

Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders

Matthew E. Gifford and Kenneth H. Kozak

M. E. Gifford (megifford@ualr.edu) and K. H. Kozak, Bell Museum of Natural History, Univ. of Minnesota, St. Paul, MN 55108, USA. Present address of MEG: Dept of Biology, Univ. of Arkansas at Little Rock, Little Rock, AR 72204, USA. KHK also at: Dept of Fisheries, Wildlife, and Conservation Biology, Univ. of Minnesota, St. Paul, MN 55108, USA.

Many animal and plant taxa reach their highest endemism and species richness in montane regions. The study of elevational range limits is central to understanding this widespread pattern and to predicting the responses of montane species to climate change. Yet, because large-scale manipulations of the distributions of most species are difficult, the causes of species' elevational range limits (e.g. competitive interactions, physiological specialization) are poorly understood. Here, we harness the power of new mechanistic approaches to dissect the factors that underlie the elevational replacement of two salamander species in the Appalachian Highlands. Our results challenge the long-held idea that competitive interactions drive the lower elevational range limits of montane species and that physiological stress prevents low-elevation species from expanding to high elevations. We show that physiological constraints drive the lower elevational range limit of the montane-endemic species, *Plethodon jordani*. Conversely, we find that competition with *P. jordani* prevents the low-elevation species, *P. teyahalee*, from expanding its range to include higher-elevation habitats. These results are broadly consistent with the biogeography and behavior of other montane species, suggesting that similar mechanisms underlie patterns of elevational zonation across a variety of taxa and montane regions. To the extent that our findings are taxonomically and geographically widespread, these results challenge the idea that competitive release at species' lower elevational range limits is driving the downslope range shifts exhibit by some montane taxa. Instead, our results raise the sobering possibility that even small changes in climate might cause erosion of the ranges of many high-elevation species.

Many animal and plant taxa reach their highest endemism and species richness in montane regions (Myers et al. 2000). Consequently, understanding the causes of species' elevational range limits has important implications for understanding global variation in biodiversity. The study of elevational range limits is also central to predicting large-scale responses of biodiversity to environmental change. Many of the species that inhabit montane biodiversity hotspots occur exclusively in high-elevation habitats (i.e. they are montane endemics) and, therefore, may be particularly susceptible to rapid changes in climate (Parmesan 2006).

Despite far-reaching implications, the factors that limit species' elevational ranges are poorly understood. In some montane regions, species are restricted to high elevations as a result of extreme climatic conditions at lower elevations. For example, in 'sky islands' of the southwestern United States, desert conditions in the lowlands limit many species to the more hospitable mesic forest habitats in the highlands (Knowles et al. 2007, Galbreath et al. 2009, Waltari and Guralnick 2009). However, in many montane regions the lower elevational range limits of species are not associated with dramatic gradients in temperature and precipitation, but rather, with the geographic distributions of closely-related species. A classic explanation for this pattern is that competition with lowland species prevents montane species

from colonizing low-elevation habitats (Diamond 1970, 1973, Jaeger 1971a, b, McArthur 1972, Terborgh and Weske 1975, Jankowski et al. 2010). Conversely, the upper limits of species' elevational ranges are often attributed harsh climatic conditions (e.g. cold) at high elevations (McArthur 1972).

Whether competition or abiotic factors drive the lower elevational limits of species is critical to predicting how taxa will respond to projected changes in climate, and also to understanding why montane species exhibit variation in the extent to which they have shifted their elevational ranges in the last century (Lenoir et al. 2010, Crimmins et al. 2011). However, given the difficulty of experimentally manipulating the distributions of species at regional scales, understanding the factors that limit species' elevational ranges remains a formidable challenge. Mechanistic niche models offer a powerful approach to untangling abiotic and biotic constraints on species' distributions (Kearney and Porter 2009). The mechanistic approach links functional traits and microclimatic data to predict spatial variation in important range-limiting parameters (e.g. growth rate, energy expenditure, activity time; Kearney and Porter 2004). Biotic interactions are also readily incorporated into mechanism-based models of species distributions (Buckley and Roughgarden 2005, 2006, Buckley 2008). Thus, unlike correlative approaches, which model species' distributions by relating occurrence

data to spatial environmental data, mechanistic niche models explicitly incorporate processes that limit the ranges of species (but see Buckley et al. 2010 for a discussion of the circumstances under which correlative models may outperform mechanistic models).

