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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a high-elevation lizard

Shu-Ping Huang · Warren P. Porter · Ming-Chung Tu · Chyi-Rong Chiou

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Abstract Warmer climates have affected animal distribution ranges, but how they may interact with vegetation patterns to affect habitat use, an important consideration for future wildlife management, has received little attention. Here, we use a biophysical model to investigate the potential thermal impact of vegetation pattern on the habitat quality of a high-elevation grassland lizard, *Takydromus hsuehshanensis*, and to predict the thermal suitability of vegetation for this species in a future warmer climate (assuming 3 °C air temperature increase). We assess the thermal quality of vegetation types in our study area (Taroko National Park in areas >1,800 m) using three ecologically relevant estimates of reptiles: body temperature (T_b), maximum active time, and maximum digestive time. The results show that increasing forest canopy gradually cools the microclimates, hence decreasing these estimates. In the current landscape, sunny mountaintop grasslands are predicted to serve as high quality thermal habitat, whereas the dense forests that are dominant as a result of forest protection are too cold to provide suitable habitat. In simulated warmer climates, the thermal quality of dense forests increases slightly but remains inferior to that of grasslands. We note that the impact of warmer climates on this reptile will be greatly affected by future vegetation patterns, and we suggest that the current trend of upslope forest movement found in many other mountain systems could cause disadvantages to some heliothermic lizard species.

Keywords Temperature · Physiology · *Takydromus hsuehshanensis* · Mountain · Niche Mapper

Introduction

Climate change has had a variety of negative impacts on reptiles (Raxworthy et al. 2008; Still et al. 1999; Mitchell et al. 2008; but see Chamaillé-Jammes et al. 2006). Investigations have proposed that vegetation can mitigate the negative impact of a warmer climate on reptiles by providing them shade to prevent overheating (Kearney et al. 2009). In cold mountain areas, however, heavy forests generate cold climates due to the reduction of solar radiation, adversely affecting reptiles (e.g., by reducing thermally suitable habitats; Pringle et al. 2003; Webb et al. 2005). Therefore, the alteration of landscape vegetation due to climate change (e.g., upslope movement of forest; Raxworthy et al. 2008) also plays a role affecting animals in future warmer climates. Quantifying the habitat suitability of the landscape vegetation is thus relevant to a better understanding of the global warming ecology of high-elevation reptiles.

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S.-P. Huang · W. P. Porter
Department of Zoology, University of Wisconsin, 250 N. Mills Street, Madison, WI, USA

W. P. Porter
e-mail: wpporter@wisc.edu

S.-P. Huang (✉) · M.-C. Tu
Department of Life Sciences, National Taiwan Normal University, Taipei, Taiwan
e-mail: sphuang0711@gmail.com

M.-C. Tu
e-mail: biofv026@ntnu.edu.tw

C.-R. Chiou
School of Forestry and Resource Conservation, National Taiwan University, Taipei, Taiwan
e-mail: esclove@ntu.edu.tw

At high elevations, the canopy cover of vegetation greatly affects the thermal quality of habitats for reptiles. Forest canopy cover provides structural complexity, influences sun penetration, and hence affects the microclimates on the forest floor (Chen et al. 1999). Owing to their temperature-dependent physiology, reptiles generally behaviorally regulate their body temperature (T_b) (e.g., by basking; Pearson and Bradford 1976; Adolph 1990; Bauwens et al. 1990) for various physiological requirements. The thermal quality of a habitat affects the effectiveness of lizards' thermoregulation (Row and Blouin-Demers 2006), which is tightly linked to their ultimate fitness (Christian and Tracy 1981). For example, the interior of heavy forests at high elevations could be very cold for a heliothermic (sun-basking) reptile that requires high T_b for physiological function, repressing physiological function and/or curtailing time for other activities (e.g., predation, reproduction). The habitat's thermal quality is species-specific and is mainly determined by the species' distinct morphological, physiological, and behavioral properties, which influence their heat and mass balances (e.g., Huang et al. 2013).

Biophysical modeling is an approach used to investigate the thermal habitat suitability of animals. Based on the principle of conservation of energy, these models compute the microclimates that the animal experiences and calculate the animal's physiological and behavioral responses (e.g., Porter and Gates 1969; Porter et al. 1973) from species-specific properties (morphology, physiology, behavior). A biophysical model may extend its application to calculate the fitness components of the animals (e.g., active time, hatching rate; Kearney and Porter 2004; Kearney et al. 2009) in a landscape. With a spatial dataset (e.g., vegetation type, climate, elevation), such a model is able to simulate thermally suitable habitats/nest areas in a landscape (Bartelt et al. 2010; Huang et al. 2013) through a mechanistic understanding of the thermal effects on animals' physiology and behavior. Understanding the causal link of environmental variables and habitat suitability of a species is important, as it can provide critical information for management plans and conservation. It can also provide robust extrapolations of animal responses to novel climates (Kearney and Porter 2009). Without the causal understanding, the time and effort spent on conservation plans could lead to poor outcomes (Green 1995; Caughley and Gunn 1996).

This study uses a biophysical model, Niche Mapper™ (Porter and Mitchell 2006), to investigate the impact of landscape vegetation on habitat use of a high-elevation lizard, *Takydromus hsuehshanensis* (Sauria: Lacertidae) and to predict the thermal suitability of vegetation for this species in a future warmer climate. This small grassland lizard is endemic to Taiwan (>1,800 m elevation; Lue et al. 1999). It generally thermoregulates by shuttling between rocky surfaces, crevices formed by overlying rocks, and short bushes. This species has apparent basking behavior, good heat tolerance (Huang and Tu 2008), and high T_b for optimal locomotion (Huang and Tu 2009). In its current high elevation range, lush forest is the most common vegetation in the landscape (Fig. 1) due to its protection by law, with grasslands located mostly in the mountain tops above the treeline (approximately 3,000–3,200 m elevation) (for a photo illustrating the landscape mosaic of forest and grasslands, see Online Resource 1). This lizard prefers sun-exposed rocky slopes in grasslands. We propose that the preference of this species for grassland habitat over forest is very likely a result of its thermal requirements, as grasslands are warmer and sunnier than forests. If this assumption is correct, an increase of air temperature in the future warmer climate might also change the thermal suitability of the vegetation for this species.

