ECOLOGY LETTERS

Ecology Letters, (2016) doi: 10.1111/ele.12645

LETTER

Climate change and habitat conversion favour the same species

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Abstract

Land-use change and climate change are driving a global biodiversity crisis. Yet, how species' responses to climate change are correlated with their responses to land-use change is poorly understood. Here, we assess the linkages between climate and land-use change on birds in Neotropical forest and agriculture. Across > 300 species, we show that affiliation with drier climates is associated with an ability to persist in and colonise agriculture. Further, species shift their habitat use along a precipitation gradient: species prefer forest in drier regions, but use agriculture more in wetter zones. Finally, forest-dependent species that avoid agriculture are most likely to experience decreases in habitable range size if current drying trends in the Neotropics continue as predicted. This linkage suggests a synergy between the primary drivers of biodiversity loss. Because they favour the same species, climate and land-use change will likely homogenise biodiversity more severely than otherwise anticipated.

Keywords

Anthropocene, bird, climate niche, countryside biogeography, deforestation, habitat conversion, homogenisation.

Ecology Letters (2016)

INTRODUCTION

The magnitude of the sixth mass extinction hinges on whether species can withstand concurrent global changes in climate and land-use (Jetz *et al.* 2007). Presently, habitat conversion is the primary driver of global endangerment for ~ 80% of vertebrate taxa (Pereira *et al.* 2012). While many species thrive in human-dominated landscapes that contain some natural vegetation (e.g. Daily *et al.* 2003; Pineda *et al.* 2005), species richness drops precipitously as land-use intensifies (e.g. Frishkoff *et al.* 2014; Newbold *et al.* 2015). Moreover, in human-dominated landscapes that contain high local diversity, species composition often differs dramatically from natural areas (Urbina-Cardona *et al.* 2006; Newbold *et al.* 2015). Why only some species thrive in human-dominated landscapes is largely unknown. Some traits, such as body size, generation time, degree of specialisation, and resource needs, are often non-randomly distributed between species that differ in their responses to land-use change (e.g. Swihart *et al.* 2003; Henle *et al.* 2004; Newbold *et al.* 2013). Yet, the effect size and even directionality of these differences varies across studies and taxa.

Unlike habitat conversion (Pereira *et al.* 2012), climate change has so far had modest effects on species endangerment (Urban 2015), perhaps in part because some species are shifting their ranges (Chen *et al.* 2011). Yet, if current emission trajectories continue, many species may go extinct over the next century, though extinction estimates differ widely depending on the taxa, spatial scale, and methods used (Bellard *et al.* 2012; Urban 2015). In general, broadly distributed species with large population sizes and wide or warm climatological niches are expected to benefit at the expense of climate-specialists and cool-adapted species (Pearson *et al.* 2014). However, even for highly vagile taxa such as birds, the rapidity of climate change is expected to outpace some species' abilities to track their climate niches (Devictor *et al.* 2008).

The combined effects of climate and land-use change are not well understood, complicating efforts to predict future biological communities and prioritise conservation (Brook *et al.* 2008; Bellard *et al.* 2012). Synergies between external threats (e.g. habitat fragmentation increasing fire risk) mean that species are often faced by multiple threats simultaneously (Laurance & Useche 2009). Additionally, the presence of one threat can make another more serious: fragmentation may prevent dispersal and limit species' abilities to track their climate niches (Opdam & Wascher 2004; Lindo *et al.* 2012).

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However, species' responses to habitat conversion may also be intrinsically tied to their climate niche because similar traits might control both. This could emerge directly because of differences in microclimates between natural and human-altered habitats. Many human-altered habitats are warmer and drier than natural ones (e.g. Frishkoff *et al.* 2015) in part because altered habitats typically lack climate-buffering canopy cover and microsites found in structurally diverse natural habitats (Scheffers *et al.* 2014). Alternatively, links between climate niche and response to land-use change may be indirect because vegetation structure in human-dominated habitats may be similar to natural habitats in specific climate regimes (e.g. warm dry areas dominated by shrubland), which would then favour species that can exploit these vegetation types. Regardless of mechanism, biological communities do seem to respond predictably to habitat conversion: a limited number of studies among European birds (Clavero *et al.* 2011; Barnagaud *et al.* 2012, 2013), and Neotropical herpetofauna (Frishkoff *et al.* 2015), report that species that thrive in agricultural or urban environments tend to have geographic ranges in warmer (lower latitude or elevation) climate zones while forest-dwelling species tend to come from cooler climes.

The consequences of linked climate-habitat niches are not fully appreciated. Previously, potential correlations between habitat and climate niche have been regarded as analytically problematic – changes in land-use could lead to 'warmer' bird communities which might then obscure potential biological signals of climate change (Devictor *et al.* 2008; Clavero *et al.* 2011). However, an additional concern is that both anthropogenic pressures could negatively affect the same species (e.g. cold-affiliated ones), causing even more dramatic biodiversity declines than currently predicted (Brook *et al.* 2008). This concern is especially relevant in the tropics because (1) biodiversity is concentrated there, (2) classical ecological thought posits that climate niches of tropical species are narrow (Janzen 1967), and (3) the tropics are expected to experience locally novel climates sooner than any other region on Earth (Mora *et al.* 2013). Despite uncertainty in precise spatial patterns, over the coming century, the Neotropics are expected to warm by 1.6–4.0 °C and to lose precipitation in some regions (Magrin *et al.* 2014). For example, in Central America, decreases in rainfall are predicted to amplify the effects of the mid-summer drought (Rauscher *et al.* 2008). If species primarily affiliated with warm or dry climate regimes are typically found in Neotropical agriculture, then climate change and further agricultural expansion may put forest-affiliated species at even greater risk.