Here, we use a mechanistic approach to dissect the ecological causes of species elevational range limits in the southern Appalachian Mountains of North America, a region that harbors exceptionally high endemism for many plant and animal taxa. Our focus is on woodland salamanders of the genus *Plethodon*, which reaches its highest endemism and species richness in the southern Appalachian Mountains (Kozak and Wiens 2010). A widespread biogeographic pattern in *Plethodon* is elevational replacement, whereby a geographically restricted high-elevation species (i.e. a montane endemic) is replaced at lower elevations by a more widespread species (Highton 1995). Although both the highlands and lowlands consist primarily of temperate deciduous forest, recent studies suggest that specialization for relatively subtle differences in temperature and precipitation may limit the elevational ranges of species (Kozak and Wiens 2006, 2010). However, there is also a large body of literature suggesting that interspecific competition among species of *Plethodon* is common (Anthony et al. 1997, Adams 2004, 2007, Marshall et al. 2004) and could play a role in the geographic replacement of species along elevational climatic gradients (Hairston 1951, 1980, Jaeger 1970, Nishikawa 1985). To date, no studies have explicitly addressed whether interspecific competition, physiological specialization, or some combination of the two, drive this pattern.

In this study, we use physiological, morphological, life-history, and microclimatic data to develop models that predict the equilibrium abundances of two species that are parapatrically distributed along an elevational gradient in Great Smoky Mountains National Park, USA. To explore the roles of competition and climatic specialization in limiting the species' distributions, we compare the abundance predictions of two mechanistic models (one without and one with competitive interactions) to field surface counts of salamanders. As a complementary approach, we also develop a biophysical threshold-based model to predict the energetically-determined range limits for both species.

Methods

To explore the ecological mechanisms underlying the elevational range limits of *P. jordani* and *P. teyahalee*, we employed two different mechanistic models: a population dynamic model that estimates spatial changes in salamander abundance in the presence and absence of interspecific competition, and a bioenergetic-threshold model that predicts the spatial distribution of suitable habitats by estimating whether salamanders can acquire sufficient energy to meet their metabolic and reproductive demands. Both models use a microclimate model (Fridley 2009) to estimate nighttime variation in operative body temperatures and evaporative water loss, which determine the amount of time that a salamander can be surface active and foraging at a given location. For each species, we mapped the predicted variation in salamander abundance and the geographic distribution

predicted by the bioenergetic-threshold model in GRASS GIS using a 90-m resolution digital elevation model (NASA Shuttle Radar Topography Mission). All modeling was conducted in R ver. 2.10.1 (code available upon request from the senior author).

Population dynamic model

The population dynamic model estimates spatial variation in salamander abundance based on the net energetic yield of foraging. The model was originally developed by Roughgarden (1997) and was extended to include temperature dependence of activity and foraging (Buckley and Roughgarden 2005, 2006). We further extended this model to include hydric constraints on potential foraging time in salamanders (*PFT*). The model incorporates empirical estimates of foraging velocity, prey density, and species-specific metabolic rates. Previous authors have discussed the modeling framework extensively (Pacala and Silander 1985, Buckley and Roughgarden 2005, 2006, Buckley 2008); therefore we only provide a brief overview of the model.

Salamanders are assumed to forage along a linear transect, which simplifies the spatial dynamics of the model and produces predictions comparable to linear transect counts. The energetic yield per unit time of foraging, $E(r)$ (kJ), within a given radius, r (m), is determined by the difference between energetic inputs and costs divided by the total time spent foraging:

$$E(r) = \frac{e_j - e_w t_w(r) - e_p t_p(r)}{t_w(r) + t_p(r)}$$

where e_j (kJ) is the energy per prey item; e_w (kJ s⁻¹) and e_p (kJ s⁻¹) are the energy expended per unit time waiting for and pursuing prey, respectively; and t_w (s) and t_p (s) represent the time spent waiting for and pursuing prey, respectively. Times spent pursuing and waiting are a function of prey density, a (arthropods m⁻¹ s⁻¹), and salamander foraging velocity, v (m s⁻¹).

