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ECOLOGICAL SOUNDINGS

Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use

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ABSTRACT

Aim The impact of multiple stressors on biodiversity is one of the most pressing questions in ecology and biodiversity conservation. Here we critically assess how often and efficiently two main drivers of global change have been simultaneously integrated into research, with the aim of providing practical solutions for better integration in the future. We focus on the integration of climate change (CC) and land-use change (LUC) when studying changes in species distributions.

Location Global.

Methods We analysed the peer-reviewed literature on the effects of CC and LUC on observed changes in species distributions, i.e. including species range and abundance, between 2000 and 2014.

Results Studies integrating CC and LUC remain extremely scarce, which hampers our ability to develop appropriate conservation strategies. The lack of CC–LUC integration is likely to be a result of insufficient recognition of the co-occurrence of CC and LUC at all scales, covariation and interactions between CC and LUC, as well as correlations between species thermal and habitat requirements. Practical guidelines for the study of these interactive effects include considering multiple drivers and processes when designing studies, using available long-term datasets on multiple drivers, revisiting single-driver studies with additional drivers or conducting comparative studies and meta-analyses. Combining various methodological approaches, including time lags and adaptation processes, represent further avenues to improve global change science.

Main conclusions Despite repeated claims for a better integration of multiple drivers, the effects of CC and LUC on species distributions and abundances have been mostly studied in isolation, which calls for a shift of standards towards more integrative global change science. The guidelines proposed here will encourage study designs that account for multiple drivers and improve our understanding of synergies or antagonisms among drivers.

Keywords

Antagonisms, climate change, community indices, land-use change, range shift, synergies

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INTRODUCTION

Over the past decades, the challenges to biodiversity presented by climate change (CC) have triggered exponential growth in the literature on the current and predicted impacts of CC on populations, species and ecological communities (e.g. Parmesan & Yohe, 2003). Evidence shows that ecosystems have already been greatly affected and that impacts will continue mostly unabated. What we still largely ignore is the magnitude of these past and, above all, future impacts (Hansen *et al.*, 2016).

Most studies on the impact of CC on species distributions have shown that species vary greatly in their responses (e.g. Parmesan & Yohe, 2003). This heterogeneity in responses reflects differences in the sensitivity of species to climate (Angert *et al.*, 2011). However, interactions amongst multiple drivers of global change have recently been identified as a major cause of uncertainty in CC attribution (Parmesan *et al.*, 2013) and CC projection (de Chazal & Rounsevell, 2009).

Despite repeated calls for a better integration of multiple drivers (Didham *et al.*, 2007; de Chazal & Rounsevell, 2009; Mantyka-Pringle *et al.*, 2012; Parmesan *et al.*, 2013; Oliver & Morecroft, 2014), several authors have highlighted that conventional CC investigations and projections privileging CC attribution remain the norm (Oliver & Morecroft, 2014; Titeux *et al.*, 2016). In the absence of integrative multi-driver approaches, limited understanding of how interactions among drivers affect observed changes will be likely to hamper reliable projections and relevant conservation recommendations (Titeux *et al.*, 2016).

To identify obstacles to integrating drivers and ways to overcome them, we analysed how the impacts of CC and land-use change (LUC) on species distributions have been, and could be, studied. Our aim was to provide a pragmatic approach to that challenge (Parmesan *et al.*, 2013; Oliver & Morecroft, 2014). We therefore addressed four questions: (1) What is the degree of integration of CC and LUC in published studies on changes in species distributions? (2) What are the consequences of insufficient integration of drivers? (3) What factors might limit integration of CC and LUC? (4) How can integrative studies of the effects of CC–LUC on species distributions be promoted?

CURRENT INTEGRATION OF CC AND LUC IN STUDIES OF SPECIES DISTRIBUTION

We analysed the peer-reviewed literature in three steps. First, we searched Web of Science (http://www.webofknowledge.com) for publications over the period 2000–14 on the effects of either CC (temperature and rainfall), LUC or both on observed or projected changes in species distributions

Table 1 Keywords selected based on title and abstracts of a large sample of publications on climate change, land-use change and species distributions.

