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Authors

Nowakowski, A Justin
Watling, James I
Whitfield, Steven M
et al.

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Tropical amphibians in shifting thermal landscapes under land-use and climate change

A. Justin Nowakowski,*#¶ James I. Watling,† Steven M. Whitfield,‡ Brian D. Todd,* David J. Kurz,§ and Maureen A. Donnelly#

*Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, CA 95616, U.S.A.
†Department of Biology, John Carroll University, University Heights, OH 44118, U.S.A.
‡Conservation and Research Department, Zoo Miami, Miami, FL 33177, U.S.A.
§Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720, U.S.A.
#Department of Biological Sciences, Florida International University, Miami, FL 33199, U.S.A.

Abstract: *Land-cover and climate change are both expected to alter species distributions and contribute to future biodiversity loss. However, the combined effects of land-cover and climate change on assemblages, especially at the landscape scale, remain understudied. Lowland tropical amphibians may be particularly susceptible to changes in land cover and climate warming because many species have narrow thermal safety margins resulting from air and body temperatures that are close to their critical thermal maxima (CT_{max}). We examined how changing thermal landscapes may alter the area of thermally suitable habitat (TSH) for tropical amphibians. We measured microclimates in 6 land-cover types and CT_{max} of 16 frog species in lowland northeastern Costa Rica. We used a biophysical model to estimate core body temperatures of frogs exposed to habitat-specific microclimates while accounting for evaporative cooling and behavior. Thermally suitable habitat area was estimated as the portion of the landscape where species CT_{max} exceeded their habitat-specific maximum body temperatures. We projected changes in TSH area 80 years into the future as a function of land-cover change only, climate change only, and combinations of land-cover and climate-change scenarios representing low and moderate rates of change. Projected decreases in TSH area ranged from 16% under low emissions and reduced forest loss to 30% under moderate emissions and business-as-usual land-cover change. Under a moderate emissions scenario (A1B), climate change alone contributed to 1.7- to 4.5-fold greater losses in TSH area than land-cover change only, suggesting that future decreases in TSH from climate change may outpace structural habitat loss. Forest-restricted species had lower mean CT_{max} than species that occurred in altered habitats, indicating that thermal tolerances will likely shape assemblages in changing thermal landscapes. In the face of ongoing land-cover and climate change, it will be critical to consider changing thermal landscapes in strategies to conserve ectotherm species.*

Keywords: CT_{max}, ectotherm, fragmentation, land cover, microclimate, thermal tolerance

Los Anfibios Tropicales en Paisajes Termales Cambiantes Debido al Uso de Suelo y el Cambio Climático

Resumen: *Se espera que el cambio climático y el uso del suelo alteren la distribución de las especies y que contribuyan a la futura pérdida de biodiversidad. Sin embargo, los efectos combinados del cambio climático y del cambio de uso de suelo sobre los ensamblajes, especialmente a escala de paisaje, siguen estando subestudiados. Los anfibios de zonas tropicales bajas pueden ser particularmente susceptibles a los cambios en la cobertura del suelo y al calentamiento climático porque muchas especies tienen márgenes estrechos de seguridad termal, resultantes de la temperatura corporal y la temperatura del aire que están cerca de su temperatura crítica máxima (TC_{max}). Examinamos cómo los paisajes térmicos cambiantes pueden alterar el área del hábitat térmico apto para los anfibios tropicales. Medimos los microclimas en seis tipos de cobertura de suelo y la TC_{max} de 16 especies de ranas en las zonas bajas del noreste de Costa Rica. Utilizamos un modelo biofísico para estimar las temperaturas nucleares del cuerpo de las ranas expuestas a los microclimas*

¶*email nowakowskia@gmail.com*
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específicos de hábitat mientras tomábamos en cuenta el enfriamiento por evaporación y el comportamiento. El área de hábitat térmico apto (HTA) se estimó como la porción de paisaje en el que la TC_{max} de las especies excedió las temperaturas corporales máximas específicas al hábitat. Proyectamos los cambios en el área de HTA a 80 años en el futuro como consecuencia unicamente del cambio en la cobertura de suelo, unicamente del cambio climático y como consecuencia de escenarios combinados del cambio en la cobertura de suelo y del cambio climático representando tasas bajas y moderadas de cambio. Las disminuciones proyectadas en el área de HTA variaron desde 16 % en condiciones de emisiones bajas y pérdida reducida de bosque a 30 % en condiciones de emisiones moderadas y el cambio usual actual de cobertura de suelo. Bajo un escenario de emisiones moderadas (A1B), el cambio climático por sí solo contribuyó a pérdidas 1.7 y hasta 4.5 veces mayores en el área de HTA que la cobertura de suelo por sí sola, lo que sugiere que las futuras disminuciones en el HTA causadas por el cambio climático podrían superar a la pérdida de hábitat estructural. Las especies restringidas a los bosques tuvieron una media más baja de TC_{max} que las especies que se encuentran en hábitats alterados, lo que indica que las tolerancias térmicas probablemente moldeen los ensamblajes en los paisajes térmicos cambiantes. Ante el al cambio continuo del uso de suelo y el cambio climático, será crítico considerar los paisajes térmicos cambiantes en las estrategias para conservar a las especies ectotermas.

