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Global change impacts 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. We here critically assess how often and efficiently the two main drivers of global changes have been simultaneously integrated into research, with the aim to provide 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 resulting from insufficient recognition of the co-occurrence of CC and LUC at all scales, co-variation and interactions between CC and LUC, as well as correlations between species thermal and habitat requirements. Practical guidelines to study 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, CC and LUC effects 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.

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 CC impacts on populations, species and ecological communities (e.g. Parmesan and 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., 2015).

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

Despite repeated calls for a better integration of multiple drivers (de Chazal and Rounsevell, 2009; Didham et al., 2007; Mantyka-pringle et al., 2012; Oliver and Morecroft, 2014; Parmesan et al., 2013), several authors have highlighted that conventional CC investigations and projections privileging CC attribution remain the norm (Oliver and 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 likely hamper reliable projections and relevant conservation recommendations (Titeux et al., 2016).

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

1. Current CC-LUC integration 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 2000-2014 period, on the effects of either CC (temperature and rainfall), LUC or both, on observed or projected changes in species distributions (i.e. species ranges and abundances) in terrestrial ecosystems (see 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 (Figure 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 around 12-14% of the total on that theme, suggesting limited CC-LUC integration regardless of whether the study focused on observed or projected changes (Figure 1).

Poor levels of true integration – We identified four levels of integration based on the abstract of the 158 publications that included both the effects of CC and LUC on observed changes in species distributions (Figure 2). Most studies (72%) mentioned CC and LUC only as 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; Popy et al., 2010; Reif et al., 2008). Only 8% of studies were specifically designed to assess the effects of both CC and LUC on species distribution (true integration; e.g. Eglington and Pearce-Higgins, 2012; Fox et al., 2014; Kampichler et al., 2012). This suggests a proportion of integrative studies even lower than what was suggested by our quantitative analysis, with truly integrative studies representing only a tiny fraction of studies on observed changes in species distributions.

Integration revealing hidden driver or combination of drivers - Most of the 13 studies designed to assess the effect of both drivers were published over the last five years. These integrative studies were of three types (see box 1 for more details). A 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 (Ameztegui et al., 2016; Bodin et al., 2013; Eglington and Pearce-Higgins, 2012; O'Connor et al., 2014). A second set showed that the impacts of CC and LUC differed among species groups, some species responding only to CC whereas others were only impacted by LUC (Fox et al., 2014; Hockey et al., 2011; Kampichler et al., 2012; Lavergne et al., 2006). Finally, a third set showed that LUC and CC acted in synergy (Christie et al., 2015; Cunningham et al., 2016; Lunney et al., 2014; Paprocki et al., 2015; Porzig et al., 2014). 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 CC-LUC integration is currently jeopardizing our understanding of global change impacts on species distribution (i.e. which driver is having an impact, where, when and why).

2. Consequences of poor CC-LUC integration in studies on species distributions

Our analysis of the literature suggests that the lack of CC-LUC integration 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 CC-LUC integration implies that biodiversity management strategies essentially derive from CC-only studies, which mainly recommend to increase landscape and habitat connectivity (Heller and 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 woody vegetation encroachment following farmland abandonment (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 CC-LUC integration hinders our ability to identify 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 CC effects through adaptive land-use management (Gaüzère et al., 2016; Princé et al., 2015). For example, Braunisch et al. (2014) showed that expected CC-driven range contractions of mountain forest birds could be partly compensated by enhancing forest structural complexity. 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 CC-LUC integration 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 and Midgley, 2009) but also concerns most situations where CC and LUC interact (Mantyka-pringle et al., 2012).

3. Reasons for poor CC-LUC's integration in studies on species distributions

Our analysis of the literature suggested that, although LUC data and LUC scenario availability and credibility may have been a limiting factor initially (before the 2000s; e.g. Verburg et al., 2002), it fails to explain the recent lack of CC-LUC integration and the increase of CC-only studies. Our review of papers designed to study CC-LUC integration (section 1) and other papers calling for more CC-LUC integration (e.g. de Chazal and Rounsevell, 2009; Oliver and Morecroft, 2014; Parmesan et al., 2013; Titeux et al., 2016) have highlighted three reasons likely to explain the ongoing lack of CC-LUC integration, for both observed and projected changes in species distributions.

