

Biodiversity Climate change Impacts Report Card Technical paper

1. Interactions between climate change and land use change impacts: addressing attribution problems

Tom H. Oliver & David B. Roy

NERC Centre for Ecology & Hydrology,

Benson Lane,

Crowmarsh Gifford,

Oxfordshire,

OX10 8BB.

Email: toliver@ceh.ac.uk; dbr@ceh.ac.uk

Summary

Following each statement, confidence in scientific understanding, following IPCC methodology, is given in brackets.

1. Climate and land use change interact in their effects of biodiversity, with potentially large negative impacts (High agreement medium evidence)
2. These interactions include:
 - Landscape structure affecting species range shifts (High agreement robust evidence)
 - Climate change affecting metapopulation persistence (Medium agreement limited evidence)
3. -Habitat and topographic heterogeneity providing broader microclimatic gradients (High agreement medium evidence)
 - Impacts of extreme climatic events being influenced by land use (Medium agreement medium evidence)
 - Climate induced community shifts being influenced by land use (Medium agreement limited evidence)
4. Mechanisms for interactions include:
 - Direct interactions between demographic parameters (High agreement robust evidence)
 - Evolutionary trade-offs and synergies (Medium agreement limited evidence)
 - Threshold effects of population size on extinction risk (High agreement robust evidence)
 - Threshold occupancy for metapopulation persistence (High agreement medium evidence)
5. To understand the significance of interaction effects well designed experiments or systematic assessments along gradients are required, and which control for one driver while exploring the effects of another.
6. Future projections of biodiversity may be prone to errors if they do not adequately address interactions between land use change and climate change. This may lead to conservation management becoming ineffective
7. Therefore, more research is needed into the synergistic effects of multiple global change drivers on biodiversity along with extent of local adaptation and the potential for rapid evolution
8. Management strategies should be adaptive and informed by spatially-replicated long term biodiversity monitoring networks
9. Interactions also offer opportunities to manage habitats and landscapes to reduce negative impacts of climate change on species. In addition, relatively simple actions, such as increasing habitat area and quality, can reduce the impacts of a number of drivers simultaneously

1. Introduction

Climate change and land use change are often assessed separately but they are likely to interact in their effects on biodiversity. These interactions could potentially have large impacts on biodiversity and important implications for habitat and landscape management. Many studies consider the combined effects of climate change and land use change, but only a few investigate the nature of interactions (e.g. antagonistic interactions or synergies), because these are much harder to study without careful experimental and analytical design, which is hard to achieve at a sufficient scale.

In this review, we briefly describe some of the key studies investigating one of the two drivers in isolation, and then consider studies looking at combined effects. We then describe some of the mechanisms by which climate and land use change can interact to affect biodiversity. Next, we highlight some of the problems in the attribution of biodiversity changes to climate or land use change and describe how errors can influence the accuracy of biodiversity projections. We conclude by identifying research gaps to improve our ability to attribute biodiversity changes and discuss the risks and opportunities for successful management provided by the existence of land use-climate change interaction effects.

2. Climate change as a driver of biodiversity change

A number of studies have considered the responses of biodiversity to past periods of climate change in the Earth's history. Biodiversity is likely to be affected by both incremental changes in mean climate parameters and also by the frequency and intensity of climatic extremes (Jentsch, Kreyling & Beierkuhnlein, 2007). Although climate changes are likely to be implicated in some mass extinction events (McGhee Jr *et al.*, 2004; Payne & Finnegan, 2007), there appears to have been relatively few extinctions during the more recent glacial to inter-glacial transition periods of rapid climate change (Dawson *et al.*, 2011). Species are expected to have survived through combinations of shifting their distribution to track climate, persisting in climatic refuges and evolving tolerance to climatic changes (Jackson & Overpeck, 2000; Coope, 2004; Willis & Bhagwat, 2009; Dawson *et al.*, 2011). However, future climate change could potentially occur at an unprecedented rate, and also against a backdrop of other drivers of change (e.g. heavily modified landscapes, pollution, eutrophication etc.). Therefore, any generalities of extinction dynamics from ancient evidence need be contextualised within current pace of climate change and synergies between drivers need to be appreciated (Brook, Sodhi & Bradshaw, 2008).

Fortunately, many studies have explored effects of modern climate change on biodiversity and several major reviews have been published (e.g. Walther *et al.*, 2002; Root *et al.*, 2003; Parmesan, 2006). The most well studied effects of climate change can be grouped into a number of active fields of research, which we briefly summarise here:

Phenology

Advances in the timing of biological events have been documented for many groups (Root *et al.*, 2003; Thackeray *et al.*, 2010). Such changes have been shown to cause temporal mismatches between interacting species, and have the potential to lead to population declines and extinctions (Visser *et al.*, 1998; Durant *et al.*, 2005; Hipfner, 2008; Post & Forchhammer, 2008; Miller-Rushing *et al.*, 2010; Thomson, 2010).

Distribution shifts

There is a large amount of evidence for expansions of species high latitude range edges towards the Earth's poles (Parmesan *et al.*, 1999; Hickling *et al.*, 2006; Chen *et al.*, 2011). There are considerable geographic and taxonomic biases in these studies with less data from the Southern hemisphere and for less charismatic groups. There is less evidence

of range retractions at low latitude range boundaries, but these may be more difficult to detect; because, for example, a grid cell of certain resolution needs to lose all individuals before a species is considered absent (Wilson *et al.*, 2005). Ultimately, whole biomes are projected to shift, with savannahs replacing rainforest and boreal forest encroaching on tundra (Bellard *et al.*, 2012). However, there is likely to be much variation in the responses of species (Warren *et al.*, 2001; Menéndez *et al.*, 2006).