Here, we characterise relationships between species' climate niches, biogeographic origins, and affiliation with human-dominated habitats to better ascertain future threats to biodiversity. To do so, we use one of the most temporally and spatially extensive data sets for any tropical taxon, encompassing 118 127 detections from more than 300 bird species across land-use gradients spanning four biomes in Costa Rica (Karp *et al.* 2012; Frishkoff *et al.* 2014). We first assess whether climatological niche axes predict species' tolerances to habitat conversion, hypothesising that species from warm and/or dry climate zones may be best equipped to cope with the conditions that characterise tropical agricultural systems. Next, we assess whether species predictably shift their habitat affiliations in regions with different climates. We then assess where Costa Rica's agriculture- and forest-affiliated species are found across the globe, in order to determine which regions and biomes are associated with Neotropical agriculture-affiliated species. Finally, we use species distribution models (SDMs) to determine whether agriculture affiliates are better equipped to tolerate future climate change.

METHODS

Bird censuses

We used a long-term bird census dataset to evaluate whether species' climate affiliations predict their responses to habitat conversion. We conducted 12 years of surveys (2001–2012) in four regions across Costa Rica. The study regions spanned wet and dry tropical biomes with native forest and agricultural systems sampled in each region (Fig. S1, Table S1). Twelve 200 m transects were placed at sites in each study region, for a total of 48 transects replicated in each of three land covers: forest reserves, diversified agriculture, and intensive agriculture. The difference between intensive and diversified agriculture was defined based on the number of crop types, amount and configuration of natural vegetation, and degree of local tree cover (Karp *et al.* 2012; Frishkoff *et al.* 2014) (Table S2). Four transects were substantially modified during the study; therefore, we restricted analyses to 44 transects – 12 in forest, 16 in diversified agriculture, and 16 in intensive agriculture. Each transect was visited between 5 am and 9 am, six times per year in two 3-visit intervals over ~ 1 week during the dry (February–May) and wet (September–November) seasons.

Climate affiliations

To assess each species' climate niche, we used range maps generated by BirdLife International (BirdLife International and NatureServe 2012). Each species' range is divided into three categories – a resident range, where it is present throughout the year, the breeding-only range, and a non-breeding-only range. We calculated climate niches in two ways. First, we considered all locations in which birds could be found during the breeding season (i.e. resident range + breeding range). For Neotropical migrants, this typically incorporates a large portion of the temperate zone. Second, we considered all locations in which a bird exists while not breeding (i.e. resident range + non-breeding range). For Neotropical migrants, this primarily includes locations in the tropics where birds overwinter. We present results from the resident + non-breeding range analysis; because latitudinal migrants and non-migrants in our dataset are both in the tropics during this period, it can be considered more conservative. Results from the breeding range analysis were qualitatively identical and are presented in the supplement.

We extracted the values of two climate variables from the WorldClim data set at a 30 arc-s resolution (mean annual temperature [Bio1], and mean annual precipitation [Bio12]) over each species' range (either resident + breeding or resident + non-breeding). For each species, we calculated the mean of the focal climate variable (considered the 'niche centre'; for Bio1, this is equivalent to the species temperature index (Devictor *et al.* 2008)) as well as the standard deviation (indicative of the 'niche breadth'). Across all species, the distribution of temperature niche centres was strongly left skewed. To reduce this skew, temperature niche centre was raised to the fourth power. Both niche breadths (i.e. temperature and precipitation) were positively correlated with their respective niche centres, such that species from hotter and rainier areas tended to have wider niches. Therefore, we regressed raw niche breadth against niche centre for both climate variables and used the residuals for analysis. The niche breadth variables that we present in the text thus indicate whether a species had a wider or narrower niche than expected based on the position of its niche centre.

Multispecies occupancy models

We analysed bird census data in a hierarchical framework that explicitly accounts for imperfect detection in order to estimate the occupancy probability of all species over all sites and years (Royle & Dorazio 2008; Tingley & Beissinger 2013; Carrillo-Rubio *et al.* 2014). We included only the 307 species that were encountered more than 25 times over the 12 years of sampling to improve model mixing and because parameter estimates for rarely detected species would be imprecise.

We examined two processes that determine occupancy: persistence (the probability that a species is present given that it was present in the previous year) and colonisation (the probability that a species is present given that it was absent in the previous year). Rates of persistence and colonisation in each land-use type were assumed to depend linearly (on a logit scale) on standardised climate niche variables, after accounting for residual region, site, and species-specific random effects. Detection probability depended on species identity and land-use type, also accounting for residual site, species, and year random effects.

We also asked whether species predictably change habitat affiliations along climate gradients. To do so, we identified the 52 and 47 species that were detected in every study region during the wet and dry seasons respectively. We obtained estimates of average annual rainfall in each region from WorldClim (Hijmans *et al.* 2005). We then built multispecies occupancy models to assess how a region's rainfall determined occupancy in each land-use type, controlling for residual species, site and year random effects.

Finally, we used a multispecies occupancy model to quantify habitat affiliation of each species in our dataset for downstream analyses. We express habitat affiliation as the log-odds of occupying agriculture (either intensive or diversified) vs. forest habitat. Because the same species tend to affiliate with both types of agriculture, we averaged across agricultural land-use categories to obtain a single species' habitat affiliation. To avoid circularity in downstream analyses, we did not include any climate traits in this model.

To confirm generality for all occupancy analyses, we split the wet and dry season samples, and ran models on each separately. We present the wet season analyses in the main text, and the dry season in the supplement – in all cases, they returned qualitatively identical results. We employed posterior predictive checks to ensure that models were able to adequately describe the data. In all cases, the model generated predictions that did not deviate significantly from the observed data ($P > 0.6$), indicating good fit. For a full description of all implemented multispecies occupancy models and JAGS code, see the supplement.

Mapping habitat affiliations

To investigate where agriculture- and forest-affiliated species in Costa Rica are found globally, we divided the western hemisphere into square grid cells (1/3° × 1/3°). In each grid cell, we used BirdLife International range maps (BirdLife International and NatureServe 2012) to identify which species (from those present in our dataset) are found within that grid cell. We then used the habitat affiliation metric of each species (see above) to calculate the mean agricultural affinity of the set of species present in each grid cell. We regressed average agricultural affinity against the temperature and precipitation present at each grid cell using linear regression, and quantified the unique contribution of each variable as the difference in parameter adjusted R^2 between the full model and a reduced model without the term in question. Additionally, we quantified how mean agricultural affiliation changes across biomes, using biomes categorised by The Nature Conservancy (available at: http://maps.tnc.org/gis_data.html). To ease visualisation and reduce total category number, we did not include rare biomes (Inland water, Mangroves, Rock and Ice), and merged temperate conifer and temperate deciduous forests as well as tropical coniferous and tropical broadleaf forest into general temperate and tropical forest categories. However, our conclusions do not change if we analyse biomes using their original categories.

