any given scale or context.

Concluding Remarks

Interactions between climate change and land use change can significantly shape biodiversity. So far, predicting their occurrence and impact has been hampered by a focus on classifying the outcomes of interactions, rather than understanding the mechanisms by which they operate. To advance our understanding of CC–LUC interactions, and to improve our ability to mitigate their potentially negative impacts on biodiversity across different geographic and taxonomic contexts, we recommend that future research focuses on investigating how the exposure and sensitivity of biodiversity to land use change, as well as its capacity to adapt to such change, is altered by climate change, and vice versa (see Outstanding Questions). A key step towards this goal will involve interdisciplinary cooperation – for example, among ecologists, physiologists, agronomists, and climate scientists – as insights from a range of fields are required to advance our understanding of how CC–LUC interactions affect biodiversity, and to develop more effective risk assessment procedures to support environmental management worldwide.

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Supplemental Information

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Outstanding Questions

How do mechanisms governing CC–LUC interactions vary across different environmental contexts? In particular, we need to know how interaction mechanisms are influenced by the geographical setting (e.g., montane versus lowland, continent versus island) and the type of biome (e.g., grassland versus forest).

How do CC–LUC interaction mechanisms vary among different types of species? Variation in interaction mechanisms may be related to differences in species ecology (e.g., herbivore versus decomposer, long lifespan versus short lifespan).

How are CC–LUC interaction mechanisms shaped by species interactions? The dynamics of underlying mechanisms may be related to the type of species interactions involved (e.g., symbiosis, competition, plant–animal, or host–pathogen) as well as the structural properties of interaction networks.

What properties of socioecological systems determine how climate change alters the exposure of biodiversity to land use change (and vice versa) in different biomes? The mechanisms by which climate change shapes the exposure of biodiversity to land use change (and vice versa) may vary systematically across regions in relation to factors such as vegetation, land use policy, and economic context (e.g., farmers' access to loans or technology).

Which characteristics predispose species, ecological communities, and ecosystems to be more sensitive to climate change in the presence of land use change (and vice versa)? Answering this question will help us to identify species and ecosystems at high risk from current and future changes in land use and climate.

Which characteristics of species, ecological communities, and ecosystems limit or promote their capacity to adapt to climate change in the presence of land use change (and vice versa)? Identifying these characteristics will be especially important for prioritising conservation attention in situations where it is impossible to mitigate climate or land use change significantly.

References

1. IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, IPCC, Geneva, Switzerland
2. Newbold, T. *et al.* (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353, 288–291
3. Visconti, P. *et al.* (2016) Projecting global biodiversity indicators under future development scenarios. *Conserv. Lett.* 9, 5–13
4. Driscoll, D.A. *et al.* (2012) Priorities in policy and management when existing biodiversity stressors interact with climate-change. *Clim. Chang.* 111, 533–557
5. Mazor, T. *et al.* (2018) Global mismatch of policy and research on drivers of biodiversity loss. *Nat. Ecol. Evol.* 2, 1071
6. Didham, R. *et al.* (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* 22, 489–496
7. Côté, I.M. *et al.* (2016) Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B* 283, 20152592
8. Oliver, T.H. and Morecroft, M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdiscip. Rev. Clim. Change* 5, 317–335
9. Keshtkar, H. and Voigt, W. (2016) Potential impacts of climate and landscape fragmentation changes on plant distributions: coupling multi-temporal satellite imagery with GIS-based cellular automata model. *Ecol. Inform.* 32, 145–155
10. Hamilton, C.M. *et al.* (2018) Slow and steady wins the race? Future climate and land use change leaves the imperiled Blanding's turtle (*Emydoidea blandingii*) behind. *Biol. Conserv.* 222, 75–85
11. Brown, C.J. *et al.* (2014) Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Divers. Distrib.* 20, 538–546
12. Brown, C.J. *et al.* (2013) Managing for interactions between local and global stressors of ecosystems. *PLoS one* 8, e65765
13. Staudt, A. *et al.* (2013) The added complications of climate change: understanding and managing biodiversity and ecosystems. *Front. Ecol. Environ.* 11, 494–501
14. Hooper, M. *et al.* (2013) Interactions between chemical and climate stressors: a role for mechanistic toxicology in assessing climate change risks. *Environment. Toxicol. Chem.* 32, 32–48
15. Noss, R. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4, 355–364
16. Kuemmerle, T. *et al.* (2013) Challenges and opportunities in mapping land use intensity globally. *Curr. Opin. Env. Sust.* 5, 484–493
17. Garcia, R. *et al.* (2014) Multiple dimensions of climate change and their implications for biodiversity. *Science* 344, 1247579
18. Valiente-Banuet, A. and Verdú, M. (2013) Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. *Front. Ecol. Environ.* 11, 408–413
19. Bregman, T. *et al.* (2015) Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology* 96, 2692–2704
20. Smith, M.D. *et al.* (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90, 2898–2907
21. Reino, L. *et al.* (2018) Modelling landscape constraints on farmland bird species range shifts under climate change. *Sci. Total Environ.* 625, 1596–1605