Population responses to altered weather

The abundance of many populations is strongly driven by weather variables (Roy *et al.*, 2001; Eglinton & Pearce-Higgins, in press). Changes in climate are therefore projected to have large impacts on populations within their existing ranges. Seasonality is an important component of this: In the UK, some insect species may decline due to the warmer wetter winters which are projected from models (Roy *et al.*, 2001; UKCP09, 2010). Spring and summer drought events may also cause future declines in some species, whilst benefitting others (Morecroft *et al.*, 2002).

Evolutionary changes

Evolutionary changes in response to climate change are less well researched than range and phenology shifts, but there is clear evidence that in some cases selection for dispersal may increase towards range boundaries (Thomas *et al.*, 2001a; Hughes, Hill & Dytham, 2003; Simmons & Thomas, 2004b). These patterns in dispersal phenotypes may be driven more by the spatial structuring of populations and the availability of suitable unoccupied habitat, rather than by climate warming directly. However, because climate change can change both these factors, it indirectly drives selection pressures. Effects of range expansion on the genetic structure of species are being increasingly explored (e.g. Buckley, Butlin & Bridle, 2012).

Community shifts

Due to interspecific variation in responses to climate change in terms of species' phenology, their distribution and population responses to altered weather patterns, community compositions are likely to change over time (Breshears *et al.*, 2008; Walther, 2010). For example, in the UK and northwest Europe, bird and butterfly communities are increasing dominated by species with warm- rather than cold distributions (Devictor *et al.*, 2012). Such community changes lead to altered interactions between species (Tylianakis *et al.*, 2008), although it is yet unclear to what degree the stability of food webs is altered by climate change. The effects of community changes on the stocks and resilience of ecosystem services is also an active field of research (Balvanera *et al.*, 2006; Montoya & Raffaelli, 2010).

To summarise thus far, there are a large number of known mechanisms by which climate change can affect biodiversity. There is also much interspecific variation in the responses. Each of these mechanisms above may interact with other drivers of change, such as land use, and we explore these interactions in later sections.

3. Land use as a driver of biodiversity change

The major human impacts on biodiversity to date are probably through land use changes and habitat loss (Millennium Ecosystem Assessment, 2005; UK National Ecosystem Assessment, 2011). Also, a whole range of other global change drivers are important including biological invasions, pollution (e.g. N and S deposition) and overexploitation (Brook, Sodhi & Bradshaw, 2008). Land use change, often to expand agriculture, causes direct habitat loss, but also has other effects such as fragmentation of remaining habitat and increased agrochemical inputs into surrounding natural (or semi-natural) habitats. Changes to the management of land (e.g. grazing regime) also have large direct impacts on biodiversity (McGovern *et al.*, 2011). Intensification often leads to an increase in nitrogen

deposition, particularly as a result of atmospheric deposition, intensive livestock rearing and fertiliser inputs. In the UK, this has led to an increase in soil fertility and increased dominance of plants preferring high-nutrient soils (Carey *et al.*, 2008).

Agricultural intensification in general has been one of the major drivers of biodiversity decline in the UK (Donald, Green & Heath, 2001; Benton *et al.*, 2002; Robinson & Sutherland, 2002; Fox, 2012). As a consequence, there is an increased recognition of need to 'join-up' landscapes (Lawton *et al.*, 2010; HM Government, 2011). Isolated populations face increased extinction risk and metapopulations (groups of connected populations) need a minimum number of sites occupied to persist (Hanski, 1999). Isolation effects may be non-linear, with greatest risks to populations when total habitat area is low (Andrén, 1994; Opdam & Wascher, 2004). However, some researchers argue that benefits of increasing connectivity through matrix management are overplayed relative to increasing patch size and quality (Thomas *et al.*, 2001b; Hodgson *et al.*, 2011). Fortunately, increasing patch size and quality is also likely to increase connectivity (through an increased number of colonists), as well as reducing local extinction risk and edge effects. However, where habitat patches are already of adequate size then it may be reasonable to focus efforts on improving connectivity through matrix management (Lawton *et al.*, 2010; Oliver *et al.*, in press).

Globally, the extent of land use change varies markedly. Many areas still have relatively pristine habitat cover (e.g. parts of tropics and the polar regions). However, in some of these areas, such as the tropics, pressures of increased agricultural expansion are greatest, and we can expect dramatic changes to biodiversity as a consequence of land use change (Sala *et al.*, 2000). Additionally, it has been suggested that in regions with a shorter history of human development, species may be more sensitive to land use change (Forister *et al.*, 2010). However, this hypothesis has not yet been tested.

In the UK, along with much of NW Europe, there is a long history of landscape modification. Priority habitats for conservation are often classed as 'semi-natural' because, although they harbour much of the remaining biodiversity and are not primarily managed for agricultural production, they require some management to maintain them (e.g. to prevent grassland succession to woodland in the absence of wild large herbivores). It is possible that conversion of land to intensive agriculture in NW Europe may have now peaked, with increased emphasis of restoring semi-natural habitat cover (e.g. through AES schemes). According to the Countryside Survey, across the UK between 1990 and 2007 there was a 9.1% decrease in arable and horticulture land cover, but also a concurrent increase in improved grassland of 5.4% (Carey *et al.*, 2008). Predicting future trends is difficult and suitable high resolution land use change scenarios are lacking (HM Government, 2010; UK National Ecosystem Assessment, 2011). In the UK, for example, European CAP reform is likely to have impacts on land use patterns, as are increased human population size and changes to planning policies. Such pressures could potentially result in increased development on green field land.

Similar to climate change, species show much variation in their responses to land use change. In the UK, species benefitting from land use change tend to be more mobile, generalist feeders with wider habitat associations (Warren *et al.*, 2001; Menéndez *et al.*, 2006).