To test the above hypothesis, we use Niche Mapper to simulate the thermally suitable habitats for *T. hsuehshanensis* in Taroko National Park (in areas >1,800 m). First, we estimate its preferred body temperatures, a trait often co-adapted with optimal performance temperatures for physiological requirements (Huey and Bennett 1987; Martin and Huey 2008). We also collect data on relevant animal properties for simulation from the literature or by measurement (Online Resource 2). We then compare the simulation results (T_b, maximum active time, and maximum digestive time in the active season) for different amounts of canopy cover (here, shade level, which refers to percent reduction of solar radiation incident on the ground) to understand the impact of forest cover on habitat suitability. Finally, we perform and analyze simulations using a landscape dataset of the study area (vegetation cover, climate, and topology) and compare the results for three major vegetation types (grasslands, coniferous forest, and coniferous–broadleaf forest).

The second goal of this study is to estimate the impact of a warmer climate on the thermal suitability of habitats for *T. hsuehshanensis*. We evaluate this effect in two steps as described above: at different shade levels and in the current landscape of Taroko National Park, assuming a 3 °C increase in air temperature (range 2.0–5.4 °C by the year 2100 predicted by the IPCC, 4th Assessment Report, A2 scenario, Meehl et al. 2007). Also, we compare the simulation results for three major vegetation types (grasslands, coniferous forest, and coniferous–broadleaf forest) to those obtained using current climate data.

Materials and methods

Animals and study areas

Takydromus hsuehshanensis is a small (snout–vent length 5–7 cm), ground-dwelling lizard. It is active from approximately May to October and hibernates the rest of the year.

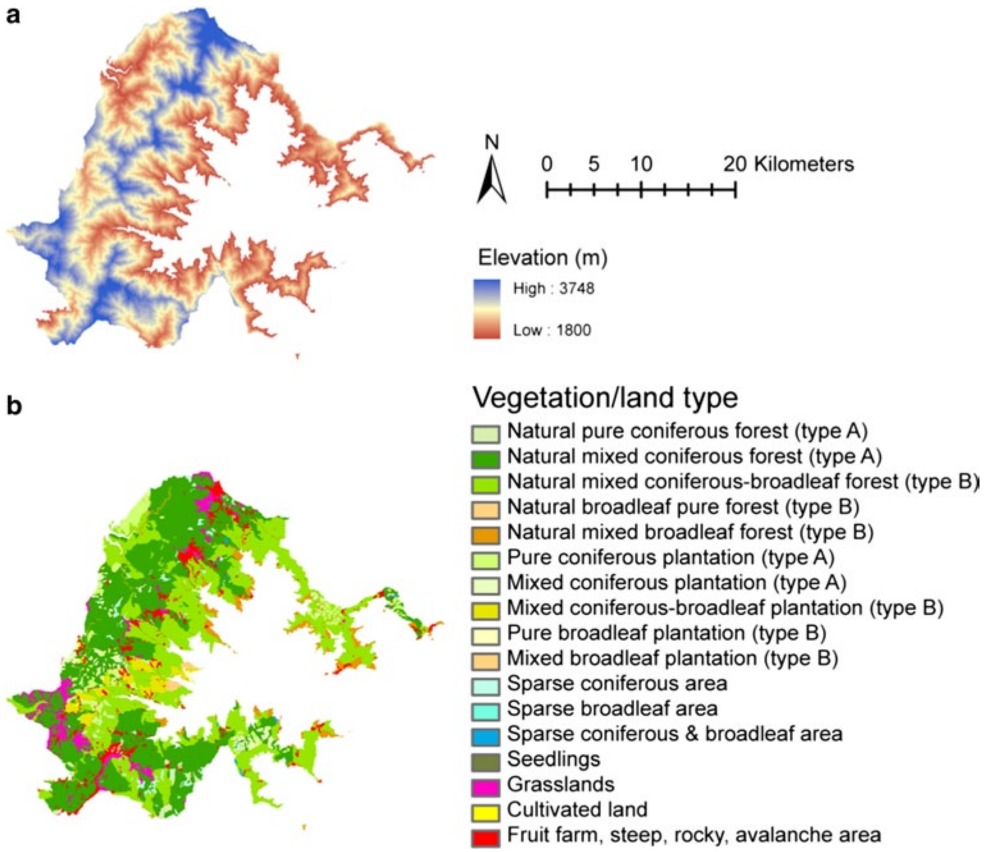

Fig. 1 **a** Elevation and **b** major vegetation/land types of the study area in Taroko National Park. The three classifications used in this study are: Type A forest (48.2 % of the study area): natural pure/mixed coniferous forest, pure/mixed coniferous plantation; Type B forest (40.7 % of the study area): natural mixed coniferous–broadleaf forest, mixed coniferous–broadleaf plantation, broadleaf forest; Grasslands (3.8 % of the study area). The grid cell size is 40 × 40 m

It prefers open habitats located in sun-exposed grasslands, characterized by large scattered stones with short bushes interspersed or clumped in the rocky substrate. During a sunny day, it generally basks on the warm stones, shuttling among open sites, crevices formed by overlying rocks, and short bushes for thermoregulation.