Palabras Clave: cobertura de suelo, CT_{max}, ectotermo, fragmentación, microclima, tolerancia termal

Introduction

Terrestrial biodiversity is threatened by ongoing climate change and the widespread conversion of forests to agriculture (Colwell et al. 2008; Vié et al. 2009). Pastures and croplands cover nearly 40% of Earth's land surface (Foley et al. 2011), resulting in loss, fragmentation, and degradation of natural habitats (Fischer & Lindenmayer 2007). As habitat conversion continues unabated in many regions, climate change is also altering species assemblages by causing latitudinal and elevational range shifts as well as local extinctions (Colwell et al. 2008; Chen et al. 2009; Cahill et al. 2013). Existing research on the interaction of these threats shows that climate change can exacerbate the effects of land-cover change (Feeley & Rehm 2012; Mantyka-Pringle et al. 2012), and potential synergies between land-cover and climate change particularly threaten tropical ectotherms (Hof et al. 2011).

Land-cover composition and change will likely mediate the effects of climate change on local ectotherm assemblages, much like the suitability of altered habitats modifies fragmentation effects (Watling et al. 2011; Nowakowski et al. 2013; Nowakowski et al. 2015*a*). Common land-cover types vary in habitat suitability for native species assemblages (Daily et al. 2001; Kurz et al. 2014) and thereby alter effective habitat area and isolation of local assemblages in forest-agriculture mosaics. Where land cover has been altered, vegetation structure (e.g., canopy stratum of tree plantations) provides varying levels of thermal refugia, allowing some species to occupy and move through altered habitats (Fischer et al. 2010; Robinson et al. 2013).

The persistence of native assemblages in forest-agricultural mosaics depends, in part, on the ability of species to tolerate changing thermal landscapes over time. We define *thermal landscapes* as the variation in temperature regimes associated with distinct landscape features, such as different land-cover types. Mean local temperatures, mediated by vegetation height and density, can differ among land-cover classes by as much as 10°C (Cosentino et al. 2011; Robinson et al. 2013). As regional temperatures increase, local temperatures will reach different maxima in different land-cover types. Therefore, thermal habitat suitability will vary spatially, according to land-cover type, as well as temporally, according to regional temperature changes. Within land-cover types, the use of shaded microhabitats can buffer ectotherms from extreme daytime temperatures (Scheffers et al. 2014); however, microhabitat temperatures are also influenced by the surrounding vegetation of a given land-cover type (Pringle et al. 2003; Robinson et al. 2013).

Variation among ectotherms in their thermal tolerances should give rise to different species responses to both land-cover and climate change. Tropical ectotherms are expected to be most sensitive to climate warming because many species are already exposed to air temperatures near their upper thermal limits (Deutsch et al. 2008). Small temperature increases in coming decades, therefore, may cause disproportionate rates of decline of ectotherms in the tropics (Deutsch et al. 2008; Catenazzi et al. 2014; Sunday et al. 2014). In particular, tropical species with low thermal tolerances may exhibit the greatest and most immediate declines in response to climate warming. Similarly, variation among species in their thermal tolerances could filter assemblages in response to land-cover change because high thermal tolerances will likely enable some species to persist in habitats with high temperatures (Duarte et al. 2012; Simon et al. 2015), including human-altered habitats with little vegetation structure.