4. Combined effects of climate and land use change on biodiversity

In addition to the direct effects described above, climate change and land use change may interact in their effects on biodiversity. Understanding such interactions between global change drivers will be essential to manage environments appropriately (Sala *et al.*, 2000; Brook, Sodhi & Bradshaw, 2008; Tylianakis *et al.*, 2008). Fortunately, an increasing number of studies have begun to examine these combined effects on biodiversity, although studies

exploring true interaction effects are less common. In this review we focus primarily on the combined effects of land use change and climate change on biodiversity. However, it should be recognised that there are a number of other key drivers that impact biodiversity, e.g. pollution and invasive species (Millennium Ecosystem Assessment, 2005; UK NEA, 2011). Another technical review paper covers invasive species (lead author Phil Hulme). Ultimately, we need to tease apart the complexity caused by interactions between all these drivers. This review paper, therefore, is a first step in outlining the types of interactions that can occur between two drivers, and discussing ways to improve attribution of biodiversity changes occurring from them.

Mantyka-Pringle et al. (2012) collated 1319 studies on the effects of habitat loss from around the globe and conducted a meta-analysis on interactions between habitat loss effects and climate. They found that the effects of habitat loss were greatest in areas with higher mean temperatures and where mean precipitation had decreased over time. This led to the conclusion that -management strategies should focus towards areas with warmer climates, especially those that are more susceptible to precipitation change. However, such a conclusion may be premature, because of the limited nature of the input data to this analysis. The effects of habitat loss on biodiversity were simply scored as a binomial variable (negative vs non-negative), potentially missing important quantitative effects. More importantly, however, the degree of habitat loss itself was not included in the analysis, presumably because data were not available. Therefore, the authors could not control for confounding correlations between habitat loss and climate variables (they did test for correlations between total habitat area and climate, but habitat area and habitat loss are not the same). For example, the extent of habitat loss could be far greater in the tropics, leading to the erroneous conclusion that effects on biodiversity are due to interactions with climate, when they are really due to direct effects from greater habitat loss.

Nevertheless, such studies attempting to understand how the combined effects of land use change and climate change across space are a step in the right direction. We would expect global differences in the magnitude of these individual drivers. Land use change is expected to continue to be a major driver in the tropics, whilst the magnitude of temperature change is expected to be greatest towards the poles (IPCC, 2007; Jetz, Wilcove & Dobson, 2007). Within countries, there may be regional differences in the intensity of land use and climate change. For example, in the UK, high intensity grazing and arable agriculture occur more in certain regions than others, whilst projections of changes in temperature and rainfall also vary regionally (UKCP09, 2010; Centre for Ecology and Hydrology, 2011).

These spatial patterns in land use and climate change cause spatial patterns in the impact on species. For example, species richness of Californian butterflies has declined at lower elevations where land use is more intensive. Additionally, this direct effect reduces the pool of species available to colonise higher elevations and exploit new opportunities provided by climate warming (Forister et al., 2010). In the UK, a qualitative analysis of several species demonstrated that projected impacts of climate change on species' varies regionally and that adaptation actions also depend on local variation in the quality, area and configuration of key habitats (Oliver *et al.*, in press). Studies such as these highlight the difficulties in teasing apart the quantitative effects of land use and climate change. Nevertheless, it is possible to qualitatively distinguish a number of ways in which climate and land use change interact to affect biodiversity. The most well known types of interaction are described below:

a. Landscape structure affects species range shifts

Certainly the most well studied interaction is the impact of land use on species' ability to shift their distributions in response to climate warming. Intensively managed landscapes may severely hinder the movement of species and their ability to cope with climate change through tracking of climatic envelopes (Coope, 2004; Thomas et al., 2004). Not all species

are equally affected, with mobile generalists more able to cope with human modified landscapes (Warren *et al.*, 2001; Menéndez *et al.*, 2006). This follows the general pattern, whereby species most able to persist in the face of synergistic global change drivers have larger geographical ranges and greater dispersal ability (Brook, Sodhi & Bradshaw, 2008).

b. Climate change affects metapopulation persistence

Direct impacts from climate change on species' local population sizes can also alter their ability to cope with habitat fragmentation (Opdam & Wascher, 2004; Verboom *et al.*, 2010). If climate change depresses mean population sizes or causes increased stochasticity in population dynamics, for example as a consequence of increased incidents of extreme events, then habitat networks may require larger patches to maintain metapopulations (Verboom *et al.*, 2010). Connectivity between habitats may also need to be improved (Lawton *et al.*, 2010). For some species, climate warming may have positive effects on dispersal, effectively increasing functional connectivity between populations (Cormont *et al.*, 2011).

b. Habitat and topographic heterogeneity provide broader microclimatic gradients

The climate experienced by species on a local scale is often a key determinant of population growth, and fundamental niche space (*sensu* Hutchinson, 1957). Microclimates can differ markedly between different topographies and habitat types (Geiger, 1965; Rosenberg, 1974). In the UK, for example, deciduous woodland buffers changes in ambient temperature, making the habitat cooler at midday and warmer at night than more exposed grasslands (Morecroft, Taylor & Oliver, 1998; Suggitt *et al.*, 2011). Soil type and structure can influence microclimate by affecting moisture retention (Rost *et al.*, 2009). Because of the strong influence of microtopography, soil and habitat type, microclimate may only be weakly correlated with macroclimate (WallisDeVries, Baxter & Van Vliet, 2011; Graae *et al.*, 2012). Indeed, within site variation in accumulated temperatures can be as high as expected from a 300m change in altitude or a climate change scenario corresponding to warming of 1.6–3.8°C (Graae *et al.*, 2012).