Animal collection and maintenance

We collected male lizards from May to July 2010 (body mass = 4.7 ± 0.9 g, snout–vent length = 61.1 ± 3.4 mm, $n = 23$) from Mt. Hehuan (2,400–3,200 m elevation, Nantou) (collection permit #201002040066, Council of Agriculture, Executive Yuan, Taiwan). We housed the lizards individually in plastic cages (20 cm long × 10 cm wide × 15 cm high) containing dry grass and a piece of paper as the substrate and a piece of tile as shelter. We provided the lizards with water ad libitum and with crickets dusted with vitamin powder twice a week. The room was maintained at 25 °C, with a photoperiod cycle of 12 h light:12 h dark. An 80-W light bulb hung above the cage during the day for thermoregulation.

Animal properties

We measured and collected data required for simulation, including body size, skin solar reflectivity from 350 to 2,500 nm (~97 % of the incident solar bandwidth), metabolic rates, preferred body temperatures, etc. (for details, see model parameterization, Online Resource 2). We measured the preferred body temperature of male individuals from July through October 2010. A stainless steel thermal gradient (160 cm long × 20 cm wide × 20 cm high) was set in a 14 °C walk-in chamber with a 12 h dark:12 h light photoperiod. This equipment generated an approximately linear gradient that allowed the lizards to maintain T_bs ranging from 5 to 45 °C (calibrated with the T_b of two deceased specimens). To generate the temperature gradient, we hung two heaters above the gradient: a 200-W ceramic heater at 5 cm and a 100-W ceramic heater at 60 cm from one end (warm end), and put a heating pad on the wall of the warm end. To create the cold temperature at the cold end, we pumped a water–glycerol mixture (0 °C) through copper pipes embedded underneath the substrate at the cold end. Inside the thermal gradient, we put a thin (~3 cm) layer of sand as substrate. We installed ten water dishes (1.5 cm in diameter and height) about 15 cm apart along the inside of the gradient for drinking.

The lizards' T_b was measured every 30 s by a data logger (type 306; Center Technology, Taiwan) with a K-type thermocouple (36 gauge) inserted 1 cm into the cloaca of the lizards and secured to the tail with surgical tape. A 160-cm-long thin stainless rod (2 mm diameter) was fastened 20 cm above the floor of the thermogradient, with a paper clip hung on it. We threaded the thermocouple wire through the paper clip and then fixed the thermocouple wire to the paper clip at about 30 cm from the test lizards to prevent tangling. The paper clip glided smoothly along the rod as the lizards moved, leaving them unimpeded.

We measured the preferred temperatures of the lizards in fasting and digesting states ($n = 11$–12/state) following 1 day of habituation in the thermal gradient. Before measurements, we deprived all the lizards of food for 2 days, but we provided the lizards in the digesting group with crickets at 0700 hours on the experimental day (crickets weighing 7.4 ± 2.8 % of lizards' body mass were consumed, mean ± 1 SD, $n = 12$). The measurement began at 0900 hours and ended at 1900 hours. For each individual, the minimum and maximum T_b value collected from 1000 to 1900 hours was taken as the voluntary T_b minimum (VT_{min}) and voluntary T_b maximum (VT_{max}), respectively. The mean of the T_b was taken as preferred temperature (T_{pref}) when data followed a normal distribution; otherwise the median value was used as T_{pref}.

Model description

(1) Microclimate model

Niche Mapper contains a microclimate model and an ectotherm model (for a detailed description, see McCullough and Porter 1971; Porter et al. 1973). The microclimate model uses macroclimate environmental data as input (see model parameterization, Online Resource 2) to compute the hourly microclimates available to a lizard, including temperature (1.0 cm above ground, and 0.2, 0.50, 1.0, and 2.0 m below ground), solar radiation, humidity, and wind velocity (1 cm above ground). At each given location, the model computed the hourly microclimate for a simulated day in both the sunniest and shadiest environments based on the setting of the shade level range in that location. The ectotherm model used the hourly climate outputs for calculation of the interaction of reptiles and their microclimates, assuming lizards can move freely between the sunniest and shadiest environments for thermoregulation.

The microclimate model has been tested in various habitats (e.g., Porter et al. 1973; Kearney and Porter 2004; Kearney et al. 2009; Bartelt et al. 2010), including our study area (Huang et al. 2013). We conducted landscape simulation with a fine-scale spatial dataset (grid cell size = 40 × 40 m), currently the finest size available. This grid cell size provides a good spatial resolution to differentiate the major vegetation types because forests and grasslands in our study area are generally much larger than the grid cell size. There are no data available to compare the lizards' maximum movement to the grid cell size. However, this lizard species tends to congregate in local grassland habitats for foraging, mating, and reproduction (S.P. Huang, personal observation). It has not been documented in the interior of heavy forests. As these large heavily forested areas were simulated with smaller grid cells, the simulation results allowed us to test whether these forests are thermally suitable habitats and/or whether they act as barriers of cold that prevent lizards from migrating between grassland habitats, by examining their T_b-related performance (e.g., active time, digestive time). We simulated lizards' physiological function on the middle day of each month, as a surrogate for all the days in the month, in the active season. Using an average monthly climate is sufficient for mechanistic models in analyzing a species' distribution range (Kearney et al. 2012).

Model parameterization for this study is shown in Online Resource 2. The model computed the air temperature of each grid cell at different elevations with an adiabatic lapse rate (for minimum daily temperature = $-4.6\ ^{\circ}\mathrm{C\ km^{-1}}$; for maximum daily temperature = $-5.3\ ^{\circ}\mathrm{C\ km^{-1}}$). The daily 2-m wind speed (expressed as minimum–maximum values) was set to 0.1–1.0 $\mathrm{m\ s^{-1}}$ for all areas except for open areas, where it was set to 0.1–4.0 $\mathrm{m\ s^{-1}}$. The relative humidity at 2 m above ground was set to 70–100 % (average annual relative humidity, Alishan at 2,413 m elevation, Yushan Station at 3,850 m elevation; Central Weather Bureau, 1981–2010). The setting of the monthly cloud cover range was based on values from satellites (MODIS-terra, MODIS-aqua) passing daily over Taroko National Park (January 2009–October 2011). The forest canopy cover determines the range of shade levels of the forest (Online Resource 3).