Density dependence emerges within the model when crowding causes territory size (i.e. home range size) to be smaller than the energetically optimal foraging radius, reducing the energetic yield for each salamander. The model assumes a transect length of 1000 m (L), which is divided among N foraging individuals (Roughgarden 1997). The production function (ΔN) is used to model population dynamics where the change in population size is a product of the population growth rate and the population size, N ;

$$\Delta N = [bE(r) - \lambda]N$$

All parameters in the model are designed to relate demography to egg production. Therefore, the death rate, λ , is the daily mortality rate times the reproductive cost of metabolism while not foraging. Thus, this parameter accounts for how egg production is reduced by maintenance costs. The birth rate, b , is the rate of reproduction per unit of energetic yield. Density dependence is included in $E(r)$, which is dependent on N . This term can be substituted into the production function and solved for equilibrium population size (carrying capacity, K ; i.e. $bE(r) - \lambda = 0$):

$$K = \frac{L \left[be_i av + \sqrt{(be_i av)^2 - 4av(be_p + \lambda)(be_w + \lambda)} \right]}{2v (be_w + \lambda)}$$

where PFT is the potential foraging time, $b = mPFT$, and $\lambda = \mu + m(24 \times 60 \times 60 - PFT)e_w$.

Interspecific competition was incorporated into the model using Lotka-Volterra approximations to the discrete time-logistic growth equations (following Buckley and Roughgarden 2006). We calculate the equilibrium abundances, N_1 and N_2 , by simultaneously solving two linear equations:

$$N_1 + a_{12}N_2 = K_1;$$

$$N_2 + a_{21}N_1 = K_2,$$

where K_i is the carrying capacity for species i and a_{ij} is the competition coefficient describing the effect of species j on species i . The carrying capacities are obtained from the solutions of the single-species production function, which are parameterized separately for each species. We explored how varying the strength and type of competition (constant competition and linearly varying competition along the elevational gradient) influences the predicted abundance patterns. Following Buckley and Roughgarden (2006), we solved for the values of a_{12} and a_{21} that minimize the sum of squares for both species across the elevational gradients.

Energy budget model

We developed an energy budget model to assess whether the range limits of *P. jordani* and *P. teyahalee* can be predicted based on physiological constraints alone. This model is based on the prediction that all organisms require a net input of energy for successful growth and reproduction and populations will not be maintained in locations where energetic costs exceed energetic inputs. Daily energetic input was estimated using an empirically-derived function describing the thermal sensitivity of plethodontid salamander food intake (Merchant 1970) and estimates of potential foraging time (see PFT below). We fit a 3rd-degree polynomial to these data ($r^2 = 0.98$, $p < 0.001$; Table 1) and used the resulting function to calculate daily energy consumption. We assumed that prey is sufficiently abundant that an average salamander can obtain the quantity of resources determined by the food intake function. Daily energetic costs were estimated by measuring the thermal sensitivity of species' basal metabolic demands (i.e. standard metabolic rate) in the laboratory and empirical estimates of the amount of energy contained in an average clutch of eggs. Locations where energetic demands were equal to, or exceeded energetic costs (i.e. discretionary energy ≤ 0), corresponded to the predicted range limit under this model. Daily estimates of energy balance (i.e. energetic inputs minus energetic costs) were multiplied by the number of days in a given month to get average monthly values and the monthly values were summed to get annual estimates.

Model parameterization

We parameterized the population-dynamic and energy budget models assuming an average salamander of each species.

Mean snout-vent length (SVL) for each species was taken from Kozak et al. (2009). Salamander body mass (g) was derived from an empirical power-law function of SVL (Table 1; *P. jordani*, $n = 63$, $r^2 = 0.92$, $p < 0.0001$; *P. teyahalee*, $n = 34$, $r^2 = 0.98$, $p < 0.0001$).

We assumed that salamanders could be surface active during nighttime hours when operative body temperature, T_p , fell within observed annual range of field body temperatures (3°C – 20°C , Feder and Lynch 1982, Feder et al. 1982). Because few data are available on geographic variation in voluntary thermal ranges in these species, we use a single value for minimum and maximum field body temperatures. Variation in the operative body temperature (T_e) and evaporative water loss for each species was modeled using fine-scale microclimatic data (see Environmental data) and the biophysical model of Campbell and Norman (2000), with adjustments in the radiant energy budget for a nocturnal, forest-dwelling amphibian (Supplementary material Appendix 1). Operationally, T_e is the air temperature increased or decreased by an increment determined by absorbed radiation, convection mediated by wind speed, and animal morphology (Bakken et al. 1985, Campbell and Norman 2000). The operative temperature estimated for a salamander enters the bioenergetic model to calculate thermally dependent parameters.