A broad range of microclimates in a local vicinity, between which species individuals can move, allows them to maintain themselves closer to their optimum environmental conditions, i.e. growth rates may be higher and populations are buffered from extreme events (Weiss, Murphy & White, 1988; Kindvall, 1996; Davies *et al.*, 2006; Oliver *et al.*, 2012a). This offers the opportunity to manage land to provide a range of microclimates and promote more resilient populations. For example, heterogeneity in habitat types and topographies may lead to more stable population dynamics (Oliver *et al.*, 2010). Indeed, future microclimatic conditions may be affected as much by land use change as by climate change (Pyke, 2004). Of course, the converse also applies, and homogenous land use with limited microclimatic variation (e.g. due to reduced soil and habitat diversity and flatter topography) may suffer greater impacts of climate change (Weibull, Bengtsson & Nohlgren, 2000; McLaughlin *et al.*, 2002; Dover & Settele, 2009; Loarie *et al.*, 2009).

c. Nutrient deposition alters microclimates

Increased nutrient deposition as a consequence of land use can alter soil fertility and increase plant growth rates (Carey *et al.*, 2008). It has been suggested that increased vegetative growth resulting from a combination of nutrient deposition and climatic warming can cause increased shading and actually lead to cooler microclimates at soil surfaces (Wallisdevries & Van Swaay, 2006). Such a hypothesis could possibly explain the contraction in habitat breadths of UK butterfly species that require open, short turf habitat types, contrary to the expectation that climatic warming should have increased the number of suitable microsites for these species (Oliver *et al.*, 2012b). However, such evidence provides only tentative support of this hypothesis and further analysis and experimentation is necessary; but a potential causal pathway does exist, whereby land use affects plant growth,

which will in turn alter surface microclimate and influence species' responses to changes in macroclimatic conditions.

d. Impacts of extreme climatic events are influenced by land use

Population response to extreme climatic events, such as drought, are likely to be affected by habitat quality, area, configuration, quality and heterogeneity (Fischer, Lindenmayer & Manning, 2006). Therefore, some authors have raised the need to consider the impacts of drought in the context of other drivers of environmental change, such as land use (Archaux & Wolters, 2006). Such research is beginning to accumulate. For example, habitat fragmentation can impact the sensitivity and recovery of insect populations to drought events (Sutcliffe *et al.*, 1997; Piessens *et al.*, 2009; Oliver, Brereton & Roy, in press).

e. Climate-induced community shifts are influenced by land use

From all the mechanisms described above, land use can influence changes in community structure under climate change (Walther, 2010). It has been observed that extreme climatic events, such as intense prolonged drought, can have drastic effects on the structure of species communities (Tilman & Haddi, 1992; Morecroft *et al.*, 2002; Archaux & Wolters, 2006; Jiguet, Brotons & Devictor, 2011), and it is likely that such effects are mediated by land use (de Vries *et al.*, 2012). For example, responses of decomposer communities to CO₂ enrichment vary depending on N deposition (Klironomos, Rillig & Allen, 1996; Sticht *et al.*, 2006). Similarly, the colonisation of plants by arbuscular mycorrhizal fungi declines with N deposition, but can increase with elevated CO₂ (Hu *et al.*, 2005; Egerton-Warburton, Johnson & Allen, 2007).

Multiple interacting global change drivers produce complex effects on communities, but from a synthesis of 688 studies Tylianakis *et al.* (2008) manage to draw a number of generalisations, including negative effects on mutualisms involving plants, context-dependent multitrophic responses of soil food webs and altered dominance of plant and animal species.

To summarise, there are a number of phenomena in which the combined effects of land use change and climate change have been shown to impact biodiversity. Interspecific variation in responses to combined effects of land use change and climate change appears to be common, as it is with the direct main effects of these drivers (Manne & Pimm, 2001; Pimm, 2008). For some species and communities, interacting effects have the potential for large negative impacts; land use change can reduce resilience to climate change and, conversely, climate change can hinder the ability of species to cope with modified land use. Therefore, there is an immediate need to better understand these interactions (Sala & *al.*, 2000; Brook, Sodhi & Bradshaw, 2008). In particular, many studies do not adequately control for the effects of one driver whilst assessing another, meaning that the importance of interactions (versus additive effects) cannot be assessed. To better investigate these effects, we below provide a review of possible interaction mechanisms to aid researchers in experiment and analysis design.

5. Demographic and evolutionary mechanisms for climate- land use interactions

In order to better adapt to climate change, it will be necessary to understanding the mechanisms behind climate- land use interactions on biodiversity. An interaction occurs when two explanatory variables have an effect upon a response variable that is greater (synergism) or lesser (antagonism) than the effects expected from the explanatory variables acting independently, i.e. effects are multiplicative, rather than additive (Figure 1).

Didham *et al* (2007) in a review of interactions between habitat loss and invasive species, suggest that interaction effects can be chain effects or modification effects (Figure 2;

adapted from Didham et al., 2007). Interaction chain effects occur when one driver (e.g. habitat loss) increases the magnitude of another driver (e.g. abundance of invasive species) and both drivers have a direct effect on the response variable. In contrast, interaction modification effects occur when the per capita effect of one driver (e.g. the negative effect of a single individual of an invasive species) changes depending on the level of another driver.

With regards to land use and climate change, direct interactions between these drivers are expected. Land use patterns across the globe will affect climates by altering the balance of carbon in terrestrial and atmospheric pools (Cramer et al., 2001). In addition, land use can effect regional climate because different land cover types have different impacts on surface fluxes of radiation, heat, moisture and momentum (Betts, 2005).