We examined the combined effects of projected land-cover and climate change on the area of thermally suitable habitat (TSH) for amphibians in the lowlands of northeastern Costa Rica. We defined TSH as the area of the

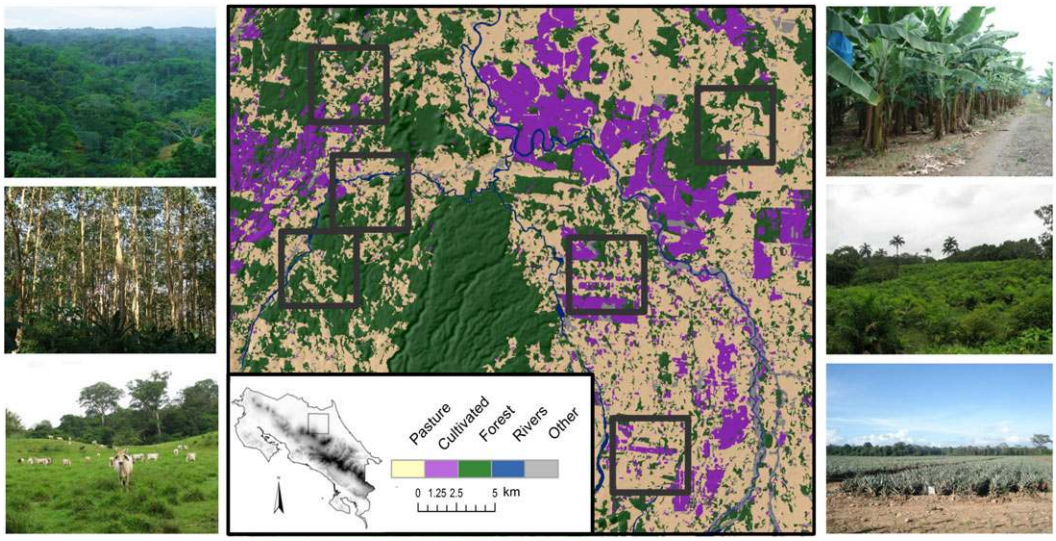

Figure 1. Map of study region in Costa Rica (squares, focal 5 × 5 km^2 landscapes analyzed). Photographs: (left, top to bottom) examples of forest, tree plantation, and pasture and (right, top to bottom) examples of banana, palmito (heart-of-palm), and pineapple farms.

landscape where species thermal safety margins (TSMs)–the difference between critical thermal maximum (CT_{max}) and maximum body temperatures–are >0. Amphibians are able to maintain body temperatures below air temperatures through behavioral thermoregulation and evaporative cooling (Wells 2007; Tracy et al. 2013). Therefore, analyses of amphibian sensitivity to climate warming increasingly account for the potential for thermoregulation to buffer body temperatures against warming air temperatures (Kearney et al. 2009; Sunday et al. 2014). The primary assumption of our analysis was that land-cover specific microclimates that inhibit maintenance of body temperatures below CT_{max} result in those habitats being unsuitable for long-term persistence of local populations owing to thermal stress (Sinervo et al. 2010; Nowakowski et al. 2015*b*).

To examine the role of thermal tolerances in species sensitivity to land-cover and climate change, we first summarized mean CT_{max} of species grouped by their habitat associations as measured by field surveys. We then used a biophysical model to estimate maximum body temperatures under current and future land-cover specific temperature regimes. Finally, we projected changes in TSH area for amphibians as a function of simulated land-cover change and climate warming over 80 years. Our primary objective was to compare the relative decrease in TSH area attributable to land-cover change, climate change, and the combination of these threats. We expected that land-cover and climate change combined would contribute to far greater rates of decrease in TSH area than either stressor alone because land-cover change will mediate local maximum temperatures experienced by ectotherms.

Methods

Study Area and Assemblage

We focused on frog assemblages in forest-agricultural landscapes in the lowlands of northeastern Costa Rica. The study area is typical of rural lowland tropical landscapes in terms of both climate and land-use composition (Ranganathan & Daily 2008). The regional climate is characterized by an annual mean temperature of 25°C and annual rainfall of approximately 4 m (Sanford et al. 1994). Temperature variation is greater over 24 h (approximately 23–27°C in forest and 23–34°C in open land-cover types) than across average daily temperatures throughout the year. Land cover in the region is dominated by fragmented wet tropical forest, cattle pastures, and cultivated areas (Fagan et al. 2013) (Fig. 1). Amphibians occupy these land-cover types to varying degrees; some species are restricted to forests and others use a range of land-cover types (Kurz et al. 2014). Although some frog species in our data set are primarily nocturnal, all have been recorded in daytime field surveys or observed by us during the day (Supporting Information; Whitfield et al. 2007; Kurz et al. 2014; Whitfield et al. 2014). Many nocturnal species in this system spend daytime hours resting on leaf surfaces or in leaf litter and are therefore also exposed to daytime temperatures.

