LETTER

Thermal biology mediates responses of amphibians and reptiles to habitat modification

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Abstract

Human activities often replace native forests with warmer, modified habitats that represent novel thermal environments for biodiversity. Reducing biodiversity loss hinges upon identifying which species are most sensitive to the environmental conditions that result from habitat modification. Drawing on case studies and a meta-analysis, we examined whether observed and modelled thermal traits, including heat tolerances, variation in body temperatures, and evaporative water loss, explained variation in sensitivity of ectotherms to habitat modification. Low heat tolerances of lizards and amphibians and high evaporative water loss of amphibians were associated with increased sensitivity to habitat modification, often explaining more variation than non-thermal traits. Heat tolerances alone explained 24–66% (mean = 38%) of the variation in species responses, and these trends were largely consistent across geographic locations and spatial scales. As habitat modification alters local microclimates, the thermal biology of species will likely play a key role in the reassembly of terrestrial communities.

Keywords

Agriculture, biodiversity, CT_{max}, ectotherm, fragmentation, global change, habitat loss, microclimate, phylogenetic signal, species traits.

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INTRODUCTION

Temperature drives much of the biology and ecology of ectotherms, including foraging, growth and reproduction (Huey & Stevenson 1979; Navas *et al.* 2016). Consequently, species-specific thermal biology is also expected to mediate the responses of ectotherms to major drivers of biodiversity loss, such as climate warming and pathogenic infection (Deutsch *et al.* 2008; Kearney *et al.* 2009; Huey *et al.* 2012; Catenazzi *et al.* 2014; Sunday *et al.* 2014; Nowakowski *et al.* 2016, 2017a). The most immediate threat to biodiversity, however, is anthropogenic habitat modification, which is causing declines of many species and altering the composition of assemblages worldwide (Gardner *et al.* 2007a; Newbold *et al.* 2014, 2016; Thompson *et al.* 2016). The filtering of ectotherm assemblages in response to habitat modification (i.e. environment by trait sorting) may depend, in part, on the ability of species to tolerate novel temperature regimes in altered habitats. By viewing the effects of habitat modification through the lens of thermal biology, biologists may better predict which species will thrive, persist or decline in the face of ongoing conversion of natural habitats (Tuff *et al.* 2016).

Despite extensive literature focused separately on thermal biology and the myriad effects of habitat modification, the integration of these two lines of research is largely nascent

(Frishkoff *et al.* 2015; Tuff *et al.* 2016; Nowakowski *et al.* 2017a). Recent work, however, shows that species that frequently occur in warm, dry climates throughout their geographic range tend to be those that persist or thrive locally in areas of human land use (Frishkoff *et al.* 2015, 2016). Microhabitat selection and macrohabitat affiliations have also been correlated with thermal tolerances; species with high heat tolerances were affiliated with open microhabitats (Brusch *et al.* 2016) and warm natural habitat types (Duarte *et al.* 2012). Thermoregulation in warm habitats is coupled with evaporative water loss (Tracy 1976; Tracy *et al.* 2013), and habitat-specific rates of water loss have been associated with survival and dispersal limitation in altered landscapes (Nowakowski *et al.* 2013, 2015; Watling & Braga 2015). Collectively, these studies suggest a potentially integral role of thermal biology in shaping species responses to habitat modification.

Anthropogenic habitat modification can substantially alter local microclimates, often by reducing canopy cover and the availability of microclimates favourable to species physiology and population persistence. At landscape scales, large differences in vegetation structure among land-cover types can result in maximum daily air temperatures that differ by as much as 10 °C between adjacent habitats (Todd & Andrews 2008; Robinson *et al.* 2013). At local scales, microhabitats within different land-cover types, such as leaf litter and

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phytotelmata, can act as thermal refugia by buffering nocturnal and diurnal ectotherms against extreme daytime temperatures (Scheffers *et al.* 2014). However, buffering microhabitats may be scarce in altered habitats, and the maximum daily temperatures of these microhabitats increase with decreasing canopy cover (Pringle *et al.* 2003), affecting daytime exposure for many diurnal and nocturnal species alike (Nowakowski *et al.* 2017a). For terrestrial ectotherms, like amphibians and reptiles, land-cover change alters the amount and distribution of thermally suitable habitat, with high local temperatures rendering some land-cover types uninhabitable for some species (Rittenhouse *et al.* 2008; Frishkoff *et al.* 2015; Nowakowski *et al.* 2015, 2017a).

Species-specific thermal biology may determine, in part, which ectotherm species persist or decline in altered habitats.

Here, we examine hypotheses describing the relationships between multiple measures of thermal biology and the sensitivity of ectotherm species to habitat modification ('habitat modification' refers here to two separate processes, fragmentation of once-continuous forest and conversion of natural forest to non-forest land uses). First, it is intuitive to expect that warm-adapted species with high heat tolerances will be less sensitive to high temperatures in altered habitats than cool-adapted species with lower heat tolerances (Fig. 1a–c). Second, species sensitivity to habitat modification may also be negatively associated with their thermal safety margins (TSM), defined here as the difference between a species' critical thermal maximum (CT_{max}) and maximum body temperature estimated using a biophysical model (Sinclair *et al.* 2016). Thermal safety margin is a measure of the interaction between
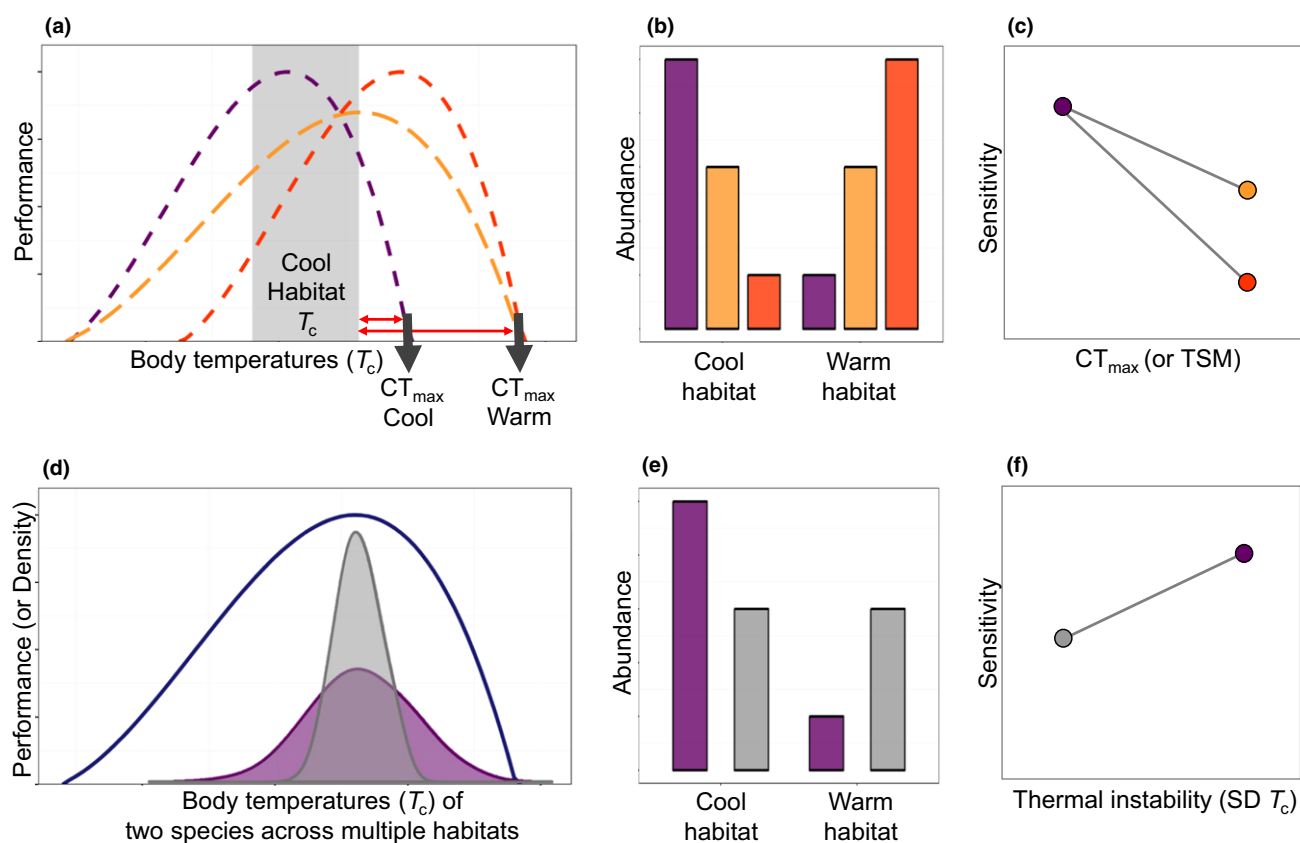