Conversely, climate change can also influence land cover and land use. Firstly, climate will directly influence the climax vegetation type expected in any given region, e.g. tropical rainforest, savannah, boreal forest etc. (Cramer et al., 2001). In addition, climate change will also affect land use through changes to socioeconomic systems (Olesen & Bindi, 2002). In Great Britain, woodland cover has now increased to 13% cover, and future changes in woodland cover or biofuel crops might be made to meet national targets for climate change mitigation (Defra Climate Change Act 2008; Forest Research, 2011). Agricultural practices may be adapted to the changing climate, e.g. through the use of different crop types such as sunflowers and maize grown further north, or altering the timing of sowing, harvesting etc. In addition, regional droughts may lead to increased irrigation of arable agriculture, altering water available for wider biodiversity. All these impacts of climate on land use, and land use on climate, may strong effects on biodiversity.

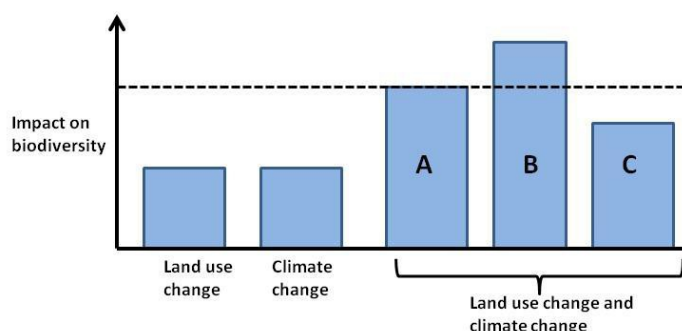


Figure 1, Combined effects of land use change and climate change on biodiversity. Effects may be additive (column A), synergistic interactions (column B) or antagonistic interactions (column C).

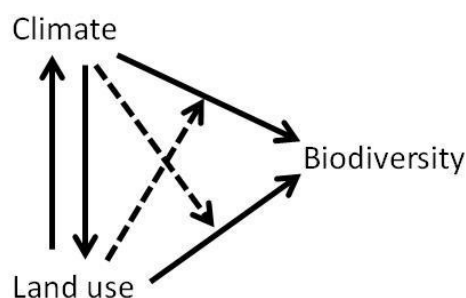


Figure 2 Interactive effects between climate change and land use on biodiversity. Interactions may arise through chain effects, whereby one driver increases the magnitude of another driver (solid arrows), or through modification effects, whereby the per unit impact of one driver on biodiversity is contingent on levels of the other driver (dashed arrows). Schematic modified from Didham et al. (2007).

In addition to these interaction chain effects, modification effects are likely to occur, where the per unit impact of climate change (e.g. per degree of temperature rise) on biodiversity is contingent on land use (e.g. levels of pollution). Similarly, the per unit impact of land use change (e.g. per hectare of habitat converted to agriculture) on biodiversity may be contingent on climate change. In this review, we focus mainly on interaction modification effects because these are less well studied than the direct effects and the interaction chain effects described above. Impacts of interaction chain effects on biodiversity can be predicted by monitoring climate or land use and by understanding their direct effects on biodiversity. In contrast, interaction modification effects can lead to unexpected, potentially large negative, impacts on biodiversity. Therefore, it is critical to better understand the extent of these interactions. Below we describe a number of mechanisms by which these interaction modification effects may occur.

A. Direct interactions between demographic parameters

Both climate change and land use can affect a number of demographic parameters and there may be interactive effects. For example, edge effects may cause desiccation and increased species mortality, which is exacerbated under extreme weather conditions (Herbst et al., 2007; Rowe, 2007). More examples are listed in Table 1. In many cases, demographic effects may be additionally mediated through altered competition between species. For example, a changing climate may push a plant species closer to the edge of its fundamental niche space, reducing its competitive ability and allowing other plant species to become dominant (hence, the realised niche space is a subset of the fundamental niche; Hutchinson, 1957).

Table 1 Examples of how climate change and land use change can have both main and interactive effects on a range of demographic parameters.

Demographic parameter	Climate change main effect	Land use change main effect	Interaction between land use change and climate change
Birth rates	Temperature dependent fecundity (Mora et al., 2007; Verboom et al., 2010).	Resource levels affect fecundity (Begon, Harper & Townsend, 1996b)	Fecundity depends on both temperature and the presence of conspecifics, which are both influenced by land use and climate (Hodek, 1973; Doumbia, Hemptinne & Dixon, 1998)
Death rates	Temperature determines species' fundamental niche space and influences mortality (Gaston, 2003)	Edge effects can increase predation risk (Laurance, 1999) ; Density-dependent mortality is determined by resource levels, which are influenced by habitat amount and quality (Begon, Harper & Townsend, 1996b).	Edge effects may cause desiccation and increased mortality, which is exacerbated under extreme weather conditions (Herbst et al., 2007); Increased pathogen infection in plants under increased temperature and nitrogen deposition (Tylianakis et al., 2008).
Immigration/Emmigration	Temperature-dependent dispersal	Matrix structure affects immigration rates (Matter	Temperature-dependent dispersal affects

	(Cormont et al., 2011).	et al., 2009). Boundary types affect emigration rates (Ricketts, 2001).	functional connectivity across landscapes which are also affected by land use change (Cormont et al., 2011). Climate affects fruiting phenology and the probability of successful seed dispersal by mutualists (Tylianakis et al., 2008).
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B. Evolutionary trade-offs and synergies

In addition to (and as a consequence of) the ecological effects of land use and climate change described above, both these drivers impose selection on populations for more tolerant genotypes. The tolerance to different environmental drivers may be correlated or uncorrelated (Vinebrooke et al., 2004). Positive correlations mean that adaptation to one driver also confers tolerance to another driver. For example, the evolution of wider environmental tolerance to spatial environmental heterogeneity may improve resilience to climate change (Bonebrake & Mastrandrea, 2010). However, this also means that increasing the homogeneity of the abiotic and biotic context, as has occurred in UK landscapes over recent decades, may reduce the ability of species to cope with climate change (Olden *et al.*, 2004; Smart *et al.*, 2006).