Characterizing CT_{max} and Habitat Associations

We measured critical thermal maxima for 16 frog species from 8 families. We captured 226 adult frogs (sample size varied among species [Supporting Information]) at La

Selva Biological Station in 2011 and transported them to a shaded, open-air laboratory on site where they were kept in plastic containers at ambient temperature (~25 °C) for 2–24 h prior to CT_{max} assays. Because all frogs were captured and assayed within the forested reserve, individuals were already acclimated to the ambient conditions under which they were tested. We measured CT_{max} of each species by placing individuals in water baths, slowly heating water from ambient temperature (approximately 25 °C) at a rate of approximately 0.5°C/min, eliciting a righting response at 1-min intervals, and recording loss of righting reflex when an individual did not exhibit a righting response for 5 s (Catenazzi et al. 2014). Temperature of water baths was measured using a thermocouple. Following the trial, we placed frogs in an ambient water bath until they recovered. Experimental protocols received approval from the Institutional Animal Care and Use Committee at Florida International University (no. 11–017).

To determine whether species that use altered habitats have higher CT_{max} than forest-restricted species, we summarized mean CT_{max} by habitat associations with previously collected survey data in remnant forests, palmito (heart-of-palm) plantations, and pastures (Kurz et al. 2014). We calculated mean CT_{max} for species that were only detected in forest and for species that were observed in multiple habitats. Because not all species for which we had CT_{max} data were detected during surveys, we statistically compared CT_{max} of forest-restricted species with habitat generalists by grouping species observed in pastures and palmito and using a nonparametric Wilcoxon rank sum test ($n = 11$).

Measuring and Projecting Thermal Landscapes

In 2011 and 2012, we measured 24-h temperature profiles in forests, tree plantations, palmito farms, banana plantations, pineapple farms, and pastures. Temperatures were measured at 3 or more replicate sites for each land-cover type and on multiple occasions with ibutton Hygrochron sensors (Maxim Integrated Products, San Jose, CA, U.S.A.). We determined placement of data loggers at each replicate site by generating random compass headings and distances from access points, ensuring that a range of microhabitats were measured (see Supporting Information for details).

We used the Dinamica EGO platform (Soares-Filho et al. 2002) to simulate land-cover change at 10-year time steps from 2010 to 2090. We projected land-cover change under reduced forest loss (RFL) and business-as-usual (BAU) scenarios representing low and moderate rates, respectively, of forest loss and land-use change relevant to the region (FAO 2011; Fagan et al. 2013). Multistep transition rates were estimated using land-cover data from 1996 and 2001 that were classified from Landsat satellite imagery (Sesnie et al. 2008; see Supporting Information for details).

To project diurnal temperature profiles in 6 land-cover types for 2020–2090, we projected temperature increases at the scale of the study region at each time step with the MarkSim weather generator (Jones & Thornton 2013; Supporting Information). Ensemble projections were created in accordance with the A1B and B1 CO_2 emissions scenarios (Nakicenovic et al. 2000) by averaging projections of 6 general circulation models. The simulated temperature increase for each period was then added to the observed temperature data in pastures (because pastures best approximate the well-exposed areas in which weather stations are generally installed [WMO 2003]) to project diurnal temperature profile for each pasture by time step combination. Estimates of future temperature profiles in the 5 nonpasture land-cover types were then derived from the observed proportional relationships between temperatures in pasture and in each land-cover type (Supporting Information).

Estimating Habitat-Specific Body Temperatures

We estimated maximum core body temperatures of the 16 frog species under land-cover and time-step specific temperatures regimes with the biophysical model Niche Mapper, which has been used to model species sensitivity to climate change (Kearney et al. 2009; Bartelt et al. 2010; Sunday et al. 2014). Details of the model are described in Porter and Mitchell (2006) and Bartelt et al. (2010). Briefly, Niche Mapper integrates a microclimate model with a mechanistic model of ectotherm heat and mass transfer. The model uses as inputs microclimate information (e.g., air temperature, humidity, and wind speed) and physiological and behavioral characteristics of species (e.g., body size, microhabitat use, and activity) to model energy budgets and core body temperatures. Estimated core temperatures account for evaporative cooling of amphibians and the ability to seek shaded microhabitats (thereby reducing air temperatures) to maintain temperatures below thermal tolerances. Previous validation with empirical body temperatures shows that Niche Mapper produces accurate core temperature estimates under a range of microclimate conditions (Kearney et al. 2009; Bartelt et al. 2010). We used physical agar models in the field, placed in forest and pasture habitats (see Supporting Information for details), to evaluate model estimates.

