Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis

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Abstract

Climate change and habitat loss are both key threatening processes driving the global loss in biodiversity. Yet little is known about their synergistic effects on biological populations due to the complexity underlying both processes. If the combined effects of habitat loss and climate change are greater than the effects of each threat individually, current conservation management strategies may be inefficient and at worst ineffective. Therefore, there is a pressing need to identify whether interacting effects between climate change and habitat loss exist and, if so, quantify the magnitude of their impact. In this article, we present a meta-analysis of studies that quantify the effect of habitat loss on biological populations and examine whether the magnitude of these effects depends on current climatic conditions and historical rates of climate change. We examined 1319 papers on habitat loss and fragmentation, identified from the past 20 years, representing a range of taxa, landscapes, land-uses, geographic locations and climatic conditions. We find that current climate and climate change are important factors determining the negative effects of habitat loss on species density and/or diversity. The most important determinant of habitat loss and fragmentation effects, averaged across species and geographic regions, was current maximum temperature, with mean precipitation change over the last 100 years of secondary importance. Habitat loss and fragmentation effects were greatest in areas with high maximum temperatures. Conversely, they were lowest in areas where average rainfall has increased over time. To our knowledge, this is the first study to conduct a global terrestrial analysis of existing data to quantify and test for interacting effects between current climate, climatic change and habitat loss on biological populations. Understanding the synergistic effects between climate change and other threatening processes has critical implications for our ability to support and incorporate climate change adaptation measures into policy development and management response.

Keywords: climate change, habitat fragmentation, habitat loss, interactions, meta-analysis, mixed-effects logistic regression

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Introduction

One of the most pressing questions of the 21st century in ecology and conservation is how do multiple stressors interact and cumulatively impact ecosystems and their biodiversity (Vinebrooke *et al.*, 2004; Brook *et al.*, 2008; Crain *et al.*, 2008)? Climate change, habitat loss, invasive species, disease, pollution, and overexploitation are typically studied and managed in isolation, although it is becoming increasingly clear that a single-stressor perspective is inadequate when ecosystems and species are threatened by multiple, co-occurring stressors (Sala *et al.*, 2000; Darling *et al.*, 2010).

Processes of climatic change and habitat loss happening concurrently are an important example where synergistic effects may occur. Yet most studies reporting

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effects of climate change (e.g. Williams *et al.*, 2003; Miles *et al.*, 2004; Parmesan, 2006) or habitat loss and fragmentation (e.g. Brooks *et al.*, 2002; Fahrig, 2003; Cushman, 2006) have examined each in isolation. If the potential combined effects of these processes are greater than those estimated individually, then current estimates of habitat loss and fragmentation effects may be misleading (de Chazal & Rounsevell, 2009). Nevertheless, substantial changes in terrestrial species' populations and distributions have already been detected world-wide in response to both of these impacts. For landscapes undergoing habitat loss and fragmentation, the effect of losing habitat is obvious: when habitat is lost, dependent species are also likely to be lost and, populations decline (e.g. Andrén, 1994; Fahrig, 1997; 2001; Bender *et al.*, 1998). Habitat fragmentation creates small populations with increased spatial isolation, which also increases the risk of extinction (Opdam, 1991; Ellstrand & Elam, 1993; Young

et al., 1996). On the other hand, the presence of scattered vegetation in a landscape may facilitate migration and gene flow among tree populations in response to climate change by providing connectivity across the landscape (Breed *et al.*, 2011).

For landscapes undergoing climate change, the effects are less clear. In terms of potential risks to biodiversity, species responses to climate change vary considerably, depending on which species are studied, whether there are any interactions between drivers, whether there are any species interactions, and the spatial and temporal scale considered (de Chazal & Rounsevell, 2009). On a global scale, many species have been or are expected to shift their ranges to higher latitudes: from the tropics to the poles (Hickling *et al.*, 2005, 2006; Wilson *et al.*, 2005). Others will retract and potentially face extinction (Pounds *et al.*, 2006; Thomas *et al.*, 2006; Sekercioglu *et al.*, 2008). The evidence for these changes, however, comes mostly from the documented shifts in the distributions of a few well-studied taxonomic groups (e.g. birds, butterflies and vascular plants) (e.g. Hickling *et al.*, 2005, 2006; Sekercioglu *et al.*, 2008).

In the few cases where studies examine both the importance of climate change and habitat loss, it is difficult to determine which stressor is the more important driver of long-term trends (e.g. Travis, 2003; Opdam & Wascher, 2004; Pimm 2008). In general, most studies indicate that, at present, habitat loss and fragmentation outweigh the responses of climate warming on species and ecosystems (Sala *et al.*, 2000; Warren *et al.*, 2001; Franco *et al.*, 2006; Jetz *et al.*, 2007), but the impact of climate change is predicted to increase over time and eventually overtake land-use modification in determining population trends (Lemoine *et al.*, 2007).

There is growing evidence to suggest that climate change will negatively interact with habitat loss and habitat fragmentation and synergistically contribute to the degradation of biological diversity at the species, genetic and/or habitat level (Schindler, 2001; McLaughlin *et al.*, 2002; Opdam & Wascher, 2004; Pyke, 2004; Brook *et al.*, 2008). Populations in fragmented landscapes are more vulnerable to environmental drivers, such as climate change than those in continuous landscapes (Travis, 2003; Opdam & Wascher, 2004). For example, forest clearance and fragmentation can cause localized drying and regional rainfall shifts, enhancing fire risk and restraining the capacity of species to move in response to shifting bioclimatic conditions (Brook *et al.*, 2008). A rapid population decline of the green salamander (*Aneides aeneus*) within a highly fragmented habitat in the southern Appalachians, USA has also been linked with an increase in temperatures since the early 1960s (Corser, 2001). Similar findings have also been reported for butterflies in the United States (McLaughlin *et al.*, 2002) and in the Mediterranean (Stefanescu *et al.*, 2004). Habitat fragmentation and overharvesting, combined with environmental warming in rotifer zooplankton resulted in populations declining up to 50 times faster when all three threats acted together (Mora *et al.*, 2007). Jetz *et al.* (2007) showed similar findings for land bird species; 950–1800 of the world's 8750 species of land birds could be imperilled by climate change and land conversion by the year 2100. Furthermore, Carroll (2007) modelled the potential impacts of climate change and logging on mammals in south-eastern Canada and the north-eastern United States; interactions between the two stressors increased overall vulnerability of both marten (*Martes americana*) and lynx (*Lynx canadensis*) populations. In contrast, there are very few studies that suggest climate change will positively interact with other impacts such as habitat loss and fragmentation on species. Those reported suggest increasing periods of thermal stress and drought may cause species to rapidly adapt, and these changes, in turn, can potentially help species counter other stressful conditions such as habitat destruction, or realize ecological opportunities arising from climate change (Cormont *et al.*, 2011; Hoffmann & Sgrò, 2011).

Clearly, the consequences of interactions between landscape change and climate change for biodiversity have the potential to be quite significant. Most climate change impact studies on species have been based on data collected in the temperate zone, where climate change is predicted to be most pronounced, and to date, there have been no global analyses of the synergistic effects of climate change and habitat loss on biological populations. We address this important issue using a global systematic review and meta-analytic techniques to estimate how current climatic conditions, climate change and habitat loss interact and synergistically impact on terrestrial biological systems. In doing so, we test hypotheses about the generality of interactions between habitat loss, climate change and current climate on biodiversity. More specifically, three hypotheses are tested:

1 The effect of habitat loss on biological populations depends on current climatic conditions and historical rates of climate change.
2 The interaction between habitat loss and climate varies with the type of habitat (i.e. vegetation type) in which a species occurs.
3 The interaction between habitat loss and climate varies with taxonomic group.

