



Original research article

Warming threat compounds habitat degradation impacts on a tropical butterfly community in Vietnam



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ABSTRACT

Species are threatened globally by multiple and often synergistic environmental changes including habitat loss, fragmentation and climate change. However, how these changes act in concert is poorly understood, especially in the tropics where the vast majority of biodiversity resides. Here, using a unique dataset covering 10 years of butterfly surveys (2003–2013) at Tam Dao National Park in northern Vietnam, we examined the combined impacts of habitat degradation (following intensive infrastructure development in 2005) and the possible threat of warming (extrapolating upon the relationship between natural climatic variation and community indices) for tropical butterfly communities. We found that both habitat degradation and warmer temperatures led to fewer narrow-range and forest-associated species comprising the sampled communities. Under projected climate change scenarios, the impact of warming was comparable to habitat degradation with respect to community change, and degraded forest communities were projected to shift towards cosmopolitan and non-forest species even more. The tropics have been heavily deforested world-wide and also suffer from heavy impacts of degradation and fragmentation, especially road construction. Warming will compound habitat degradation impacts such that the conservation of tropical biodiversity will require addressing these multiple global changes simultaneously.

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1. Introduction

Climate change is anticipated to have large and significant impacts on biodiversity world-wide (Pacifiçi et al., 2015; Urban, 2015). However, most research on the subject has taken place outside the tropics (Parmesan, 2006; Pacifiçi et al., 2015). Thus despite being home to the majority of global biodiversity, considerable uncertainty persists as to the possible impacts of climate change in the tropics (Bonebrake, 2013). Recent physiological and gradient based models have highlighted possible high vulnerabilities of tropical species to climate change, particularly for ectotherms (Deutsch et al., 2008; Bonebrake and Deutsch, 2012; Corlett, 2012; Araújo et al., 2013; Sunday et al., 2014). Many studies have documented upslope and poleward shifts of species distributions, particularly throughout North America and Europe (Chen et al., 2011; Breed et al., 2013). Yet, empirical evidence for any climate change impacts in the tropics is scant, though a few recent studies have demonstrated strong upward shifts in the elevation of tropical montane species (Chen et al., 2009; Freeman and Freeman, 2014).

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There are innumerable conservation threats to tropical forests aside from climate change, especially habitat loss and degradation, which threaten biodiversity hotspots in tropical regions (Brodie et al., 2012; Laurance et al., 2014a). One of the biggest threats to tropical biodiversity is forest loss and disturbance, especially via agricultural expansion (Gibson et al., 2011; Laurance et al., 2014a). Road building is a major driver of this forest loss and is expected to dramatically increase in extent this century (Laurance et al., 2014b). Roads themselves have large impacts on tropical species and encourage exotic species invasion, increase edge effects, cause vehicle-related mortality and create sources for chemical and nutrient pollution (Laurance et al., 2009).

Multiple additive and interacting threats are projected to have especially strong, non-additive and detrimental impacts on species diversity (Hof et al., 2011; Parmesan et al., 2013). For example, habitat fragmentation has had the most impact in areas of high temperature and precipitation change over the past century (Mantyka-Pringle et al., 2012). Additionally, climate change impacts are projected to be compounded in biomes with low habitat intactness (Eigenbrod et al., 2015). Climate change could also worsen land-use change impacts on bird and mammal species by 20%–40% globally (Mantyka-Pringle et al., 2015). However, how the combined effects of climate change and habitat degradation will affect biodiversity generally, especially in the tropics, remains uncertain. A lack of long-term data in tropical biodiversity-rich communities (Bonebrake et al., 2010; Corlett, 2011) has limited our capacity to understand these critical conservation threats.

Here we take advantage of a unique long-term monitoring programme to examine how a large-scale habitat degradation event and variation in environmental temperatures altered butterfly communities. In the late 1980s and early 1990s, a series of studies conducted on the butterfly fauna of Tam Dao National Park in northern Vietnam showed that many species were confined to forest habitats and that forest habitats tended to harbour a greater proportion of locally distributed, non-cosmopolitan species than open and disturbed habitats (Spitzer et al., 1993, 1997). Elsewhere in the park, butterfly communities were surveyed from 2003 to 2013 along six 700 m transects across forest and open habitats (Vu and Yuan, 2003; Vu et al., 2015). In 2005, development and road construction around the town of Tam Dao disrupted much of the habitat within these transects (Fig. 1). This provided an opportunity to examine the impacts of habitat degradation by comparing butterfly communities pre and post disturbance. Specifically we evaluated the impacts on butterfly communities using the forest association and distribution (locally distributed vs. regionally or globally widespread) species characterizations provided by Spitzer et al. (1993). The results presented here provide an examination of possible cumulative impacts of warming and habitat degradation on a species rich and biodiverse tropical butterfly community.