Misrepresentation of the scale of CC and LUC impacts - The ongoing lack of CC-LUC integration can first be explained by the fact that CC has been expected to impact species distributions at broader spatial and temporal scales (regional-continental, >50 years) and LUC at finer (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-altitudinal temperature shifts, but also via progressive shifts in local climate (Lenoir and Svenning, 2015). Conversely, LUC has been shown to massively impact 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 misrepresentation previously described, most studies on latitudinal or altitudinal species shifts focused on CC only, whereas most studies on local long-term changes in species abundance focused on LUC only. However, geographic variation in land cover is highly correlated with geographic variation in bioclimatic variables (e.g. Thuiller et al., 2004) and altitudinal gradients are often correlated with land-use intensity gradients (e.g. Archaux, 2004). This implies that LUC represents a likely driver to latitudinal or altitudinal species shifts, habitat gains explaining range expansion (e.g. Elmhagen et al., 2015) and habitat 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 and 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 optimum 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 both species and land-cover distributions, e.g. 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 northern 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).

4. Recommendations for future research on CC-LUC interactions

Building on the obstacles for CC-LUC integration identified here (section 3), and solutions developed in studies that have genuinely integrated CC and LUC (section 1), we propose three main recommendations to design a more effective integrative global-change science (see synthesis and illustration in Figure 3).

1. 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 US; 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 and Pearce-Higgins, 2012). The availability of long-term climatic and remote-sensing data should facilitate this integration. Most local studies in the literature considered 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 and Altwegg, 2015).

2. 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 to assess the complex interactive effects of multiple drivers (Oliver and 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 and 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 and Schurr, 2012).

3. Question the role of multiple processes in species requirements and distribution– Species thermal optimum or latitudinal distribution and species habitat requirements may be correlated. Comparing distribution 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 to quantify 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 (Kuussaari et al., 2009; Menéndez et al., 2006), 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, to 1) consider time-lags in species response to environmental changes; 2) use long-term data to check for interactions between environmental drivers and population dynamics (e.g. Wittwer et al., 2015), and 3) reinforce the links between macro-ecological studies and macroevolution (e.g. Lancaster et al., 2015; Lavergne et al., 2013) .

Conclusion

Despite repeated calls, the interactive effects of multiple drivers on species distribution changes 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 in the public, of the relative importance of specific drivers, and may represent a major impediment to accurate biodiversity projections 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.

Table 1. Key words selected based on title and abstracts of a large sample of publications on climate change, land-use change and species distributions. We consulted the Web of Science database (http://www.webofknowledge.com) for the last 15 years (2000-2014). 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 key words used in these studies. As a result, we believe that our search may have, if anything, only slightly underestimated the number of publications on land-use changes.