Figure 1 (a–c) The predicted relationships between species-specific critical thermal maxima (CT_{max}) or thermal safety margins (TSM) and species sensitivity to habitat modification. (a) Hypothetical thermal performance curves (e.g. for locomotion) and CT_{max} (black vertical arrows) for a low-temperature specialist (purple), a generalist (orange) and a high-temperature specialist species (dark orange). The TSM for each species is the difference between maximum core body temperature (T_c; hypothetical range of T_c in cool, unmodified habitat illustrated by shaded area) and CT_{max} (illustrated by horizontal red arrows). (b) Expected abundance patterns for cool- (purple) and warm-adapted species (orange, dark orange) in cool (e.g. forested) and warm (e.g. cleared) habitats. (c) Sensitivity to habitat modification (*y*-axis) is quantified here as the ratio of a species' abundance in cool, natural habitats to abundance in warm, altered habitats (e.g. the ratio of abundances in panel b). In this example, we expect species sensitivity to habitat modification to decrease with increasing CT_{max} or TSM, regardless of the exact shape and breadth of the associated performance curve; however, the shape and breadth of performance curves could affect the slope of this relationship. High sensitivity indicates that a species reaches its highest abundances in cool, natural habitats, moderate values indicate similar abundances across habitats and low sensitivity indicates highest abundances in warm, altered habitats. (d) Two hypothetical species that differ in thermal instability, one with highly variable T_c (purple density distribution) and one with stable T_c (grey distribution), in relation to their thermal performance curve (blue line). We define thermal instability as variation in body temperatures across habitats. (e) Species with highly labile body temperatures under a range of habitats/microclimates (purple) are expected to be more sensitive to habitat modification because they are more likely to experience thermal stress in warm habitats than species that can maintain relatively stable body temperatures across habitats (grey). (f) The predicted relationship between species-specific thermal instability and sensitivity to habitat modification.

tolerance and exposure to high temperatures, while accounting for the ability of ectotherms to lower body temperatures through microhabitat selection and evaporative cooling. Thermal safety margins have been used to predict variation in species' vulnerability to climate warming (Sunday *et al*. 2014; Gunderson & Stillman 2015) and may provide a useful metric for modelling vulnerability to novel thermal environments that result from habitat modification. Third, we expect that sensitivity to habitat modification will be positively associated with intraspecific variation in body temperatures across different microclimates (Fig. 1d–f). Differences between body temperatures and environmental temperatures experienced by ectotherms arise from species-specific behaviour, physiology and morphology (e.g. body size; Tracy *et al*. 2010), and the inability of some species to maintain body temperatures near thermal optima across different microclimates may increase their sensitivity to thermal gradients resulting from habitat modification. Finally, we predict that sensitivity to habitat modification will be positively associated with species-specific rates of water loss (as a proportion of body mass) because organisms in warm, dry habitats are challenged with regulating body temperature through behaviour and evaporative cooling while also maintaining water balance (Porter *et al*. 1973; Tracy 1976).

We examine general support for these hypotheses for amphibians and reptiles by drawing on multiple case studies from Costa Rica and Colombia and by synthesising data from the literature. The case studies show interspecific responses to habitat modification in two tropical landscapes where habitat modification is the most pervasive threat to diverse assemblages, and the literature data set illustrates the generality of responses across a broad range of environmental contexts. We examine the relative importance of each thermal variable described above, contrast thermal traits with non-thermal traits (e.g. clutch size and microhabitat use) and draw our inferences from the level of concordance of patterns across systems and spatial scales (i.e. local case studies and meta-analysis).

MATERIALS AND METHODS

Field surveys

We compiled four data sets consisting of records from standardised field surveys of amphibians (frogs and salamanders) and reptiles (lizards). We used the first data set to estimate sensitivity of amphibians to forest fragmentation in the Caribbean lowlands of Costa Rica (see Supporting Information for detailed methods). From 2009 to 2012, we sampled amphibians along transects at six sites within *c*. 1500 ha private preserve and in 17 nearby forest fragments, resulting in 3488 observations of 39 species. We used the remaining three data sets to estimate amphibian and reptile sensitivity to habitat conversion (i.e. conversion of forest to non-forest land uses). In 2011, we sampled transects in 10 forest remnants and in paired areas of converted habitats (five sites in pastures and five sites in heart-of-palm plantations) in the Caribbean lowlands of Costa Rica, resulting in 482 observations of 25 amphibian species and 173 observations of 12 lizard species (see Kurz *et al*. 2014 for full description of

methods). In May and June of 2015 and 2016, we used multiple methods to survey amphibians and reptiles in eight forest remnants and adjacent pastures in the Magdalena River Valley in Colombia, resulting in 138 observations of 19 species (see Supporting Information for detailed methods). Finally, we searched the literature for studies reporting amphibian abundances in natural habitats and adjacent converted habitats from standardised field surveys, resulting in 6016 observations of 32 species from 21 studies for this analysis (see Nowakowski *et al*. 2017b and Supporting Information for detailed methods).

Thermal traits

In Costa Rica, we measured CT_{max} of 26 amphibian and lizard species by placing individuals in water baths and slowly increasing water temperature at a rate of *c*. 0.5 °C per min. At 1-min intervals, we elicited a righting response and recorded the temperature at which individuals lost their righting reflex for ≥ 5 s (Navas *et al*. 2007; Catenazzi *et al*. 2014). We captured all individuals within the forest preserve and maintained individuals in an ambient-air laboratory in the preserve prior to assays; therefore, all individuals were exposed to similar habitat conditions and were already acclimated to similar thermal regimes (Brusch *et al*. 2016; Nowakowski *et al*. 2017a). We used a similar approach to measure CT_{max} of 19 amphibian and lizard species in Colombia, but increased water temperature at a rate of 1 °C per min. Our estimates of CT_{max} in Costa Rica and Colombia, therefore, may not be directly comparable because of differences in rates of warming. Finally, we cross-referenced species abundance records from the literature with CT_{max} estimates compiled in Sunday *et al*. (2014). We also added CT_{max} estimates to the database by conducting our own literature search and by matching our CT_{max} estimates described above with published abundance estimates to maximise the number of species retained in the literature data set. For all data sets, we calculated mean CT_{max} for each species.