Meta-analysis is a quantitative method for synthesizing existing data from multiple studies to test specific hypotheses (Schulze, 2004). By systematically

combining studies, one attempts to overcome limits of size or scope in individual studies to obtain more reliable and general information about treatment effects (Berman & Parker, 2002). There has been some controversy about its validity (LeLorier *et al.*, 1997; Garg *et al.*, 2008; Stewart, 2010), but even knowing its limitations, meta-analysis is considered an ideal framework within which to assess the accumulation of scientific evidence (Berman & Parker, 2002; Garg *et al.*, 2008) in ecology (Gurevitch *et al.*, 2001; Leimu & Koricheva, 2004; Luiselli, 2008) and in conservation biology (Ojeda-Martinez *et al.*, 2007; Aronson *et al.*, 2010; Marczak *et al.*, 2010). Given the high volume of studies and lines of evidence concerning climate change and habitat loss to date, we believe undertaking a meta-analysis is warranted and timely, and is the best way to test for the generality of such interactions at a global scale.

Materials and methods

To test for interactions between climate change, current climate and habitat loss, we created a database of existing data on habitat loss effects using a systematic review of the literature and then identified relationships between the patterns of habitat loss effects and climate data using mixed-effects logistic-regression models.

Criteria for publication selection and data extraction

The first goal of the study was to quantitatively review the results of published studies that statistically analysed the effects of habitat loss (i.e. loss of native habitat) on population density and diversity. Figure 1 shows the process of study identification, study selection and data extraction. A list of research articles published between 1989 and 2009 were generated using the key-words '(habitat loss OR habitat fragmentation) AND (species abundance OR species distribution) AND (impact)' under TOPIC in the database of ISI Web of Science,
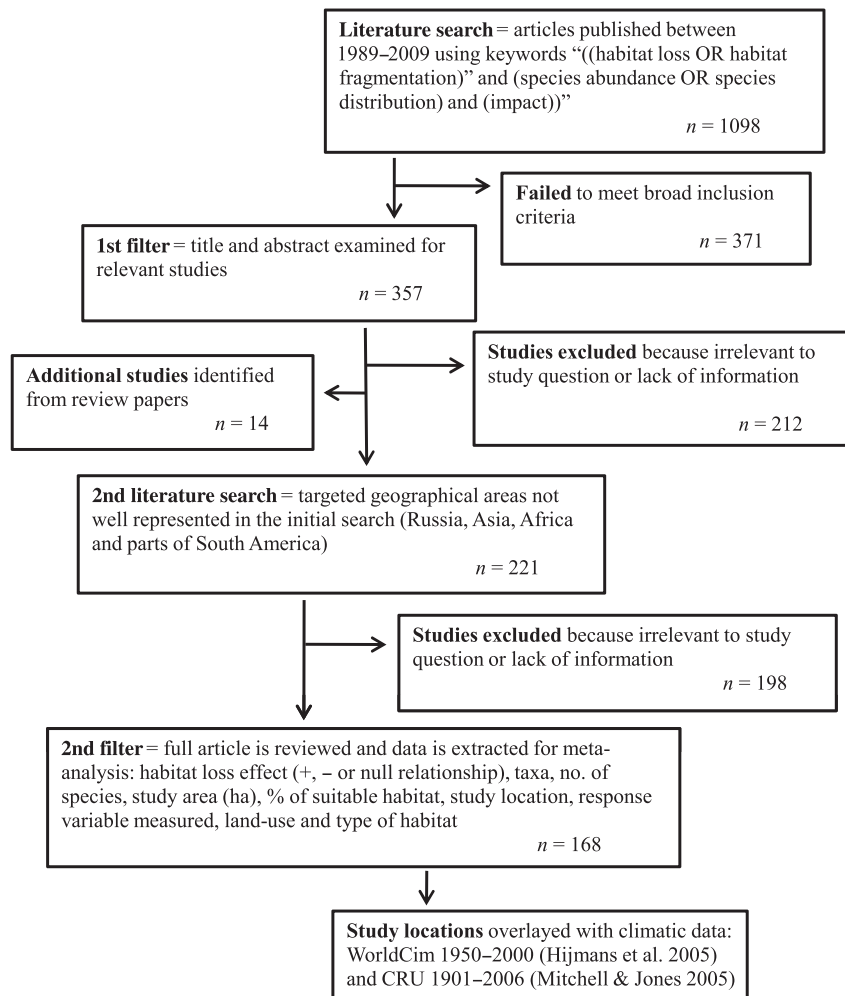

Fig. 1 Flow chart detailing the process of study identification, selection and data extraction for studies included in the meta-analysis.

revealing 1098 studies. The use of these key-words allowed for the identification of a broad inclusive set of studies on the effects of habitat loss and associated habitat fragmentation on biological populations.

From the list of 1098 articles, we examined each title and abstract to determine whether they met the criteria for inclusion in the meta-analysis. Inclusion criteria comprised impacts on species abundances, density, diversity and/or richness due to habitat loss. The impact of habitat loss caused by anthropogenic pressures was the only effect measure considered. However, it was not always clear whether a study looked at the impact of habitat loss, habitat fragmentation, patch size effect, isolation or a combination of these, since they are almost always correlated (Fahrig, 2003). Thus, if a study measured habitat fragmentation and/or habitat loss it was included in our analysis. Because our focus was on empirical evidence, theoretical studies and review papers were excluded during this first filter. However, the reference lists in these papers were scrutinized for further studies. Additional studies identified in the course of reading were also included. At each stage of the review, the numbers and identities of articles retrieved, accepted and rejected were recorded (Fig. 1). Remaining articles were then reviewed in full to determine whether they contained relevant and usable data (second filter). The estimated habitat loss effects on species (positive, negative or null relationships) were extracted from the final set of studies (see Appendix S1). If a study reported individual species effects, the effect on each species was recorded. If a study reported only an overall effect for a group of species, a single effect on that group of species was recorded. If the results were not statistically tested, then the study was excluded or only those results that were statistically tested were included in the database. The total size of the study area for each study and the proportion of the landscape area covered by suitable habitat were also recorded. For any studies that did not measure the proportion of area covered by suitable habitat, it was sometimes possible to calculate or access the data by other means (see Appendix S1). For 31 studies, this was calculated from the text, tables or graphs, or estimated from their study map. In 27 cases, the primary authors were contacted for unpublished data and in three cases, we were able to obtain the missing information from another paper that studied the same study region. The study location, study coordinates (if not reported in the paper, Google Earth was used to identify the coordinates), year that the study was completed (if no study year was reported, the year that the paper was published was recorded), response variable measured (density, richness, diversity or probability of occurrence), type of habitat/vegetation type (forest, rainforest, woodland, wetland, savanna/grassland, shrubland/heathland or other) and land-use (agriculture, grazing, urban, natural fragmentation or other) were also tabulated. Finally, each species was classified into one of six taxonomic groups: birds, plants, arthropods, mammals, amphibians or reptiles. After the second filter we went back and performed another search using the same key-words and time span as above, but substituted the word 'impact' for 30 individual countries or regions (Russia, Siberia, China, Turkey, Kazakhstan, Mongolia, Iran, Saudi Arabia, Korea, Egypt, Libya, Pakistan, Algeria, North Africa, Ethiopia, Somalia, Chad, Niger, Mali, Nigeria, Ghana, Guinea, Angola, Congo, Madagascar, Greenland, Denmark, Venezuela, Peru and Alaska) to target geographical areas that were not well represented ($n = 221$). Of these 221 papers, 23 were identified suitable for the meta-analysis using the same criteria as previously.

