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

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1 **Global change impacts on species distributions: obstacles and solutions to integrate climate and**  
2 **land use**

3

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22

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24

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26

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30

31 **Abstract**

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

37 **Location** Global

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

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

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

54

## 55 **Introduction**

56 Over the past decades, the challenges to biodiversity presented by climate change (CC) have triggered  
57 exponential growth in the literature on the current and predicted CC impacts on populations, species  
58 and ecological communities (e.g. Parmesan and Yohe, 2003). Evidence shows that ecosystems have  
59 already been greatly affected and that impacts will continue mostly unabated. What we still largely  
60 ignore is the magnitude of these past and, above all, future impacts (Hansen et al., 2015).

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

66 Despite repeated calls for a better integration of multiple drivers (de Chazal and Rounsevell,  
67 2009; Didham et al., 2007; Mantyka-pringle et al., 2012; Oliver and Morecroft, 2014; Parmesan et al.,  
68 2013), several authors have highlighted that conventional CC investigations and projections  
69 privileging CC attribution remain the norm (Oliver and Morecroft, 2014; Titeux et al., 2016). In the  
70 absence of integrative multi-driver approaches, limited understanding of how interactions among  
71 drivers affect observed changes will likely hamper reliable projections and relevant conservation  
72 recommendations (Titeux et al., 2016).

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

80

81           **1. Current CC-LUC integration in studies of species distribution**

82   We analysed the peer-reviewed literature in three steps. First, we searched Web of Science  
83   (<http://www.webofknowledge.com>) for publications over the 2000-2014 period, on the effects of  
84   either CC (temperature and rainfall), LUC or both, on observed or projected changes in species  
85   distributions (i.e. species ranges and abundances) in terrestrial ecosystems (see complete list of  
86   keywords used for each criterion in Table 1). Second, we read the abstract of all publications on the  
87   effects of both CC and LUC on observed changes in species distributions. We then qualitatively  
88   assessed the level of driver integration in any given relevant publication based on its abstract. Finally,  
89   we read the full text of all publications truly designed to integrate both drivers and assessed their  
90   outcome. For the second and third steps, we also included publications on the effects of both CC and  
91   LUC on observed changes in species distributions from 2015 and 2016.

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

102           **Poor levels of true integration** – We identified four levels of integration based on the abstract  
103   of the 158 publications that included both the effects of CC and LUC on observed changes in species  
104   distributions (Figure 2). Most studies (72%) mentioned CC and LUC only as a general context while  
105   focusing on a single driver (context only), or acknowledged that other drivers could influence  
106   observed changes (acknowledgement). Some studies (20%) attempted to control for potential

107 confounding effects of CC and LUC on species distribution (integration attempt), for example by  
108 accounting for species habitat as a covariate in studies on the impact of CC or by selecting study sites  
109 without LUC (e.g. Franco et al., 2006; Popy et al., 2010; Reif et al., 2008). Only 8% of studies were  
110 specifically designed to assess the effects of both CC and LUC on species distribution (true  
111 integration; e.g. Eglinton and Pearce-Higgins, 2012; Fox et al., 2014; Kampichler et al., 2012). This  
112 suggests a proportion of integrative studies even lower than what was suggested by our quantitative  
113 analysis, with truly integrative studies representing only a tiny fraction of studies on observed changes  
114 in species distributions.

115 **Integration revealing hidden driver or combination of drivers** - Most of the 13 studies  
116 designed to assess the effect of both drivers were published over the last five years. These integrative  
117 studies were of three types (see box 1 for more details). A first set showed that, in some cases, despite  
118 strong expectations that observed changes were driven by CC, the effects of LUC clearly overrode  
119 those of CC (Ameztegui et al., 2016; Bodin et al., 2013; Eglinton and Pearce-Higgins, 2012;  
120 O'Connor et al., 2014). A second set showed that the impacts of CC and LUC differed among species  
121 groups, some species responding only to CC whereas others were only impacted by LUC (Fox et al.,  
122 2014; Hockey et al., 2011; Kampichler et al., 2012; Lavergne et al., 2006). Finally, a third set showed  
123 that LUC and CC acted in synergy (Christie et al., 2015; Cunningham et al., 2016; Lunney et al.,  
124 2014; Paprocki et al., 2015; Porzig et al., 2014). None of the studies assessing both CC and LUC  
125 concluded that only CC had an impact on species distributions. This suggests that the lack of CC-LUC  
126 integration is currently jeopardizing our understanding of global change impacts on species  
127 distribution (i.e. which driver is having an impact, where, when and why).