We used the biophysical model NicheMapper to estimate core body temperatures (T_c) and rates of water loss for species, while accounting for their potential to alter T_c via behavioural thermoregulation and evaporative cooling (Porter & Mitchell 2006; Bartelt *et al*. 2010). Our estimates of T_c and water loss integrated data on local microclimates and species-specific behaviour, physiology and physical characteristics. NicheMapper combines a microclimate model with an ectotherm model that iteratively solves a heat–mass balance equation to estimate core body temperatures of frog- and lizard-shaped ectotherms (Porter & Mitchell 2006; Bartelt *et al*. 2010). The model has been used in previous studies to examine the importance of thermoregulation to species' sensitivity to climate change (Kearney *et al*. 2009; Sunday *et al*. 2014) and performs well when T_c estimates have been validated with data from physical models and observed body temperatures (Kearney *et al*. 2009; Bartelt *et al*. 2010; Nowakowski *et al*. 2017a). We also validated estimates of water loss, here, for 13 species in Costa Rica using a flow chamber; estimates from the model closely predicted variation among species in the observed rates of water loss ($R^2 = 0.93$;

Fig. S1). As inputs for the ectotherm model, we specified species-specific mass, maximum voluntary temperatures (assumed to be a function of CT_{max}), wet or dry skin for amphibians and lizards (respectively), activity period, climbing behaviour and burrow use based on available natural history information and our own field observations. We used default values for other parameters. As inputs for the microclimate model, we extracted air temperature and relative humidity for each site at 0.5 m from the ground under a range of shade conditions (0, 25, 50, 75, 100%) from the microclim data set (Kearney *et al.* 2014). We used T_c estimates to calculate TSMs and thermal instability (SD of max T_c across habitats) for downstream analyses. We used estimates of the maximum rate of evaporative water loss (g h^{-1}) in downstream analyses, transforming the rate to a percentage of each species' body mass. We obtained information on other species traits, including body size, clutch size and larval and adult microhabitat use, from natural history accounts and primary literature (Supporting Information).

Sensitivity to habitat modification and statistical analyses

We analysed data sets separately because of disparate sampling methodologies and to evaluate the level of agreement across systems. To evaluate relative importance of predictors of species sensitivity to habitat modification, we conducted two sets of analyses using different measures of sensitivity. First, we fit generalised least squares (GLS; for local data sets) or linear mixed effects model (LMM; for literature data set) that allowed for flexibility in evaluating residual correlations structures, estimating goodness of fit (R^2) and partitioning variance. Consistent with the literature on comparative species analyses (i.e. species are the unit of observation; Purvis 2008; Murray *et al.* 2014), we summarised field observations here by calculating species-specific indices of sensitivity to habitat modification. We estimated sensitivity to forest fragmentation for each species using the residuals from a linear regression with species abundances in continuous forest as the dependent variable and abundances in forest fragments as the independent variable (e.g. Bell & Donnelly 2006). This relationship was positive and linear (Fig. S2; $R^2 = 0.55$), and deviations from predicted values provided a continuous index of relative sensitivity to fragmentation that simultaneously accounts for the differences in sampling effort between continuous and fragmented forest in this data set. Positive residuals indicated species that were more abundant in continuous forest than predicted by the regression model, and those species were interpreted as being sensitive to fragmentation, whereas species with negative residuals were more abundant in forest fragments than predicted and were considered relatively tolerant of fragmentation. To estimate sensitivity to habitat conversion, where sampling effort was standardised between habitats, we calculated response ratios of a species abundance in forest to its abundance in nearby converted habitats. Response ratios were calculated as $\ln([N_n + 1]/[N_c + 1])$, where N_n was abundance in natural habitat and N_c was abundance in converted habitats (Nowakowski *et al.* 2017b). Again, positive values indicated species that were sensitive to habitat conversion, negative values indicated species that were

tolerant of or favoured converted habitats and values near zero indicated species that were similarly abundant in forest and converted habitats (i.e. generalists).

For local field data sets (Costa Rica and Colombia), we evaluated relationships between species traits and sensitivity to habitat modification using GLS and phylogenetic GLS (PGLS) models. We first assessed multicollinearity of trait data (Figs S3–S8) and dropped variables for which variance inflation factors (VIFs) were > 4 (VIFs for remaining variables were ≤ 3.06) while retaining thermal traits in analyses when possible (Table S1). We also graphically examined stability of parameter estimates for remaining variables across models. Next, we fit full GLS and PGLS models with all predictors and compared multiple phylogenetic correlations structures using AIC_c (Table S2). We obtained branch lengths from two time-calibrated phylogenies, one composed of 2871 extant amphibian species (Pyron & Wiens 2011) and the other containing 9755 squamate reptiles (Tonini *et al.* 2016). We added six species from across our data sets that were missing from the amphibian phylogeny by randomly attaching branches along the subtree representing the genus of a given species. We generated competing phylogenetic correlation structures using the corStruct function in package 'ape' (Paradis *et al.* 2004). To evaluate single-variable importance, we fit all-subsets of the full model and calculated the sum of Akaike weights across all models containing each variable. To formally compare competing models, we fit a full model, a model with all thermal variables (CT_{max}, thermal instability and water loss), a model with 'non-thermal' traits (body size, clutch size, larval habitat and adult microhabitat), each single variable model and a null model; we evaluated fit of competing models using AIC_c.

For analyses of the literature data set, we fit sets of LMMs and PGLS models. We fit global LMMs with varying intercepts for source studies reporting abundance data and for studies reporting CT_{max} (thereby controlling for differences in experimental protocols) together in the same model and each separately and compared competing structures using AIC_c. We also fit PGLS models with different phylogenetic correlation structures and assessed relative variable importance from all subsets of the best supported full model as described above. For all data sets, we performed variance partitioning using the varPart function in package modEVA. Also, we assessed phylogenetic signal of residuals from the full and single-variable models using the corPagel structure implemented in package 'ape' for all data sets. Because model residuals may not exhibit phylogenetic signal even when constituent variables do (Revell 2010), we also assessed phylogenetic signal of individual variables using the phylosig function in package 'phytools' (Revell 2012).

As a second analytical approach and means of validation, we fit generalised linear mixed models (GLMMs) with binomial errors to analyse individual-level observations from field surveys, thereby using the full number of field observations in each data set and increasing statistical power. For analyses of sensitivity to habitat conversion, individuals observed in forest were coded as 0 and those observed in converted habitats were coded as 1 (e.g. Frishkoff *et al.* 2015). Sensitivity in this set of analyses was calculated as 1-probability of occurring in

converted habitats. We fit all models with a random intercept for species. We analysed sensitivity to fragmentation in Costa Rica using GLMMs as above; however, to account for unequal sampling effort between forest fragments and continuous forest sites, we standardised species abundances by total transect area searched in each habitat type and then fit aggregated binomial models (Supporting Information; McElreath 2016). For the literature data set, we also fit aggregated binomial GLMMs because data consisted of total number of observations in each habitat type (as opposed to sample-level data), and we evaluated models fit with additional random intercepts for the CT_{max} source study and the field survey source study. We report models fit with random effects of species and CT_{max} source study below. We calculated relative variable importance and evaluated competing models using AIC_c as described above. All GLMMs were fit using the glmer function in package lme4 in R (Bates et al. 2014; version 3.4.1, R Core Team 2017).