2. Methods

2.1. Study site and sampling

Butterfly surveys took place in Tam Dao National Park (21.3°N, 105.4°E) (Fig. 1). Six transects of 700 m were set up in multiple habitats which can be classified into forest (three transects: bamboo forest, open road in forest, and secondary forest) and open habitats (three rural transects). The forest sites are a mixture of primary and secondary forest with a history of disturbance (e.g. logging, though protected since 1977 and designated a National Park in 1996) while the rural sites represent a mixture of small croplands and residential properties (Fig. 2; Vu and Yuan, 2003; Vu, 2009). All transects were sampled between 2003 (but the bamboo forest sampling began in 2005) and 2013 though no surveys were conducted 2009–2011. Detailed descriptions of transects are available in Vu (2009) and Vu et al. (2015). Transects were surveyed during the wet season from May to November. However, sampling effort was focused in June (early wet season) and October (late wet season), and all sampled years conducted surveys in each of these months (but in 2004 only a July survey was conducted) with varied effort across years for May, Aug, Sept and Nov (Table A1). Over the course of the study period we conducted 574 surveys across the six transects.

One of the authors (LVV) conducted most of the surveys himself over the 10-year period though trained research assistants have also taken part in surveys. Each survey consists of a walking transect where all individuals within 10 m of the surveyor are identified and recorded across the 700 m transect. Most species could be identified on the wing but netting and photography were necessary for some species (e.g. some Lycaenidae and Hesperidae). Further details on the survey approach are available in Vu et al. (2015).

2.2. Observed changes in community composition

Major development in Tam Dao occurred in 2005 when roads were built and paths paved directly upon or close to the established transects (Vu et al., 2015). Development was not even across all transects—but in general, rural transects experienced paving while forest transects had extensive path widening into roads (Fig. 2). This provided a unique opportunity to compare butterfly communities before the development event (in 2003 and 2004) and after (2005–2013). For the community analysis we pooled survey data for each year and transect and used non-metric multidimensional scaling (NMDS) to ordinate and examine similarities and differences between forest and open habitat communities. However, we kept the bamboo forest distinct given its unique community properties as highlighted in Vu et al. (2015). Using the NMDS we also examined pre and post road building communities. Butterflies not identified to species level were excluded from analysis. The NMDS plot was based on Bray–Curtis similarities.

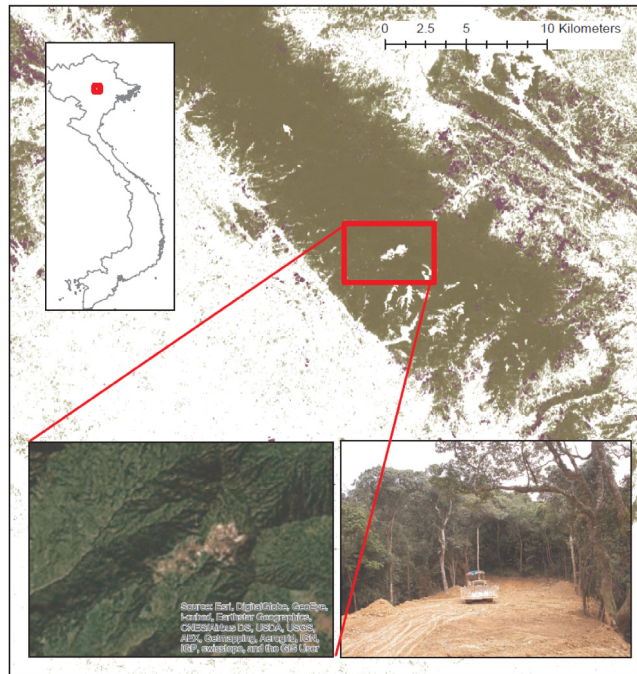


Fig. 1. Map of the study site (Tam Dao) showing forest cover in 2000 (in green) and forest loss from 2000 to 2014 (in purple) (Source: Hansen/UMD/Google/USGS/NASA). Inset photo illustrates the road construction that occurred in the study site in 2005 (Photo by Lien Van Vu). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 2. Photos of the transects post road construction (2012–2013) in both the forest sites (a, b) and in the rural sites (c, d) (Photos by Lien Van Vu).