Key words 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

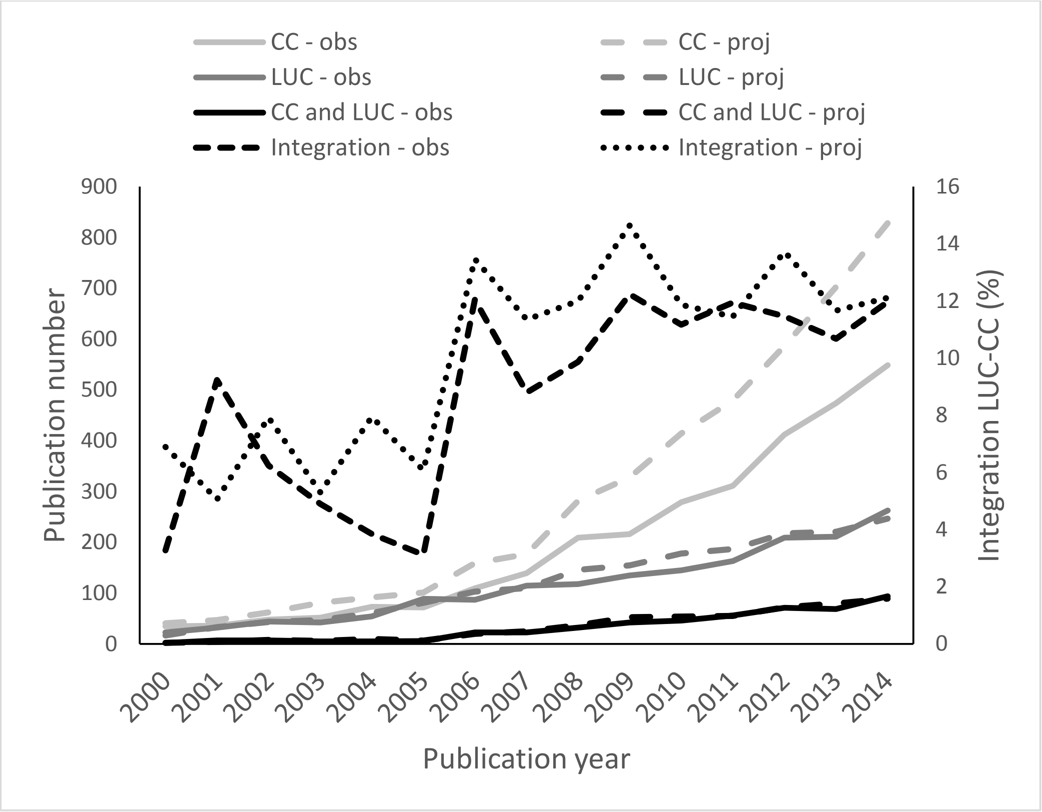
Figure captions

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 % of publications integrating land-use change (LUC) and climate change (CC) in publications on observed (Integration-obs) and projected (Integration-proj) effects (i.e. 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 2000-2014 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 publications title, abstract and keywords.

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

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).

Figure 1.


CC - obs
CC - proj
LUC - obs
LUC - proj
CC and LUC - obs
CC and LUC - proj
Integration - obs
Integration - proj
Publication number
900
800
700
600
500
400
300
200
100
0
Integration LUC-CC (%)
16
14
12
10
8
6
4
2
0
2000
2001
2002
2003
2004
2005
2006
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2008
2009
2010
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2012
2013
2014
Publication year

Figure 2.