RESULTS

Across all data sets, we found a negative association between species' CT_{max} and their sensitivity to habitat modification (Figs 2 and S9). Results of GLS and GLMM analyses were qualitatively similar, indicating that results were robust to the specific modelling approach and sensitivity index used. We present GLMM results in Table 1 and Fig. 2 (where sensitivity is plotted as 1-probability of occurring in modified habitats). The GLMMs fit with only CT_{max} predicted a 1.7- to 115-fold (mean = 22) increase in the odds of occurring in modified habitat with each standard deviation increase in CT_{max} [responses to: habitat conversion in published literature ($\beta = 1.44$, SE = 0.48, $P = 0.007$); fragmentation in Costa Rica ($\beta = 0.57$, SE = 0.25, $P = 0.018$); habitat conversion in Costa Rica – amphibians ($\beta = 0.67$, SE = 0.56, $P = 0.239$) and lizards ($\beta = 0.94$, SE = 0.76, $P = 0.211$); habitat conversion in Colombia – amphibians ($\beta = 4.75$, SE = 2.31, $P = 0.006$) and lizards ($\beta = 1.80$, SE = 1.04, $P = 0.010$)].

Results of GLS analyses (Figs S9 and S10; Table S3) showed that CT_{max} alone explained 24–66% (mean = 38%) of the variation in sensitivity to habitat modification [responses to: habitat conversion in published literature (R^2 marginal = 0.24, R^2 conditional = 0.36, $\beta = -1.04$, SE = 0.35, $P = 0.003$); fragmentation in Costa Rica ($R^2 = 0.50$, $\beta = -0.69$, SE = 0.17, $P < 0.001$); habitat conversion in Costa Rica – amphibians ($R^2 = 0.24$, $\beta = -0.60$, SE = 0.30, $P = 0.061$) and lizards ($R^2 = 0.32$, $\beta = -0.78$, SE = 0.51, $P = 0.187$); habitat conversion in Colombia – amphibians ($R^2 = 0.32$, $\beta = -0.91$, SE = 0.44, $P = 0.067$) and lizards ($R^2 = 0.66$, $\beta = -0.89$, SE = 0.26, $P = 0.014$)]. We found weak or no phylogenetic signal in model residuals (for models fit with corPagel, λ was ≤ 0.20 for the literature data set and < 0.0 for all local data sets). We present the best-fitting models that were uncorrected for phylogeny (Revell 2010; models with and without phylogenetic correlation structures are presented in Tables S4–S9). We did not include CT_{max} and TSM in the same analyses because CT_{max} was used to calculate TSM, and consequently, these metrics were highly correlated. In analyses where TSM was substituted for CT_{max}, results

were qualitatively similar, with TSM explaining 18–75% (mean = 40%) of the variation in sensitivity to habitat modification in GLS models (Figs S9 and S10; Table S3).

Across most data sets, we found weak associations between species' sensitivity to habitat modification and thermal instability. The odds of occurring in modified habitat changed by a factor of 0.04–3.4 (mean = 0.94) with increasing thermal instability according to GLMM analyses. Thermal instability explained less variation in sensitivity to habitat modification, 5–47% (mean = 19%), than did CT_{max} and TSM according to GLS models, and typically had low relative variable importance (Figs 2 and S9). In Costa Rica and Colombia, evaporative water loss was positively associated with sensitivity to habitat conversion. In GLMM analyses, the odds of occurring in modified habitat changed by a factor of 0.06–1.02 (mean = 0.56), typically decreasing, with each standard deviation increase in water loss (Fig. 2). According to GLS models, water loss explained 3–58% (mean = 21%) of variation in the responses and was among the top-ranked models in these analyses for amphibians in Costa Rica and Colombia (Fig. S9; Table S3).

Across most data sets, and for both sets of analyses, the relative importance of thermal traits was greater than that of 'non-thermal' traits retained in analyses (Figs 2 and S9; Tables 1 and S3); however, in our analyses of amphibians exposed to habitat conversion in Costa Rica, larval habitat also ranked among the most important variables. Much of the explained variation in sensitivity to habitat modification was attributed both independently to thermal traits and to the covariation between thermal traits and other species traits (Fig. S11). For example, CT_{max} was correlated with the larval aquatic index in most data sets, with terrestrial breeding amphibians often having the lowest CT_{max} (Figs S3–S8). Some non-thermal traits (e.g. body size) were highly correlated with thermal traits (e.g. water loss) and were, therefore, dropped from analyses to reduce VIFs (Table S1). Tests for phylogenetic signal further revealed that variation in multiple traits, including CT_{max}, body size and clutch size, was in some cases tightly linked with phylogenetic position (Fig. 3; Table S10), even though model residuals did not exhibit phylogenetic non-independence (Revell 2010; Tables S4–S9).