Keywords included	LUC-obs	LUC-proj	CC -obs	CC -proj	CC and LUC - obs	CC and LUC - proj
Species distribution: "species diversity" OR "distribution range*" OR "range expansion*" OR "range contraction*" OR "distributional shift*" OR "range shift*" OR "elevation* distribution*" OR "altitudinal distribution*" OR "latitudinal distribution*" OR "species distribution*" OR "species abundance*" OR "species composition" OR "community composition" OR "population change*" OR "population decline*" OR "species range*" OR "species richness"	x	x	x	x	x	x
Land-use change: "land-use change*" OR "habitat change*" OR "habitat degradation" OR "habitat loss*" OR "habitat fragmentation" OR "land use change*" OR "land cover change*" OR "land abandonment" OR "agricultural intensification" OR "rural depopulation" OR "urbanization"	x	x			x	x
Climate change: "climate change" OR "global warming" OR "temperature increase" OR "precipitation loss" OR "drought" OR "flood" OR "extreme event"			x	x	x	x
Observed: "observed" OR "historical" OR "past" OR "current"	x		x		x	
Projected: "predict*" OR "project*" OR "scenario" OR "future"		x		x		x
NOT: "Pleistocene" OR "Paleo" OR "fossil" OR "glacial" OR "quaternary" OR "Holocene" OR "marine" OR "ocean*" OR "sea"	x	x	x	x	x	x

We consulted the Web of Science database (http://www.webofknowledge.com) for the last 15 years (2000–14). We ran the following searches: LUC-obs = effect of land-use change (LUC) on observed changes; LUC-proj = effects of LUC on projected changes; CC-obs = effects of climate change (CC) on observed changes; CC-proj = effects of CC on projected changes; CC and LUC-obs = effects of both LUC and CC on observed changes; CC and LUC-proj = effects of both LUC and CC on projected changes. We tried to include as many terms as possible related to LUC to include the wide diversity of keywords used in these studies. As a result, we believe that our search may have, if anything, only slightly underestimated the number of publications on LUC.

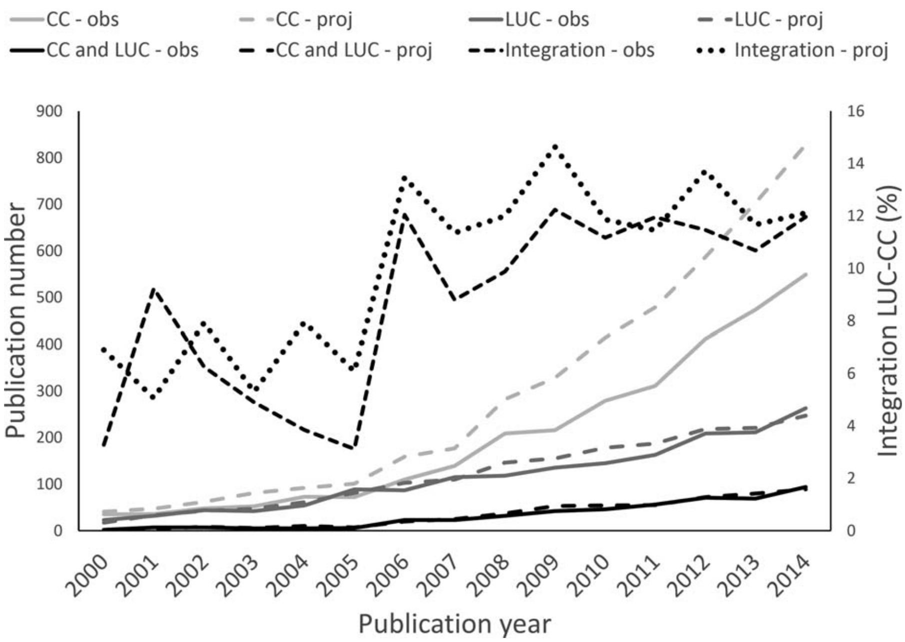

Figure 1 Temporal variations in (1) the number of publications on the observed (-obs) or projected (-proj) effects of climate change (CC), land-use change (LUC) and both combined in the same publication (CC-LUC), on species distributions and abundances, and (2) the percentage of publications integrating LUC and CC in publications on observed (Integration-obs) and projected (Integration-proj) effects (i.e. the percentage of publications including both drivers simultaneously over all publications including either one of the drivers represented along the secondary axis). This figure is restricted to the period 2000–14 since referencing for years 2015 and 2016 in Web of Science was not complete at the time of the review. This analysis is based on publication title, abstract and keywords.