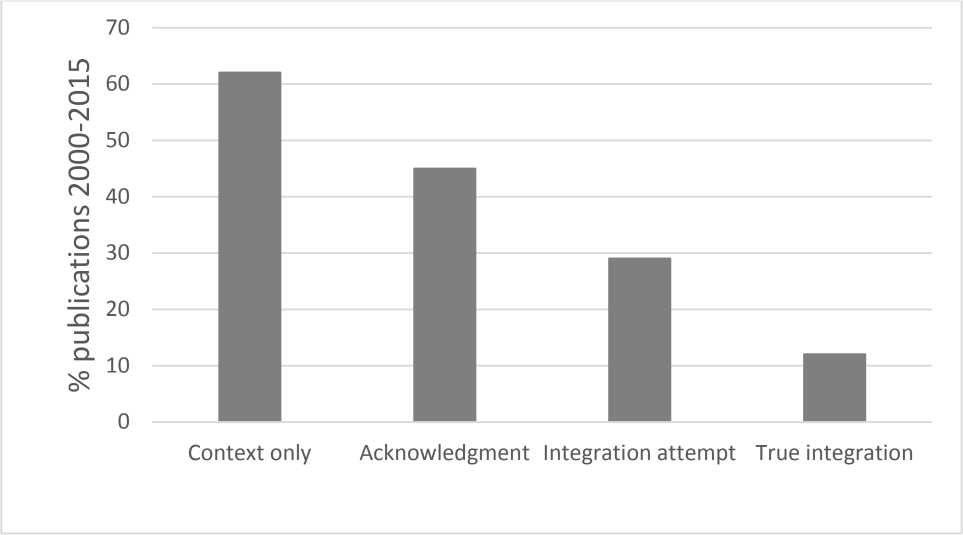
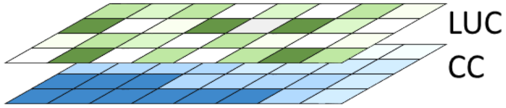
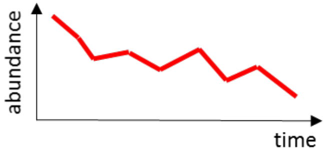
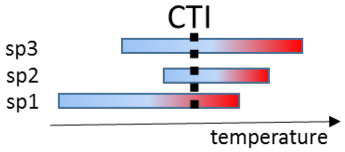
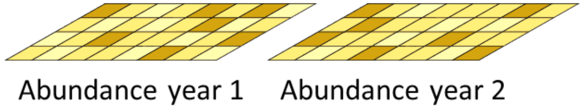
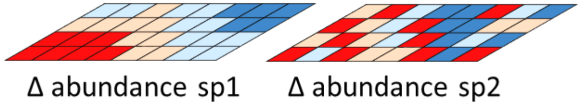
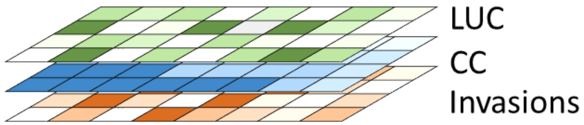
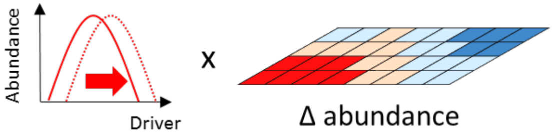
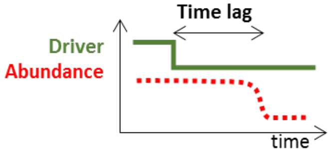

% publications 2000-2015
70
60
50
40
30
20
10
0
Context only
Acknowledgment
Integration attempt
True integration

Figure 3.

	1. Consider multiple drivers	**2. Assess interactions**	**3. Question processes at species level**
Design	Consider alternative drivers at any scale, in particular CC and LUC	Consider alternative hypotheses: confounding, synergystic, antagonistic effects	Consider that species distribution and requirements result from multiple processes
Data	Use available data on multiple drivers *e.g. Stürck et al., 2015* 	Use long-term monitoring schemes *e.g. NEON* 	Use and develop community indicators *e.g. CTI - Kampichler et al., 2012* 
Methods Must-do	Revisit existing datasets and studies *e.g. Péron and Altwegg, 2015* 	Conduct meta-analysis *e.g. Mantyka-Pringle et al., 2012* 	Compare guilds or species *e.g. Konvicka 2003* 
Methods Wish-list	Include more than two drivers *e.g. Benning et al., 2002* 	Combine methodological approaches *e.g. Tayleur et al., 2015* 	Include time-lags and adaptation processes *e.g. Menéndez et al., 2006* 

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

Outcomes of publications designed to study the effects of both LUC and CC on species distribution and abundance.s

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

Eglington and Pearce-Higgins (2012) showed that despite more stable land-use intensity in recent years, climate change 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 climate change in the study area. Similarly, Bodin et al. (2013) showed that the shift of forest species along an elevation gradient in Southeast France resulted from the maturation of forests due to land abandonment rather than climate change. 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 land-use and climate change influenced range shifts of different types of South African bird species. Kampichler et al. (2012) showed that interactions between climate and land-use change 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 land-use changes (human population growth and habitat loss) have been hiding the significant contribution of climate changes (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, U.S.A., 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 raptors populations in southwest Idaho, U.S.A., were influenced by northward distributional shifts due to climate change 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.