DISCUSSION

Habitat modification is the primary driver of species imperilment, yet responses to habitat modification vary considerably among species (Newbold et al. 2014; Todd et al. 2017). We found that simple measures of thermal biology – CT_{max} and TSM – explained as much as 75% (mean = 39%) of the variation in responses of amphibians and reptiles to habitat modification, even though interactions of ectotherms with their thermal environments are complex. As expected, species able to tolerate warmer temperatures (i.e. those with high CT_{max}) and those expected to maintain body temperatures far below their CT_{max} (i.e. those with large TSMs) were typically less sensitive to habitat modification than species with low CT_{max} and narrow TSMs. The strength of these relationships varied across data sets, possibly owing to differences in methodologies, the influence of species interactions or the relative
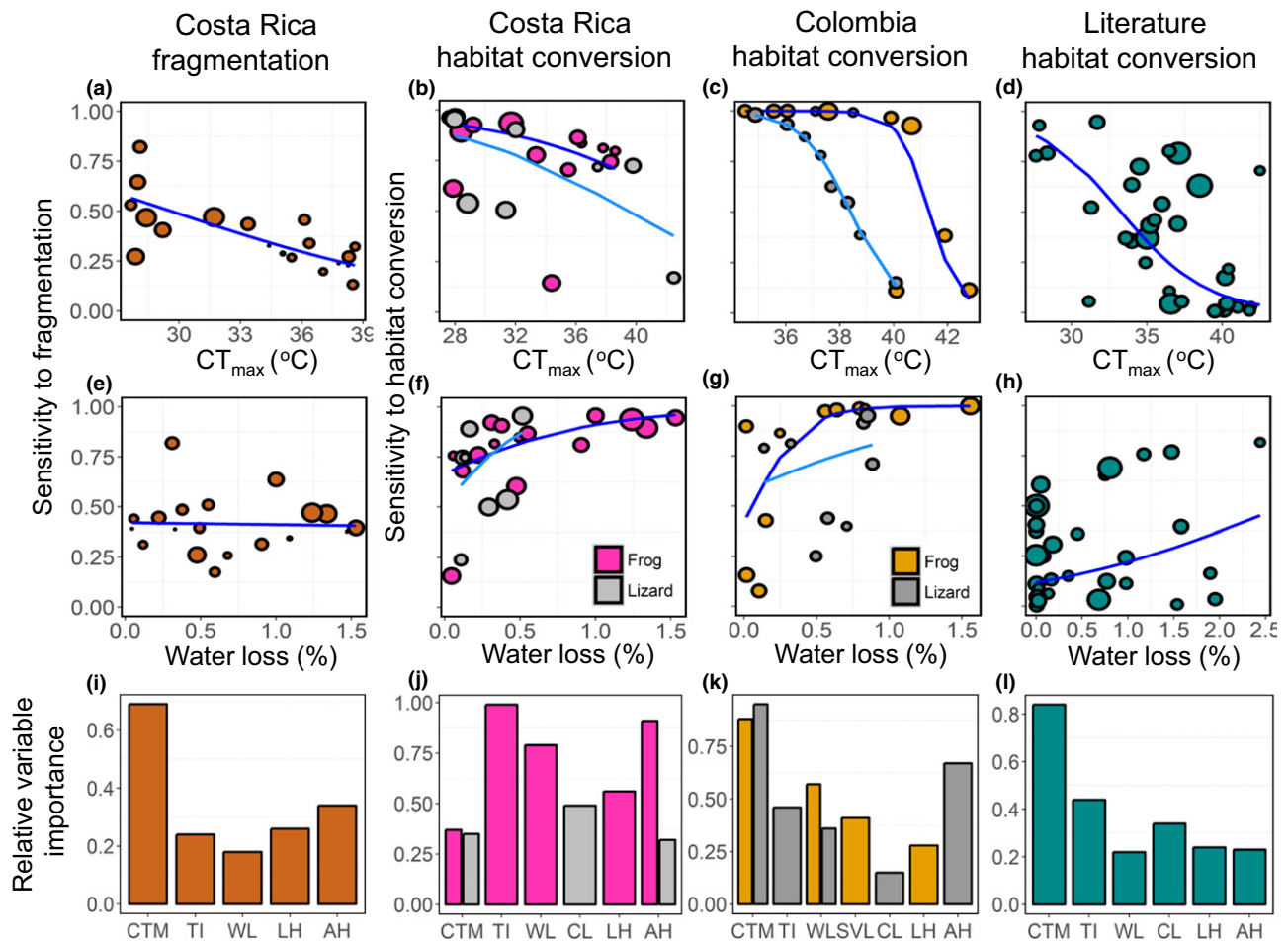
Figure 2 Species sensitivity to habitat fragmentation (far left panels) or habitat conversion (i.e. non-forest land use) in response to species-specific critical thermal maxima (CT_{max}; a–d) and water loss (% of body mass; e–h). Sensitivity is plotted as 1-probability of occurring in modified habitats; all *y*-axes for panels a–h range from 0 to 1. Points show predicted sensitivity for each species from a generalised linear mixed model while accounting for the random effect of species, and point size is proportional to the number of observations for each species. Blue lines show the mean, overall fit of the model. Water loss was estimated for each species using the biophysical model NicheMapper under a range of microclimatic conditions (see Supporting Information for model validation). Species sensitivity to habitat modification was estimated from field surveys in continuous forest vs. forest fragments (for sensitivity to fragmentation) and forest habitat vs. adjacent areas of land use (for sensitivity to habitat conversion). (i–l) Bar graphs show relative variable importance in explaining variation in sensitivity to habitat modification calculated as the cumulative Akaike weights from all subsets of a full model; predictor variables are CT_{max} (CTM), thermal instability (TI), water loss (WL), clutch size (CL), snout to vent length (SVL), adult microhabitat (AH) and larval microhabitat (LH). Some variables were dropped from all subsets analysis so that variance inflation factors were < 4 (Table S1). Bar widths vary depending on whether variable was present in analysis for both taxa (frogs and lizards; panels j, k). Thermal safety margin was highly correlated with CT_{max} and was, therefore, included in a separate model set from CT_{max} (Supporting Information).

importance of additional limiting factors, such as water loss. There was partial support for the importance of water loss, but little support for thermal instability, as predictors of sensitivity to habitat modification. The general trends for CT_{max} and TSM, however, were largely consistent across multiple types of habitat modification, spatial scales and vertebrate classes, despite differences in thermal physiology between amphibians and reptiles. Collectively, these results indicate that certain aspects of thermal biology likely play a key role in determining responses of ectotherms to habitat modification in addition to other major drivers of biodiversity loss, such as climate change and disease (Huey *et al.* 2012; Catenazzi *et al.* 2014; Sunday *et al.* 2014; Nowakowski *et al.* 2016, 2017a).

Our results suggest plausible mechanisms underlying variable species responses to habitat modification. Species with low heat tolerances were those less likely to maintain abundant local populations in fragments and in converted habitats, possibly owing to physiological limits placed on survival, activity and foraging efficiency. Acute or chronic thermal stress can directly reduce survival of individuals in habitats where maximum daily temperatures, including those in daytime refugia, regularly approach their CT_{max} (Rittenhouse *et al.* 2008; Nowakowski *et al.* 2015). Diurnal organisms may reduce their activity to avoid overheating, but this can result in population declines as they forgo opportunities for foraging and reproduction (Sinervo *et al.* 2010). When active, body temperatures that deviate far from thermal optima will reduce

Table 1 Support for competing models explaining variation in species sensitivity to habitat modification

Model	Costa Rica Amphibians Fragmentation			Costa Rica Amphibians Habitat Conversion			Costa Rica Lizards Habitat Conversion		
	AIC_c	ΔAIC_c	P	AIC_c	ΔAIC_c	P	AIC_c	ΔAIC_c	P
Global	110.8	11.3	0.052	**266.5**	**0.00**	**0.001**	192.8	3.3	0.353
All non-thermal traits	103.3	3.7	0.075	274.8	8.3	0.064	**190.7**	**1.2**	**0.198**
All thermal traits	105.7	6.1	0.089	270.1	3.6	0.007	–	–	–
CT_{max}	**99.6**	**0.0**	**0.018**	276.9	10.4	0.239	**190.2**	**0.8**	**0.211**
Thermal instability	104.7	5.1	0.478	273.5	7.1	0.030	–	–	–
Water loss	105.2	5.6	0.941	275.6	9.1	0.103	–	–	–
Body size	–	–	–	–	–	–	–	–	–
Clutch size	–	–	–	–	–	–	**189.5**	**0.0**	**0.128**
Larval habitat	102.8	3.3	0.123	273.0	6.5	0.022	–	–	–
Adult habitat	103.7	4.2	0.227	278.0	11.5	0.615	191.7	2.2	0.772
Null	102.4	2.8	–	276.2	9.8	–	**189.7**	**0.2**	–

Model	Colombia Amphibians Habitat Conversion			Colombia Lizards Habitat Conversion			Literature Amphibians Habitat Conversion		
	AIC_c	ΔAIC_c	P	AIC_c	ΔAIC_c	P	AIC_c	ΔAIC_c	P
Global	49.8	2.0	0.016	29.6	6.5	0.011	260.1	11.7	0.055
All non-thermal traits	56.8	9.0	0.686	31.2	8.1	0.464	257.3	8.9	0.233
All thermal traits	48.3	0.5	0.010	26.2	3.1	0.019	251.1	2.7	0.015
CT_{max}	**47.8**	**0.0**	**0.006**	**23.2**	**0.0**	**0.010**	**248.5**	**0.0**	**0.007**
Thermal instability	–	–	–	28.2	5.1	0.219	252.8	4.3	0.086
Water loss	51.7	3.9	0.055	29.7	6.5	0.811	254.4	6.0	0.255
Body Size	55.3	7.5	0.742	–	–	–	–	–	–
Clutch size	–	–	–	29.3	6.1	0.509	252.4	4.0	0.068
Larval habitat	54.7	6.8	0.393	–	–	–	253.0	4.6	0.098
Adult habitat	–	–	–	28.3	5.1	0.230	255.0	6.6	0.397
Null	53.3	5.4	–	27.0	3.9	–	253.1	4.7	–

We used corrected Akaike's information criterion (AIC_c) to compare generalised linear mixed models. Models within $2\Delta AIC_c$ of best-supported models are in bold. Models fit with thermal traits are highlighted in grey. Some predictor variables were dropped from model sets to reduce variance inflation resulting from correlated traits (Table S1).

efficiency of foraging, predator escape and reproduction, which can reduce population growth (Huey *et al.* 2009; Navas *et al.* 2016). Higher temperatures will also affect many nocturnal organisms that are behaviourally inactive, but exposed during the day (Fig. S12); nocturnal species may experience thermal stress (e.g. Welbergen *et al.* 2008) or increased metabolic rate, thus requiring increased foraging time to supplement dietary intake at the expense of reproduction. These mechanisms are not mutually exclusive and may operate in concert to limit abundances of species with low heat tolerances in altered habitats.