Future range size estimation

To ask which birds will tolerate future climate change, we estimated bird range sizes under different future climate change scenarios. First, we cleaned observation data obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org) for North and South America to include only observations by humans, and removed georeferencing errors (e.g. in middle of oceans, or single points on continents where the species is not found; Fig. S2). Presence locations for each species were tested for sampling bias using the average nearest neighbour index in ArcGIS 9.1 (ESRI, Redland, CA, USA). Where nearest neighbour ratios were significant ($P > 0.05$), we spatially filtered the data by randomly removing points within 10 km of one another (Boria *et al.* 2014). We then used all 19 climate variables from WorldClim at a spatial resolution of 5 arc-min (Hijmans *et al.* 2005) to develop SDMs with MaxEnt (Phillips *et al.* 2006). SDMs were run with five-fold cross validation using the default convergence threshold (10^{-5}) with a maximum of iterations (5000) and regularisation multiplier of 1. MaxEnt's inbuilt method for regularisation is efficient at dealing with correlated variables (Elith *et al.* 2011), alleviating some concern regarding model over-fitting with correlated climate data. This reduces the need to exclude correlated variables or preprocess covariates (e.g. by using PCA), which can downgrade model performance (Elith *et al.* 2011). Model accuracy was evaluated against withheld data by assessing the area under the curve (AUC) of the receiver-operating characteristic (ROC). All species' out-of-sample AUC was > 0.92, indicating that, in absolute terms, potential model over-fitting was not so great as to impede predictive power.

Next, we projected current species distributions into the future using simulated climate from 11 general circulation models for the year 2070 (average for 2061–2080) and four standard greenhouse gas concentration trajectories (representative concentration pathways [RCP]2.6, RCP4.5, RCP6.0 and RCP8.5) (Meinshausen *et al.* 2011; van Vuuren *et al.* 2011) from WorldClim (Hijmans *et al.* 2005). These pathways simulate different scenarios of land-use and energy use that will generate a combined radiative forcing equal to 2.6–8.5 W m^{-2} by 2100.

To calculate habitable range sizes from each model, we used the 10th percentile training presence as the threshold value, above which the species is assumed to be present (Morueta-Holme *et al.* 2010). This cut-off eliminates the most extreme training presence records granting greater confidence in the predicted distributions when some error exists in the data.

To assess the proportion of a species' current range that will be habitable in the future (assuming no dispersal), we focused only on points within a species current range and calculated the change in range size between current and future conditions. Because proportions are bounded by 0 and 1, we normalised residuals and linearised the expected relationship with a logit transformation. We also tested whether our results were robust to a universal dispersal scenario, in which species could occupy locations outside their current ranges with suitable climate conditions. In this case, changes in range size were bounded by 0 (but not 1), so we used a $\log_2$ transformation. For both dispersal scenarios, we regressed change in range size for each species against its habitat affiliation. For each RCP, we used a linear mixed effect model with fixed intercepts and habitat affiliation slopes for each general circulation model, and random intercepts for species.

Even if a local climate regime is favourable for a species, land-use characteristics may make certain areas inhospitable. Therefore, to verify that changes in land-use did not confound our SDMs' predictions, we parameterised a second series of SDMs with the same climate variables as well as five land-use variables extracted from the Land-use Harmonization project (Hurtt *et al.* 2011), and projected into the future varying both climate and land-use, or climate only. See supplement for full details.

RESULTS

Climate niche and colonisation-extinction dynamics in human-dominated landscapes

We estimated occupancy and detection parameters for 307 species of birds across forest reserves, diversified agriculture and intensive agriculture. We found that precipitation niche centre was the only niche property that consistently predicted whether birds are affiliated with agriculture or forest (Figs 1a, b and S3, Table S3). On average, species had higher interannual persistence probabilities in forest (0.88) than in diversified agriculture (0.80) or intensive agriculture (0.68). Yet, species with precipitation niches centred in dry climate zones (944 mm rainfall per year, i.e. two standard deviations below mean) were able to continuously persist in both diversified and intensive agriculture (persistence probabilities of 0.97 and 0.94 respectively) but not forest (persistence probability 0.64). Similarly, while colonisation probabilities were low on average (0.04 for forest, 0.04 for diversified agriculture and 0.02 for intensive agriculture), the most dry-affiliated species were much more likely to colonise unoccupied agricultural sites than forest sites (0.01 for forest, 0.32 for diversified agriculture and 0.11 for intensive agriculture) (Fig. 1c,d). These effects were robust both to the exclusion of migrant birds and to the calculation of niche characteristics from breeding or non-breeding ranges (Fig. S4).

Habitat switching

Individual species predictably changed habitat preferences between regions, more often occupying agricultural sites in wetter regions and forest sites in drier areas (Figs 2 and S5). For example, the Orange-chinned Parakeet shifted from being a strong agriculture affiliate in our wettest region (> 100X more likely to occupy agriculture than forest) to being strongly forest affiliated in the driest region (23X more likely to occupy forest). Of the 52 species observed in all regions, 40% significantly increased their occupancy probabilities in either diversified or intensive agriculture relative to forest as rainfall in a region increased, while none showed the opposing trend.

Biogeography of agriculture affiliation

Agricultural affinities in the wet and dry seasons were highly correlated (diversified agriculture: $R^2 = 0.89$, $P < 0.001$, intensive agriculture: $R^2 = 0.84$, $P < 0.001$), and species responded similarly to diversified and intensive agriculture (dry season: $R^2 = 0.78$, $P < 0.001$, wet season: $R^2 = 0.73$, $P < 0.001$). Yet, species varied extensively in their response to agriculture. The most agriculture-affiliated species was the House Wren (> 100X more likely to occupy agriculture over forest), while the most forest-affiliated was the White-breasted Wood Wren (> 100X more likely to occupy forest over agriculture). In all, 131 species out of 307 (42%) were more likely to occupy agriculture than forest.