(i.e. species ranges and abundances) in terrestrial ecosystems (see the complete list of keywords used for each criterion in Table 1). Second, we read the abstract of all publications on the effects of both CC and LUC on observed changes in species distributions. We then qualitatively assessed the level of driver integration in any given relevant publication, based on its abstract. Finally, we read the full text of all publications truly designed to integrate both drivers and assessed their outcome. For the second and third steps, we also included publications on the effects of both CC and LUC on observed changes in species distributions from 2015 and 2016.

Increase in the proportion of CC-only studies

We found 15,593 publications on CC or LUC and species distributions. We observed an increasing number of papers published per year for all types of publications, a pattern reminiscent of the period's general publication trends. Between 2000 and 2005, publications on CC and publications on LUC increased at a similar pace (Fig. 1). We detected a steeper increase in the number of CC publications relative to LUC publications after 2005. Currently, there are more than three times more publications on CC than on LUC for projected changes and twice more publications on CC than on LUC for observed changes. The proportion of publications including both CC and LUC almost doubled after 2005 but remained at around 12–14% of the total on that theme, suggesting limited integration of CC and LUC regardless of whether the study focused on observed or projected changes (Fig. 1).

Poor levels of true integration

We identified four levels of integration based on the abstract of the 158 publications that included the effects of

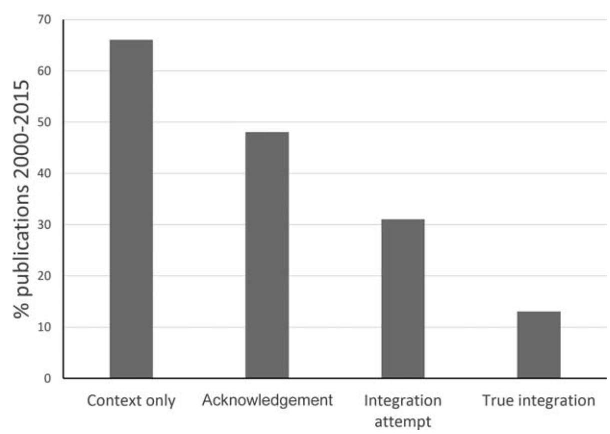

Figure 2 Level of driver integration in publications on observed changes in species distribution and abundance considering both climate change and land-use change in our literature search. This analysis is based on the full text of the publications.

Box 1. Review of the outcomes of 12 publications designed to study the effects of both LUC and CC on species distribution and abundance.

Case 1. The effects of LUC override the effect of CC

Eglington and Pearce-Higgins (2012) showed that despite more stable land-use intensity in recent years, CC has not overtaken land-use intensity as the dominant driver of UK bird populations. Ametzegui *et al.* (2016) showed that the cessation of human activity drove forest dynamics at the tree line in the Catalan Pyrenees, Spain, and revealed a very low or even negligible signal of CC in the study area. Similarly, Bodin *et al.* (2013) showed that the shift of forest species along an elevational gradient in south-east France resulted from the maturation of forests due to land abandonment rather than CC. O'Connor *et al.* (2014) showed that changes to soil surface temperatures caused by increased grazing had a more consistent influence than air temperature increases on the recovery of the Adonis blue butterfly in the UK.

Case 2. LUC and CC impact different sets of species

Lavergne *et al.* (2006) showed that changes in land use and climate influenced the occurrence of different plant species in Mediterranean France. Similarly, Hockey *et al.* (2011) showed that LUC and CC influenced range shifts of different types of South African bird species. Kampichler *et al.* (2012) showed that interactions between CC and LUC differed between habitats for Dutch breeding bird communities. Fox *et al.* (2014) showed that changes in land use and climate influenced distributional changes of different types of British moths but not all species of a given type behaved similarly, suggesting complex interactions between these two drivers.