Temperature regulation and water balance are tightly linked through evaporative cooling (Tracy 1976). Environmental temperature and humidity are typically inversely correlated across the landscape (Chen *et al.* 1999; Laurance 2004), and organisms in hot, dry habitats must avoid overheating, in part, by dissipating heat via evaporative water loss (Tracy 1976). Amphibians, with their highly permeable skin, can reduce body temperatures by > 10 °C below air temperatures through rapid evaporative cooling; however, amphibians quickly risk dehydration, especially small-bodied species, without seeking shade or remaining in contact with water (Tracy 1976; Tracy *et al.* 2013; Nowakowski *et al.* 2015). In our analyses, rates of water loss among amphibians in Costa Rica and Colombia (more so than lizards) were positively correlated with their sensitivity to habitat conversion (Fig. 2). However, heat tolerances were more consistently associated with sensitivity to habitat modification across systems and taxa.

Several major assumptions of our approach represent critical avenues for future research on how thermal traits mediate responses of ectotherms to habitat modification. First, species may adapt to new thermal environments. Existing research reveals both potential for local adaptation as well as genetic constraints that limit adaptation of thermal tolerances (Grigg & Buckley 2013; Hoffmann *et al.* 2013; Richter-Boix *et al.* 2015; Llewelyn *et al.* 2016). Adaptive potential may, therefore, be insufficient to keep pace with rapid temperature shifts associated with climate change and habitat alteration (Araujo *et al.* 2013; Grigg & Buckley 2013; Hoffmann *et al.* 2013; Quintero & Wiens 2013; Richter-Boix *et al.* 2015). Second, upper thermal tolerances exhibit some plasticity, suggesting potential for acclimation of CT_{max} to new thermal regimes (e.g. CT_{max} of frogs and lizards increased by a mean of *c.* 0.13 °C with each 1 °C increase in acclimation temperature; Clusella-Trullas & Chown 2014; Simon *et al.* 2015). However, a meta-analysis of thermal performance at subcritical temperatures showed limited acclimation potential for amphibians and reptiles (Seebacher *et al.* 2014). The degree to which
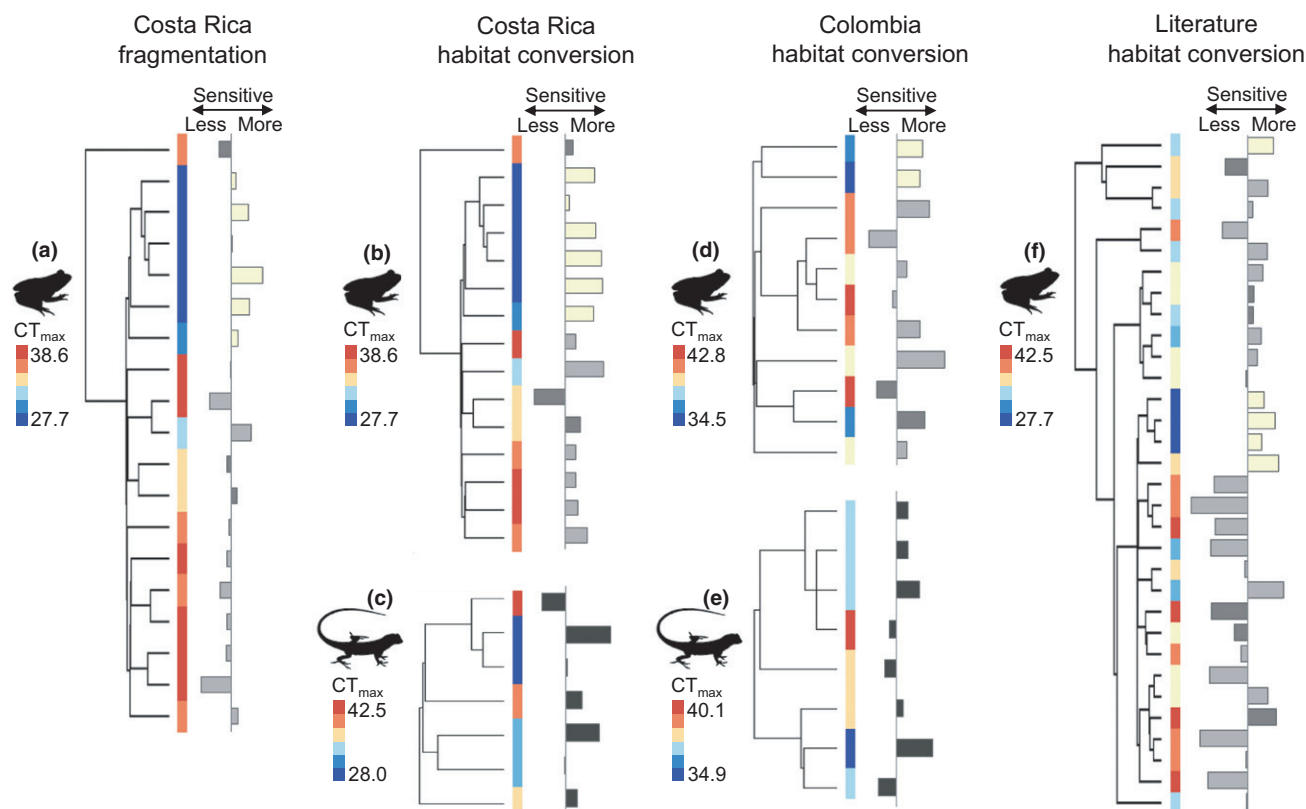
Figure 3 The phylogenetic associations of CT_{max} and sensitivity to habitat modification for each data set. We mapped CT_{max} onto community phylogenies with cool colours (dark and light blue) representing low CT_{max} and warm colours (yellow, orange, red) representing high CT_{max} relative to other species in the community. The bars show sensitivity to habitat modification (direction and magnitude), and for amphibians, shades represent the aquatic index (cream = fully terrestrial development; light grey = aquatic larvae specialised for either lotic or lentic habitats; dark grey = aquatic generalist larvae). Community phylogenies were obtained from large scale, time-calibrated phylogenies for amphibians and squamate reptiles (Pyron & Wiens 2011; Tonini *et al.* 2016). (a, b, f) Values of CT_{max} exhibit significant phylogenetic signal in the Costa Rican amphibians and literature data sets but not in other data sets (c–e; Table S10). We detected no phylogenetic signal in sensitivity to habitat modification at the current scale using likelihood ratio tests. Community phylogenies with tips labelled with species names are shown in Figs S13–S16.

thermal acclimation can reduce vulnerability to rapid microclimatic changes resulting from habitat modification remains an open question. Acclimation could contribute to unexplained variation in species responses observed in this study and may provide insights into why some species with relatively low CT_{max} can persist in refugia within altered habitats (Robinson *et al.* 2013). Third, there is intraspecific variation in thermal tolerances (Riquelme *et al.* 2016), and using point estimates of mean CT_{max} for species does not capture this variation. However, interspecific variation in CT_{max} is typically greater than intraspecific variation (Araujo *et al.* 2013). Intraspecific variation is often associated with life stage, environmental gradients and geographic clines, possibly resulting from selection over long time periods (Floyd 1983; Richter-Boix *et al.* 2015; Riquelme *et al.* 2016; von May *et al.* 2017). Here, we examined local responses to habitat modification occurring over short ecological time scales, and intraspecific variation in CT_{max}, measured locally, was lower than interspecific variation for well-sampled taxa. Determining the degree to which these sources of variation in CT_{max}, as well as other thermal traits (e.g. thermal optimum), influence species responses will help advance our understanding of how habitat modification

filters assemblages and interacts with other drivers of global change.