Climate data

To test for the interaction effect between habitat loss, climate change and current climate we spatially mapped the location of each study site and overlayed the locations on high-resolution global climate data (Fig. 2). For current climatic conditions, we used four bioclimatic variables (1 km^2 resolution grid) from the WorldClim database (1950–2000 averaged values; Hijmans *et al.*, 2005) without modifications: maximum
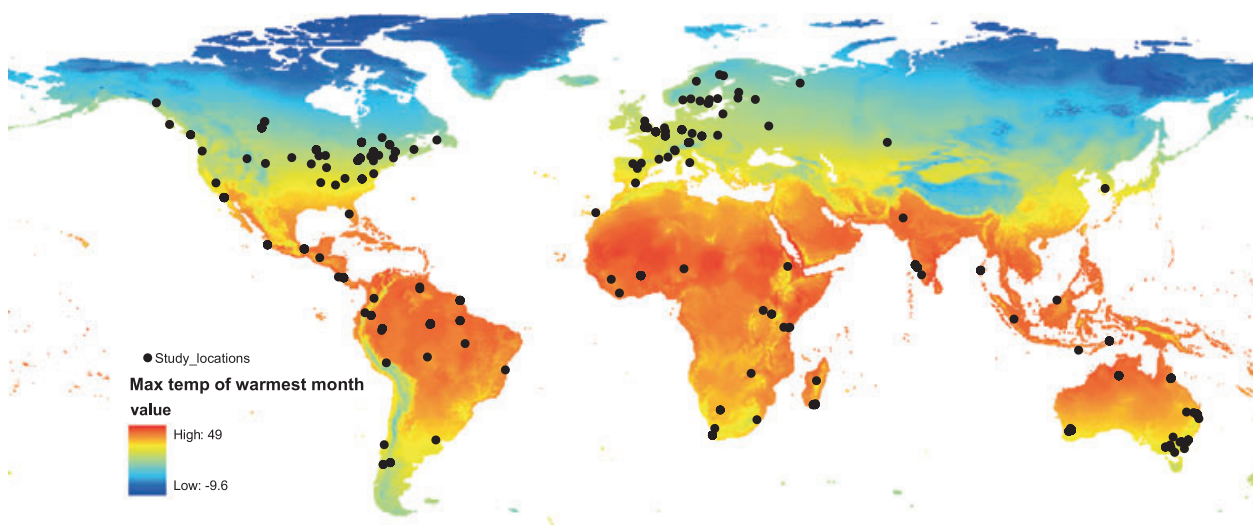

Fig. 2 Location of studies and maximum temperature of warmest month, WorldClim 1950–2000 (Hijmans *et al.*, 2005) ($n = 168$).

temperature of warmest month, precipitation of driest month, temperature seasonality and precipitation seasonality. For climatic change, we used two variables: monthly average daily maximum temperature and average monthly precipitation (0.5 km^2 resolution grid), from the Climatic Research Unit (CRU) at the University of East Anglia (1901–2006) (Mitchell & Jones, 2005). From the original CRU climate data variables we calculated the change in temperature and precipitation over time as the difference in mean values between the periods 1977–2006 and 1901–1930 (1977–2006 minus 1901–1930). The two time periods were chosen based on availability of data: using the latest and earliest available years from the CRU data at the time of analysis (2010). Thirty-year time periods were also chosen as a period long enough to eliminate year-to-year variations.

Logistic-regression models

Mixed-effects logistic-regression models were used to model the relationship between the habitat loss effects and the climatic variables, while accounting for variation among studies, taxonomic groups, habitats and land-uses. Mixed-effect models are preferable in ecological data synthesis because their assumption of variance heterogeneity is more likely to be satisfied (Gurevitch et al., 2001). In this case, the climatic variables and habitat amount were used as the explanatory variables and a binomial habitat loss effect (negative vs. non-negative) was used as the dependent variable. Prior to analysis, correlations among variables were calculated using Pearson's correlation coefficient to test for collinearity among the climatic variables and habitat amount. Habitat amount was not significantly correlated with any of the climatic variables ($r < 0.5$, $P > 0.05$). However, temperature seasonality and precipitation seasonality were identified as being correlated ($r > 0.5$, $P < 0.05$) with maximum temperature of warmest month or precipitation of driest month. Temperature seasonality and precipitation seasonality were therefore removed from the models to reduce the effect of collinearity (Graham 2003). The remaining bioclimatic variables (maximum temperature of warmest month, precipitation of driest month, annual temperature difference and annual precipitation difference) and habitat amount were standardized to have a mean of zero and standard deviation of one prior to running the meta-analysis.

We used a step-wise forward selection analysis to test the significance of random effects before including them in the logistic-regression analyses (Beale et al. 1967). Initially, all climatic predictors and habitat amount were incorporated as fixed effects and study response type (i.e. response variable measured in each study: density, richness, diversity, probability of occurrence) was incorporated as a random intercept effect. Random effects were then sequentially added and tested for statistical significance with likelihood ratio tests using the lme4 package in R 2.11.1 (R Development Core Team, 2010).

Once the significant random effects had been identified, an information theoretic approach using Akaike's Information Criteria (AIC) (Burnham & Anderson, 2002) was then used to rank competing models with all combinations of predictors. Model-averaged logistic-regression coefficients were then calculated with unconditional standard errors to identify the magnitude of important relationships (Burnham & Anderson, 2002). Finally, for each variable, its relative importance was quantified through an index constructed by summing the Akaike weights for all models containing the variable (Burnham & Anderson, 2002). To assess the fit of the most parsimonious model, we visually inspected a goodness-of-fit quantile–quantile (Q–Q) plot developed by Landwehr et al. (1984) with simulations replicated 1000 times. Logistic-regression Q–Q plots are useful for assessing whether the error distribution of the data is modelled correctly and to detect more general departures from model assumptions (Landwehr et al. 1984; Rhodes et al., 2009).

Results

Summary of the effects of habitat loss on biodiversity

Of the 1319 papers that we reviewed, a total of 168 studies were identified as suitable for our meta-analysis. Many studies, however, reported habitat loss or fragmentation effects on multiple species and/or on several taxa, and so from the 168 studies we had 1779 data points for our analyses (Appendix S1). The number of publications that cited significantly positive or no habitat loss/fragmentation effects on single species or a group of species ($n = 1132$; 312 positive and 820 null) exceeded the number that reported significantly negative effects ($n = 647$). Although the number of negatives ($n = 647$) exceeded the number of positives ($n = 312$), their combined total ($n = 959$), opposed to the number of no effects ($n = 820$) was not driven by a sample size effect (logistic regression, $\chi^2 = 406.51$, df = 1, $P = 0.434$). Of the 1779 effect sizes included, 1017 (57%) referred to birds, 389 (22%) arthropods, 166 (9%) mammals, 126 (7%) plants, 52 (3%) reptiles and 29 (2%) amphibians (Appendix S1). Approximately 59% ($n = 1057$) referred to forest habitats, 12% ($n = 207$) woodland, 10% ($n = 183$) shrubland or heathland, 8% ($n = 140$) rainforest, 5% ($n = 93$) savanna or grassland, 2% ($n = 27$) wetlands, and 4% ($n = 72$) described other various habitats, such as farmland, pasture, salt marsh, meadows, coastal sage scrub and coastal dunes (Appendix S1). Papers primarily examined changes in species density (83%, $n = 266$) or species richness (11%, $n = 36$), with only 6% reporting changes in the probability of occurrence ($n = 13$) or species diversity ($n = 6$) (Appendix S1). Figure 2 shows an overview of the geographical spread of studies included in our analyses. It can be seen that most studies were conducted in North America and in Europe; however, areas throughout South America, Africa, Asia and Australia are also represented.