Biogeographic analyses of bird ranges confirmed that agriculture-affiliated species in Costa Rica disproportionately came from drier regions of the western hemisphere (Fig. 3a–c). Precipitation and temperature together explained a large portion of the variance in mean agricultural affiliation across the tropics (multiple linear regression: Total $R^2 = 0.69$, $P < 0.001$; Fig. S6). However, precipitation and temperature were correlated ($r = 0.5$), and we found that precipitation was more predictive of mean agriculture affiliation than temperature (Precipitation attributable $R^2 = 0.31$, Temperature attributable $R^2 = 0.06$).

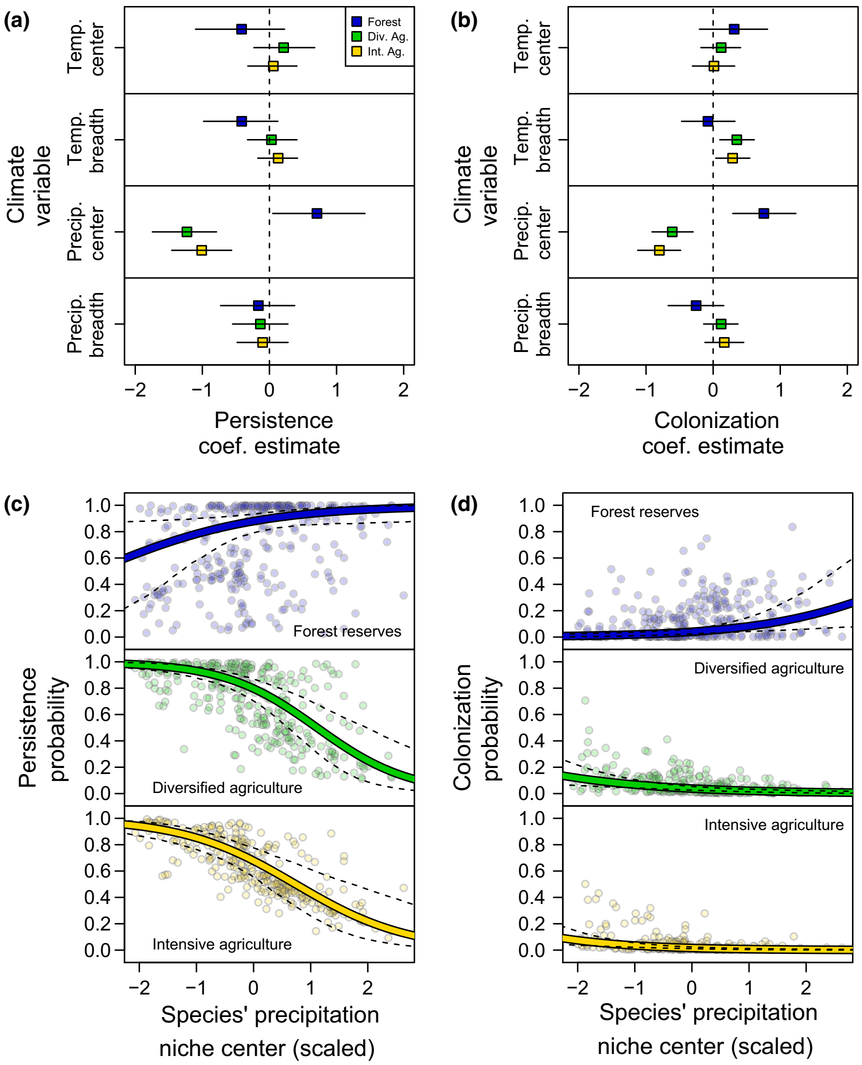

Figure 1 Species from drier regions are more likely to occupy agriculture than forest. (a & b) Summary of parameter estimates for the effects of species' climatological niche characteristics on persistence and colonisation rates in forest (dark blue), diversified agriculture (green) and intensive agriculture (yellow) during the wet season sample. The dry season data are presented in the supplement (Fig. S3). Points depict posterior means, and lines show 95% Bayesian credible intervals. (c & d) Posterior estimates of persistence and colonisation rates for all 307 bird species in each of the three investigated land-uses (averaged across the four study regions) depicting the effect of species' precipitation niche centre. Points represent posterior means for each species, while the best-fit line represents the expectation based on the posterior means of parameters governing how precipitation niche influences persistence and colonisation probabilities, with dashed lines indicating 95% BCIs around these expectations.

Biomes differed significantly in the average agriculture affiliation of their species (ANOVA, $R^2 = 0.62$, $P < 0.001$). We found that dry regions such as the grasslands of Venezuela, southern Brazil, Argentina, and the central United States, the deserts of western North America and Chile, and the scrublands of California and Chile contain species that affiliate strongly with agriculture in Costa Rica (Fig. 3d,e). Across all biomes, scrubland habitats possessed bird faunas that were most likely to be encountered in Costa Rican agriculture – the average scrubland species had an agriculture affiliation score of 3.13, indicating it would be 23X more likely to occupy agriculture over forest. Only tropical forest biomes were enriched for Costa Rican birds that affiliated with forests over agriculture.