Responses to habitat modification were associated with phylogenetically constrained traits, indicating that ongoing forest conversion will cause non-random extirpations within local assemblages (i.e. community filtering). Although species thermal traits best predicted sensitivity to habitat modification, often explaining a greater fraction of variation than other traits, suites of associated traits likely contribute to species sensitivity (Fig. S11). For example, frogs with terrestrial development often had low CT_{max}, and these species have also frequently evolved small bodies and clutch sizes compared to aquatic breeders (Gomez-Mestre *et al.* 2012). Small clutches can result from a trade-off with the production of large eggs that are less prone to desiccation in terrestrial habitats than small eggs. Ultimately, the reliance of terrestrial-developing species on humid forest resources for reproduction (e.g. leaf litter), their reduced fecundity and thermal inertia (of very small-bodied species), and their sensitivity to extreme temperatures all may constrain distributions globally, to wet tropical and subtropical zones (Gomez-Mestre *et al.* 2012; Sunday *et al.* 2014), as well as locally, to relatively cool, moist forest

habitats. Furthermore, upper thermal tolerances are often conserved within clades (Grigg & Buckley 2013; Hoffmann *et al.* 2013), with intra- and interspecific variation associated with mean environmental temperatures and temperature variation (Clusella-Trullas & Chown 2014; Richter-Boix *et al.* 2015). Adaptation under limited temperature variation has likely given rise to thermal specialisation in tropical clades (Bonetti & Wiens 2014). Thermal specialists are expected to perform better than generalists under a narrow range of temperatures (Clavel *et al.* 2011), possibly explaining why numerically dominant species in lowland forests of Costa Rica have low CT_{max} and are sensitive to habitat modification (i.e. these species may be cool-habitat specialists).

Thermal biology is likely a critical filter shaping ectotherm assemblages confronted with habitat modification. Although few studies have integrated thermal biology into research on habitat modification (Tuff *et al.* 2016), many of the approaches used to estimate sensitivity of ectotherms to climate change can be adapted to research on altered microclimates resulting from habitat conversion, thereby generating new insights for conservation. Information on species thermal traits could also provide new criteria for conservation prioritisation as practitioners frequently need to make decisions and assess the status of species in a data vacuum (Gardner *et al.* 2007b; Catenazzi 2015). In the absence of robust population data for many species, assessment and monitoring efforts could be directed, in part, towards sensitive groups using information on easily characterised traits, such as larval habitat (Nowakowski *et al.* 2017b) and thermal traits. Our results illustrate a widespread link between thermal traits of species and their sensitivity to habitat modification and point to new lines of inquiry that will allow conservation planners to better understand and ameliorate the effects of habitat modification on ectotherms.

AUTHORSHIP

AJN designed the study, collected and analysed the data and drafted the manuscript; JIW designed the study, collected the data and edited the manuscript; MET, GAB, AC, SMW, DJK, ASM and AAG collected the data and edited the manuscript; MAD and BDT contributed to the design of the study and edited the manuscript.

DATA ACCESSIBILITY

The data used in this study are archived on Figshare: https://doi.org/10.6084/m9.figshare.5632873.

REFERENCES

Araujo, M.B., Ferri-Yanez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013). Heat freezes niche evolution. *Ecol. Lett.*, 16, 1206–1219.

Bartelt, P.E., Klaver, R.W. & Porter, W.P. (2010). Modeling amphibian energetics, habitat suitability, and movements of western toads, *Anaxyrus* (=*Bufo*) *boreas*, across present and future landscapes. *Ecol. Model.*, 221, 2675–2686.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: linear mixed effects models using Eigen and S4*. Available at: http://cran.r-project.org/web/packages/lme4/index.html. Last accessed September 2017.

Bell, K.E. & Donnelly, M.A. (2006). Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conserv. Biol.*, 20, 1750–1760.

Bonetti, M.F. & Wiens, J.J. (2014). Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proc. R. Soc. Lond. B Biol. Sci.*, 281, 20133229.

Brusch, G.A., Taylor, E.N. & Whitfield, S.M. (2016). Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia*, 180, 325–334.

Catenazzi, A. (2015). State of the world's amphibians. *Annu. Rev. Env. Resour.*, 40, 91–119.

Catenazzi, A., Lehr, E. & Vredenburg, V.T. (2014). Thermal physiology, disease, and amphibian declines on the eastern slopes of the Andes. *Conserv. Biol.*, 28, 509–517.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D. *et al.* (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, 49, 288–297.

Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9, 222–228.

Clusella-Trullas, S. & Chown, S.L. (2014). Lizard thermal trait variation at multiple scales: a review. *J. Comp. Physiol. B.*, 184, 5–21.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. *et al.* (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA*, 105, 6668–6672.

Duarte, H., Tejedo, M., Katzenberger, M., Marangoni, F., Baldo, D., Beltrán, J.F. *et al.* (2012). Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Glob. Chang. Biol.*, 18, 412–421.

Floyd, R.B. (1983). Ontogenetic change in the temperature tolerance of larval *Bufo Marinus* (Anura: Bufonidae). *Comp. Biochem. Physiol.*, 75A, 267–271.

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.

Frishkoff, L.O., Karp, D.S., Flanders, J.R., Zook, J., Hadly, E.A., Daily, G.C. *et al.* (2016). Climate change and habitat conversion favour the same species. *Ecol. Lett.*, 19, 1081–1090.

Gardner, T.A., Barlow, J. & Peres, C.A. (2007a). Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biol. Conserv.*, 138, 166–179.

Gardner, T.A., Barlow, J., Parry, L.W. & Peres, C.A. (2007b). Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, 39, 25–30.

Gomez-Mestre, I., Pyron, R.A. & Wiens, J.J. (2012). Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution*, 66, 3687–3700.

Grigg, J.W. & Buckley, L.B. (2013). Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol. Lett.*, 9, 20121056.

Gunderson, A.R. & Stillman, J.H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B.: Roy. Soc.*, 282, 20150401.

Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S. & Fox, C. (2013). Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct. Ecol.*, 27, 934–949.

Huey, R.B. & Stevenson, R. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.*, 19, 357–366.

Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.Á. *et al.* (2009). Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. Lond. B Biol. Sci.*, 276, 1939–1948.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M. & Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 1665–1679.

Kearney, M., Shine, R. & Porter, W.P. (2009). The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc. Natl Acad. Sci. USA*, 106, 3835–3840.

Kearney, M.R., Isaac, A.P. & Porter, W.P. (2014). microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Scientific data*, 1, 140006.

Kurz, D.J., Nowakowski, A.J., Tingley, M.W., Donnelly, M.A. & Wilcove, D.S. (2014). Forest-land use complementarity modifies community structure of a tropical herpetofauna. *Biol. Conserv.*, 170, 246–255.