The studies we reviewed reported habitat cover (proportion of the area covered by suitable habitat) (Appendix S1) at various spatial scales. Of the 168 studies included, 83 reported habitat cover at the landscape scale, 39 reported habitat cover at the site or treatment scale and 26 reported treatment effects, but we were only able to obtain habitat cover data at the landscape scale. For 20 of the 168 studies (11.9%), we were unable to obtain the proportion of suitable habitat remaining for either the study landscape or study sites.

The influence of climatic factors on habitat loss and fragmentation effects

The climate data used in the models varied substantially across the study areas. Maximum temperature of warmest month ranged from −1.7 to 41.9 °C, minimum precipitation of driest month from 0 to 202 mm, mean precipitation change from −311.1 to 247.38 mm and mean temperature change from −1.14 to 1.8 °C. Tests of significance indicated that random slopes for study response type and land-use, and random intercepts for taxonomic group, habitat type and land-use were not significant ($P > 0.05$), and therefore were excluded from the logistic-regression models. Random slopes for taxonomic group and habitat type and a random intercept for study response type were significant ($P < 0.05$) and therefore were included (Table 1).

The most parsimonious model according to AIC was a model containing maximum temperature, mean precipitation change and mean temperature change (AIC = 629.2; Table 2). This model had a comparably high Akaike weight ($W_i = 0.68$) indicating that the combined effects of these three climate variables have good support from the data relative to other models. A model containing maximum temperature and mean precipitation change was the second best model (AIC = 632.1, ΔAIC = 2.9, $W_i = 0.16$), but according to Burnham & Anderson (2002) only models with AIC differences between 0 and 2 have substantial support. The good-

ness-of-fit Q–Q plot for the best model showed a slight lack of fit at the lower and upper quantiles (Appendix S2). This appears to be due to an inability of the model to account for some of the variation in the tails of distribution of the residuals, rather than a misspecified functional form for the model. Overall, the most important variable was maximum temperature ($w_i = 0.999$), followed by precipitation change ($w_i = 0.857$), and temperature change ($w_i = 0.825$). We found little evidence for the importance of minimum precipitation ($w_i = 0.147$) and habitat amount ($w_i = 0.011$; Table 2).

The model-averaged coefficients revealed that maximum temperature was positively related to habitat loss/fragmentation impacts and had the strongest effect compared to the other climatic factors (Fig. 3). The positive relationship indicates that, as maximum temperature increases, the probability of negative habitat loss/fragmentation impacts also increases. On the other hand, effect sizes for minimum precipitation and precipitation change were negative. The negative relationships indicate that as minimum precipitation increases, the probability of negative habitat loss/fragmentation impact declines. Similarly, the probability of a negative habitat loss/fragmentation effect is lowest where rainfall has increased most over time. Coefficients for temperature change and habitat amount were small in magnitude.

Taxonomic group and habitat type variation

There were very few differences in the habitat loss/fragmentation effect sizes among taxa (Fig. 4). Apart from arthropods, habitat loss/fragmentation effects on species were large and positive for maximum temperature (Fig. 4a). This indicates that, in general, as temperature increases, the chance of a species being negatively affected by habitat loss/fragmentation also increases, especially for reptiles, which had the largest coefficient of 23.026. For arthropods, the effect size was still relatively large but, as temperature increases, the

Table 1 List of parameters included in the logistic-regression analyses to test whether study habitat loss/fragmentation effect sizes are related to current climate and/or climatic change

Parameter	Description	Type of variance/effect
Taxa	Taxonomic group	Random slope effect
Habitat	Type of habitat	Random slope effect
Study response	Response variable measured	Random intercept effect
Habitat amount	Proportion of the area covered by suitable habitat	Fixed effect
Max temperature	Maximum temperature of warmest month (1950–2000)	Fixed effect
Min precipitation	Precipitation of driest month (1950–2000)	Fixed effect
Mean precipitation change	Annual average precipitation difference [(1977–2006) − (1901–1930)]	Fixed effect
Mean temperature change	Annual average temperature difference [(1977–2006) − (1901–1930)]	Fixed effect

Table 2 Logistic-regression models with habitat loss/fragmentation effects as the dependent variable and climatic parameters and habitat amount as independent variables

Table 2 (continued)

Model	Variables	AIC	ΔAIC	Model weights (W_i)
XIX	mtwm + precdiff + tmxdiff	**629.2**	0.0	0.68
VII	mtwm + precdiff	632.1	2.9	0.16
XVII	mtwm + podm + tmxdiff	632.4	3.2	0.14
XX	mtwm + precdiff + habper	637.7	8.5	0.01
VI	mtwm + podm	639.4	10.2	0.00
XXVI	mtwm + podm + precdiff + tmxdiff	639.4	10.2	0.00
VIII	mtwm + tmxdiff	641.7	12.5	0.00
XVI	mtwm + podm + precdiff	642.4	13.2	0.00
XXIX	mtwm + precdiff + tmxdiff + habper	643.7	14.5	0.00
IX	mtwm + habper	645.7	16.5	0.00
XXVIII	mtwm + podm + tmxdiff + habper	646.5	17.3	0.00
I	mtwm	648.8	19.6	0.00
XVIII	mtwm + podm + habper	649.9	20.7	0.00
XXI	mtwm + tmxdiff + habper	650.0	20.8	0.00
XXV	precdiff + tmxdiff + habper	652.8	23.6	0.00
XXVII	mtwm + podm + precdiff + habper	654.9	25.7	0.00
XXXI	mtwm + podm + precdiff + tmxdiff + habper	659.3	30.1	0.00
XXII	podm + precdiff + tmxdiff	660.6	31.4	0.00
XXIV	podm + tmxdiff + habper	665.6	36.4	0.00
XXX	podm + precdiff	665.7	36.5	0.00

Model	Variables	AIC	ΔAIC	Model weights (W_i)
	+ tmxdiff + habper			
XIV	precdiff + habper	669.1	39.9	0.00
XI	podm + tmxdiff	669.3	40.1	0.00
XIII	precdiff + tmxdiff	670.0	40.8	0.00
XXIII	podm + precdiff + habper	678.6	49.4	0.00
XV	tmxdiff + habper	680.8	51.6	0.00
V	habper	693.0	63.8	0.00
III	precdiff	695.1	65.9	0.00
XII	podm + habper	695.3	66.1	0.00
X	podm + precdiff	695.5	66.3	0.00
IV	tmxdiff	698.2	69.0	0.00
II	podm	703.9	74.7	0.00
N	Null	716.8	87.6	0.00
Individual variable weights (w_i)	mtwm 0.999	precdiff 0.857	tmxdiff 0.825	podm 0.147 habper 0.011

Random-effect variables coding for study (intercept), taxonomic group (slope) and habitat type (slope) were included in all models. The table indicates the fixed-effect variables included in each model, the Akaike's information criterion scores (AIC), the difference between the AIC for a given model and the best fitting model (ΔAIC), AIC weights (W_i) and the individual variable weights (w_i).
Models are ranked by ΔAIC values; bold indicates lowest AIC value in model set.
mtwm, maximum temperature of warmest month; podm, precipitation of driest month; precdiff, annual average precipitation difference; tmxdiff, annual average temperature difference; habper, proportion of the area covered by suitable habitat.