Case 3. LUC and CC act in synergy

Lunney *et al.* (2014) showed that overwhelming LUC (human population growth and habitat loss) has been hiding the significant contribution of CC (temperature increase and drought) to the long-term shrinkage in the distribution of the koala in south-eastern New South Wales, Australia. Porzig *et al.* (2014) showed that temporal variations in Californian birds were best explained by temporal changes in vegetation, but that variations in rainfall also had a significant effect for four of the seven species studied. Christie *et al.* (2015) showed that temporal variations in pronghorn abundance in North Dakota, USA, were primarily due to variations in winter weather but were also negatively affected by the increase in road and oil/gas well density that has recently increased and is likely to impede pronghorn movement to more hospitable areas during winter storms. Paprocki *et al.* (2015) showed that temporal changes in wintering raptor populations in south-west Idaho, USA, were influenced by northward distributional shifts due to CC as well as temporal changes in local habitat conditions. Finally, Cunningham *et al.* (2016) showed that pied crow numbers in south-western South Africa have increased in response to climate warming, with their spread facilitated by electrical infrastructure.

both CC and LUC on observed changes in species distributions (Fig. 2). Most studies (72%) mentioned CC and LUC only in a general context while focusing on a single driver (context only), or acknowledged that other drivers could influence observed changes (acknowledgement). Some studies (20%) attempted to control for potential confounding effects of CC and LUC on species distribution (integration attempt), for example by accounting for species habitat as a covariate in studies on the impact of CC or by selecting study sites without LUC (e.g. Franco *et al.*, 2006; Reif *et al.*, 2008; Popy *et al.*, 2010). Only 8% of studies were specifically designed to assess the effects of both CC and LUC on species distribution (true integration; e.g. Eglington & Pearce-Higgins, 2012; Kampichler *et al.*, 2012; Fox *et al.*, 2014). This suggests that the proportion of integrative studies is even lower than suggested by our quantitative analysis, with truly integrative studies representing only a tiny fraction of studies on observed changes in species distributions.

Integration revealing a hidden driver or combination of drivers

Most of the 13 studies designed to assess the effect of both drivers were published over the last 5 years. These integrative studies were of three types (see Box 1 for more details). The first set showed that, in some cases, despite strong expectations that observed changes were driven by CC, the effects of LUC clearly overrode those of CC (Eglington & Pearce-Higgins, 2012; Bodin *et al.*, 2013; O'Connor *et al.*, 2014; Amezteguі *et al.*, 2016). The second set showed that the impacts of CC and LUC differed among species groups, some species responding only to CC whereas others were only affected by LUC (Lavergne *et al.*, 2006; Hockey *et al.*, 2011; Kampichler *et al.*, 2012; Fox *et al.*, 2014). Finally, the third set showed that LUC and CC acted in synergy (Lunney *et al.*, 2014; Porzig *et al.*, 2014; Christie *et al.*, 2015; Paprocki *et al.*, 2015; Cunningham *et al.*, 2016). None of the studies assessing both CC and LUC concluded that only CC had an impact on species distributions. This suggests that the lack of integration of CC and LUC is currently jeopardizing our understanding of the impacts of global change on species distribution (i.e. which driver is having an impact, where, when and why).

CONSEQUENCES OF POOR INTEGRATION OF CC AND LUC IN STUDIES ON SPECIES DISTRIBUTIONS

Our analysis of the literature suggests that the lack of integration of CC and LUC in studies on species distributions and the dominance of CC-only studies is likely to result in inappropriate management strategies or missed conservation opportunities, and may even trigger, in some cases, a relaxation in appropriate conservation efforts.

Overemphasis on connectivity

The lack of integration of CC and LUC implies that biodiversity management strategies essentially derive from CC-only studies, which mainly recommend increasing landscape and habitat connectivity (Heller & Zavaleta, 2009). Yet, focusing on the restoration of corridors, stepping stones or 'softening' of the anthropogenic matrix may divert attention away from the primary objective of maintaining habitat area (Hodgson *et al.*, 2009). Moreover, a 'blind' increase in connectivity based on patterns observed at the community level or at large scales, while neglecting the local context or habitat requirements of specialist species, may also fragment other habitats, favour species invasions and/or decrease species adaptive potential (Caplat *et al.*, 2016). For example, open habitat species already negatively affected by the encroachment of woody vegetation following the abandonment of farmland (e.g. in the Mediterranean; Sirami *et al.*, 2008) may be further affected by the systematic creation of undisturbed wooded corridors (Eggers *et al.*, 2010).