We used partial redundancy analysis (pRDA) to (1) test if butterfly communities significantly differed across different habitats and pre and post disturbance and (2) remove the effect of sampling effort by including the number times a transect was sampled in the analysis. To further examine the effect of disturbance on butterfly communities in different habitats, we ran pairwise comparisons by building reduced models which included the pre and post disturbed butterfly communities of a specific site and ran the pRDA again. Prior to the pRDA, Hellinger transformation was used on the community data. The NMDS and pRDA were implemented in R using package *vegan* (Oksanen et al., 2015, see Appendix A).

2.3. Relationship between climate and butterfly communities

Transect temperature was not recorded during every survey (we have temperature data for 59% of transects), so to predict temperature we constructed a candidate set of generalized linear models to model known transect temperature against interactions between the maximum temperature in Hanoi (closest available long-term temperature dataset), habitat type (open, closed) and disturbance (pre-disturbed, post-disturbed) with additive impacts of time of day (AM or PM) and weather (clear, cloudy or mixed). We then used the most parsimonious model with lowest AICc (as $\Delta AIC > 2$) to predict transect temperature for each sampling event.

2.4. Model of climate change threat to butterfly communities

To model the impact of temperature and disturbance on community characteristics, across open and forest habitats, we used the distribution and forest association indices developed by Spitzer et al. (1993). Each species was scored on its distribution (1 = northern Indochina, 2 = India and Indochina, 3 = Indo-Malayan region, 4 = Australasian tropics, 5 = throughout the palaotropics, 6 = larger than the paleotropics) and its forest association based on a canonical correspondence analysis conducted on a habitat gradient study (e.g., less than 1 for a ruderal species, and greater than 2 for a forest associated species) by Spitzer et al. (1993). For each sampling event we used scores for all individuals counted to compute an index mean for each assemblage for both forest association and distribution. These assemblage indices were then modelled against interactions between predicted temperature (from the above model), habitat type and disturbance using Gaussian generalized linear models. We checked the residuals of all models to verify that model assumptions were satisfied.

Using the relationship between Hanoi maximum temperature and the transect temperature, we then simulated future temperatures projected out to 2070 (2061–2080 averaged) from three global circulation models (IPSL-CM5A-LR, BCC-CSM1-1, and HadGEM2-AO) and three concentration pathways (RCPs 2.6, 4.5 and 8.5). We used this climate change temperature data (temperature change) and applied it to the Hanoi temperature data in order to predict transect temperatures under future warming conditions. We then used these forecasted warming temperatures and the most parsimonious models (as $\Delta AIC > 2$) to predict the impacts of warming and disturbance on the distribution and forest association of butterfly communities exposed to these pressures over the study duration. In other words, if the transects had been sampled in 2070 (and also experienced a development/disturbance event two years after the initiation of sampling) how might the community responses differ from those observed under the current climate. Our basic approach, modelling species abundance and community changes with respect to climate and using that relationship to project under warming, comes with number of uncertainties including the assumption that current climate-species responses will hold into the future. Despite significant uncertainties associated with this approach, previous studies have demonstrated the utility of these types of methods (e.g. Johnston et al., 2013). All analyses were conducted in R (R Core Team, 2013), and scripts are available in the supplementary material (Appendix A).