128

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

130 Our analysis of the literature suggests that the lack of CC-LUC integration in studies on species  
131 distributions and the dominance of CC-only studies is likely to result in inappropriate management

132 strategies or missed conservation opportunities, and may even trigger, in some cases, a relaxation in  
133 appropriate conservation efforts.

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

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

154 **Insufficient conservation efforts** – Finally, the lack of CC-LUC integration and the  
155 dominance of CC-only studies assessing observed shifts in species distribution is likely to have  
156 resulted in overrating the effects of CC and downplaying the negative effects of LUC. This is likely to  
157 divert funds and efforts away from more immediate conservation priorities (Maxwell et al., 2016).

158 The risk of insufficient local conservation efforts is extremely acute for species declines inaccurately  
159 attributed to CC (e.g. Hockey and Midgley, 2009) but also concerns most situations where CC and  
160 LUC interact (Mantyka-pringle et al., 2012).

161

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

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

170 **Misrepresentation of the scale of CC and LUC impacts** - The ongoing lack of CC-LUC  
171 integration can first be explained by the fact that CC has been expected to impact species distributions  
172 at broader spatial and temporal scales (regional-continental, >50 years) and LUC at finer (habitat-  
173 landscape, <20 years; Parmesan et al., 2013). This has resulted in the assumptions that CC overrides  
174 LUC at regional scales (Thuiller et al., 2004), and that LUC overrides CC at local scales (Bailey et al.,  
175 2002). CC has been recently shown to affect species distributions not only through broad latitudinal-  
176 altitudinal temperature shifts, but also via progressive shifts in local climate (Lenoir and Svenning,  
177 2015). Conversely, LUC has been shown to massively impact contemporaneous broad scale changes  
178 in species distributions (e.g. Barbet-Massin et al., 2012).

179 **Lack of recognition of covariations and interactions between CC and LUC** – Partly as a  
180 consequence of the misrepresentation previously described, most studies on latitudinal or altitudinal  
181 species shifts focused on CC only, whereas most studies on local long-term changes in species  
182 abundance focused on LUC only. However, geographic variation in land cover is highly correlated  
183 with geographic variation in bioclimatic variables (e.g. Thuiller et al., 2004) and altitudinal gradients

184 are often correlated with land-use intensity gradients (e.g. Archaux, 2004). This implies that LUC  
185 represents a likely driver to latitudinal or altitudinal species shifts, habitat gains explaining range  
186 expansion (e.g. Elmhagen et al., 2015) and habitat losses explaining range contraction (e.g. Franco et  
187 al., 2006). Similarly, CC represents a likely driver to explain local long-term changes in species  
188 abundance and community composition (e.g. Lemoine et al., 2007). Moreover, interactions between  
189 CC and LUC are likely to be the norm rather than the exception (Parmesan et al., 2013). For example,  
190 land cover influences microclimate, and therefore the local effects of CC (e.g. Carlson and Traci  
191 Arthur, 2000); landscape structure affects the ability of species to shift their distribution (e.g. Hill et  
192 al., 2001); and climate affects the effects of habitat loss (e.g. Mantyka-pringle et al., 2012).

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

204

#### 205 **4. Recommendations for future research on CC-LUC interactions**

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

210 **1. Consider multiple drivers at any scale** - When working at broad spatial scales, consider potential  
211 broad scale gradients in drivers other than CC, in particular LUC (e.g. the South-North LUC gradient  
212 in Europe or LUC gradients in the US; Ordonez et al., 2014). The availability of data on past LUC/CC  
213 (e.g. Wang et al., 2015) and LUC scenarios (e.g. Stürck et al., 2015) at various scales should facilitate  
214 this integration. When working at local scales, account for local processes such as LUC or species  
215 invasions as well as fine-grained spatio-temporal variation in temperature and precipitation patterns  
216 (e.g. Eglington and Pearce-Higgins, 2012). The availability of long-term climatic and remote-sensing  
217 data should facilitate this integration. Most local studies in the literature considered only one driver,  
218 but the increased availability of data on other drivers offers new avenues for integrative analyses.  
219 These studies could therefore be revisited from a multiple-driver perspective, with the novel  
220 integration of two or possibly more drivers (e.g. Benning et al., 2002), for example by comparing  
221 existing long-term datasets and new datasets available on CC and LUC (e.g. Péron and Altwegg,  
222 2015).