22. Trisurat, Y. *et al.* (2015) Assessing potential effects of land use and climate change on mammal distributions in northern Thailand. *Wildlife Res.* 41, 522–536
23. Lemoine, N. *et al.* (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conserv. Biol.* 21, 495–503
24. Bremer, L. *et al.* (2018) Bringing multiple values to the table: assessing future land-use and climate change in North Kona, Hawai i. *Ecol. Soc.* 23, 33
25. Hoiss, B. *et al.* (2013) Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Divers. Distrib.* 19, 386–395
26. Heubes, J. *et al.* (2013) The projected impact of climate and land use change on plant diversity: an example from West Africa. *J. Arid Environ.* 96, 48–54
27. Zhou, G. *et al.* (2002) Responses of grassland ecosystems to precipitation and land use along the Northeast China Transect. *J. Veg. Sci.* 13, 361–368
28. Aleman, J. *et al.* (2017) Tree cover in Central Africa: determinants and sensitivity under contrasted scenarios of global change. *Sci. Rep.* 7, 41393
29. Mantyka-Pringle, C.S. *et al.* (2014) Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. *J. Appl. Ecol.* 51, 572–581
30. Kuemmerlen, M. *et al.* (2015) An attack on two fronts: predicting how changes in land use and climate affect the distribution of stream macroinvertebrates. *Freshw. Biol.* 60, 1443–1458
31. Lang, Y. *et al.* (2017) Responses of the water-yield ecosystem service to climate and land use change in Sancha River Basin, China. *Phys. Chem. Earth* 101, 102–111
32. Young, H. *et al.* (2017) Interacting effects of land use and climate on rodent-borne pathogens in central Kenya. *Philos. T. R. Soc. B.* 372, 20160116
33. Conenna, I. *et al.* (2017) Interactive effects of climate and forest canopy cover on Goshawk productivity. *J. Ornithol.* 158, 799–809
34. Benot, M. *et al.* (2014) Stronger short-term effects of mowing than extreme summer weather on a subalpine grassland. *Ecosystems* 17, 458–472
35. Jaramillo, J. *et al.* (2013) Climate change or urbanization? Impacts on a traditional coffee production system in East Africa over the last 80 years. *PLoS One* 8, e51815
36. Senior, R.A. *et al.* (2018) Tropical forests are thermally buffered despite intensive selective logging. *Glob. Change Biol.* 24, 1267–1278
37. Carón, M. *et al.* (2018) Regeneration responses to climate and land-use change of four subtropical tree species of the southern Central Andes. *Forest Ecol. Manag.* 417, 110–121
38. Frishkoff, L.O. *et al.* (2015) Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. *Glob. Change Biol.* 21, 3901–3916
39. Frishkoff, L.O. *et al.* (2016) Climate change and habitat conversion favour the same species. *Ecol. Lett.* 19, 1081–1090
40. Klaus, V. *et al.* (2016) Plant diversity moderates drought stress in grasslands: Implications from a large real-world study on 13C natural abundances. *Sci. Total Environ.* 566, 215–222
41. Gimona, A. *et al.* (2012) Woodland networks in a changing climate: threats from land use change. *Biol. Conserv.* 149, 93–102
42. Darling, E.S. and Côté, I.M. (2008) Quantifying the evidence for ecological synergies. *Ecol. Lett.* 11, 1278–1286
43. Crain, C.M. *et al.* (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315
44. Piggott, J.J. *et al.* (2015) Reconceptualizing synergism and antagonism among multiple stressors. *Ecol. Evol.* 5, 1538–1547
45. Sala, O. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774
46. Halpern, B.S. *et al.* (2008) Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean Coast. Manag.* 51, 203–211
47. Folt, C.L. *et al.* (1999) Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44, 864–877
48. Schäfer, R.B. and Piggott, J.J. (2018) Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Glob. Change Biol.* 24, 1817–1826
49. Mantyka-Pringle, C.S. *et al.* (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Glob. Change Biol.* 18, 1239–1252
50. Turner, B. *et al.* (2003) A framework for vulnerability analysis in sustainability science. *Proc. Natl. Acad. Sci. U. S. A.* 100, 8074–8079
51. Polsky, C. *et al.* (2007) Building comparable global change vulnerability assessments: the vulnerability scoping diagram. *Glob. Environ. Change* 17, 472–485
52. IPCC (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press
53. Young, W.B. and Foden, B.E. (2016) *IUCN SSC Guidelines for Assessing Species' Vulnerability to Climate Change*, IUCN, Cambridge, UK and Gland, Switzerland
54. Schröter, D. *et al.* (2005) Assessing vulnerabilities to the effects of global change: an eight step approach. *Mitig. Adapt. Strateg. Glob. Change* 10, 573–595
55. Bland, L.M. *et al.* (2017) *IUCN Guidelines for the Application of IUCN Red List of Ecosystems Categories and Criteria, version 1.1*, IUCN, Gland, Switzerland
56. Žurovec, O. *et al.* (2017) Quantitative assessment of vulnerability to climate change in rural municipalities of Bosnia and Herzegovina. *Sustainability* 9, 1208
57. Ameca y Juárez, E.I. *et al.* (2013) Assessing exposure to extreme climatic events for terrestrial mammals. *Conserv. Lett.* 6, 145–153
58. Mantyka-Pringle, C.S. *et al.* (2015) Climate change modifies risk of global biodiversity loss due to land-cover change. *Biol. Cons.* 187, 103–111
59. Woodroffe, R. *et al.* (2017) Hot dogs: high ambient temperatures impact reproductive success in a tropical carnivore. *J. Animal Ecol.* 86, 1329–1338
60. Pereira, H.M. *et al.* (2004) A framework for assessing the relative vulnerability of species to land-use change. *Ecol. Appl.* 14, 730–742
61. Lee, C. *et al.* (2018) A new framework to assess relative ecosystem vulnerability to climate change. *Conserv. Lett.* 11, e12372
62. Almeca y Juárez, E.I. *et al.* (2012) Natural population die-offs: causes and consequences for terrestrial mammals. *Trends Ecol. Evol.* 27, 272–277
63. Greenwood, O. *et al.* (2016) Using *in situ* management to conserve biodiversity under climate change. *J. Appl. Ecol.* 53, 885–894
64. Bebi, P. *et al.* (2009) Snow avalanche disturbances in forest ecosystems. State of research and implications for management. *Forest Ecol. Manag.* 257, 1883–1892
65. Seidl, R. and Rammer, W. (2017) Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Lands. Ecol.* 32, 1485–1498
66. Opdam, P. and Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117, 285–297
67. Pitelka, L.F. *et al.* (1997) Plant migration and climate change: a more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity. *Am. Sci.* 85, 464–473
68. Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142
69. García-Valdés, R. *et al.* (2015) Evaluating the combined effects of climate and land-use change on tree species distributions. *J. Appl. Ecol.* 52, 902–912
70. Barros, C. *et al.* (2017) Extreme climate events counteract the effects of climate and land-use changes in Alpine tree lines. *J. Appl. Ecol.* 54, 39–50
71. Vellend, M. (2004) Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* 85, 3043–3055