(2) Ectotherm model

The ectotherm model simulated the maximum hours lizards were able to be active or digesting for the middle day of each active month (May–October) in the given location. This model first estimated hourly T_bs by iteratively solving the steady-state heat balance equation:

$$Q_{\mathrm{gen}} + Q_{\mathrm{solar}} + Q_{\mathrm{IR,\ in}} = Q_{\mathrm{evap}} + Q_{\mathrm{conv}} + Q_{\mathrm{IR,\ out}} + Q_{\mathrm{cond}}$$

where Q_{gen} refers to generated metabolic heat, Q_{solar} refers to solar energy absorbed, $Q_{IR,\ in}$ and $Q_{IR,\ out}$ are incoming and outgoing thermal infrared radiation, and Q_{evap}, Q_{conv}, and Q_{cond} are evaporative heat, convective heat, and conductive heat transfer, respectively. Mechanism equations for each term are described elsewhere (Porter et al. 1973; Porter and Mitchell 2006). The hourly air and ground temperatures output from microclimate model was used for calculating heat exchange between the animal and its environments in each grid cell. Also, as this lizard species normally goes underground when above ground environments are not suitable (e.g., avoiding extreme cold and high temperatures, predators), our model assumed that lizards would retreat below ground if the above-ground environment did not allow them to maintain their T_b in the range between VT_{min} and VT_{max}. The model simulated the lizards' maximum active time and digestive time as well as the daytime T_b (i.e., mean of hourly estimated T_bs from 0700 to 1900 hours). The active and digestive times are the maximum number of hours that lizards can maintain T_b within the fasting VT range and the digesting VT range, respectively.

Shade-level and landscape simulations

We simulated the maximum active and digestive times of adult lizards (body mass = 4.5 g, total length = 19.4 cm) under two conditions: (1) in five shade levels (0, 25, 50, 75, 100 %) representing the percentage of solar radiation reduction by the forest canopy, at 3,000 m elevation, and (2) within the landscape of Taroko National Park (the area above 1,800 m).

According to empirical work by other investigators (F.S. Chou, C.K. Yang, C.K. Liao, and T.T. Chen, personal communication, 2005), four major vegetation types are classified in our study area: (1) alpine thicket formation: mainly composed of Yushan cane (*Yushania niitakayamensis*) thickets and scattered single seed juniper (*Juniperus squamata*) thickets, characterized by short bushes (0.5–1 m average height) in rocky places; (2) needle-leaf forest formation: mainly composed of Taiwan fir (*Abies kawakamii*) and Chinese hemlock (*Tsuga chinensis*) (20–25 m average height), generally with Yushan cane and small bushes as dominant understory plants; (3) needle-leaf and broadleaf mixed forest formation: Formosa pine (*Pinus taiwanensis*) forest type and Taiwan rhododendron (*Rhododendron leptosanthum*)—Chinese hemlock forest type; and (4) evergreen broadleaf forest formation: Kusano machilus (*Machilus japonica*)—arishan oak (*Cyclobalanopsis stenophylloides*) forest type, with a variety of plants as understory (e.g., small bushes, *Pourthiaea beauverdiana*, *Symplocos stellaris*) and groundcover (e.g., ferns, *Plagiogyria formosana*, *Monachosorum henryi*).

Here, we selected three major vegetation types (92.8 % of the total study area) for further analyses, with consideration of vegetation features and occupied area: (1) grasslands (Yushan cane thickets, main type of alpine thicket formation, 3.9 % of the total study area); (2) needle-leaf forest formation (termed Type A forest, 48.2 % of the total study area), including coniferous forest and coniferous plantation; and (3) needle-leaf and broadleaf mixed forest formation and evergreen broadleaf forest formation (termed Type B forest, 40.7 % of the total study area), including mixed coniferous–broadleaf forest, coniferous–broadleaf plantation, and broadleaf forest. Furthermore, we analyzed the simulation results for these vegetation types at three elevation ranges (3,000–3,784, 2,400–2,999, 1,800–2,399 m).

We prepared the spatial dataset for Taroko National Park, including latitude, longitude, elevation, aspect, slope, and vegetation/land types for each grid cell (40 × 40 m per cell, 363,804 grid cells). We calculated the elevation, aspect, and slope from a digital terrain map (40 × 40 m grid cell; Aerial Survey Office, Taiwan Forestry Bureau) using ESRI ArcMap v.9.1. Figure 1 illustrates the elevation and the major vegetation/land types in the study area. We assigned specific shade levels to each type of vegetation/land use (Taiwan Forestry Bureau) during the active season (from May to October): Type A forest, 70–90 %; Type B forest 70–90 % from May to August, 50–80 % in September, 40–70 % in October; grasslands: 10–40 %. These assignments are based on our previous work (Huang et al. 2013) using approaches that combined data collected from aerial photo-based spatial datasets (Taiwan Forestry Bureau) and fisheye lens photos to estimate canopy cover for major forest types (details described in Online Resource 3).

Statistics

We tested the normality of the distribution of the T_{pref}, VT_{min}, and VT_{max} data using the Shapiro–Wilk *W* test. We tested whether the VT_{min} and VT_{max} differed between fasting and digestive states using the Student's *t* test when the data followed a normal distribution; otherwise, we used the Mann–Whitney *U* test. We conducted the statistical tests using JMP 5.0.1 (SAS Institute, NC, USA, 2003). We presented all values as the mean ± 1 standard deviation or median with range unless otherwise noted.