Conversely, the tolerance to different drivers may be uncorrelated or negatively correlated, in which case genetic variation will be eroded by selection from one driver reducing the capacity to adapt to the other (Etterson & Shaw, 2001; Chevin, Lande & Mace, 2010). For example, in a microcosm experiment Mora et al. (2007) found that population declines caused by reduced immigration and environmental warming were up to 36 times worse when these drivers occurred simultaneously. They speculated the smaller population sizes from reduced immigration may have impaired the ability of populations to adapt to warming. An alternative hypothesis is that tolerance to environmental warming is negatively correlated with fecundity or development time (Sgro & Hoffmann, 2004).

C. Threshold effects of population size on extinction risk

Even if the combined effects of land use and climate change on demographic parameters are additive, there may still be interactive effects on other population parameters such as extinction risk. All demographic parameters have the potential to influence equilibrium population size (Begon, Harper & Townsend, 1996a), and there may be non-linear relationships between local population size and extinction risk. In particular, small populations may suffer greater risk of extinction due to genetic drift, inbreeding depression, inability to find mates and increased susceptibility to environmental and demographic stochasticity (Gilpin & Soulé, 1984; Fagan & Holmes, 2006). Therefore, additive effects of land use and climate change drivers on population size may result in multiplicative effects on extinction risk (Figure 3a).

D. Threshold occupancy for metapopulation persistence

Many species exist in metapopulations or patchy populations, whereby local extinctions of sub-populations may occur relatively frequently, but these are re-colonised through dispersal from occupied patches. Both land use change and climate change can lead to local extinction events.

Theory has shown that when the proportion of patches falls below a threshold level, the extinction of the entire metapopulation can rapidly follow (Amarasekare, 1998; Zhou &

Wang, 2004). Therefore, even if the effects of land use and climate change are additive for any individual population, the total combined effects may lead to multiplicative effects on metapopulation extinction risk (Figure 3b).

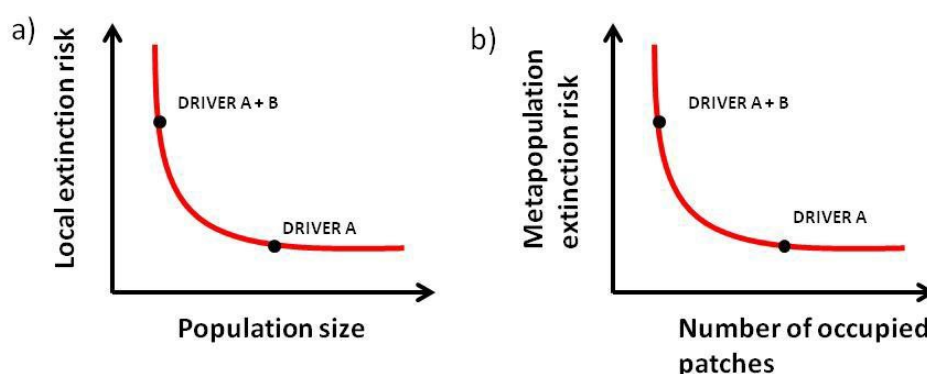


Figure 3, Non-linear effects between local population size and extinction risk (panel a) and patch occupancy and metapopulation persistence (panel b) can lead to interactive effects of global change drivers on extinction risk.

6. Addressing attribution problems

How do we know that climate change has caused all the changes that are attributed to it?

In order to usefully inform conservation and climate policy, it is essential that we can reasonably attribute changes in species' populations to climate and/ or land use change. In order to do this, well designed experiments and analyses are required, which control for one driver while exploring the effects of another. A basic requirement is to have measures on the degree to which land use and local climate has changed in any area, concurrent with measurements of biodiversity change. Sufficient independent samples are needed to allow statistical analyses which give an appropriate degree of confidence in associations. In these analyses, it is important that spatial autocorrelation is accounted for, to prevent anti-conservative estimates of the significance of associations ('pseudoreplication'). Also, land use change and climate change measures must not be too well-correlated, so that regression techniques can reliably attribute associations. If these conditions are met, then researchers can potentially ascertain whether changes in biodiversity across a number of sites are primarily due to climate or land use change, including quantification of uncertainty in any conclusions.

In some cases, clear significant effects of either land use change or climate change may be identified (e.g. see examples in sections 2 and 3). However, in other cases it may be difficult to separate out effects of land use and climate change. For example, in the UK, butterfly communities have changed over the last three decades, probably as a result of both drivers (Warren *et al.*, 2001; Fox *et al.*, 2006; Fox *et al.*, 2010). In addition, as this review describes, in many cases there may be strong interactions between the effects of climate and land use upon biodiversity. Therefore, in order to successfully attribute effects, interactions need to be explicitly considered in experimental and analytical designs.

Investigating interactions

Microcosm experiments are ideal to consider interactions, allowing sufficient replication and with influences beyond the variables of interest kept constant (Mora *et al.*, 2007). However, their transferability to real world situations (e.g. other species and real landscapes) may be limited (Huston, 1999).

Experiments in real landscapes are often lacking, however, due to the practicalities of manipulating land use and climate and achieving sufficient replication. One of the most efficient approaches may be to exploit natural gradients in climate and land use and use long term ecological monitoring schemes to assess effects on biodiversity. With sufficient spatial replication, climate patterns across space can be used as a surrogate for temporal patterns, and replicated across different land use classes. However, extrapolating from spatial patterns to temporal predictions can be error prone if the response variable has not achieved an equilibrium state, e.g. metapopulations may be in 'extinction debt' where the negative impacts of habitat fragmentation show a time-lag (Bulman et al., 2007). Alternatively, if populations are locally adapted to their environment, then space-for-time substitutions may produce erroneous conclusions (Randin et al., 2006; Broennimann et al., 2007).