Projecting Changes in Thermally Suitable Habitat Area over Time

We modeled thermal landscapes by assigning land-cover specific maximum temperatures to corresponding cells within 6, 5 × 5 km focal landscapes (Fig. 1). We generated thermal landscapes at 10-year time steps for 8 scenarios: land-cover change only (BAU or RFL scenarios); climate

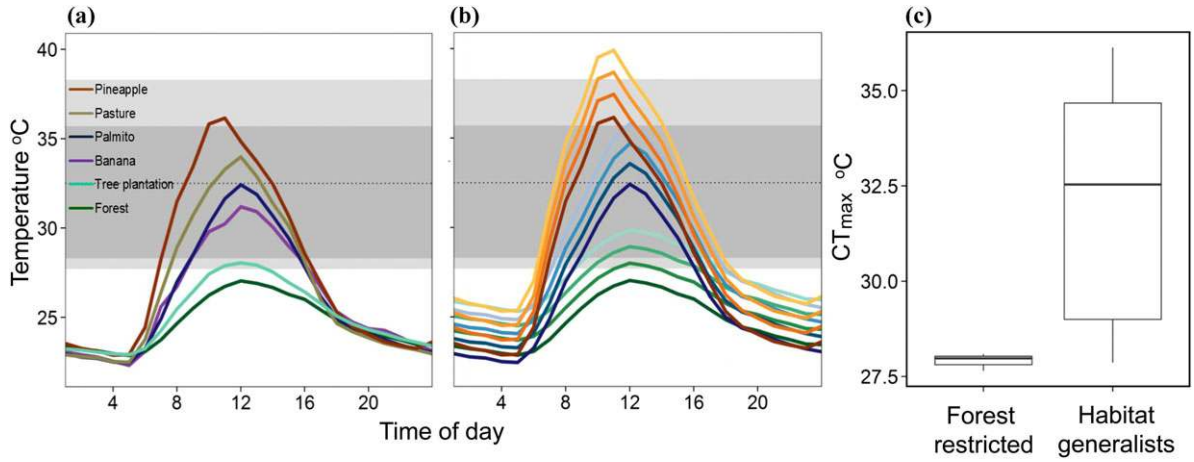

Figure 2. In northeastern Costa Rica, mean 24-h temperature profiles (a) from 2012 in 6 land-cover types and (b) in forest, palmito, and pineapple in 2012 (darkest lines) and projected for 2030, 2060, and 2090 under the A1B emissions scenario (lighter line shades, respectively, from bottom to top) (horizontal line, median of critical thermal maxima [CT_{max}] measured for frogs; dark shading, interquartile range of CT_{max}; light shading, range of CT_{max}). (c) The median, interquartile range, and range of CT_{max} for frog species restricted to forest (n = 3 species) and for frog species observed in forest and disturbed habitats (i.e., habitat generalists) (n = 8) during surveys.

change only (A1B or B1 IPCC emissions scenarios); and combined land-cover- and climate-change scenarios, including A1B + BAU, A1B + RFL, B1 + BUA, and B1+ RFL. We did not consider elevation–temperature relationships because our primary objective was to examine the effects of variation in temperatures among land-cover types in the lowlands, and elevation varied little within (SD of elevation = 18.7 m) and among focal landscapes (SD of mean landscape elevation = 64.2 m).

For each species, we calculated amount of TSH as the area of the landscape where TSMs were > 0. We defined TSM as the difference between a species' CT_{max} and its maximum core body temperature in a given land-cover type (estimated using Niche Mapper). The TSH area was calculated for all species, landscapes, time steps, and scenarios. We further validated the use of TSH area as a predictor of species distributions by examining correlations between our estimates of TSH area derived from CT_{max} data and estimates of habitat area derived from field surveys. We also examined (graphically) mean species richness in multiple land-cover types in relation to mean maximum air temperatures and mean CT_{max} of species occupying those land-cover types (Kurz et al. 2014; Supporting Information).

We analyzed trends in TSH area over time and across scenarios, averaging TSH area across species. We then plotted mean change in TSH area among scenarios and as a function of CT_{max}. To analyze mean decreases in TSH area between the first and last time step of our projections (our response), we fit a linear mixed-effects model with landscape as a random effect and land-cover-change scenario, climate scenario, and the interaction of land-cover and climate change as fixed effects. We also analyzed variation in modeled deviations of core body temperatures from air temperature as a function of mass and relative humidity with generalized linear models. Analyses were implemented in R lme4 package (Bates et al. 2013).