Responses to future climate change

Based on future climate projections for the year 2070, we found that agriculture-affiliated species were more robust to global change than forest-affiliated species. For example, under RCP 6.0 and averaging across general circulation models, we found that most forest-affiliated species are expected to lose nearly 60% of their currently habitable ranges by 2070, while the most agricultural species would lose < 30% (linear mixed model, d.f. = 11, $\chi^2 = 163$, Marginal $R^2 = 0.10$, Conditional $R^2 = 0.92$, $P < 0.001$, Fig. 4). This relationship was significant in every climate model and RCP considered. If species disperse freely and colonise areas outside their current ranges, these trends were maintained across most climate

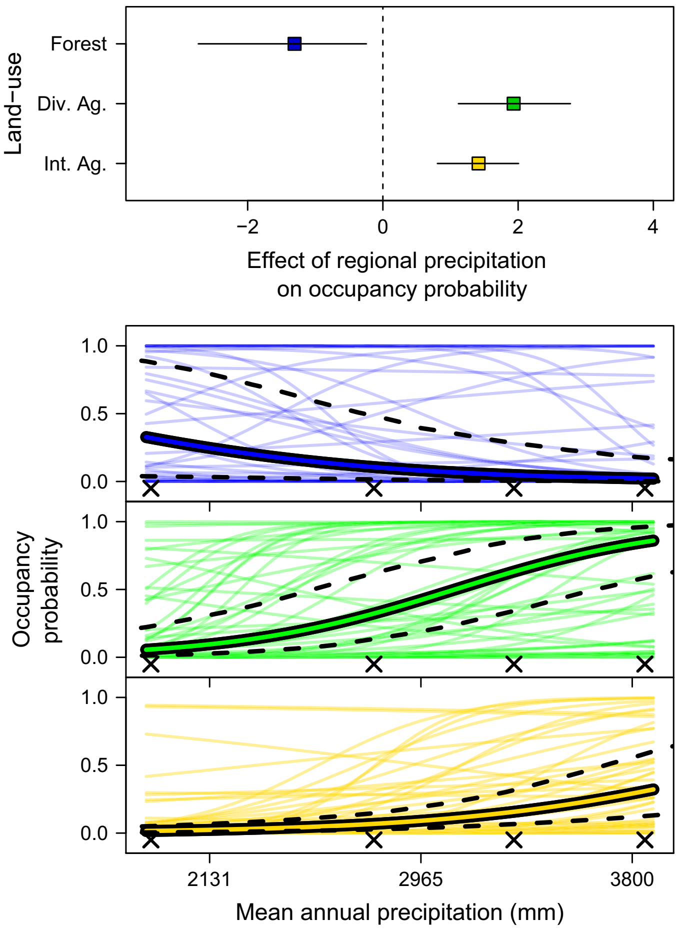

Figure 2 Evidence of habitat switching along a rainfall gradient among the 52 species encountered in all four regions. Top panel depicts the effect of regional rainfall on species' occupancy in each habitat type (posterior mean ± 95% Bayesian credible interval). The bottom panel shows overall occupancy probability across the rainfall gradient. Large lines depict mean effects across species in each habitat (forest = blue, div. ag. = green, int. ag. = yellow), dashed black lines show 95% credible bands, and thin coloured lines show responses of each of the 52 individual species, based on fitted multispecies occupancy model. Figure depicts wet season sample. The dry season data are presented in the supplement (Fig. S5). Rainfall in each of the four regions is indicated by an 'X'.

models and RCPs, though trends weakened in the highest RCP scenarios: variance in species responses to climate change, regardless of habitat affiliation, increased greatly (Fig. S7). When land-use was incorporated in SDMs, agricultural species always fared significantly better than forest species, even when land-use was held constant at current conditions, so projections only reflected climate change's contribution to range size shifts (Figs S7, S8, S9 and S10).

DISCUSSION

Links between climate affiliation and land-use affiliation

We found that birds' climate niches strongly predicted their tolerance to tropical habitat conversion: dry climate-affiliated species were much more likely to persist in and colonise agriculture while wet-climate affiliated species were more likely to persist in and colonise forest. The correlation between climate niche and resilience to land-use change was similar across intensive and diversified agriculture. While these habitats differ in mean occupancy and species richness, past studies have found that both agricultural communities are similar in their level of phylogenetic clustering and, further, that the community occupying intensive agriculture can be viewed as a subsample of the community occupying diversified agriculture (Frishkoff *et al.* 2014).

The correlation between a species' climate niche and its affiliation with agricultural habitats may have arisen via two mechanisms. First, different species may have different fundamental niches, such that the microclimates of agriculture preclude the survival of select species. This is the case for Neotropical amphibians: frog species that are more common in agriculture possess warm-adapted physiologies (Frishkoff *et al.* 2015). *A priori* it also seems possible that hotter temperatures in agriculture might preclude cool-adapted birds, as agricultural fields can be + 10 °C warmer than adjacent forest patches (Fig. S11). However, when controlling for precipitation niche, we did not detect temperature effects (Fig. 1a,b), suggesting that temperature is not a filter for Neotropical birds in agriculture. Similarly, tropical birds' fundamental temperature niches do not appear to control species distributions across elevational gradients (Freeman 2016). Previous analyses that linked species' temperature niches to habitat use in temperate zones (e.g. Clavero *et al.* 2011; Barnagaud *et al.* 2013) did not control for the precipitation niche and are, thus, not directly comparable.

While precipitation niche was correlated with agriculture affiliation, and while agriculture is drier than forest (Fig. S12), it seems unlikely that birds respond directly to increased precipitation or moisture. In some circumstances, bird demography may be under direct climatological control: periods of intense precipitation have been correlated with reduced survival and fecundity, perhaps because heavy rain restricts foraging time (Gullett *et al.* 2014). However, if this mechanism were operating, then birds that can least tolerate heavy rain (dry climate niche species), would likely affiliate most with forest where there is more cover from rainfall. This is the opposite of the pattern that we observed.

Instead, we posit that climate is impacting birds indirectly. Species from drier geographic zones may preferentially occupy agriculture because it resembles the shrubbier vegetation of the drier regions from which they originated (Figs S13 and S14). Rainfall is known to directly control vegetative structure: precipitation is the best predictor of average plant height (Moles *et al.* 2009) and loss of precipitation results in declines in ecosystem-wide plant biomass (Liu *et al.* 2013). In fact, deforestation and loss of rainfall can result in similar signatures in remotely sensed plant biomass data (Liu *et al.* 2013). This link between vegetation structure and rainfall means that, in some sense, by clearing forests, humans are converting a region's ecosystem into a structure more characteristic of drier biomes. This signature subsequently carries over to the bird communities: the mean precipitation niche centre of the average forest community in our dataset is 2196 mm compared to 1899 mm for the average agricultural community.