Results

Animal properties

Animal properties used for model simulation are listed in Table S1 (Online Resource 2). In the preferred body temperature data, we detected two outliers; these two lizards remained at the same place in the gradient during the experiment (mean = 13.2 ± 0.2 °C in the fasting lizard and 21.2 ± 0.2 °C in the digesting lizard). The T_{pref} was not significantly different between fasting and digesting states with the outliers omitted (=32.1 ± 1.6 °C for both states, $n = 10–11$, $P = 0.86$) or with the outliers included (fasting state: median = 32.1 °C, range = 13.2–34.0 °C, $n = 11$; digesting state: median = 32.2 °C, range = 21.2–34.0 °C, $n = 12$). The VT_{max} in the fasting state (median = 37.1 °C, range = 32.5–38.5 °C) did not significantly differ from that in the digesting state (median = 37.4 °C,

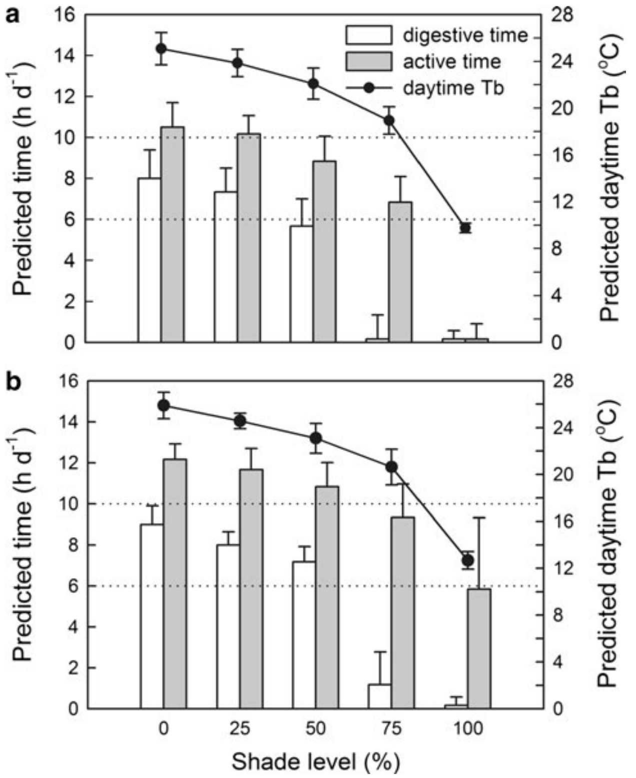

Fig. 2 The active time, digestive time, and daytime body temperature (mean ± 1SD) of *Takydromus hsuehshanensis* predicted at 5 shade levels in **a** the current climate and **b** a warmer climate during the active season. Values are the average of estimated results for the middle day of each month from May to October. Daytime T_b:T_bs estimated from 0700 to 1900 hours, using VT range = 23.0–38.6 °C for simulation. Wind speed at 2 m = 0.1–1.0 m s^{-1}. Values for other parameters are listed in Table S1 (Online Resource 2)

range = 35.4–40.1 °C) ($P > 0.05$). Although the VT_{min} in the fasting state (median = 23.9 °C) was not significantly different from that in the digesting state (median = 25.9 °C), it had a larger variance (range = 9.0–30.2 °C) than in the digesting state (range = 18.9–28.6 °C) ($P < 0.001$, Levene's test).

We used the VT ranges, defined as the range between the lower 95 % CI of the mean VT_{min} and the upper 95 % CI of the mean VT_{max} (digesting VT range = 23.0–38.6 °C; fasting VT range = 14.8–37.8 °C) in the model to simulate the maximum active and digestive times.

Niche Mapper simulation

(1) Impact of canopy cover on daytime $\boldsymbol{T_b}$, and maximum active and digestive times

The simulated daytime T_b, maximum active time, and maximum digestive time drop with increasing shade levels. In the current climate (Fig. 2a), the maximum active and digestive times drop from highest (active time = 10.5 h day^{-1}, digestive time = 8.0 h day^{-1}) at 0 % shade level to very minimal at 100 % shade level (0.2 h day^{-1} for both active and digestive times). Similarly, the predicted daytime T_b dropped from 25.1 ± 0.8 °C at 0 % shade level to 9.8 ± 0.7 °C at 100 % shade level. In the simulated warmer climate, all these estimates are higher than those the model predicted for the current climate. Note that, though the maximum active time increases, the digestive time remains very short at 75 % (1.1 h day^{-1}) and 100 % shade levels (0.2 h day^{-1}; Fig. 2b).

(2) Thermally suitable habitats in Taroko National Park (area >1,800 m)

A. Landscape simulation In the current climate, the predicted active times were higher along the border and lower in the central part of the study areas (Fig. 3a). The model predicted that most places provide reasonable activity time (90.0 % with >6 h day^{-1}). In contrast, only 7.3 and 28.9 % of the study area can provide sufficient digestive time, >6 and >3 h day^{-1}, respectively; most of the area (71.0 %) provides very short digestive times (<3 h day^{-1}) (Fig. 3b).

The predicted active and digestive times increase in response to future warmer climates (Fig. 3c, d). For example, the areas providing active and digestive times for more than 6 h day^{-1} increase to 90.0 and 25.6 %, respectively. Up to 69.0 % of the area provides digestive time for more than 3 h day^{-1}.