Potential foraging time (PFT) was calculated as a subset of the time in which T_e was considered suitable for surface activity. We followed Feder (1983) and Feder and Londos (1984) and designated PFT as the amount of time required for a salamander to lose 10% of its body mass through evaporative water loss, after which time the animal was assumed to return to a moist refuge. The skin of plethodontids acts as a free-water surface (Spotila and Berman 1976). We therefore modeled evaporative water loss, using the following equation:

$$\lambda E = A \left(\frac{1}{r_e} \right) (\rho_s - RH\rho_a)$$

where λE is the rate of water loss (kg s^{-1}), A is the surface area (m^2 ; calculated from body mass using the relation from Whitford and Hutchinson [1967]). Because heat and mass transfer are accomplished by the same mechanisms there is a close relationship between their coefficients, a relationship known as the Lewis rule (Spotila et al. 1992). We define r_e as the external resistance to water vapor transport ($r_e = 0.93\rho_c/h_c \text{ s m}^{-1}$; Spotila et al. 1992), RH is relative humidity (%) and ρ_s and ρ_a are the saturation vapor densities at the skin surface and in the air (kg m^{-3}), respectively. The convection coefficient, h_c , is taken from Campbell and Norman (2000) ($h_c = 1.4 \times 0.135 \times \text{sqrt}(ud)$, where u is the wind speed experienced by the animal and d is the characteristic dimension, SVL (cm)).

We estimated how metabolic rate varies with temperature in 57 salamanders (27 *P. jordani* and 30 *P. teyahalee*) at 10°C , 15°C , and 20°C using automated closed-system respirometry (Sable Systems International, Hendersonville, NV). During measurements, salamanders rested inside respirometry chambers that were housed in a digitally controlled incubator. The order of temperatures was randomized for each individual. All metabolic measurements were

Table 1. Relationships used to parameterize the mechanistic models and their sources.

	Relation	Source
Salamander parameters		
Snout-vent length (mm)	55 68	Kozak et al. 2009
Mass, M (g) from snout-vent length, SVL (mm)	$M_{jordan} = 1.0310^{-5}(SVL^{2.53})$ $M_{teyahalee} = 2.0310^{-6}(SVL^{3.01})$	This study
Resting metabolic rate, from \log_{10} mass, M, and temperature ($^{\circ}\text{C}$) (O_2 consumption, $\text{mL O}_2 \text{ h}^{-1}$)	$\log_{10}MR_r = 0.036(T) + 0.57(\log_{10}M) - 1.95$ $\log_{10}MR_t = 0.035(T) + 0.59(\log_{10}M) - 1.83$	This study
Salamander surface area (cm^2)	$9.62 \times M^{0.614}$	Whitford and Hutchinson 1967
Sprinting speed (m s^{-1})*	0.15	Austin and Shaffer 1992
Prey size, L (mm)	4.5	Mitchell and Taylor 1986
Digestive efficiency	$DE = -0.0094(T) + 0.99$	Bobka et al. 1981
Foraging intake (FI, $\text{cal g}^{-1} \text{ d}^{-1}$)	$FI = 0.015(T^3) - 0.81(T^2) + 12.76(T) - 43.06$	Merchant 1970
Annual survival (%)	0.49	Hairston 1983
Age at maturity (yr)	3	Hairston 1983
Mature ovum size, diameter (mm)	3.5	Hairston 1983
Ovum dry weight, DW (mg) from ovum volume (mm^3)	0.48	Kaplan 1980
Energy content of salamander ova (kJ mg DW^{-1})	0.025	Kaplan 1980
Foraging window parameters		
Activity temperature range ($^{\circ}\text{C}$)	3 – 20	Feder et al. 1982
Potential foraging time, PFT (s)	$PFT = (0.1 \times M)/WL$	Feder 1983
from water loss rate, WL, and mass, M		Feder and Londos 1984
Prey parameters		
Arthropod abundance, a (arthropods $\text{m}^{-2} \text{ s}^{-1}$)	0.029 (95% quantiles = 0.023–0.046)	This study
Prey dry mass, M (mg) from length, L (mm)	$M = 0.28 \times L^{2.45}$	Schoener 1977
Prey energy content kJ mg^{-1} dry mass	0.02385	Reichle 1971

*Assumed to remain constant across temperatures. These salamanders rarely use rapid bursts of speed to secure prey (unpubl).