Missed conservation opportunities

The lack of integration of CC and LUC hinders our ability to identify the relevant drivers of changes in species distributions, to appropriately project future trends and therefore to provide efficient conservation recommendations. Moreover, it prevents us from detecting antagonistic CC–LUC effects and therefore from mitigating adverse effects of CC through adaptive land-use management (Princé *et al.*, 2015; Gaüzère *et al.*, 2016). For example, Braunisch *et al.* (2014) showed that expected CC-driven range contractions of birds in mountain forests could be partly compensated by enhancing the structural complexity of forests. The dominance of both LUC-only and CC-only studies is therefore likely to hamper the development of effective conservation strategies (but see Faleiro *et al.*, 2013).

Insufficient conservation efforts

Finally, the lack of integration of CC and LUC and the dominance of CC-only studies assessing observed shifts in species distribution is likely to have resulted in overrating the effects of CC and downplaying the negative effects of LUC. This is likely to divert funds and efforts away from more immediate conservation priorities (Maxwell *et al.*, 2016). The risk of insufficient local conservation efforts is extremely acute for species declines inaccurately attributed to CC (e.g. Hockey & Midgley, 2009) but also concerns most situations where CC and LUC interact (Mantyka-Pringle *et al.*, 2012).

REASONS FOR POOR INTEGRATION OF CC AND LUC IN STUDIES ON SPECIES DISTRIBUTIONS

Our analysis of the literature suggested that although LUC data and the availability and credibility of LUC scenarios may have been a limiting factor initially (before the 2000s; e.g. Verburg *et al.*, 2002), this fails to explain the recent lack of integration of CC and LUC and the increase of CC-only studies. Our review of papers designed to study the integration of CC and LUC (see 'Current integration of CC and LUC in studies of species distribution') and other papers calling for more integration of CC and LUC (e.g. de Chazal & Rounsevell, 2009; Parmesan *et al.*, 2013; Oliver & Morecroft, 2014; Titeux *et al.*, 2016) have highlighted three reasons likely to explain the ongoing lack of integration of CC and LUC, for both observed and projected changes in species distributions.

Misrepresentation of the scale of the impact of CC and LUC

The ongoing lack of integration of CC and LUC can first be explained by the fact that CC has been expected to affect species distributions at broader spatial and temporal scales (regional–continental, >50 years) and LUC at finer scales (habitat–landscape, <20 years; Parmesan *et al.*, 2013). This has resulted in the assumptions that CC overrides LUC at regional scales (Thuiller *et al.*, 2004) and that LUC overrides CC at local scales (Bailey *et al.*, 2002). CC has been recently shown to affect species distributions not only through broad latitudinal–elevational temperature shifts, but also via progressive shifts in local climate (Lenoir & Svenning, 2015). Conversely, LUC has been shown to have a massive impact on contemporaneous broad-scale changes in species distributions (e.g. Barbet-Massin *et al.*, 2012).

Lack of recognition of covariations and interactions between CC and LUC

Partly as a consequence of the previously described misrepresentation, most studies on latitudinal or elevational species shifts focused on CC only, whereas most studies on local long-term changes in species abundance focused on LUC only. However, geographical variation in land cover is highly correlated with geographical variation in bioclimatic variables (e.g. Thuiller *et al.*, 2004) and elevational gradients are often correlated with land-use intensity gradients (e.g. Archaux, 2004). This implies that LUC represents a likely driver to latitudinal or elevational species shifts, habitat gains explaining range expansion (e.g. Elmhagen *et al.*, 2015) and habitat