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

237 **3. Question the role of multiple processes in species requirements and distribution**– Species  
238 thermal optimum or latitudinal distribution and species habitat requirements may be correlated.  
239 Comparing distribution changes among species with diverse habitat requirements, uncorrelated with  
240 their thermal requirements, or species with diverse range limits, uncorrelated with land cover limits,  
241 may be a good approach (e.g. Konvicka et al., 2003). Another solution could be to expand hypotheses  
242 on CC indicators to LUC in order to develop novel indicators allowing to quantify the respective roles  
243 of, and interactions between, multiple drivers (e.g. Kampichler et al., 2012). Finally, there is now  
244 considerable evidence that species respond with varying time-lags to LUC and CC (Kuussaari et al.,  
245 2009; Menéndez et al., 2006), which is likely to impede our understanding of species requirements,  
246 and, as a result, our understanding of the interactive effects of CC and LUC. There are also subtle  
247 interplays between the time species need to adapt to changes and the pace of the evolutionary  
248 processes shaping their distributions (e.g. plant dispersal evolution; Caplat et al., 2013).  
249 Consequently, to better assess the interactive effects of multiple drivers on species distribution, we  
250 recommend, if possible, to 1) consider time-lags in species response to environmental changes; 2) use  
251 long-term data to check for interactions between environmental drivers and population dynamics (e.g.  
252 Wittwer et al., 2015), and 3) reinforce the links between macro-ecological studies and macroevolution  
253 (e.g. Lancaster et al., 2015; Lavergne et al., 2013) .

254

## 255 **Conclusion**

256 Despite repeated calls, the interactive effects of multiple drivers on species distribution changes are  
257 too often neglected by researchers, leading to an overemphasis on the effects of CC. This may have  
258 biased our perception, both in science and in the public, of the relative importance of specific drivers,  
259 and may represent a major impediment to accurate biodiversity projections and effective conservation.  
260 To develop truly integrative global science, we need to better acknowledge correlations and  
261 interactions among drivers, in particular CC and LUC, and multiple-driver studies should become the

262 norm. The increasing availability of datasets and methods can help overcome the challenges posed by  
263 studying multiple processes.

264

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434

435 **Biosketch**

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

442

443

444 Table 1. Key words selected based on title and abstracts of a large sample of publications on climate  
 445 change, land-use change and species distributions. We consulted the Web of Science database  
 446 (<http://www.webofknowledge.com>) for the last 15 years (2000-2014). We ran the following searches:  
 447 LUC-obs = effect of land-use change (LUC) on observed changes; LUC-proj= effects of LUC on  
 448 projected changes; CC-obs = effects of climate change (CC) on observed changes; CC-proj = effects of  
 449 CC on projected changes; CC and LUC-obs = effects of both LUC and CC on observed changes; CC  
 450 and LUC-proj = effects of both LUC and CC on projected changes. We tried to include as many terms  
 451 as possible related to LUC to include the wide diversity of key words used in these studies. As a result,  
 452 we believe that our search may have, if anything, only slightly underestimated the number of  
 453 publications on land-use changes.  
 454

Key words included	LUC-obs	LUC-proj	CC-obs	CC-proj	CC and LUC-obs	CC and LUC-proj
<b>Species distribution:</b> "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
<b>Land-use change:</b> "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
<b>Climate change:</b> "climate change" OR "global warming" OR "temperature increase" OR "precipitation loss" OR "drought" OR "flood" OR "extreme event"			x	x	x	x
<b>Observed:</b> "observed" OR "historical" OR "past" OR "current"	x		x		x	
<b>Projected:</b> "predict*" OR "project*" OR "scenario" OR "future"		x		x		x
<b>NOT:</b> "Pleistocene" OR "Paleo" OR "fossil" OR "glacial" OR "quaternary" OR "Holocene" OR "marine" OR "ocean*" OR "sea"	x	x	x	x	x	x