72. Des Roches, S. *et al.* (2020) Climate-driven habitat change causes evolution in Threespine Stickleback. *Glob. Change Biol.* 26, 597–606
73. Reusch, T.B. and Wood, T.E. (2007) Molecular ecology of global change. *Mol. Ecol.* 16, 3973–3992
74. Maron, M. *et al.* (2015) Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Divers. Distrib.* 21, 731–743
75. Morelli, T.L. *et al.* (2012) Anthropogenic refugia ameliorate the severe climate-related decline of a montane mammal along its trailing edge. *Proc. R. Soc. B* 279, 4279–4286
76. De Chazal, J. and Rounsevell, M.D. (2009) Land-use and climate change within assessments of biodiversity change: a review. *Global Environ. Change* 19, 306–315
77. Farber, D.A. (2015) Separated at birth: addressing the twin crises of biodiversity and climate change. *Ecology LQ* 42, 841
78. Vinebrooke, R.D. *et al.* (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos* 104, 451–457
79. Katayama, N. *et al.* (2014) Landscape heterogeneity–biodiversity relationship: effect of range size. *PLoS One* 9, e93359
80. Bennett, J.M. *et al.* (2015) Climate drying amplifies the effects of land-use change and interspecific interactions on birds. *Landsc. Ecol.* 30, 2031–2043
81. Benning, T.L. *et al.* (2002) Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci. U. S. A.* 99, 14246–14249
82. Willis, C.G. *et al.* (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl. Acad. Sci. U. S. A.* 105, 17029–17033
83. Gómez-Ruiz, E.P. and Lacher Jr., T.E. (2019) Climate change, range shifts, and the disruption of a pollinator-plant complex. *Sci. Rep.* 9, 1–10
84. Norberg, J. and Moor, H. (2019) Amplitude and timescale of metacommunity trait-lag response to climate change. *BioRxiv* Published online November 21, 2019. https://doi.org/10.1101/850289