B. Effect of three major vegetation types on active and digestive times Both the predicted active and digestive times decrease with increasing elevation in all of the three vegetation types (Fig. 4). In the current climate, grasslands were predicted to provide more time in activity (8.9–10.0 h day^{-1}) and digestion (6.7–7.7 h day^{-1}) than the two forest types (active time = 5.5–9.7 h day^{-1}, digestive time = 0.3–2.9 h day^{-1}) (Fig. 4a, c). In the simulated warmer climate, both the predicted active and digestive times increase in all three vegetation types (Fig. 4b, d), but the digestive time remains very low in the two forest types at high elevations (>3,000 m, 0.9–1.9 h day^{-1}) (Fig. 4d). Note that the predicted digestive time in both forest types in the warmer climate remains lower than that predicted for grasslands.

C. Sensitivity analyses The results of our model are sensitive to the settings of solar radiation and wind speeds. In general, increasing solar radiation increases the benefit to this species, while increasing wind speed reduces the benefit to or exacerbates the negative effect on this species. In landscape simulation results, a higher wind speed (compared with values listed in Table S1, Online Resource 2) results in forests and grasslands that are less thermally suitable. Detailed descriptions are in sensitivity analyses (Online Resource 4).

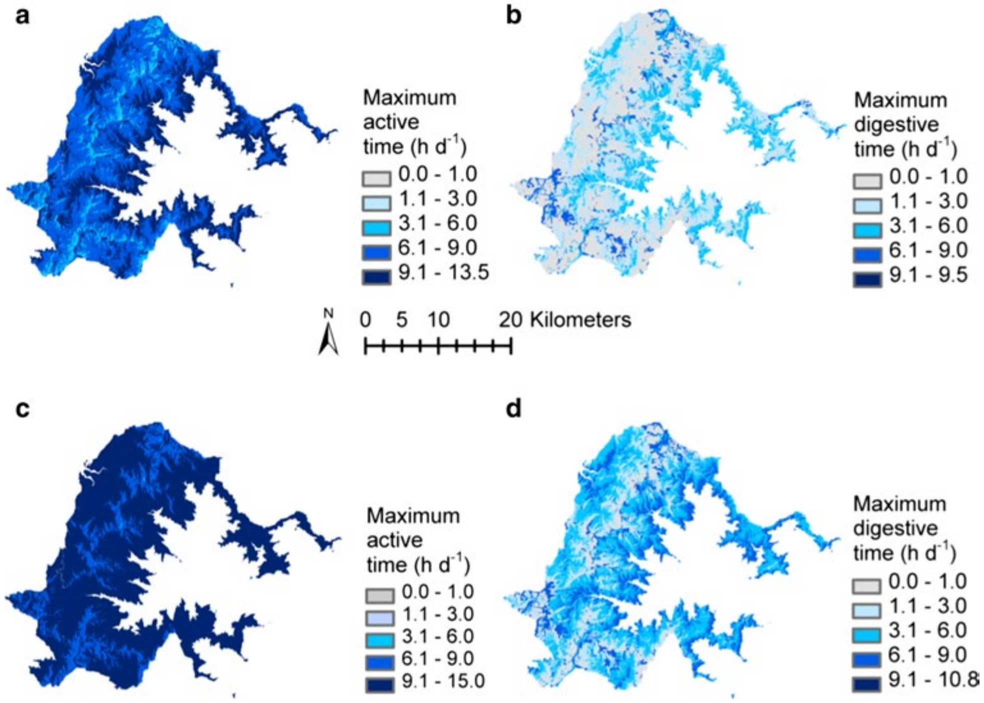

Fig. 3 The predicted maximum active and digestive times in Taroko National Park in **a**, **b** the current climate and **c**, **d** an increase in 3 °C air temperature given the current vegetation pattern. The maximum times are the average daily hours simulated for the middle day of each month from May to October. The grid cell size is 40 × 40 m