Results

Observed mean maximum daily temperatures ranged from 27°C in forest to 36 °C in pineapple farms; temperatures in other land-cover types were intermediate (Fig. 2a). Projected regional temperature increases of 2.8–3.9 °C over 80 years under the A1B CO_2 emissions scenario translated to mean maximum daily temperatures of 29.8 °C and 39.9 °C in forest and pineapple, respectively (Fig. 2b). Eighty-year temperature increases under the B1 scenario resulted in mean maximum daily temperatures of 29.0 °C in forest and 38.7 °C in pineapple. Mean CT_{max} of individual species ranged from 27.6 to 38.3°C; across 16 species, the median CT_{max} was 32.5°C (Fig. 2 & Supporting Information). Under both emissions scenarios, daytime maximum forest temperatures in 2090 exceeded the thermal tolerances of species with the lowest CT_{max} values, predominantly species from the family Craugastoridae. The mean CT_{max} of species restricted to forest was lower than for species that also occurred in disturbed habitats ($p = 0.048$) (Fig. 2c).

Evaporative cooling and thermoregulatory behavior resulted in estimated core temperatures that were up to 9°C lower than maximum daily air temperatures under certain circumstances (Supporting Information). The difference between modeled core body temperature and air temperature was largely driven by

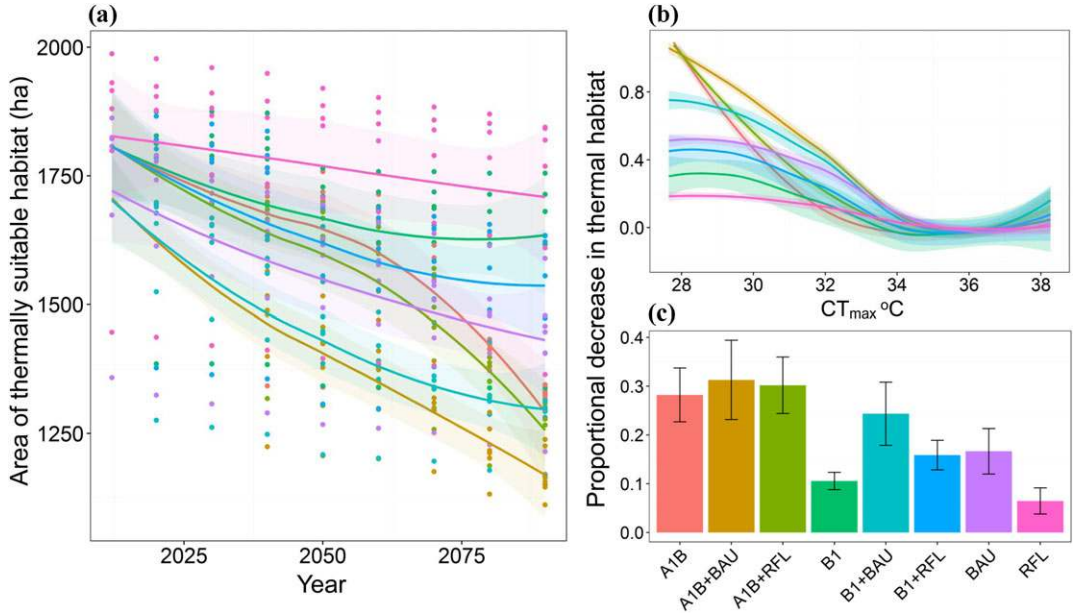

Figure 3. (a) Mean area of landscape in northeastern Costa Rica predicted to be thermally suitable (thermal safety margins >0) over time under multiple land-cover and climate-change scenarios (trend lines, loess smoothers; bands, confidence intervals; key to scenarios is provided by scenario labeling on the x-axis in graph [c]). (b) Predicted proportional decrease in thermally suitable habitat over 80 years under multiple land-cover and climate-change scenarios for frog species as a function of their critical thermal maxima (CT_{max}). (c) Predicted proportional decrease in thermally suitable habitat over 80 years under land-cover (BAU, business-as-usual; RFL, reduced forest loss) and climate-change scenarios (A1B and B1 emissions) (climate scenarios are as defined by the Intergovernmental Panel on Climate Change [Nakicenovic et al. 2000]).

minimum relative humidity ($p < 0.001$); in low-humidity microclimates, these differences were greatest. There was also a body-size threshold (approximately 1 g) at which small-bodied frogs were unable to reduce core temperatures below ambient temperatures (Supporting Information). Agar-model temperatures best approximated core temperature profiles of small-bodied frogs estimated using Niche Mapper ($R^2 = 0.87–0.92$). Differences in mean maximum agar-model temperatures and maximum estimated core temperatures of small-bodied frogs were 0.08°C in pasture and 1.11°C in forest, whereas Niche Mapper estimates of body temperatures were cooler than agar-model temperatures in pasture for large-bodied species (Supporting Information).