Errors in space-for-time substitutions can also arise if the correlation between explanatory variables and response is not directly causal but driven by some other confounding factor (White & Kerr, 2006). For example, Canadian butterfly assemblages are more species rich in areas of high human population density. Taking this association as directly causal, one would predict that increasing human populations density should increase species richness. However, the opposite is, in fact, true. The spatial association between human population density and butterfly species richness is driven by the co-variation of both these factors with climate (White & Kerr, 2006).

Conversely, attributing biodiversity changes to climate can sometime be confounded by land use. For example, the community temperature index (CTI) is an increasingly used metric of the balance of cold- and warm- associated species in a given location. Under incremental climate warming, the replacement of cold-associated species in communities with more warm adapted species is expected, leading to an increase in CTI scores. Across Europe, both bird and butterfly assemblages show this general pattern, although the rates of community change do not seem to be keeping track with the pace of climate change (Devictor et al., 2012).

These examples illustrate the difficulty in attributing changes in biodiversity to either land use change or climate change. Analyses need to be appropriately designed with adequate spatiotemporal data on both drivers. For example, a recent study by Eglinton and Pearce-Higgins (in press) compares the relative impact of climate change (temperature and rainfall) versus land use change (degree of agricultural intensification) on bird populations. Results suggest that land use change has been a more significant driver of bird declines compared with climate change. Although, their model did not consider interaction effects between climate and land use, these could potentially be included in the analytical framework.

Influences on biodiversity change projections

Understanding relationships between biodiversity and drivers of change will facilitate the prediction of the impacts of land use decisions. However, current predictions for biodiversity rarely incorporate multiple drivers or interactions (Sala & al., 2000; Mora *et al.*, 2007). Interactions may only be relatively unimportant where the effects of a single driver are very great (Brook, Sodhi & Bradshaw, 2008). However, it is probably more often the case than multiple drivers act together to impact biodiversity (Tylianakis et al., 2008).

Some sources suggest that climate change will overtake habitat loss as the greatest driver of biodiversity decline (Millennium Ecosystem Assessment, 2005; UK National Ecosystem Assessment, 2011). However, others suggest that land use change will continue to be the most significant pressure (Jetz, Wilcove & Dobson, 2007; Haines-Young, 2009; Eglinton & Pearce-Higgins, in press). This discrepancy may partly depend on the species group and region being studied (Bonebrake & Mastrandrea, 2010). Impacts of climate change will vary between and within countries, as will land use change (IPCC, 2007). Some researchers

have suggested that greater future land use will occur in the tropics (Sala & al., 2000; Jetz, Wilcove & Dobson, 2007). Others have suggested that regions at mid-latitude, such as Mediterranean grasslands, will experience both significant land use and climate changes and, therefore, we might expect the effect of land use-climate interactions to be most apparent in these regions (Sala & al., 2000). For the UK, climate projections vary regionally, with hotter drier summers predicted in the South East, whilst some areas in Scotland are predicted to become wetter (UKCP09, 2010). For land use change, future trends are uncertain, as this depends on drivers such as reform of the EU Common Agricultural Policy, implementation of the National Planning Policy Framework and responses of land owners to food prices and climate change.

In addition to spatial variation in land use and climate change, within any region, species will also differ in their sensitivity to these drivers. For example, where species are closer to climatically-determined range boundaries they are likely to be more sensitive to the effects of climate change and, consequently, any interactions between land use and climate change (Sala & al., 2000; Oliver *et al.*, 2009; Oliver *et al.*, 2012a).

Most predictive models of biodiversity change currently simply consider one driver or combined effects of multiple drivers in very crude ways. For example, an analysis by Jetz *et al.* (2007) classified land cover for each global 0.5° grid cell as changing either due to human land use *or* due to climate change, with subsequent effects on biodiversity proportional to the amount of original habitat cover lost. Clearly, such a framework is not appropriate to consider interaction effects between land use and climate change.

Some predictive models, however, are beginning to take into account interaction effects. For example bioclimatic envelope models and being integrated with demographic models to understand how species range shifts occur in the context of altered landscape structures (Keith *et al.*, 2008; Anderson *et al.*, 2009). For example a model by Carroll (2007) suggests that logging and climate change have interactive effects on martens in Canada and the USA. As a consequence of the dependency of species range shifts on both land use and climate change, an increasing number of studies are considering how reserve networks might be designed to promote more resilient populations (Hannah, 2008; Vos *et al.*, 2008; Carroll, Dunk & Moilanen, 2010; Verboom *et al.*, 2010). However, such models would benefit from better data on species movement (Eycott, Marzano & Watts, 2011) and finer resolution climate and land use data, in order to better identify topographic and habitat refugia (Wiens & Bachelet, 2009). Also, most models assume static land cover. To incorporate land use change, however, will require better scenarios of land use change. Coarse resolution land use scenarios do exist (Jetz, Wilcove & Dobson, 2007), but projections of land use at local scales are difficult to achieve due to the large uncertainties in future land use policy and unseen changes in world food markets.

Finally, predictive models for other land use-climate interactions changes, beyond species range shifts, are far less common. The effects of these interactions first need to be better quantified. For example, only when we better understand how land use moderates species responses to drought events, will be in a position to predict how community structures might change in different regions under climate change (Oliver, Brereton & Roy, in press).