3. Results

We observed 28,446 individuals of 300 species over 574 transect samples. Butterfly communities within open habitats pre-disturbance and post-disturbance were similar to one another and to the post-disturbance forest communities; however, pre-disturbance forest communities were substantially different to all other habitats (Fig. 3). The pRDA of the full model demonstrated that the impact of disturbance significantly differed between habitats (Habitat*Disturbance, $F_{1,38} = 2.73$, semi-partial $R^2 = 0.04$, $p = 0.01$; Sampling effort $R^2 = 0.06$). Pairwise comparisons revealed that disturbance significantly affected butterfly species compositions in forest ($F_{1,19} = 5.91$, semi-partial $R^2 = 0.22$, $p = 0.001$; Sampling effort $R^2 = 0.07$) but less significantly in open habitats ($F_{1,13} = 1.63$, semi-partial $R^2 = 0.10$, $p = 0.03$; Sampling effort $R^2 = 0.07$). Furthermore, pre-disturbance communities had the greatest proportion of species that were locally distributed and forest-associated (Fig. 4; Distribution index: Habitat = 0.44 ± 0.05 [standard error], $p < 0.001$, Disturbance = -0.24 ± 0.09 , $p = 0.01$, Disturbance*Habitat = 0.10 ± 0.11 , $p = 0.39$, Forest association index: Habitat = -1.11 ± 0.08 , $p < 0.001$, Disturbance = 1.05 ± 0.16 , $p < 0.001$, Disturbance*Habitat = -0.77 ± 0.20 , $p < 0.001$). The transect temperature at the time of sampling also significantly affected the proportion of locally distributed and forest associated species in addition to habitat (open vs. forest) and disturbance (pre and post road construction) (Table 1; Figure A1).

To further examine abundance of individuals we defined forest associated species as forest association index < 0 and widely distributed species as distribution index > 2.5 and then analysed counts of individuals within these species

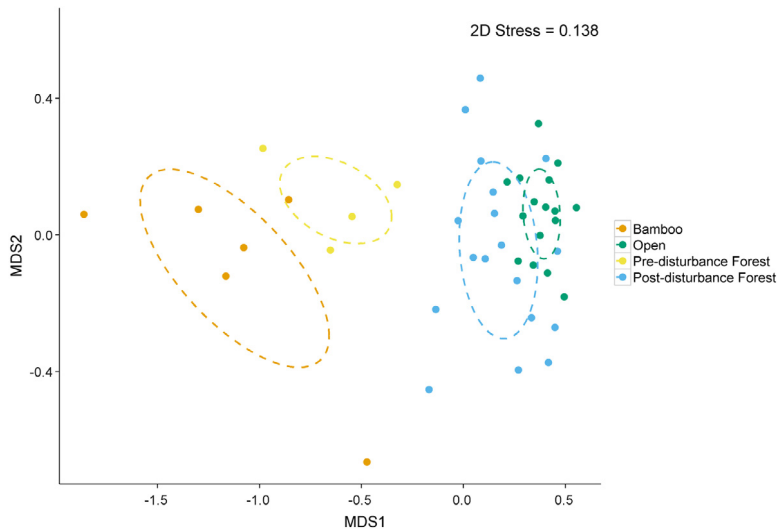


Fig. 3. Community dissimilarity across habitats (open grassland, closed forest and bamboo forest) and before and after the habitat degradation event. Each point represents pooled data by year for each transect. Ellipses represent the standard deviation of the multivariate mean of each group.

Table 1

Results of linear model selections examining the effects of regional temperature (Max temperature in Hanoi), habitat (forest and open), time of day (morning and afternoon) and weather (clear and cloudy) on transect temperature and the effects of temperature, habitat (forest and open) and disturbance (undisturbed and disturbed) on the proportion of species that are locally distributed and forest associated.

Parameters	K	AICc	Delta_AICc	AICcWt	LL
Transect temperature model					
Max * Habitat * Disturb + Time + Weather	14	1403.07	0	0.94	−686.84
Max * Habitat * Disturb + Time	11	1408.65	5.58	0.06	−692.89
Max * Habitat + Time + Weather	10	1421.27	18.19	0	−700.27
Max * Habitat + Time	7	1426.52	23.44	0	−706.08
Max * Habitat * Disturb + Weather	12	1426.79	23.72	0	−700.88
Max * Habitat * Disturb	9	1435.54	32.47	0	−708.48
Max * Habitat + Weather	8	1439.75	36.67	0	−711.64
Max * Habitat	5	1448.08	45.01	0	−718.94
Distribution warming model					
Temp * Habitat * Disturb	9	429.49	0	0.86	−205.45
Temp * Habitat	5	433.12	3.63	0.14	−211.47
Temp * Disturb	5	466.34	36.85	0	−228.07
Temp	3	467.82	38.33	0	−230.87
Forest association model					
Temp * Habitat * Disturb	9	715.43	0	1	−348.42
Temp * Habitat	5	755.03	3.63	0	−372.42
Temp * Disturb	5	863.02	36.85	0	−426.41
Temp	3	873.74	38.33	0	−433.83