chance of a species being negatively affected by habitat loss/fragmentation declines. On average, all taxonomic groups (excluding plants) had relatively large negative coefficients for precipitation change; in general, habitat loss/fragmentation effects declined in areas where rainfall has increased most over time (Fig. 4c). Plants, on the other hand, displayed no response to precipitation change. For minimum precipitation, negative coefficients were observed for all taxa except birds, which showed no response (Fig. 4b), indicating that as current precipitation increases, habitat loss/fragmentation effects decline. Effect sizes varied considerably for habitat amount (Fig. 4e). Amphibians and mammals
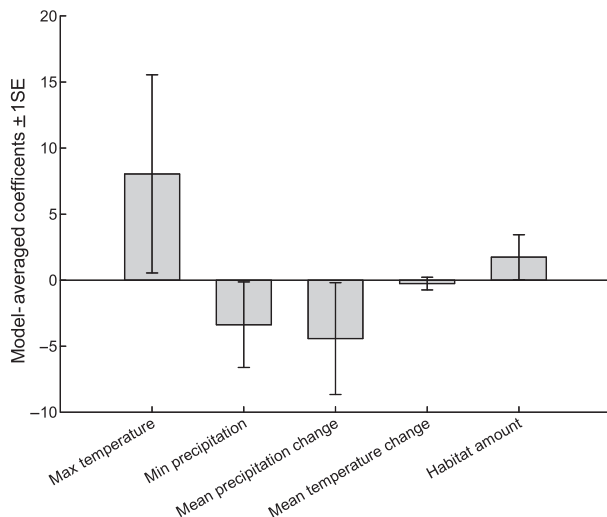
Fig. 3 Coefficient averages from the logistic-regression models in Table 2 explaining the variation in habitat loss and fragmentation effects on biological populations as influenced by current climate, climatic change and amount of habitat. max temperature represents maximum temperature of warmest month; min precipitation represents precipitation of driest month; mean precipitation change represents annual average precipitation difference; mean temperature change represents the annual average temperature difference; habitat amount represents proportion of the area covered by suitable habitat.

displayed larger positive coefficients, whereas plants and reptiles displayed smaller negative coefficients. This indicates that, as habitat amount increases, the chance of a plant or reptile species being negatively affected by habitat loss/fragmentation declines. In contrast, as habitat amount increases, the chance of an amphibian or mammal species being negatively affected by habitat loss/fragmentation increases. The coefficients for birds and arthropods in relation to habitat amount, and all taxa in relation to temperature change were small (Fig. 4d and e).

Effect sizes for different habitat types showed several distinct differences (Fig. 5). First, the coefficients were more variable than for taxonomic groups, indicating that habitat type probably drives most of the variation in the dataset. Coefficients for forest, savanna/grassland, rainforest and wetland habitats were large and positive for maximum temperature, indicating that as current temperature increases the chance of a species being negatively affected by habitat loss/fragmentation in these habitats also increases (Fig. 5a). Coefficients for woodland, shrubland/heathland and other habitats were negative, but smaller in magnitude, suggesting that the effects of temperature on habitat loss/fragmentation effects in these habitats were relatively minor. For precipitation change, the majority of coefficients (excluding wetlands and other habitats) were negative;

habitat loss/fragmentation effects in these habitats were lowest in areas where rainfall has increased most over time (Fig. 5c). The wetland coefficient was small, but for other habitats positive, indicating that habitat loss/fragmentation effects in other habitats were highest in areas where rainfall has increased most over time. Apart from shrubland/heathland, the coefficients for minimum precipitation were relatively small (Fig. 5b). For shrubland/heathland, the chance of a species being negatively affected by habitat loss/fragmentation declines as precipitation increases. Effect sizes varied considerably for temperature change (Fig. 5d). Woodland, shrubland/heathland and rainforest displayed negative coefficients; habitat loss/fragmentation effects were lowest in areas where temperature has increased most over time. In contrast, habitat loss/fragmentation effects on species in wetlands and other habitats were highest in areas where temperature has increased most. Forest and shrubland/heathland coefficients were small. For habitat amount, the shrubland/heathland, savanna/grassland and wetland coefficients were positive, indicating that as habitat amount increases, the chance of a species in these habitats being negatively affected by habitat loss/fragmentation also increases. All other coefficients were small, except for rainforest; suggesting that the chance of a rainforest species being negatively affected by habitat loss/fragmentation declines as habitat amount increases.

Discussion

We have presented here the first empirical synthesis to quantify and test for interacting effects among current climate, climatic change and habitat loss on terrestrial biological populations at a global scale. Our empirical approach demonstrates that habitat loss and fragmentation effects were greatest where maximum temperature of warmest month was highest (i.e. effects were greatest in areas with high temperatures). Conversely, habitat loss and fragmentation effects were lowest in areas where precipitation has increased most (i.e. smaller effects occurred in areas where average rainfall has increased over time than in areas where rainfall has decreased). These were the two most important variables, with mean temperature change as the third. Therefore, both current climate (i.e. maximum temperature) and climate change (i.e. precipitation change) appear to be key determinants of habitat loss and fragmentation effects on terrestrial biodiversity.

Model interpretation

Our results suggest that areas with high current temperatures and where average rainfall has decreased
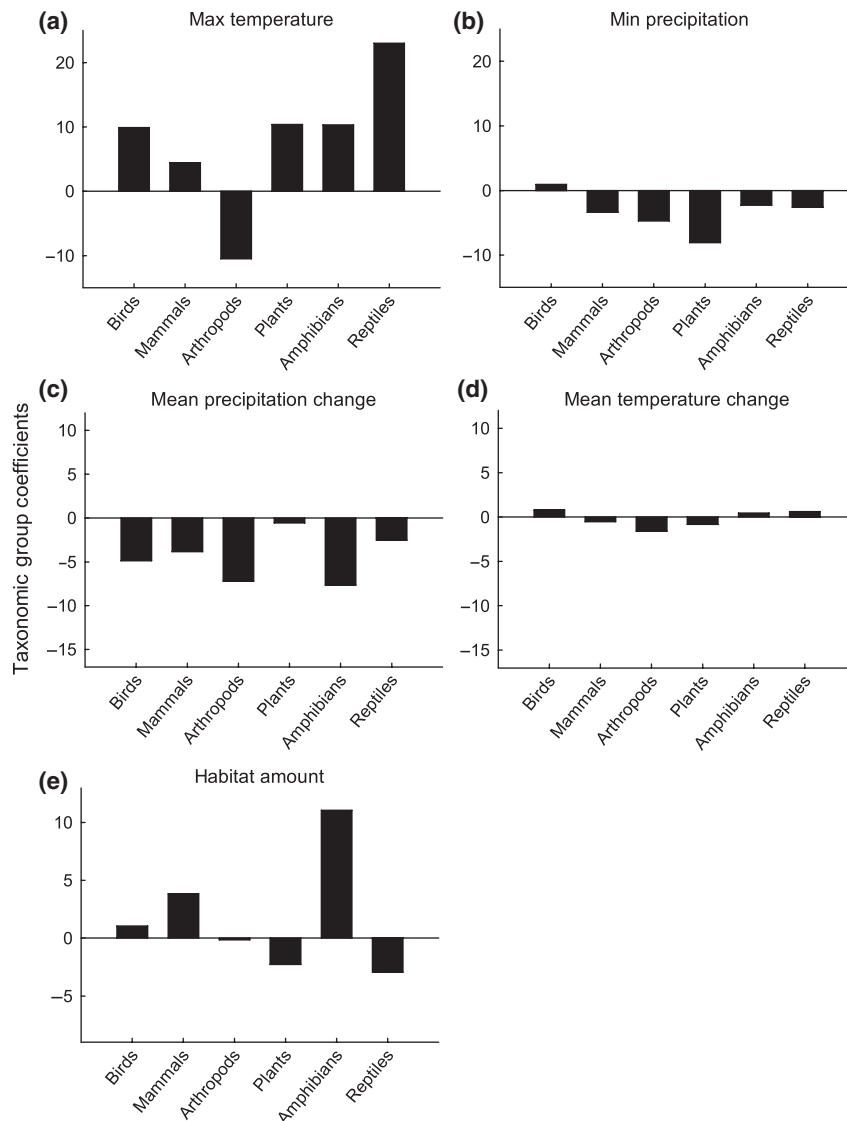
Fig. 4 Logistic-regression coefficients for each taxonomic group averaged across all models and combined with the fixed-effect model-averaged coefficients. Positive associations exist between habitat loss/fragmentation effects and (a) maximum temperature of warmest month, (b) minimum precipitation of driest month, (c) mean annual precipitation difference, (d) mean annual temperature difference or (e) habitat amount for taxonomic groups with coefficients greater than zero. Negative associations exist for those taxonomic groups with coefficients less than zero.