made on animals in a post-absorptive state. Seven animals were measured over five evenly spaced automated cycles of 10 min each during a given day. The minimum rate of O_2 consumption (ml h^{-1}) was calculated using equations from Withers (1977). During each trial CO_2 -free air was pumped (at a known flow rate) through a water bubbler prior to entering respirometry chambers to prevent desiccation of salamanders. Excurrent air was scrubbed of both CO_2 and water vapor prior to entering the oxygen analyzer (FC-10a, Sable Systems International, Las Vegas, NV). Metabolic rate and body mass data were \log_{10} transformed to linearize their relationship. We parameterized the models with species-specific functions to estimate metabolic rate from temperature and body mass (Table 1). We assume that, while active, salamander metabolism is 1.5 times that of resting levels (Bennett and Houck 1983). Digestive efficiency (DE) tends to vary strongly with temperature and has only been measured in a single plethodontid, *Plethodon cinereus* (Bobka et al. 1981). We use these data to derive a linear relationship between temperature and DE ($DE = -0.0094(T) + 0.99$). The energetic content per prey item, e_p , is reduced by a factor determined by DE .

Daily survival (μ) was computed from annual survival estimated in Hairston (1983) and is included in Table 1. We estimate m (no. eggs kJ^{-1}) by calculating the energetic content of an average salamander egg. We assume an average egg is 3.5 mm diameter, approximated from data in Hairston (1983). We calculate egg volume, assuming a sphere,

and convert egg volume to dry mass (mg ; $0.48 \text{ mm}^3 \text{ mg}^{-1}$ DW, Kaplan 1980). Energetic content (per unit dry mass) of amphibian eggs is similar across taxa (-0.024 – 0.027 kJ mg^{-1} DW; Kaplan 1980); we assume an energetic conversion of 0.025 kJ mg^{-1} DW. We assume a clutch size of 14 eggs (Hairston 1983). The estimated energetic cost to produce a clutch of eggs is thus 3.78 kJ, which is similar to empirically estimated reproductive costs in other plethodontids (3.38 kJ, Fitzpatrick 1973).

Salamanders eat a broad array of prey items of a variety of sizes (Powders and Teitjen 1974, Jaeger 1981, Mitchell and Taylor 1986). The size of prey taken by *Plethodon* does vary weakly with body size (Mitchell and Taylor 1986), but this effect is inconsistent across seasons (Powders and Teitjen 1974). We therefore assume a single prey size is consumed (prey length = 4.5 mm, Powders and Teitjen 1974). We determined prey dry mass (mg) from prey length (mm) using a regression for arthropods from a temperate deciduous forest (Schoener 1977; Table 1). Prey dry mass is converted to energy content per prey item, e_p , assuming $0.0239 \text{ kJ mg}^{-1}$ dry mass (Reichle 1971, Andrews and Asato 1977). We measured prey abundance at four sites along the elevation gradient using the methods of Buckley and Roughgarden (2005, 2006). At each site we placed four replicates of four paper plates coated with a sticky substance (Tree Tanglefoot, Tanglefoot Company, Grand Rapids, MI) in a 0.25 m^2 grid. Plates were recovered after 24 h. We convert arthropods captured ($\text{m}^{-2} \text{ s}^{-1}$) to number of arthropods

($\text{m}^{-1} \text{s}^{-1}$) by assuming that each salamander forages within 0.5 m to each side of the linear transect. Among sites, arthropod abundances were broadly overlapping and no significant differences were detected (Mann–Whitney U, $p = 0.36$). The abundance distribution is skewed, so we used kernel density estimation to estimate the modal value of prey abundance across all sites combined. Kernel density estimation approximates a probability density function of a random variable and has been applied in other ecological situations (Manly 1996, Rabosky et al. 2007, Adams and church 2008).

Environmental data

We used a fine-scale model (90 m spatial resolution) of daily temperature variation for Great Smoky Mountains National Park (Fridley 2009) and empirically-derived estimates of relative humidity and wind speed to parameterize the environmental variables in the mechanistic models. The temperature model provides estimates of near-ground air temperatures (~ 1 m) after accounting for the effects of incoming solar radiation, topographic shading, slope, aspect, and soil moisture, and its parameters and predicted values were cross-validated by dividing field temperature sensors into training and test datasets (Fridley 2009). Given that the nighttime temperatures of the air, soil, and surfaces of plants in closed-canopy forests are extremely similar to each other (Spotila et al. 1992, Gifford and Kozak unpubl.), the T_c of salamanders is approximated by the near-ground air temperature. Moreover, temperature and desiccation rate (which constrain surface activity of salamanders) are strongly correlated (Spotila 1972), suggesting that daily variation in near-ground temperatures can be used to estimate salamander surface activity times. The air near the forest floor in the southern Appalachian forests is saturated for most of the year (nighttime relative humidity ranges from 90–100%; Hairston 1949, Petranka and Smith 2005). We therefore assumed that relative humidity was 95% during the time in which salamanders were surface active. We used average monthly wind-speed data (10' resolution, New et al. 2002) to model wind speed at the level of a salamander (~ 5 mm above ground) after accounting for attenuation through a forest canopy. The attenuation coefficient is calculated using a leaf area index (LAI) calculated for southern Appalachian deciduous forests (Bolstad et al. 2001, Supplementary material Appendix 1).