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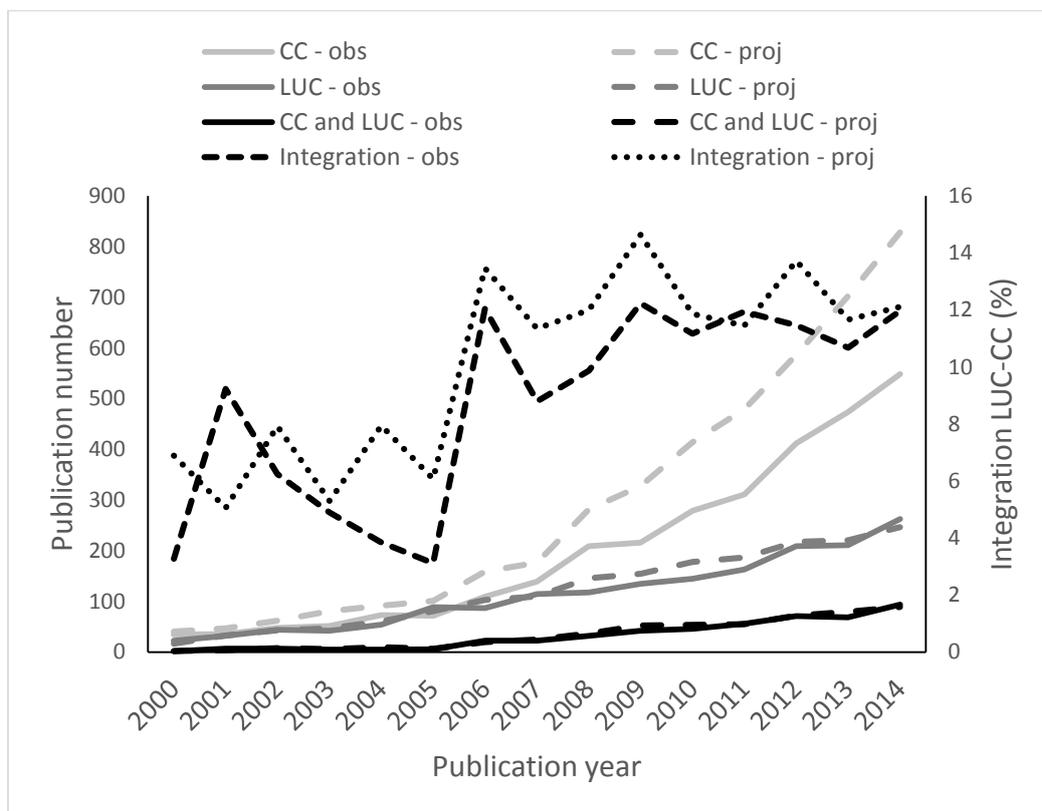
458 **Figure captions**

459 Figure 1. Temporal variations in 1) the number of publications on the observed (-obs) or projected (-  
460 proj) effects of climate change (CC), land-use change (LUC), and both combined in the same  
461 publication (CC-LUC), on species distributions and abundances, and 2) the % of publications  
462 integrating land-use change (LUC) and climate change (CC) in publications on observed (Integration-  
463 obs) and projected (Integration-proj) effects (i.e. percentage of publications including both drivers  
464 simultaneously over all publications including either one of the drivers represented along the  
465 secondary axis). This figure is restricted to the period 2000-2014 since referencing for years 2015 and  
466 2016 in Web of Science was not complete at the time of the review. This analysis is based on  
467 publications title, abstract and keywords.

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

471  
472 Figure 3. Synthesis of the three major recommendations for effective integrative global change  
473 science regarding the study design, data available and methods that can easily be implemented (must-  
474 do). We also suggest several avenues to further improve global change science (wish-list).