Vegetation structure may also be behind our observed patterns of decreasing affiliation with forest and increasing affiliation with

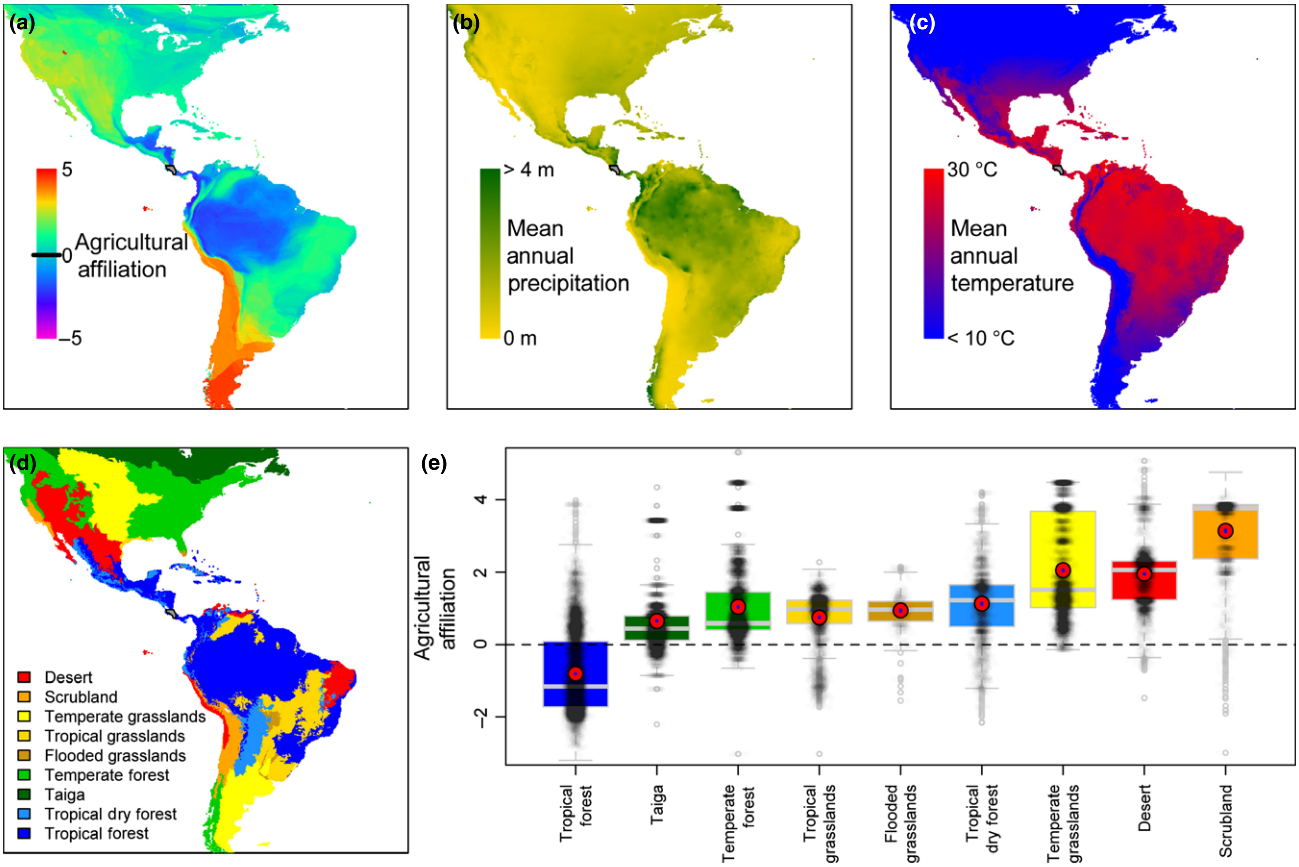

Figure 3 Agricultural birds in Costa Rica tend to be found in drier biomes. (a) Map depicting the average agricultural affinity of Costa Rican species whose ranges overlap with each depicted location on the globe. (b) Annual precipitation correlates strongly with the expected habitat affiliation of the birds, while (c) temperature plays a secondary role. (d) Major biomes across the western hemisphere (see also Fig. S6). (e) Boxplot depicts median and interquartile ranges of average agricultural affiliation in each of the major biomes of the western hemisphere (colours as in d); means are marked by a red points. The dashed line indicates equal affiliation with forest and tropical agriculture. In panel (e), each semi-transparent black point represents a 1/3° × 1/3° grid cell. They have been jittered to better show the distribution of the data. Costa Rica (where the habitat affiliations are generated) is indicated in grey in all maps.

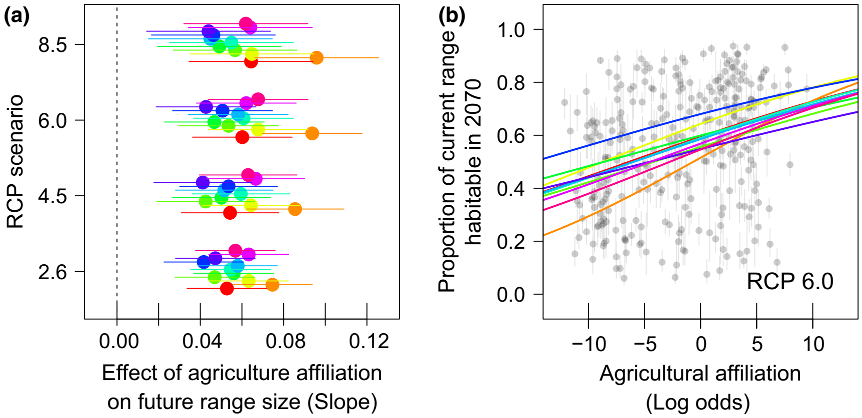

Figure 4 Forest species will, on average, lose more than half their currently habitable range due to climate change, while most agricultural species are more buffered. (a) Estimated effects of agricultural affiliation on the proportion of range still habitable in 2070 for all RCP scenarios (equivalent to slope in panel b). Coloured points show maximum likelihood estimate for each general circulation model, and bars show 95% bootstrap CIs. (b) Example of projected range decline under RCP 6.0. Points represent species mean change in suitable habitat across 11 general circulation models (grey lines indicate standard deviation across circulation models). Coloured lines represent best fit for each circulation model. These figures reflect the assumption of no dispersal beyond species' current range boundaries, and use only climate data to generate species distributions. The supplement contains alternative assumptions regarding universal dispersal, and the effects of land-use on distributions (Figs S7–S10).

agriculture along rainfall gradients for widespread species. Dry forests have much lower canopy heights than tropical wet forests (Fig. S14), and agriculture in dry regions is also typically shorter (e.g. rice or melon) than agriculture practiced in wetter regions (e.g. coffee or banana cultivation).