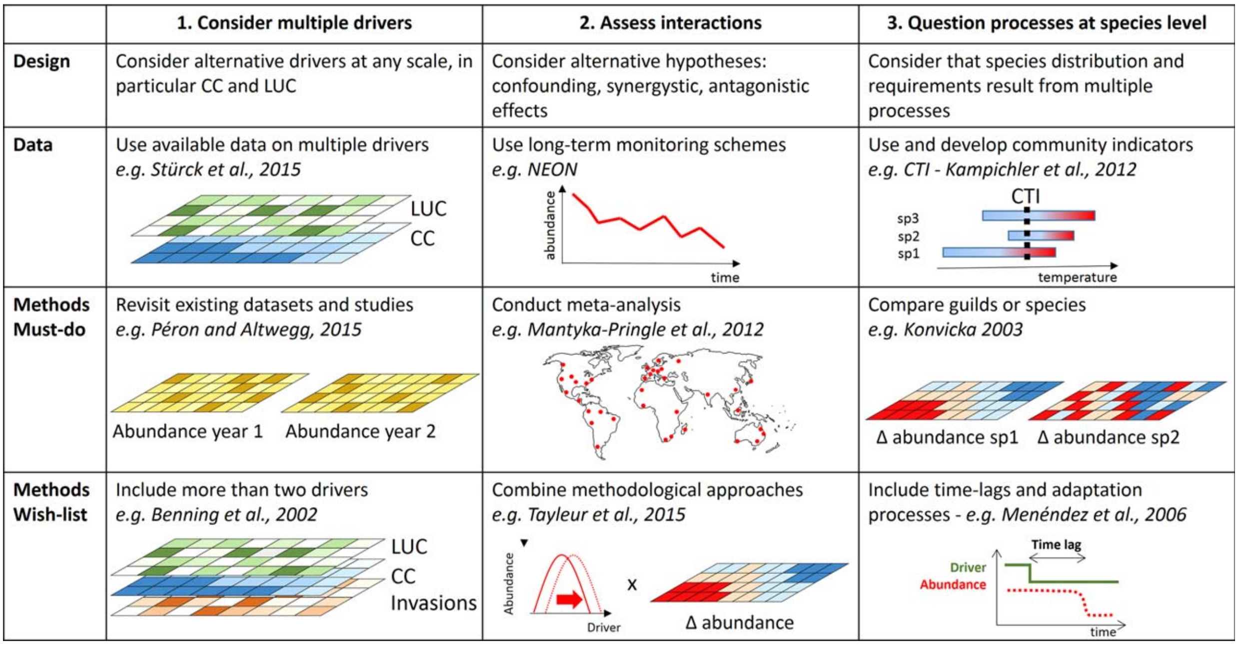

Figure 3 Synthesis of the three major recommendations for effective integrative global change science regarding the study design, data available and methods that can easily be implemented (must-do). We also suggest several avenues to further improve global change science (wish-list). CC, climate change; LUC, land-use change; NEON, National Ecological Observatory Network; CTI, community temperature index.

losses explaining range contraction (e.g. Franco *et al.*, 2006). Similarly, CC represents a likely driver to explain local long-term changes in species abundance and community composition (e.g. Lemoine *et al.*, 2007). Moreover, interactions between CC and LUC are likely to be the norm rather than the exception (Parmesan *et al.*, 2013). For example, land cover influences microclimate, and therefore the local effects of CC (e.g. Carlson & Traci Arthur, 2000); landscape structure affects the ability of species to shift their distribution (e.g. Hill *et al.*, 2001); and climate affects the effects of habitat loss (e.g. Mantyka-Pringle *et al.*, 2012).

Lack of recognition of correlations between species thermal and habitat requirements

Finally, species thermal optima and habitats have repeatedly been used to assess the effects of CC and LUC, respectively (e.g. Lemoine *et al.*, 2007). However, climate is the major driver of the distribution of both species and land cover, for example across Europe (Thuiller *et al.*, 2004). As a result, species thermal and habitat requirements may equally be influenced by climate and land use. For example, in the Mediterranean, forest bird species have more northerly distributions and colder thermal optima than open-habitat bird species (Suarez-Seoane *et al.*, 2002). As a result, species traits and community indicators based on thermal requirements only, or habitat associations only, do not constitute a reliable way to disentangle the effects of CC and LUC unless potential correlations between the effects of these two drivers are explicitly recognized, or their respective causal effects disentangled (Clavero *et al.*, 2011).

RECOMMENDATIONS FOR FUTURE RESEARCH ON THE INTERACTIONS OF CC AND LUC

Building on the obstacles to integration of CC and LUC identified here ('Reasons for poor integration of CC and LUC in studies on species distributions'), and solutions developed in studies that have genuinely integrated CC and LUC ('Current integration of CC and LUC in studies of species distribution'), we propose three main recommendations to design a more effective integrative global-change science (see synthesis and illustration in Fig. 3).