475 Figure 1.

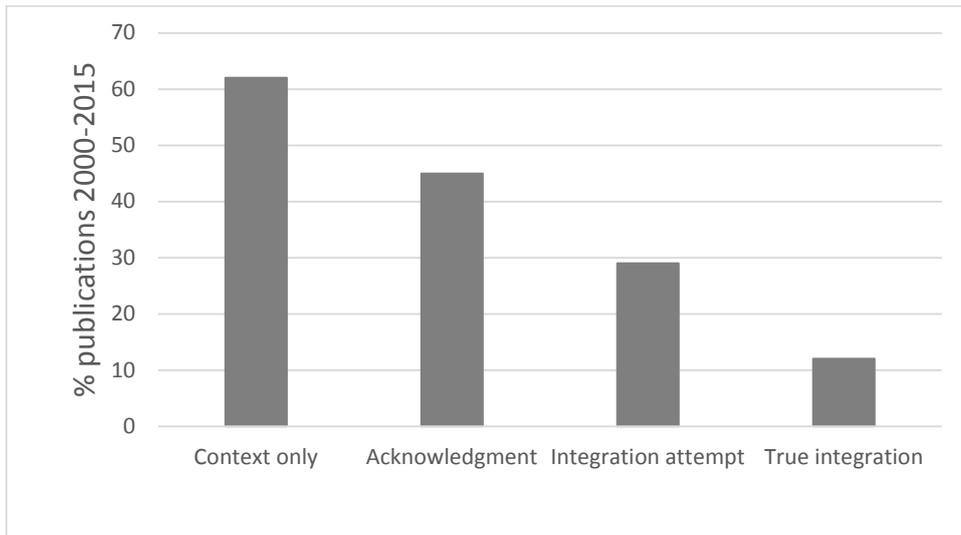


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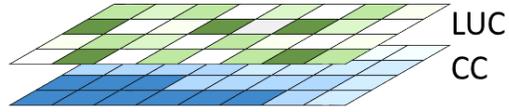
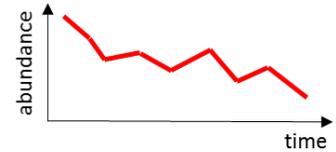
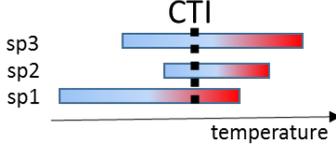
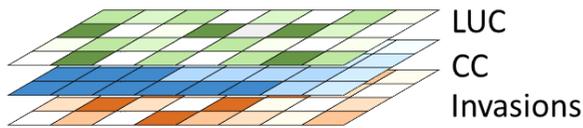
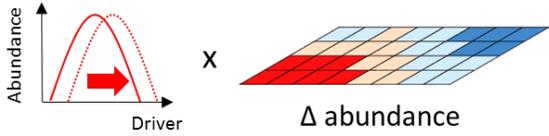
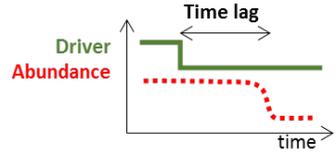
479 Figure 2.  
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482

1 Figure 3.

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

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

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

3  
4 **Case 1. The effects of LUC overrides the effect of CC**

5 Eglinton and Pearce-Higgins (2012) showed that despite more stable land-use intensity in recent years, climate change has not overtaken land-use  
6 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  
7 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)  
8 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  
9 than climate change. O'Connor et al. (2014) showed that changes to soil surface temperatures caused by increased grazing had a more consistent influence  
10 than air temperature increases on the recovery of the Adonis blue butterfly in the UK.

11  
12 **Case 2. LUC and CC impact different sets of species**

13 Lavergne et al. (2006) showed that changes in land use and climate influenced the occurrence of different plant species in Mediterranean France.  
14 Similarly, Hockey et al. (2011) showed that land-use and climate change influenced range shifts of different types of South African bird species. Kampichler  
15 et al. (2012) showed that interactions between climate and land-use change differed between habitats for Dutch breeding bird communities. Fox et al. (2014)  
16 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  
17 similarly, suggesting complex interactions between these two drivers.

18  
19 **Case 3. LUC and CC act in synergy**

20 Lunney et al. (2014) showed that overwhelming land-use changes (human population growth and habitat loss) have been hiding the significant  
21 contribution of climate changes (temperature increase and drought) to the long-term shrinkage in the distribution of the koala in south-eastern New South  
22 Wales, Australia. Porzig et al. (2014) showed that temporal variations in Californian birds were best explained by temporal changes in vegetation, but that  
23 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  
24 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  
25 well density that has recently increased and is likely to impede pronghorn movement to more hospitable areas during winter storms. Paprocki et al. (2015)  
26 showed that temporal changes in wintering raptors populations in southwest Idaho, U.S.A., were influenced by northward distributional shifts due to climate  
27 change as well as temporal changes in local habitat conditions. Finally, Cunningham et al. (2016) showed that pied crow numbers in south-western South  
28 Africa have increased in response to climate warming, with their spread facilitated by electrical infrastructure.

29