over time exacerbate the negative effects of habitat loss and fragmentation on species density and/or diversity. Over the last 10–15 years, key findings on the ecological effects of high temperatures and extended droughts in terrestrial ecosystems have accumulated (e.g. Davis & Shaw, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Thomas *et al.*, 2004; Bates *et al.*, 2005; Parmesan, 2006; Allen *et al.*, 2010). Evidence suggests that stressful conditions appear to drive local population dynamics; however, the responses of both flora and fauna to drought, heat and rain, can vary (Parmesan, 2006; Pearson, 2006). Species react differently to

climate change depending on their life-history characteristics, individual thresholds and many environmental factors (Walther *et al.*, 2002). It is also important to recognize that the threshold of climate change below which species extinction occurs or populations severely decline is likely to be determined by the pattern of habitat loss (Opdam & Wascher, 2004; Keith *et al.*, 2008). For instance, Travis (2003) used a lattice model to investigate the combined impacts of climate change and habitat loss on a hypothetical species and showed that during climatic change, the habitat loss threshold occurs sooner. Habitat loss and fragmentation may
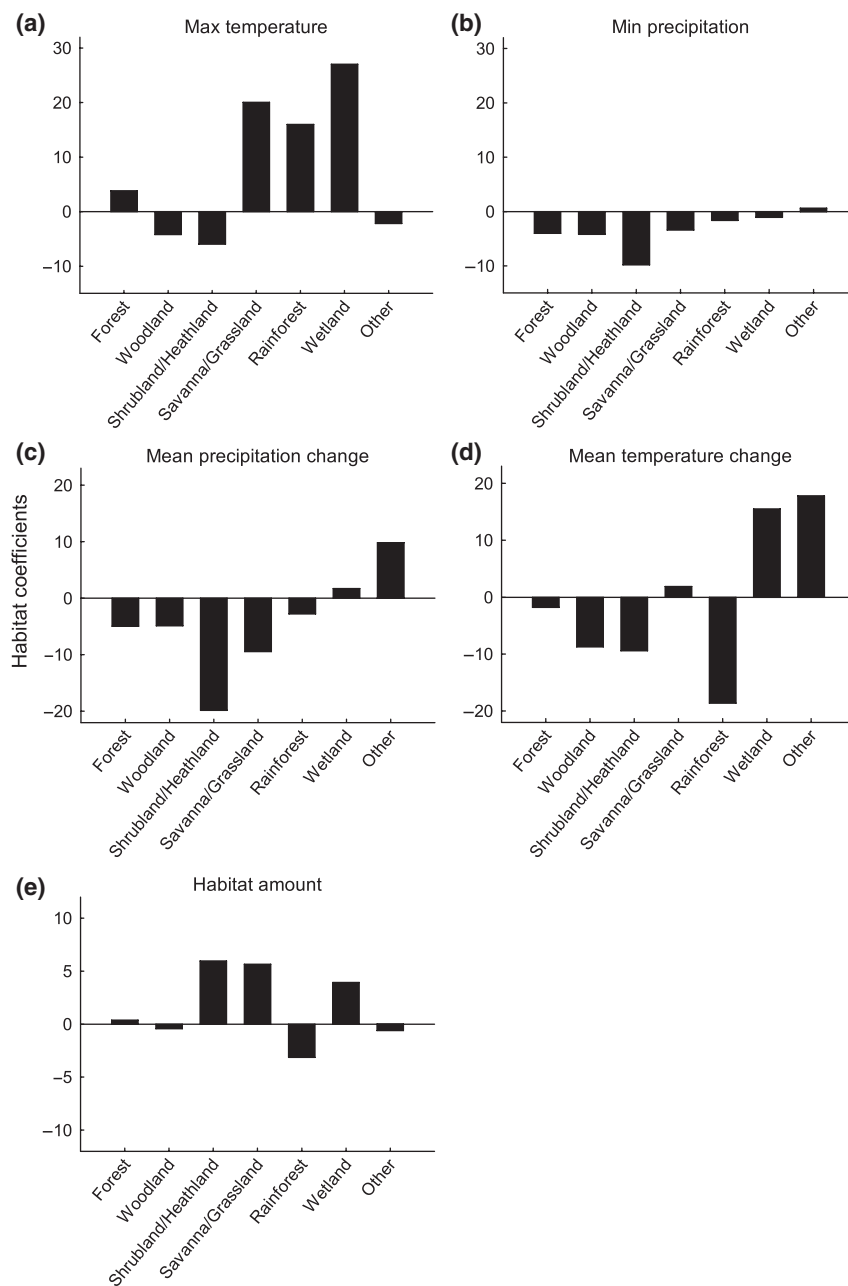
Fig. 5 Logistic-regression coefficients for each habitat type averaged across all models and combined with the fixed-effect model-averaged coefficients. Positive associations exist between habitat loss/fragmentation effects and (a) maximum temperature of warmest month, (b) minimum precipitation of driest month, (c) mean annual precipitation difference, (d) mean annual temperature difference or (e) habitat amount for habitats with coefficients greater than zero. Negative associations exist for those habitats with coefficients less than zero.

increase species susceptibility to climate change by limiting their ability to track climate variations across space (Thomas *et al.*, 2004). In contrast, species within high temperature and lower precipitation regions may be more susceptible to fragmentation and habitat destruction because they are unable to adapt rapidly enough to their environmental conditions.

We hypothesized that different taxonomic groups might show different interactions between habitat loss and climate change depending on their functional niche and habitat requirements. In spite of the diverse number of taxonomic groups and species included in the meta-analysis, arthropods were the only group to show little interaction between current

temperature and habitat loss effects compared with other taxa. Studies of these taxa do not appear to be outliers, but rather indicate that differences among taxa may reflect the choice of species sampled. For example, previous studies of insects have reported that single drought years and manipulated water availability cause drastic crashes in some species while leading to population booms in others (Mattson & Haack, 1987; Schowalter *et al.*, 1999). The arthropods included in our meta-analysis varied greatly from ants, termites, dung beetles, moths, flies, bees, scorpions, amphipods, spiders, cockroaches to butterflies, and included a wide range of specialists, generalists, opportunists, and even hot climate specialists. The range of plants, mammals, reptiles and amphibians, on the other hand, were much more limited. Thus, it is possible that diverse animal groups are more resistant or resilient on average because they are more likely to include various heat-tolerant and drought-resistant species. Specialist species are more prone to extinction during climate change because they tend to have low colonization ability and limited dispersal, whereas generalist species with relatively wider ranges tend to be more resilient (Travis, 2003; Thomas *et al.*, 2004). Consequently, to thoroughly understand how the combined effects of current climate, climate change and habitat loss vary between animal groups, further investigations into specific taxa, functional groups and ecological traits are required. It seems clear, however, at least at the broad taxonomic level that higher order species on average are being more adversely affected by habitat loss and climate interactions.