Consider multiple drivers at any scale

When working at broad spatial scales, consider potential broad-scale gradients in drivers other than CC, in particular LUC (e.g. the south–north LUC gradient in Europe or LUC gradients in the USA; Ordonez *et al.*, 2014). The availability of data on past LUC/CC (e.g. Wang *et al.*, 2015) and LUC scenarios (e.g. Stürck *et al.*, 2015) at various scales should facilitate this integration. When working at local scales, account for local processes such as LUC or species invasions as well as fine-grained spatio-temporal variation in temperature and precipitation patterns (e.g. Eglington & Pearce-Higgins, 2012). The availability of long-term climatic and remote-sensing data should facilitate this integration. Most local studies in the literature consider only one driver, but the increased availability of data on other drivers offers new avenues for integrative analyses. These studies could therefore be revisited from a multiple-driver perspective, with the novel integration of two or possibly more drivers (e.g. Benning *et al.*, 2002), for example by comparing existing long-term datasets and new datasets available on CC and LUC (e.g. Péron & Altwegg, 2015).

Assess interactions among multiple drivers

Changes in species distributions are likely to result from multiple interacting drivers, resulting in synergies and antagonisms. National monitoring schemes (e.g. the National Ecological Observatory Network, NEON) and international initiatives (e.g. the Group on Earth Observations – Biodiversity Observation Network, GEO BON) represent valuable datasets for assessing the complex interactive effects of multiple drivers (Oliver & Morecroft, 2014). Comparing local studies conducted in regions with uncorrelated CC and LUC may also provide a suitable framework for disentangling the effects of the two drivers and assessing their interactions (e.g. within formal meta-analysis; Mantyka-Pringle *et al.*, 2012; Parmesan *et al.*, 2013). Finally, whenever possible, we recommend using the methods recently developed to better account for multiple processes, for example by analysing distribution changes along multiple metrics (e.g. Lenoir & Svenning, 2015), quantifying change along multiple gradients (e.g. Tayleur *et al.*, 2015), combining short-term and long-term data with species attributes and environmental variables (e.g. Jørgensen *et al.*, 2016), or integrating key aspects of population dynamics and habitat preferences in models (e.g. Pagel & Schurr, 2012).

Question the role of multiple processes in species requirements and distribution

Species thermal optima or latitudinal distribution and species habitat requirements may be correlated. Comparing distributional changes among species with diverse habitat requirements, uncorrelated with their thermal requirements, or species with diverse range limits, uncorrelated with land-cover limits, may be a good approach (e.g. Konvicka *et al.*, 2003). Another solution could be to expand hypotheses on CC indicators to LUC in order to develop novel indicators allowing the quantification of the respective roles of, and interactions between, multiple drivers (e.g. Kampichler *et al.*, 2012). Finally, there is now considerable evidence that species respond with varying time lags to LUC and CC (Menéndez *et al.*, 2006; Kuussaari *et al.*, 2009), which is likely to impede our understanding of species requirements and, as a result, our understanding of the interactive effects of CC and LUC. There are also subtle interplays between the time species need to adapt to changes and the pace of the evolutionary processes shaping their distributions (e.g. plant dispersal evolution; Caplat *et al.*, 2013). Consequently, to better assess the interactive effects of multiple drivers on species distribution, we recommend, if possible: (1) the consideration of time lags in species response to environmental changes; (2) the use of long-term data to check for interactions between environmental drivers and population dynamics (e.g. Wittwer *et al.*, 2015); and (3) reinforcement of the links between macro-ecological studies and macroevolution (e.g. Lavergne *et al.*, 2013; Lancaster *et al.*, 2015).

CONCLUSIONS

Despite repeated calls, the interactive effects of multiple drivers on changes in species distribution are too often neglected by researchers, leading to an overemphasis on the effects of CC. This may have biased our perception, both in science and among the public, of the relative importance of specific drivers, and may represent a major impediment to accurate projections of biodiversity and effective conservation. To develop truly integrative global science, we need to better acknowledge correlations and interactions among drivers, in particular CC and LUC, and multiple-driver studies should become the norm. The increasing availability of datasets and methods can help overcome the challenges posed by studying multiple processes.

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BIOSKETCH

The authors are global change ecologists and conservation ecologists working on a wide range of biological models, ecosystems or countries and at various spatial and temporal scales. They have published numerous papers in high-ranked journals on the effects of climate change and/or land-use change on observed changes in species distribution and abundance. They are also deeply involved in conservation actions and have experienced how detrimental the lack of integration can be on the ground.

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