Laurance, W.F. (2004). Forest-climate interactions in fragmented tropical landscapes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 359, 345–352.

Llewelyn, J., Macdonald, S.L., Hatcher, A., Moritz, C., Phillips, B.L. & Franklin, J. (2016). Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. *Divers. Distrib.*, 22, 1000–1012.

von May, R., Catenazzi, A., Corl, A., Santa-Cruz, R., Carnaval, A.C. & Moritz, C. (2017). Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. *Ecol. Evol.*, 7, 3257–3267.

McElreath, R. (2016). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. CRC Press, Boca Raton, FL, USA.

Murray, K.A., Verde Arregoitia, L.D., Davidson, A., Di Marco, M. & Di Fonzo, M.M.I. (2014). Threat to the point: improving the value of comparative extinction risk analysis for conservation action. *Glob. Chang. Biol.*, 20, 483–494.

Navas, C.A., Antoniazzi, M.M., Carvalho, J.E., Suzuki, H. & Jared, C. (2007). Physiological basis for diurnal activity in dispersing juvenile *Bufo granulosus* in the Caatinga, a Brazilian semi-arid environment. *Comp. Biochem. Physiol. A*, 147, 647–657.

Navas, C.A., Gomes, F.R. & De Domenico, E.A. (2016). Physiological ecology and conservation of anuran amphibians. In *Amphibian and Reptile Adaptations to the Environment: Interplay Between Physiology and Behavior*. (ed D. Vieira de Andrade, C. R. Bevier, and J. E. de Carvalho). CRC Press, Boca Raton, FL, USA, pp. 155–188.

Newbold, T., Hudson, L.N., Phillips, H.R.P., Hill, S.L.L., Contu, S., Lysenko, I. *et al.* (2014). A global model of the response of tropical and su-tropical foest biodiversity to anthropogenic pressures. *Proc. R. Soc. Lond. B Biol. Sci.*, 281, 20141371.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Gray, C.L., Scharlemann, J.P. *et al.* (2016). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, 39, 1151–1163.

Nowakowski, A.J., Otero Jiménez, B., Allen, M., Diaz-Escobar, M. & Donnelly, M.A. (2013). Landscape resistance to movement of the poison frog, *Oophaga pumilio*, in the lowlands of northeastern Costa Rica. *Anim. Conserv.*, 16, 188–197.

Nowakowski, A.J., Veiman-Echeverria, M., Kurz, D.J. & Donnelly, M.A. (2015). Evaluating connectivity for tropical amphibians using empirically derived resistance surfaces. *Ecol. Appl.*, 25, 928–942.

Nowakowski, A.J., Whitfield, S.M., Eskew, E.A., Thompson, M.E., Rose, J.P., Caraballo, B.L. *et al.* (2016). Infection risk decreases with increasing mismatch in host and pathogen environmental tolerances. *Ecol. Lett.*, 19, 1051–1061.

Nowakowski, A.J., Watling, J.I., Whitfield, S.M., Todd, B.D., Kurz, D.J. & Donnelly, M.A. (2017a). Tropical amphibians in shifting thermal landscapes under land-use and climate change. *Conserv. Biol.*, 31, 96–105.

Nowakowski, A.J., Thompson, M.E., Donnelly, M.A. & Todd, B.D. (2017b). Amphibian sensitivity to habitat modification is associated with population trends and species traits. *Global Ecol. Biogeogr.*, 26, 700–712.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Porter, W.P. & Mitchell, J.W. (2006). *Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals*. Google Patents.

Porter, W.P., Mitchell, J.W., Beckman, W.A. & DeWitt, C.B. (1973). Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia*, 13, 1–54.

Pringle, R.M., Webb, J.K. & Shine, R. (2003). Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology*, 84, 2668–2679.

Purvis, A. (2008). Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Evol. Syst.*, 39, 301–319.

Pyron, R.A. & Wiens, J.J. (2011). A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.*, 61, 543–583.

Quintero, I. & Wiens, J.J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol. Lett.*, 16, 1095–1103.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at: http://www.r-project.org. Last accessed September 2017.

Revell, L.J. (2010). Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.*, 1, 319–329.

Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217–223.

Richter-Boix, A., Katzenberger, M., Duarte, H., Quintela, M., Tejedo, M. & Laurila, A. (2015). Local divergence of thermal reaction norms among amphibian populations is affected by pond temperature variation. *Evolution*, 69, 2210–2226.

Riquelme, N.A., Diaz-Paez, H. & Ortiz, J.C. (2016). Thermal tolerance in the Andean toad *Rhinella spinulosa* (Anura: Bufonidae) at three sites located along a latitudinal gradient in Chile. *J. Therm. Biol*, 60, 237–245.

Rittenhouse, T.A., Harper, E.B., Rehard, L.R. & Semlitsch, R.D. (2008). The role of microhabitats in the desiccation and survival of anurans in recently harvested oak–hickory forest. *Copeia*, 2008, 807–814.

Robinson, D., Warmsley, A., Nowakowski, A.J., Reider, K.E. & Donnelly, M.A. (2013). The value of remnant trees in pastures for a neotropical poison frog. *J. Trop. Ecol.*, 29, 345–352.

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.

Seebacher, F., White, C.R. & Franklin, C.E. (2014). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Change*, 5, 61–66.

Simon, M.N., Ribeiro, P.L. & Navas, C.A. (2015). Upper thermal tolerance plasticity in tropical amphibian species from contrasting habitats: implications for warming impact prediction. *J. Therm. Biol*, 48, 36–44.

Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S. *et al.* (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.*, 19, 1372–1385.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M. *et al.* (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. *et al.* (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl Acad. Sci. USA*, 111, 5610–5615.

Thompson, M.E., Nowakowski, A.J. & Donnelly, M.A. (2016). The importance of defining focal assemblages when evaluating amphibian and reptile responses to land use. *Conserv. Biol.*, 30, 249–258.

Todd, B.D. & Andrews, K.M. (2008). Response of a reptile guild to forest harvesting. *Conserv. Biol.*, 22, 753–761.

Todd, B.D., Nowakowski, A.J., Rose, J.P. & Price, S.J. (2017). Species traits explaining sensitivity of snakes to human land use estimated from citizen science data. *Biol. Conserv.*, 206, 31–36.

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W. & Pyron, R.A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.*, 204, 23–31.

Tracy, C.R. (1976). A Model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecol. Monogr.*, 46, 293–326.

Tracy, C.R., Christian, K.A. & Tracy, C.R. (2010). Not just small, wet, and cold: effects of body size and skin resistance on thermoregulation and arboreality of frogs. *Ecology*, 91, 1477–1484.

Tracy, C.R., Christian, K.A., Burnip, N., Austin, B.J., Cornall, A., Iglesias, S. *et al.* (2013). Thermal and hydric implications of diurnal activity by a small tropical frog during the dry season. *Austral Ecol.*, 38, 476–483.

Tuff, K.T., Tuff, T. & Davies, K.F. (2016). A framework for integrating thermal biology into fragmentation research. *Ecol. Lett.*, 19, 361–374.

Watling, J.I. & Braga, L. (2015). Desiccation resistance explains amphibians distributions in a fragmented tropical forest landscape. *Landscape Ecol.*, 30, 1449–1459.

Welbergen, J.A., Klose, S.M., Markus, N. & Eby, P. (2008). Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. R. Soc. Lond. B Biol. Sci.*, 275, 419–425.

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