7. Risks and opportunities

Interactions between climate change and land use change present a number of risks for biodiversity conservation, but also several opportunities. Firstly, the complex nature of interactions between global change drivers means that we may never have accurate predictive models for biodiversity impacts. For example, the effects of increased drought under climate change may be moderated by local land use, but climate change also affects species phenology which will influence their sensitivity depending on when in the year a

drought occurs. In addition to interaction chain and modification effects between drivers, the effects on individual species may cascade through communities causing unanticipated effects (Brook, Sodhi & Bradshaw, 2008). These problems are in addition to the fact that there are clear difficulties in obtaining reliable projections of land use and climate change on which to base our projections for biodiversity. Therefore, predicting combined effects of multiple drivers on biodiversity is particularly challenging (Willis & Bhagwat, 2009).

Despite this difficulty, however, it is necessary to anticipate potential future trends, otherwise current conservation practice may become ineffective. Inappropriate habitat management could exacerbate biodiversity declines. For example, under a warmer UK climate, prescriptions for scrub clearance on sites vulnerable to high soil moisture deficit may reduce the availability of cooler moister microclimatic refuges which will allow species to persist. At a larger scale, the location of protected areas may need to be re-assessed in light of shifts in species ranges and sea level rises (Mascia & Pailler, 2011); although whilst currently protected areas may become less suitable for some species, other new species may colonise them preferentially (Thomas *et al.*, 2012).

Because of the difficulty in predicting impacts accurately, management for biodiversity will benefit from being adaptive, whereby observations of unexpected impacts can rapidly feed back to influence management decisions (Willows & Connell, 2003; Maris & Bechet, 2009). To achieve this, spatially replicated long term biodiversity monitoring will be essential. Such monitoring should aim for good coverage across land use and climate gradients. Current monitoring is often spatially, temporally and taxonomically biased (Pereira, Navarro & Martins, 2012). In the UK, for example, less monitoring occurs in more sparsely populated areas of Scotland and Wales and there is less monitoring of species which are not charismatic, but which nonetheless may have important functional roles in ecosystems (UK NEA, 2011).

To reduce uncertainty in biodiversity predictions, research on the synergistic effects of multiple global change drivers needs to continue (Sala & *al.*, 2000; Bellard *et al.*, 2012). Both climate and land use change will also interact with other drivers. For example, climate change may increase probability of biological invasions (Didham *et al.*, 2007; Walther, 2010) and disease susceptibility (Harvell *et al.*, 2002). In addition, the ability of populations to cope with these drivers through rapid evolution needs more investigation (Hairston *et al.*, 2005; Bradshaw & Holzapfel, 2006). For example, local adaptation to climate conditions and land use patterns are likely to affect species responses to these threats (Simmons & Thomas, 2004a; Phillimore *et al.*, 2010; Buckley, Butlin & Bridle, 2012). To address this question, transplant experiments could be conducted, or genetic data could be collected across species ranges (e.g. by volunteers) and analysed together with population data from long term spatially replicated monitoring schemes.

In addition to the risks described above, interactions between land use change and climate change can also offer opportunities of new ways to address the impacts on biodiversity. For example, the existence of interactions means that we can potentially reduce the negative impacts of climate change on biodiversity through changes to land use. These opportunities to 'adapt' to climate change have been collated into a number of general principles (Hopkins *et al.*, 2007; Huntley, 2007; Mitchell *et al.*, 2007; Smithers *et al.*, 2008; Heller & Zavaleta, 2009; e.g. Mawdsley, O'Malley & Ojima, 2009). For example, one suggestion is to promote habitat and topographic heterogeneity to provide broader microclimatic gradients, another is to increase the functional connectivity between populations. Appropriate implementation of these principles may vary geographically depending on landscape context and other types of threats faced by species. Therefore, decision frameworks for climate change adaptation will need to integrate these factors (Oliver *et al.*, in press).

A better understanding of interactions will lead to more successful habitat management in the face of climate change. For example, recent research suggests that optimum turf height for conservation of *Maculinea* butterflies is changing with increasing mean temperatures (Thomas, 2009). Therefore, with this knowledge and with ongoing assessment of the situation, management prescriptions can be updated to increase their effectiveness.

Although the complexity of interactions between global change drivers can be daunting, it is reassuring the relatively simple actions may reduce the impacts of a number of drivers simultaneously. For example, increasing habitat quality or area (e.g. by creating or restoring habitat adjacent to occupied patches) can reduce the impact of edge effects and increase population sizes, making populations less susceptible to extinctions induced by environmental and demographic stochasticity. Simultaneously, these actions also increase functional connectivity of populations (by increasing propagule pressure and colonisation probability; Hodgson *et al.*, 2011) and increase the genetic variation within populations, giving them greater capacity to evolve tolerance to environmental drivers (Mora *et al.*, 2007).

To conclude, climate change and land use change may interact to impact biodiversity through a wide range of mechanisms. Understanding these interactions will be necessary to more reliably project changes in biodiversity under different land use and climate scenarios and to manage the habitats appropriately. There are also opportunities to reduce the negative impact of climate change on biodiversity through adaptation strategies (e.g. Natural England, 2012), and relatively simple actions such as increasing habitat quality and extent can simultaneously address multiple drivers. However, land use decisions can also have negative impacts on the 'adaptive capacity' of populations (Williams *et al.*, 2008). Land use is driven by socioeconomic and climatic factors, potentially with complex feedbacks; but if we cannot suitably address the negative impacts of land use change, then we close off our options for dealing with climate change (Hannah, 2011). With a growing recognition of the existence of interactions between global change drivers, conservation strategies and biodiversity projections that only address a single driver are inadequate. Future research needs to understand and quantify the major mechanisms by which global change drivers interact, in order to minimise risks and increase opportunities for the conservation of biodiversity.

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