The variation in effects among habitats was far more complex than among taxonomic groups. Species of the same taxa are often similar in both morphology and ecology, yet they can respond differently in different habitats or distributions depending on the local conditions (Schlichting, 1986). For example, it has been well documented that species can change physiologically and morphologically to adapt to their environment (e.g. Davis & Shaw, 2001; Losos & Ricklefs, 2009; Berg *et al.*, 2010; Hofmann & Todgham, 2010; Hill *et al.*, 2011). This ability is particularly important in plants, whose sessile life-history requires them to deal with ambient conditions (Wilson *et al.*, 1980; Dudley, 1996; Aiba *et al.*, 2004; Puijalon *et al.*, 2005). Other species have adapted to unpredictable habitat availability in space and time by developing high mobility, and consequently are less susceptible to human-induced fragmentation, for example, species from coastal habitats and early succession stages of ecosystems (Opdam & Wascher, 2004). In contrast, species in systems with less natural variability, like

forests, heathlands and wetlands, have evolved under fairly predictable conditions. Species in those habitats that were found not to be negatively impacted by habitat loss and climate interactions, may therefore be caused by the adaptability or phenotypic plasticity of the species in each habitat, the natural variability of the ecosystem, or both, rather than the type of habitat alone.

Another theory for species not being negatively impacted by habitat loss and climate interactions, within specific habitats, is the notion that the amount of habitat in the landscape and the spatial distribution of remaining habitat may influence the degree to which climate interacts with habitat loss (Opdam & Wascher, 2004; Pyke, 2004). It has been hypothesized that fragmentation effects should be most pronounced at low levels of habitat cover (Andrén, 1994; Bascompte & Solé, 1996; Fahrig, 1997; Swift & Hannon, 2010). Forests, grasslands and wetlands often become highly fragmented with habitat loss, while shrublands, heathlands and other ecosystems such as farmland and pastures are regarded as less vulnerable. Species in highly fragmented ecosystems, when responding to climate change, may therefore be limited by the amount and spatial configuration of habitat (Opdam & Wascher, 2004; Pyke, 2004). This concept may help to explain some of the variation found among the habitat types in this study, especially in relation to maximum temperature effects. Differences in how authors classify habitats across the globe, and the relatively small number of wetland ($n = 27$) and savanna or grassland ($n = 93$) samples included in our meta-analysis may also explain some of the variation.

Model limitations

An assumption of meta-analyses is that the studies examined have collected data in a sufficiently similar manner that they can be pooled to identify meaningful patterns. Although habitat cover (proportion of the area covered by suitable habitat) was shown to have little importance in explaining habitat loss/fragmentation effects in our model, the resolution of the habitat amount data was variable and could not be improved, because of inconsistencies in the spatial scales reported among studies and missing data (Appendix S1). Therefore, it is possible that the logistic-regression models may have underestimated the impact of habitat cover as a predictor. Despite this limitation, we believe that our results are valid and the lack of a habitat amount effect does not affect our conclusions about the climate effects, which is the main focus of the study. Furthermore, there is a slight lack of fit at the lower and upper quantiles of our model (Appendix S2). This is primarily

due to the model failing to capture all of the variation among studies and not a result of a misspecified functional form. However, because the main aim of the model was to understand how the effects of current climate, climate change and habitat loss interact and synergistically impact on biological systems rather than as a general predictive model we do not believe this affects our overall conclusions. As discussed earlier, the relationships among habitats that may explain the unexplained variation are complex and should be explored in more detail in future work.

Implications for conservation

The results of this study have important implications for conservation of biodiversity under climate change. A plethora of modelling studies have already shown the potential impacts of climate change on the distributions and abundances of species (e.g. Easterling et al., 2000; Berry et al., 2002; Midgley et al., 2003; Thomas et al., 2004; Thuiller, 2004; Harrison et al., 2006; Márquez et al., 2010). While many studies have postulated about the potential for synergetic effects between climate change and other stressors (e.g. Harvell et al., 2002; Pyke, 2004, 2005; Christensen et al., 2006; Brook et al., 2008) few studies have examined these interactions explicitly. The analysis conducted in this study provides an empirical test using direct examples to inform conservation biologists of what responses we can expect to see more of in the coming decades.

Integrated assessments, such as this one, on how species and ecosystems respond to climate and habitat loss can help to identify appropriate actions for biodiversity conservation and assist in preparing for future conservation challenges. The overall breakthrough that emerges from this article is the discovery that areas with high temperatures where average rainfall has decreased over time augment the negative effects of habitat loss on species density and/or diversity. The question now is whether existing management strategies for conserving biodiversity are still appropriate under predicted climatic conditions? Management strategies should focus towards areas with warmer climates, especially those that are more susceptible to precipitation change. In the case where biodiversity is threatened by interactions among climate change and other stressors, there are essentially two main approaches to minimizing loss. Where climate change interactions are expected to be relatively small and knowledge and capacity high, the best feasible option might be to continue what we are already doing. That is, building resilience in a system to climate change, for example, through habitat restoration, and continued management of other stressors,

such as pest management, and fire and grazing management. Existing measures against drought, such as protecting and creating migration corridors (Anderson & Jenkins, 2006) should also be intensified, to reduce the negative interaction between habitat loss and climate change, especially in fragmented landscapes. However, in areas where the effects of climate change and interactions are expected to be severe, our current suite of management actions may be ineffective. It may be appropriate in these cases to use a mixture of more proactive management strategies instead; such as species translocation (McDonald-Madden et al., 2011), engineering habitat to reduce impact of interactions (Brook et al., 2008), and even abandoning effort on saving species in one area in favour of other areas (Bottrill et al., 2008). Monitoring that informs management is thus essential here to pre-emptively identify populations that may suffer decline, and to assess cost-effective and feasible management actions (Field et al., 2004; Carwardine et al., 2011).

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References

Aiba S, Kitayama K, Takyu M (2004) Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. Plant Ecology, **174**, 147–161.

Allen CD, Macalady AK, Chenchouni H et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, **259**, 660–684.

Anderson AB, Jenkins CN (2006) Applying Nature's Design: Corridors as a Strategy for Biodiversity Conservation. Columbia University Press, New York.

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos, **71**, 355–366.

Aronson J, Blignaut JN, Milton SJ et al. (2010) Are socioeconomic benefits of restoration adequately quantified? A meta-analysis of recent papers (2000–2008) in restoration ecology and 12 other scientific journals Restoration Ecology, **18**, 143–154.

Bascompte J, Solé RV (1996) Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology, **65**, 465–473.

Bates JW, Thompson K, Grime JP (2005) Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. *Global Change Biology*, **11**, 757–769.

Beale EML, Kendall MG, Mann DW (1967) The discarding of variables in multivariate analysis. *Biometrika*, **54**, 357–366.

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.

Berg MP, Kiers ET, Driessen G *et al.* (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587–598.