Our land-use change simulations projected annual forest loss of 0.3%/year (RFL) and 1.3%/year (BAU); the latter value approximated well the deforestation rate in the study region from 1996 to 2011 (1.38%/year [Fagan et al. 2013]). We projected the greatest mean loss of TSH area under the combined A1B climate and BAU land-cover change scenario (approximately 30% loss over 80 years); however, this was only marginally higher than all other scenarios that included A1B climate change (Fig. 3). Under the most conservative land-cover + climate-change scenario that combined low emissions (B1) and RFL land-cover change, we projected a 16% decrease in TSH area over 80 years. When comparing loss of TSH area attributable solely to land-cover change or climate change, TSH loss was 1.7–4.5 greater under the moderate emissions scenario (A1B) than BAU or RFL land-cover change scenarios, respectively (Fig. 3c). There was a significant interaction between climate and land-cover change scenarios explaining TSH loss ($p < 0.001$) (Fig. 3c & Supporting Information).

Proportional decreases in TSH area from 2012 to 2090 were negatively associated with CT_{max}; species with $CT_{max} > 34$°C experienced little loss of TSH, whereas species with low CT_{max} (~28°C) experienced complete loss of TSH under some scenarios (Fig. 3b). There was general agreement between expected TSH area derived from CT_{max} and survey data at low-to-medium values of CT_{max} and low agreement (i.e., low R^2) at high values of CT_{max} (Supporting Information). Mean maximum temperature was lowest in forest, and mean species richness of amphibians was greater in forest than in palmito plantations and pastures (Kurz et al. 2014; Supporting Information).

Discussion

Climate and land-cover change are reshaping the distributions of species and the structure of native

communities (Colwell et al. 2008; Sheldon et al. 2011; Newbold et al. 2015). Because the behavior, reproduction, and physiology of amphibians are highly temperature-dependent (Wells 2007), thermal gradients affect their habitat selection (Freidenburg & Skelly 2004) and movement (Nowakowski et al. 2015*a*), thereby shaping amphibian distributions (Frishkoff et al. 2015). Projected decreases in TSH area attributable to the combined effects of land-cover and climate change ranged from 16% under low emissions (B1) and RFL to 30% under moderate emissions (A1B) and BAU land-cover change. This loss of TSH may contribute to the attrition of lowland amphibian faunas. Our results suggest that, at the landscape scale, loss of TSH from climate warming may become an equally or more severe threat to lowland amphibians than the structural loss of forest. Under a moderate emissions scenario (A1B), declines in TSH area from climate change alone were 1.7–4.5 times greater than declines attributable to land-cover change only, suggesting that future losses of TSH from climate warming could outpace the effects of land-cover change.

Both climate and land-cover change will alter future thermal landscapes for amphibians, reducing TSH area as species increasingly encounter temperatures that exceed their thermal tolerances. The B1 and A1B emissions scenarios considered here represent low and moderate rates of projected temperature increase, respectively. However, CO_2 emissions of the last decade tracked slightly above the A1B projection, suggesting that these scenarios could be conservative (Peters et al. 2013). Our land-cover change scenarios are also consistent with contemporary rates of annual forest loss in Central America (1.19%/year) and South America (0.45%/year) (FAO 2011). It is important to note that rates of forest loss in some Neotropical countries (e.g., Brazil) are greater than in our scenarios (Bianchi & Haig 2013); therefore, the combined effects of forest conversion and climate change will likely be more pronounced in other tropical regions.

Assumptions

We assumed that near-term potential for acclimation or selection to shift thermal tolerances in response to climate warming is negligible. There is evidence of some plasticity associated with CT_{max} in ectotherms, suggesting that studies relying on point estimates of CT_{max} may overestimate sensitivity to climate warming (Simon et al. 2015). However, results of a recent study showed that potential for acclimation in ectotherms is generally limited and will be insufficient to buffer most species against climate warming (Gunderson & Stillman 2015). Reviews of existing evidence suggest that heritable variation in thermal tolerances is also low in model taxa (e.g., *Drosophila*), and that many ectotherms likely have limited adaptive potential to keep pace with current rates of temperature increase (Parmesan et al. 2000; Hoffmann et al. 2013).