classifications. Changes in community composition in response to temperature were in part the result of abundance changes of forest-associated and locally distributed species. Forest associated species declined under warmer conditions in both pre-disturbance and post-disturbance transects (Temp = -0.58 ± 0.20 , $p = 0.004$, Disturbance = 0.75 ± 1.37 , $p = 0.59$). The number of individuals of widely distributed species also increased with increasing temperatures in both pre-disturbance and post-disturbance transects (Temp = 1.12 ± 0.47 , $p = 0.02$, Disturbance = -4.20 ± 2.90 , $p = 0.15$).

We found that local habitat temperatures could be reasonably approximated using a model of regional weather maximum temperatures (from Hanoi) if accounting for habitat type and disturbance (Table 1; $R^2 = 0.38$, $p < 0.001$). Using this relationship and the linear model of temperature effects on proportion of locally distributed and forest associated species (Table 1), we modelled the impact of climate change on the butterfly communities by simulating warming under three models (IPSL-CM5A-LR, BCC-CSM1-1, and HadGEM2-AO) and three representative concentration pathways (RCPs 2.6, 4.5 and 8.5) for the entire ten year dataset. Warming is projected to decrease the proportion of locally distributed species in forest habitats and the impact is greatest in undisturbed forest (Fig. 5). Forest associated species are also projected to decline under warming though not in disturbed open habitats where few of these species live anyway (Fig. 6). These trends were generally consistent across the three GCMs and RCPs (supplementary material).

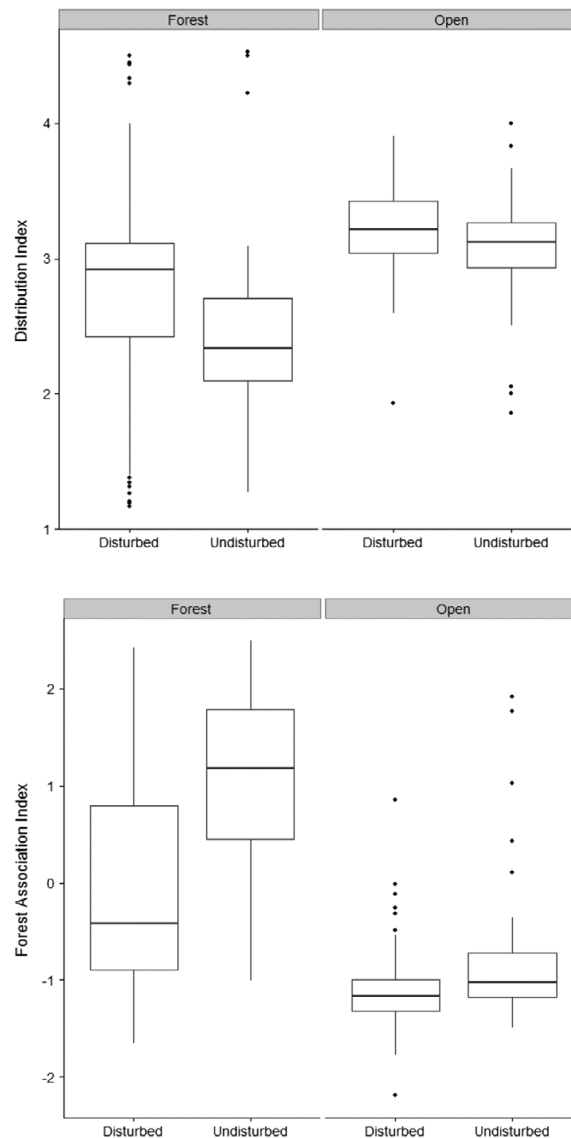


Fig. 4. Boxplots of butterfly communities surveyed pre-road construction (Undisturbed) and post-road construction (Disturbed) in forest and open habitats. Impacts of the disturbance event on the distribution index (top) where higher numbers indicate communities with more individuals of broad distributions and impacts on the forest association index (bottom) where higher numbers indicate communities with more individuals that are forest associated.