Berman NG, Parker RA (2002) Meta-analysis: neither quick nor easy. *BMC Medical Research Methodology*, **2**, 10.

Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453–462.

Bottrill MC, Joseph LN, Carwardine J *et al.* (2008) Is conservation triage just smart decision making? *Trends in Ecology & Evolution*, **23**, 649–654.

Breed MF, Ottewell KM, Gardner MG, Lowe AJ (2011) Clarifying climate change adaptation responses for scattered trees in modified landscapes. *Journal of Applied Ecology*, **48**, 637–641.

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

Brooks TM, Mittermeier RA, Mittermeier CG *et al.* (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909–923.

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* Springer-Verlag, New York.

Carroll C (2007) Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. *Conservation Biology*, **21**, 1092–1104.

Carwardine J, O'Connor T, Legge S, Mackey B, Possingham HP, Martin TG (2011) *Priority Threat Management to Protect Kimberley Wildlife.* CSIRO Ecosystem Sciences, Brisbane.

de Chazal J, Rounsevell MDA (2009) Land-use and climate change within assessments of biodiversity change: a review. *Global Environmental Change-Human and Policy Dimensions*, **19**, 306–315.

Christensen MR, Graham MD, Vinebrooke RD, Findlay DL, Paterson MJ, Turner MA (2006) Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, **12**, 2316–2322.

Cormont A, Malinowska A, Kostenko O, Radchuk V, Hemerik L, WallisDeVries M, Verboom J (2011) Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. *Biodiversity and Conservation*, **20**, 483–503.

Corser JD (2001) Decline of disjunct green salamander (*Aneides aeneus*) populations in the southern Appalachians. *Biological Conservation*, **97**, 119–126.

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, **11**, 1304–1315.

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation*, **128**, 231–240.

Darling ES, McClanahan TR, Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conservation Letters*, **3**, 122–130.

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

Dudley SA (1996) The response to differing selection on plant physiological traits: evidence for local adaptation. *Evolution*, **50**, 103–110.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Ellstrand NC, Elam DR (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217–242.

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, **61**, 603–610.

Fahrig L (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Field SA, Tyre AJ, Jonzen N, Rhodes JR, Possingham HP (2004) Minimizing the cost of environmental management decisions by optimizing statistical thresholds. *Ecology Letters*, **7**, 669–675.

Franco AMA, Hill JK, Kitschke C *et al.* (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545–1553.

Garg AX, Hackam D, Tonelli M (2008) Systematic review and meta-analysis: when one study is just not enough. *Clinical Journal of the American Society of Nephrology*, **3**, 253–260.

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**, 2809–2815.

Gurevitch J, Curtis PS, Jones MH (2001) Meta-analysis in ecology. *Advances in Ecological Research*, **32**, 199–247.

Harrison PA, Berry PM, Butt N, New M (2006) Modelling climate change impacts on species' distributions at the European scale: implications for conservation policy. *Environmental Science & Policy*, **9**, 116–128.

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. *Science*, **296**, 2158–2162.

Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hill JK, Griffiths HM, Thomas CD (2011) Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143–159.

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology*, **72**, 127–145.

Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, 1211–1219.

Keith DA, Akçakaya HR, Thuiller W *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.

Landwehr JM, Pregibon D, Shoemaker AC (1984) Graphical methods for assessing logistic regression models. *Journal of the American Statistical Association*, **79**, 61–71.

Leimu R, Koricheva J (2004) Cumulative meta-analysis: a new tool for detection of temporal trends and publication bias in ecology. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 1961–1966.

LeLorier J, Gregoire G, Benhaddad A, Lapierre J, Derderian F (1997) Discrepancies between meta-analyses and subsequent large randomized, controlled trials. *New England Journal of Medicine*, **337**, 536–542.

Lemoine N, Bauer HG, Peintinger M, Bohning-Gaese K (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology*, **21**, 495–503.

Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. *Nature*, **457**, 830–836.

Luiselli L (2008) Community ecology of African reptiles: historical perspective and a meta-analysis using null models. *African Journal of Ecology*, **46**, 384–394.

Marczak LB, Sakamaki T, Turvey SL, Deguise I, Wood SLR, Richardson JS (2010) Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis *Ecological Applications*, **20**, 126–134.

Márquez A, Real R, Olivero J, Estrada A (2010) Combining climate with other influential factors for modelling the impact of climate change on species distribution. *Climatic Change*, **108**, 1–23.

Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. *BioScience*, **37**, 110–118.

McDonald-Madden E, Runge MC, Possingham HP, Martin TG (2011) Optimal timing for managed relocation of species faced with climate change. *Nature Climate Change*, **1**, 261–265.

McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 6070–6074.

Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, **112**, 87–97.

Miles L, Grainger A, Phillips O (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **13**, 553–565.

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, **25**, 693–712.

Mora C, Metzger R, Rollo A, Myers RA (2007) Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1023–1028.

Ojeda-Martinez C, Bayle-Sempere JT, Sanchez-Jerez P, Forcada A, Valle C (2007) Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data. *Marine Biology*, **151**, 1153–1161.

Opdam P (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology*, **5**, 93–106.

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285–297.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pearson RG (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, **21**, 111–113.

Pimm SL (2008) Biodiversity: climate change or habitat loss - which will kill more species? *Current Biology*, **18**, R117–R119.

Pounds JA, Bustamante MR, Coloma LA *et al.* (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.

Puijalon S, Bornette G, Sagnes P (2005) Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. *Journal of Experimental Botany*, **56**, 777–786.

Pyke CR (2004) Habitat loss confounds climate change impacts. *Frontiers in Ecology and the Environment*, **2**, 178–182.

Pyke CR (2005) Interactions between habitat loss and climate change: implications for fairy shrimp in the central valley ecoregion of California, USA. *Climatic Change*, **68**, 199–218.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) Glmm applied on the spatial distribution of koalas in a fragmented landscape. In: *Mixed Effects Models and Extensions in Ecology With R* (eds Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM), pp. 469–492. Springer, New York.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Sala OE, Chapin FS, Armesto JJ *et al.* (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Schindler DW (2001) The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 18–29.

Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics*, **17**, 667–693.

Schowalter TD, Lightfoot DC, Whitford WG (1999) Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *American Midland Naturalist*, **142**, 281–290.

Schulze R (2004) *Meta-Analysis: A Comparison of Approach*. Hogrefe & Huber, Toronto.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Stefanescu C, Herrando S, Paramo F (2004) Butterfly species richness in the northwest Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography*, **31**, 905–915.

Stewart G (2010) Meta-analysis in applied ecology. *Biology Letters*, **6**, 78–81.

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews*, **85**, 35–53.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thomas CD, Franco AMA, Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**, 415–416.

Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 467–473.

Vinebrooke RD, Cottingham KL, Norberg J, Scheffer M, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos*, **104**, 451–457.

Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Warren MS, Hill JK, Thomas JA *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 1887–1892.

Wilson J, Ludlow M, Fisher M, Schulze E (1980) Adaptation to water stress of the leaf water relations of four tropical forage species. *Functional Plant Biology*, **7**, 207–220.

Wilson K, Pressey RL, Newton A, Burgman M, Possingham H, Weston C (2005) Measuring and incorporating vulnerability into conservation planning. *Environmental Management*, **35**, 527–543.

Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, **11**, 413–418.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Studies used in the meta-analysis.
Appendix S2. Goodness-of-fit quantile–quantile plot for Model XIX, containing maximum temperature of warmest month, mean annual precipitation difference and mean annual temperature difference with 95% pointwise confidence bounds.

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