We did not account for topography, which can modify thermal landscapes (Sears et al. 2011), especially when there are appreciable changes in elevation. Assuming an adiabatic lapse rate of –5.5°C/1000 m for warm, moist air masses (Poage & Chamberlain 2001), variation in temperature among land-cover types is an order of magnitude greater than elevation-mediated temperature variation within our study system because of the shallow elevational gradient (SD of elevation within landscapes = 18.7 m). Microclimate variation associated with fine-scale topographic complexity (e.g., north-facing slopes) is likely most important in remnant forests in the system that often remain on steeper slopes that are unsuitable for cultivation; relatively flat areas have been preferentially cleared for agriculture in the study area (Fig. 1) and elsewhere in the tropics (Grau & Aide 2008).

Moist-skinned amphibians lower their body temperatures through evaporative cooling, which can keep their body temperatures below ambient temperatures, given adequate hydration (Wells 2007). Without constant hydration, evaporative cooling may only reduce body temperature below ambient temperatures for a matter of minutes in open habitats during the warmest times of day (Tracy et al. 2013). In our study system, small amphibians can experience rapid water loss during dry, daytime conditions in open habitats (Nowakowski et al. 2015*b*). We assumed amphibians could access adequate moisture during the warmest times of the day in all habitats, which may have resulted in conservative estimates of TSH loss.

Thermally Suitable Habitat Area as a Landscape Metric

By integrating information on microclimate and species thermal physiology, TSH area provides a useful index for evaluating sensitivity of species and assemblages to both land-cover and climate change. Habitats in which some species are regularly unable to maintain body temperatures below physiological tolerances are unlikely to support local populations of those species. Consequently, assemblages may be filtered according to species thermal tolerances and thermal landscape change (Figs. 2c & 3b). Thermal landscapes are changing in spatially complex ways as regional temperatures increase and land-cover transitions alter local temperature regimes. However, TSH area, as defined here, is a conservative metric in 2 important ways. First, organismal performance decreases steeply from thermal optima as temperatures approach thermal maxima (Huey et al. 2012). Although local extinctions are expected for populations frequently exposed to temperatures $\geq CT_{max}$, declines and elevated extinction risk may occur before body temperature exceeds CT_{max}.

Second, TSH may represent an upper limit to the area of the landscape that is potentially accessible. Areas that are thermally suitable may be inhospitable in other ways, such as scarcity of resources for reproduction and foraging, the presence of pathogens and predators, the quantity and type of agrochemicals applied, and the intensity of mechanical site preparation. Therefore, in most cases, the area that is actually used by a species will be lower than the TSH area (Supporting Information). We suggest that TSH area, measured using TSMs, could serve as useful base landscape model on which to build more complex models of effects of anthropogenic change. For example, accounting for TSH area may provide new insights into fragmentation effects on ectotherms because effective habitat area and connectivity are expected to increase with increasing thermal tolerances.

Our analysis highlights the need to consider near-term changes in TSH area at landscape scales. Most notably, we found that a complete loss of thermally available habitat was projected for some species with low thermal tolerances (Fig. 3b). For these species, daytime maximum body temperatures in forest may already exceed optimum temperatures, and thermal stress could be an important factor contributing to observed gradual declines (Whitfield et al. 2007). Complete loss of TSH area for some species may result in nonrandom extirpations that could denude leaf-litter amphibian assemblages currently dominated by direct-developing lineages with low thermal tolerances. Our results may be broadly relevant to other tropical ectotherm systems because thermal landscapes affect the distributions of ectotherms, and TSH area is likely decreasing for many species. Therefore, consideration of the combined effects of land-cover and climate change in modifying thermal landscapes should be a fundamental component of conservation strategies in the coming decades.

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Supporting Information

Additional detailed methods, observed daytime microhabitat use by diurnal and nocturnal species (Appendix S1), mean $CT_{max,}$ and species-specific parameters of the Niche Mapper ectotherm model for 16 amphibian species (Appendix S2), significance of predictors in the linear mixed-effects model (Appendix S3), photographs of nocturnal amphibians encountered during diurnal surveys and their microhabitat use (Appendix S4), workflow for the analyses (Appendix S5), a comparison of MarkSim simulated temperatures with weather station data for 2012 (Appendix S6), a comparison of Niche Mapper estimates with agar-model temperatures (Appendix S7), sources of variation in model estimates (Appendix S8), and model validation based on survey data (Appendix S9) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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