The connection between the precipitation niche and agriculture affiliation may partially help explain why past studies have found that latitudinal migrants tend to be better at exploiting tropical agriculture (Newbold *et al.* 2013). Migrants spend much of the year in high-latitude biomes, which tend to receive less rainfall and have scrubbier vegetation than that found in the tropics.

Our methods relied on correlative models that correct for imperfect detection to assess links between species' climate niches and their response to agriculture, as well as substitute space for time to understand how habitat affiliations shifts as a region's rainfall declines. While these correlative approaches represent powerful means to elucidate trends, truly understanding direct and indirect links between climate change, land-use change, shifts in vegetation structure and animal responses, requires long-term data sets that track these processes at local scales over multidecadal time scales. Our current dataset spans only 12 years – still too short to robustly infer whether fluctuations in occupancy patterns are due to shifts in climate given the need to account for time lags and temporal autocorrelation. Accumulation of longer term datasets would solidify the mechanistic underpinnings of the patterns we report here.

Biogeography of the Anthropocene

Anthropogenic changes are recasting the biogeographic patterns laid down over millions of years of evolutionary history. Human transport of organisms across the globe has garnered appreciable attention lately for its ability to modify the predictions of island biogeography (Helmus *et al.* 2014) and create new species distributions that reflect climatological constraints rather than dispersal limitation (Capinha *et al.* 2015). Our findings suggest that human land-use also may reshuffle biological communities, breaking down older biome-based biogeographic realms. Through land clearing, the species pool in tropical forest regions appears to be transitioning to include more taxa from higher latitude grassland and scrubland biomes. This suggests that many agriculture-affiliated birds in the tropics are not forest-gap specialists but, instead, may have origins outside of tropical forests altogether. Indeed, previous analyses have shown that forest-gap specialists are unlikely to be found in agriculture (Frishkoff *et al.* 2014). These observations raise the possibility that some taxa currently considered 'native' to tropical forest regions may, in fact, be 'exotic', having been biogeographically restricted to true scrubland and grassland biomes prior to anthropogenic land clearing. Future analyses that employ historical, paleontological, or population genetic data could evaluate this hypothesis.

Responses of Neotropical avifauna to future climate and land-use change

On top of changes in vegetative structure brought about by agriculture, Central America and tropical South America are expected to lose precipitation over the coming century – perhaps by > 20% (Magrin *et al.* 2014). These climate trends are expected to result in loss of tropical forest and the expansion of habitats structurally similar to tropical agriculture, such as savannah (Magrin *et al.* 2014). Our data suggest that species affiliated with tropical agriculture will be the most resilient to such global changes in climate and land use. While the amount of habitable space suitable for strongly forest-affiliated species will decline, agriculture affiliates will, on average, either be capable of occupying the majority of their current ranges if dispersal is limited or expand their ranges if they can disperse to newly habitable areas. Moreover, our data suggest that as habitats dry, species that are today found in agriculture may move into forests and compete with current forest-affiliated species (Fig. 2). These findings highlight the need to preserve tropical forest habitat and to foster connectivity between forest fragments to ensure that forest specialists are able to disperse to newly habitable areas over the next century.

Our specific predictions hinge on the assumption that species are either completely dispersal limited or free to disperse to available habitat without restraint. Most species will fall somewhere between these two extremes. Further, it is probable that agriculture-affiliated species are better dispersers than forest-restricted species, as some strongly forest-affiliated species do not fly outside a closed canopy (Laurance *et al.* 2004). If this is the case, then differences in future range size between forest- and agriculture-affiliated species may be further exacerbated.

CONCLUSION

Research investigating the environmental impacts of land-use change on the biogeographical patterns that have been laid down over millennia is still in its infancy (Helmus *et al.* 2014). Focusing our efforts on local community dynamics may improve our predictive power in the face of future environmental challenges. Here, the predictive capacity of the climate niche revealed a potential synergy between Earth's two greatest environmental challenges – climate change and habitat conversion. Specifically, we found that climate change-induced drying will likely favour agriculture-affiliated species. At large scales, the most important determinant of biodiversity is the degree to which sites differ in their species compositions (Flohre *et al.* 2011). If climate change and habitat conversion do threaten and favour similar species, then global biodiversity may homogenise even more rapidly than previously predicted, truly ushering in the 'Homogocene' (Baiser *et al.* 2012).

ACKNOWLEDGEMENTS

We thank the Organization for Tropical Studies and Los Cusingos Bird Sanctuary for providing logistical support in collecting field data. Support was provided by a Ward Wilson Woods, Jr. Fellowship in Environmental Studies to LOF and a Killam Postdoctoral Fellowship to DSK. Data collection was made possible by donors to the Center for Conservation Biology and grants to GCD from the Heinz, Moore Family, and Winslow foundations and the LuEsther T. Mertz and the Pew Charitable trusts. This work was conducted in collaboration with the FuturAgua Project, funded by the Belmont Forum. Original transect data are available at Dryad (10.5061/dryad.fv921).

AUTHORSHIP

LOF, DSK and LKM designed the study, GCD designed transect data collection, JZ collected the transect data, LOF and LKM performed occupancy model analysis, LOF, DSK and LKM performed biogeographic analysis, JRF generated species distribution models and LOF performed downstream analysis, LOF wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

REFERENCES

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L. & McKinney, M.L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proc. R. Soc. B*, 279, 4772–4777.

Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I. & Archaux, F. (2012). Relating habitat and climatic niches in birds. *PLoS ONE*, 7, e32819.

Barnagaud, J.-Y., Barbaro, L., Hampe, A., Jiguet, F. & Archaux, F. (2013). Species' thermal preferences affect forest bird communities along landscape and local scale habitat gradients. *Ecography (Cop.)*, 36, 1218–1226.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.*, 15, 365–377.

BirdLife International and NatureServe (2012). *Bird Species Distribution Maps of the World*. BirdLife International, Cambridge, UK; NatureServe, Arlington, TX.

Boria, R.A., Olson, L.E., Goodman, S.M. & Anderson, R.P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Modell.*, 275, 73–77.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.*, 23, 453–460.

Capinha, C., Essl, F., Seebens, H., Moser, D. & Pereira, H.M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348, 1248–1251.

Carrillo-Rubio, E., Kéry, M., Morreale, S.J., Sullivan, P.J., Gardner, B., Cooch, E.G. *et al.* (2014). Use of multispecies occupancy models to evaluate the response of bird communities to forest degradation associated with logging. *Conserv. Biol.*, 28, 1034–1044.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.

Clavero, M., Villero, D. & Brotons, L. (2011). Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS ONE*, 6, e18581.

Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G. & Sánchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv. Biol.*, 17, 1814–1826.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proc. Biol. Sci.*, 275, 2743–2748.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.*, 17, 43–57.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R. *et al.* (2011). Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecol. Appl.*, 21, 1772–1781.

Freeman, B.G. (2016). Thermal tolerances to cold do not predict upper elevational limits in New Guinean montane birds. *Divers. Distrib.*, 22, 309–317.

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C. *et al.* (2014). Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science*, 345, 1343–1346.

Frishkoff, L.O., Hadly, E.A. & Daily, G.C. (2015). Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. *Glob. Chang. Biol.*, 21, 3901–3916.

Gullett, P., Evans, K.L., Robinson, R.a. & Hatchwell, B.J. (2014). Climate change and annual survival in a temperate passerine: partitioning seasonal effects and predicting future patterns. *Oikos*, 123, 389–400.

Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.*, 13, 207–251.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.

Hurtt, G.C., Chini, L.P., Frolking, S., Betts, R.a., Feddema, J., Fischer, G. *et al.* (2011). Harmonization of land-use scenarios for the period 1500-2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change.*, 109, 117–161.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.*, 5, e157.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. & Daily, G.C. (2012). Intensive agriculture erodes β-diversity at large scales. *Ecol. Lett.*, 15, 963–970.

Laurance, W.F. & Useche, D.C. (2009). Environmental synergisms and extinctions of tropical species. *Conserv. Biol.*, 23, 1427–1437.

Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. (2004). Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia. *Conserv. Biol.*, 18, 1099–1109.

Lindo, Z., Whiteley, J. & Gonzalez, A. (2012). Traits explain community disassembly and trophic contraction following experimental environmental change. *Glob. Chang. Biol.*, 18, 2448–2457.

Liu, Y.Y., van Dijk, A.I.J.M., McCabe, M.F., Evans, J.P. & de Jeu, R.A.M. (2013). Global vegetation biomass change (1988-2008) and attribution to environmental and human drivers. *Glob. Ecol. Biogeogr.*, 22, 692–705.

Magrin, G.O., Marengo, J.A., Boulanger, J.-P., Buckeridge, M.S., Castellanos, E., Poveda, G. *et al.* (2014). Central and South America. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. and White, L.L., *et al.*). Cambridge University Press, Cambridge, UK; New York, NY, pp. 1499–1566.

Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M.L.T., Lamarque, J.-F. *et al.* (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Clim. Change.*, 109, 213–241.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E. *et al.* (2009). Global patterns in plant height. *J. Ecol.*, 97, 923–932.

Mora, C., Frazier, A.G., Longman, R.J., Dacks, R.S., Walton, M.M., Tong, E.J. *et al.* (2013). The projected timing of climate departure from recent variability. *Nature*, 502, 183–187.

Morueta-Holme, N., Flojgaard, C. & Svenning, J.C. (2010). Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS ONE*, 5(4), e10360. doi:10.1371/journal.pone.0010360

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioglu, Ç.H., Alkemade, R., Booth, H. *et al.* (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B*, 280, 20122131.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

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

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-lammens, M.E., Ersts, P.J., Horning, N. *et al.* (2014). Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Chang.*, 4, 217–221.

Pereira, H.M., Navarro, L.M. & Martins, I.S. (2012). Global biodiversity change: the bad, the good, and the unknown. *Annu. Rev. Environ. Resour.*, 37, 25–50.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.*, 190, 231–259.

Pineda, E., Moreno, C., Escobar, F. & Halffter, G. (2005). Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz. *Mexico. Conserv. Biol.*, 19, 400–410.

Rauscher, S.A., Giorgi, F., Diffenbaugh, N.S. & Seth, A. (2008). Extension and intensification of the Meso-American mid-summer drought in the twenty-first century. *Clim. Dyn.*, 31, 551–571.

Royle, J. & Dorazio, R. (2008). *Hierarchical Modeling and Inference in Ecology. The Analysis of Data from Populations, Metapopulations and Communities*. Academic Press, London.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E. & Evans, T.A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Glob. Chang. Biol.*, 20, 495–503.

Swihart, R.K., Gehring, T.M., Kolozsvary, M.B. & Nupp, T.E. (2003). Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Divers. Distrib.*, 9, 1–18.

Tingley, M.W. & Beissinger, S.R. (2013). Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology*, 94, 598–609.

Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science*, 348, 571–573.

Urbina-Cardona, J.N., Olivares-Perez, M., Reynoso, V.H. & Olivares-Pérez, M. (2006). Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz. *Mexico. Biol. Conserv.*, 132, 61–75.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K. *et al.* (2011). The representative concentration pathways: an overview. *Clim. Change.*, 109, 5–31.

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Editor, Nick Haddad
Manuscript received 13 January 2016
First decision made 10 February 2016
Second decision made 12 May 2016
Manuscript accepted 29 May 2016