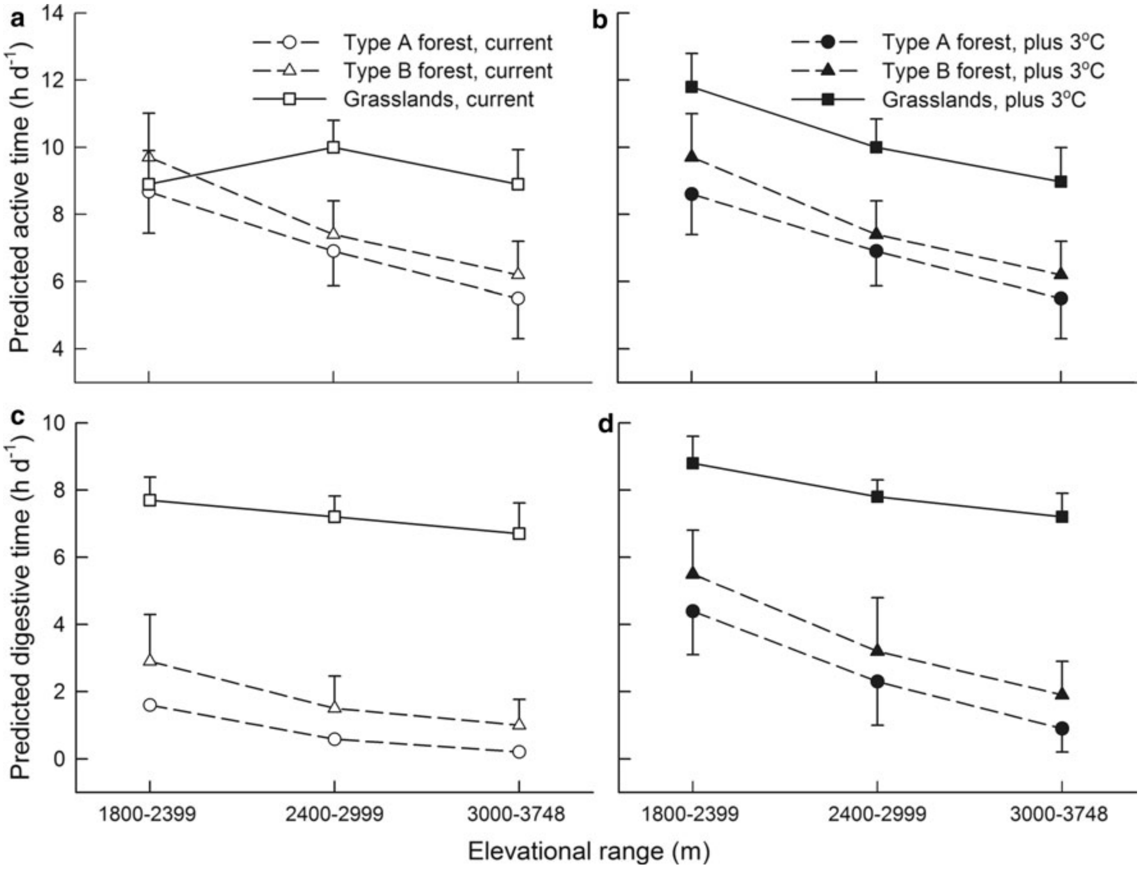

Fig. 4 **a**, **b** Maximum active time and **c**, **d** digestive time (mean ± 1SD) predicted for *T. hsuehshanensis* in three vegetation types at 3 elevational ranges on the middle days of active months in the current climate (*hollow symbols*) and a warmer climate (*filled symbols*). Type A forest (*circles*): coniferous forest, coniferous plantation; type B forest (*triangles*): coniferous–broadleaf forest, coniferous–broadleaf plantation, and broadleaf forest; grasslands (*squares*)

Discussion

Our study investigates the thermally suitable habitats of the high-elevation reptile *T. hsuehshanensis* and predicts its potential response to future warmer climates. Our results indicate (1) an increase in forest cover reduces the thermal suitability of habitats, (2) the grasslands are more thermally suitable over current heavy forests for thermal physiological requirements, and (3) the future landscape vegetation pattern will impact the response of this species to a warmer climate.

Habitat quality, landscape vegetation, and thermal requirements of *T. hsuehshanensis*

Evaluation of the habitat quality for reptiles requires the integration of many factors (e.g., thermal quality, habitat attributes, resource availability). Here, we address the effect of vegetation features, an essential component affecting microclimate (Chen et al. 1999), on the habitat thermal quality of *T. hsuehshanensis*. At most high elevation areas in Taiwan, the forests are aggregated into large areas due to their protection by law. Vertical stratification of the forests (for details, see "Materials and methods") can block up to 81 % of the solar radiation incident on the coniferous forest floor (Wei and Lin, personal communication), resulting in very cold floor temperatures for the terrestrial reptiles. On the other hand, grasslands are characterized by short homogeneous structure on rocky areas, allowing more solar radiation to be absorbed by the ground. From the lizard's perspective, thermal environments in the grasslands were warmer, as the lizard can elevate its T_b by basking and absorbing heat by conduction and thermal radiation from warm rocky ground. A warm ground will also locally warm the air creating convective warming, too.

Our results indicate that the current grassland provides more thermally suitable habitats for *T. hsuehshanensis* than heavy forest for its thermal requirements. Several pieces of data also indicate that this species requires high T_b for physiological functions. For example, this species has high T_{pref} (32.1 °C) and optimal T_b for locomotion (e.g., ~35.0 °C; Huang and Tu 2009). The T_{pref} is often co-adapted with the optimal performance temperature to meet physiological requirements (Huey and Bennett 1987; Martin and Huey 2008). Temperature-dependent locomotor performance also affects an individual's fitness in critical activities (capturing prey, Jayne and Bennett 1990; escaping predators, Christian and Tracy 1981). In addition, this species elevates T_b by basking at high elevations ($T_b = 32.0$–36.2 °C, $n = 4$ at air temperature ~15 °C at 3,000 m; S.P. Huang, personal observation).

We illustrate that the level of forest canopy cover is a critical element affecting thermal habitats for this species (Fig. 2). As the shade level increases, the thermal environment gradually cools, decreasing lizards' T_bs and curtailing the maximum time for activity and digestion. Owing to its broad fasting VT range, the model predicts that this species has the capability (judged by active time) to exploit a wide range of shade levels. However, even if small lizards are able to find sunny spots anywhere, the thermal environments created by different vegetation types can impact their T_b differently. Basking lizards would dissipate heat to cold surroundings such as the forest floor, while they may absorb heat from warm surroundings such as warm rocks in open sunny places. Since their T_bs predicted at high shade levels are very low (e.g., 18 °C predicted for 75 % shade) for digestion, the digestive time is restricted. The individuals seen on our field trips ($n = 94$, years 2005–2010) were in cells predicted to provide reasonable digestion time (62 % cells: >7.0 h day^{-1}, 38 % cells: 3.0–6.9 h day^{-1}, 42 grid cells total). From an energetic perspective, sunny places rather than heavy forest are more thermally suitable to this species, consistent with results predicted for another heliothermic reptile from the same study area (Huang et al. 2013). Many reptiles choose open habitats and adopt basking behavior in high elevations (Adolph 1990; Bauwens et al. 1990; Christian 1998; Huey and Webster 1976; Pearson and Bradford 1976). Other empirical studies also report that removing forest canopy cover restored a reptile assemblage (Pike et al. 2011), that an increase of canopy cover reduces habitat suitability for a nocturnal snake (Pringle et al. 2003), and that expanding forests could be related to the local extinction of mountain reptile populations (Jäjji and Baur 1999).