4. Discussion

Endemic species tend to be at greater risk of extinction under climate change than widely distributed species (Urban, 2015). Endemic and locally distributed species are also more heavily impacted by habitat loss and fragmentation than widespread species, which can displace endemic species (Thomas, 1991; Waltert et al., 2011). Our results suggest that warming could have detrimental impacts on communities by favouring generalist cosmopolitan (widely distributed) species. In combination, warming and habitat disturbance will interact to further the biotic homogenization of ecosystems occurring worldwide that comes from generalist species replacing specialists (Clavel et al., 2010; Frishkoff et al., 2016).

We observed significant changes in community composition and characteristics of the butterfly communities following road construction. Consistent with other studies on temperate butterfly communities (Börschig et al., 2013; Eskildsen et al., 2015), ecological specialists with respect to habitat (forest associated species) and geography (narrow distributions) (Spitzer et al., 1993) were replaced by generalists following increased land use intensity. Interestingly, the establishment of cosmopolitan species following disturbance and edge effects can at times increase butterfly diversity in some systems (Bonebrake et al., 2010). Yet, this often comes at the loss of ecologically sensitive species, e.g. forest species (Leidner et al., 2010). From a landscape scale, obvious large scale land use change did not occur within our study site (Fig. 1). However, the

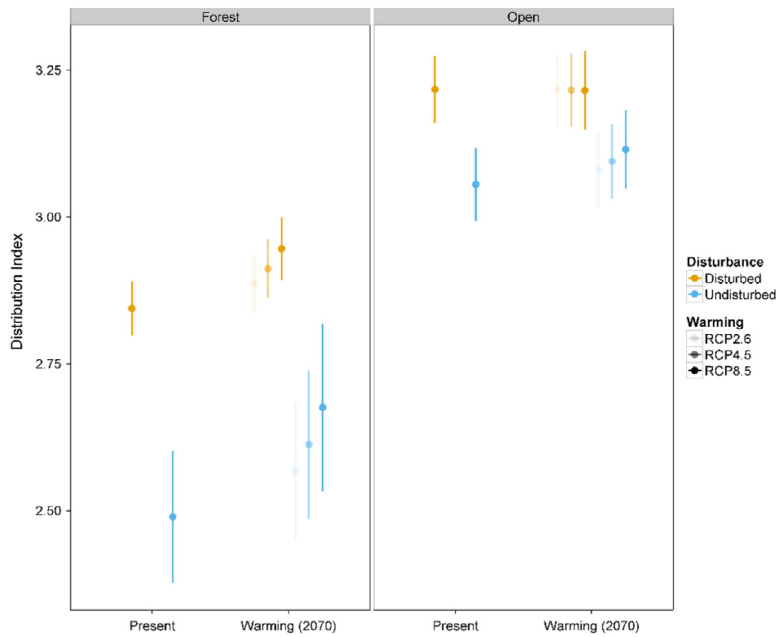


Fig. 5. Disturbance in the form of road building results in a higher proportion of cosmopolitan species, especially in forest habitats. Warming (IPSL-CM5A-LR) was projected to also lead to greater proportions of cosmopolitan species. Error bars indicate standard errors of model predictions (Table 1).

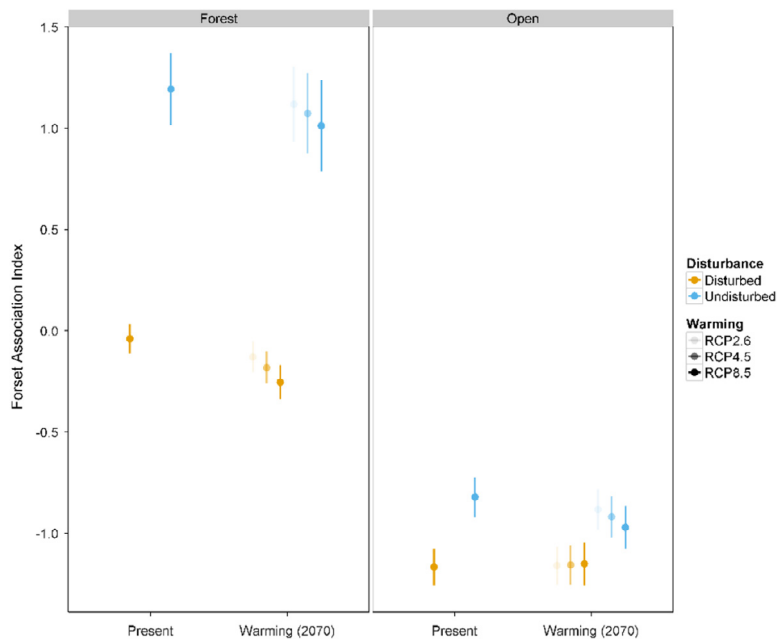


Fig. 6. The proportion of forest associated species reduced substantially when forest habitat was disturbed through road building. Warming (IPSL-CM5A-LR) was also projected to also decrease the proportion of forest associated species. Error bars indicate standard errors of model predictions (Table 1).

disturbance event of the road construction and the local impacts on the local butterfly community are clear in the results, emphasizing the importance of understanding habitat degradation and road impacts on biodiversity in the tropics (Laurance et al., 2009).

In addition to this disturbance event, we found that temperature caused significant community alterations in both pre- and post-disturbance environments. Consistent with this observation, we also found declines in abundance of forest-associated species and narrowly distributed species with increasing temperatures. These results are also consistent with previous studies showing that specialist species respond more strongly to warming than generalists (Warren et al., 2001;

Gough et al., 2015). However, additional life history traits beyond geographic distribution not examined in this study are likely contributing to warming vulnerability (Menéndez et al., 2007; Heikkinen et al., 2010).

A lack of long-term studies in tropical insect and butterfly conservation has caused significant difficulties in evaluating possible habitat loss and climate change threats to these diverse communities (Bonebrake et al., 2010; Basset et al., 2015). This study demonstrates the utility of pursuing such long-term monitoring programmes. However, the butterfly walking transects employed here do have some limitations including an emphasis on butterfly activity (rather than abundance per se), transect visibility, understory species (rather than canopy), and conspicuous species (Basset et al., 2013). In this case, though we have shown how communities vary in response to environmental variation, we lack a mechanistic understanding of why species respond differentially to warming (and habitat degradation) or if extinction is playing any role in the community changes (Cahill et al., 2013). For example, it is possible that lower abundance of endemic species on high temperature days could simply be a consequence of inactivity—yet, even in under such circumstances detrimental consequences of the warmer temperatures (e.g. missed foraging or reproduction opportunities) are likely (Bonebrake et al., 2014).

Precipitation and changes in precipitation are also known to be important in understanding the interactions between habitat loss and climate change impacts on biodiversity (Mantyka-Pringle et al., 2012; Roland and Matter, 2013). For example, Cleary and Mooers (2006) found that, relative to cosmopolitan species, endemic and locally restricted butterfly species declined in response to logging and to fires induced by an El Niño Southern Oscillation event in Borneo. Rainfall changes and other disturbances (e.g. fire) are therefore likely to have additional primary and significant impacts on tropical communities in addition to warming and habitat loss (Bonebrake and Mastrandrea, 2010; Wilcove et al., 2013).

Synergistic consequences of climate change and habitat loss should be a focus of future research efforts. For example, habitat degradation, and road construction specifically, will affect forest species communities both directly and indirectly. Infrastructure development can cause big changes in forest structure, fire frequency and microclimate, all of which can result in changes to ecological communities (Laurance et al., 2009). That warmer conditions – apart from disturbance – cause reductions in forest area and endemic species demonstrates that both warming itself and any warming resulting from habitat degradation (in addition to more direct changes in forest structure) will cumulatively impact forest ecology. Land use changes generally alter local climates which interact with large scale climate change and can result in complex biological responses (Diamond et al., 2014). For example, Daily and Ehrlich (1996) found that butterflies were more adversely impacted by forest fragmentation than moths, quite likely due to greater climatic barriers in daytime hours vs. nighttime hours (higher temperatures and solar radiation impacts) in a tropical landscape.

Though recent studies have impressed upon the importance of habitat degradation and climate change interactions causing biodiversity changes (Mantyka-Pringle et al., 2012; Segan et al., 2016) a lack of empirically collected data has limited our understanding of these impacts, especially in the tropics. Our study emphasizes the negative impacts of habitat degradation for tropical species and demonstrates how warming could compound the threat and exacerbate declines of sensitive forest endemic species. Conservation efforts must then seriously consider the multitude of environmental changes transforming tropical ecosystems to achieve outcomes of effective protection of the world's biodiversity.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.09.003>.

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