Here, our simulation results show that thermal environments generated by the landscape vegetation patterns affect the thermal habitat suitability for this lizard species. Our model predicts that, in Taroko National Park, sunny open places like grasslands are more thermally habitable for this species (Fig. 4). In the current landscape, these thermally suitable habitats are scarce and sparsely distributed, while the coniferous, coniferous–broadleaf, and broadleaf forests occupy up to 88.9 % of the total area (Fig. 1b) due to the ban on forest logging and thinning. Even in summer, the air temperature in the spruce forest interior is too low (mean ± 1SD, 11.0 ± 2.9 °C, hourly temperature recordings: range: 5.7–17.1 °C, 3,005 m; July 1–15, 2005; Taiwan Endemic Species Research Institute), for this lizard species' normal function, which supports our assertion that forest is thermally disadvantageous to this species.

Potential effect of vegetation pattern on altitudinal distribution of *T. hsuehshanensis*

Although a species' distribution ranges can be shaped by factors other than temperature, such as historical events and biological or abiotic factors (Gaston 2003), here we suggest that the thermal environment generated by current landscape vegetation cover plays an important role in the current altitudinal range of *T. hsuehshanensis*. This species is a high-temperature specialist and requires open places/grasslands to meet its thermal requirements at high elevations. The predominant high-elevation vegetation types, however, generate a very cold environment; their distribution pattern likely constrains this lizard species to the small patches of available grassland and impedes it from moving downslope. Moreover, the fog zone currently below its elevation range (~2,400 m) can enhance the cooling impact of forest as fog further blocks solar radiation, generating a "cold barrier" that prohibits this species from spreading downslope.

Potential responses of *T. hsuehshanensis* to a warmer temperature due to climate change

We predict that, when the vegetation cover remains unchanged, *T. hsuehshanensis* may benefit from a warmer climate by having more time for activity and digestion (Fig. 3c, d). This prediction is consistent with other studies of cold climate lizards (e.g., Deutsch et al. 2008; Huey et al. 2009). Empirical studies have also shown a benefit gained by ectotherms from increased warmth in the past decade(s) (e.g., lizard: increased survival rates, body size, female fecundity, Chamaillé-Jammes et al. 2006; frog: increased winter viability, McCaffery and Maxell 2010; insect: increased thermally suitable habitats, Thomas et al. 2001; Davies et al. 2006).

However, we also note that the response of *T. hsuehshanensis* to climate change will be greatly affected by the vegetation pattern of the future. The coniferous forest has been expanding into grasslands and moving upslope in our study area during the past decades (C.T. Chen, unpublished data), like other mountain vegetation around the world (Walther 2003). If forest expansion continues, *T. hsuehshanensis* may experience reductions in population size due to a shrinking of suitable habitat area (e.g., Hokit and Branch 2003). This species may also exploit less suitable forest habitats and/or move downslope, as forest habitats at lower elevations are more thermally suitable than they are at high elevations (Fig. 4d). Other factors can also affect the response of this species. For example, if the warmer habitats become drier, lizards might not be as active as we suggest due to behavioral changes related to dehydration (Wilson et al. 1989; Lorenzon et al. 1999). Biological factors, such as prey and predator abundance and a potential increase in competition due to the upslope movement of lowland lizard species (e.g. Raxworthy et al. 2008), could also affect this species' response.

The potential influence of wind speed on our findings merits discussion because our model is very sensitive to wind speed ("Results" see Online Resource 4). We found that the prediction of a negative effect on this species from dense vegetation remains robust because wind speeds that are higher than our setting (0.1–1.0 m s^{-1}) intensify the negative effect of heavy forest on lizards. On the other hand, the predicted advantage of this species in grasslands should generally be greater in calmer sites and lesser in windier sites relative to that predicted with the default wind speed setting (0.1–4.0 m s^{-1}). If wind speeds in the future warmer climate are stronger than the default setting, the predicted advantage for this species in grasslands may also be reduced.

Potential warming effects on reptiles living in mountain ecosystem

We note that the impact of future warming effects on the reptiles can be modulated by changes in thermally suitable habitats, due to alteration of landscape vegetation patterns of the future. Currently, the empirical studies regarding the impact of the warming climate on mountain reptiles still remain scarce. Mountain endemics are sensitive to climate change caused impacts such as habitat loss and upslope displacement of species distributions (Rull and Vegas-Vilarrúbia 2006). These changes have been documented to crucially threaten the mountain herpetological assemblage in the tropics, e.g., Madagascar (Raxworthy et al. 2008). Nevertheless, current warming climates were observed to benefit some mountain reptiles, such as the common lizard (*Lacerta vivipara*) inhabiting southern France, by increasing survival rates, body size, and female fecundity (Chamaillé-Jammes et al. 2006). As the effect of climate warming on species can act on species through multiple complex ways (changes in climates, vegetation, species interaction, human activity), species-specific responses to future climate change are therefore challenging to forecast; however, a prediction based on causal relationships between vegetation pattern and reptiles' thermal requirements could help orient species' conservation, through management of wildlife habitats, and potentially reduce negative impacts of climate warming changes on these species.

Future perspectives

Although results from our mechanistic model remain preliminary, they have the potential to help guide further species conservation and forest management. Here, we propose three perspectives to consider for future studies on mountain ectotherms. First, many studies to date have addressed heliothermic species (e.g., this study; Chamaillé-Jammes et al. 2006), which are generally expected to benefit from a warmer climate. More studies are required for non-heliothermic and forest interior lizards, which could be more susceptible to temperature and hence warmer climates. Second, examination of whether or not a species' physiology can rapidly adjust to a changing climate (e.g., Leal and Gunderson 2012) should be an important consideration in future studies. Finally, regional climate data (precipitation, humidity, temperature range, etc.) are often not available, yet are important for future studies.

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