Due to the difficulty in estimating daily variation in precipitation, we were unable to explicitly include this parameter in our models. Although precipitation affects salamander surface activity (Grover 2000) across the Great Smoky Mountains annual mean temperature and precipitation are strongly spatially correlated ($r = -0.91$, $p = 0.0001$). However, we caution that in other montane regions (e.g. those in which closed-canopy forests are absent at higher elevations), precipitation and temperature may exhibit more complex relationships, making it difficult to estimate surface activity times from microclimate models of temperature alone.

Model evaluation and performance

We compared the elevational pattern of salamander abundance predicted by the population-dynamic model to field

estimates of salamander surface activity. We used ANCOVA to test whether the empirical relationship between salamander surface activity and elevation had a significantly different slope and/or intercept than was predicted by the models. Salamander surface activity was estimated using linear transect counts at 10 elevationally separated sites in Great Smoky Mountains National Park (Supplementary material Appendix 1, Table A1). At each site, we searched a 100×1 m linear transect for a constant time period (1 h). We captured each salamander that we encountered (to avoid double-counting of individuals) and released all salamanders at the conclusion of the sampling period. All sites were surveyed during peak salamander activity time (21:00–01:00 h; Hairston 1949).

Because many of the salamanders in a local population are not surface active on a given night, surface counts underestimate population size. However, mark–recapture estimates of salamander abundance are strongly positively correlated with surface counts ($r^2 = 0.84$; Smith and Petranka 2000). Therefore, while our surface counts are not equivalent to actual salamander population sizes, they are expected to parallel the elevational trends in abundance which are the foci of our analyses. Similarly, although salamander detectability may decrease with elevation and soil moisture (Bailey et al. 2004), it seems unlikely that such biases drive our results for two reasons. First, we expect that any elevational variation in detectability is also correlated with overall abundance (i.e. salamanders are harder to detect at drier, low-elevation sites, because those locations are less suitable, and therefore, support smaller populations). Second, despite 50 yr of field sampling, *P. jordani* has never been taken at low elevations and *P. teyahalee* has never been found at high elevations.

To examine the extent to which each model discriminated between known presence and absence locations for *P. jordani* and *P. teyahalee*, we used receiving operator characteristic (ROC) analysis. We calculated the area under the ROC curve (i.e. AUC) for each model. The AUC assesses whether a randomly chosen positive observation (i.e. species presence) has a higher rank than a randomly chosen negative observation (i.e. species absence). AUC values ≤ 0.50 indicate that a model fails to discriminate between presence and absence; AUC = 1.00 indicates that a model perfectly discriminates between presence and absence (i.e. presence locations are always ranked higher than absence locations).

Georeferenced presence and absence locations for each species were obtained from the collection of R. Highton, now deposited at the U.S. National Museum. This dataset contains over 600 locations that document the geographic distributions of *P. jordani* and *P. teyahalee*. We acknowledge that failure to find a species at a given location is not proof of its absence. However, we point out that many of these sites have been searched multiple times over a 50-yr period (mean visits per site = 2, range = 1–37), and despite considerable sampling effort (mean = 24 plethodontid specimens collected per site, range = 1–1158), a species that is considered absent from the site has not been found.

Finally, we evaluated the ability of the energy budget model to predict the range limits *P. jordani* and *P. teyahalee*. This approach required that we delimit a threshold value for presence vs absence. Given that we do not expect viable populations to be maintained in locations where energetic costs exceeded energetic inputs, we classified grid cells with

discretionary energy ≤ 0 as unsuitable. Based on this bioenergetic threshold, we calculated the proportions of true presences (sensitivity index, Manel et al. 2001) and true absences (the specificity index, Manel et al. 2001), and the proportion of all locations that were correctly predicted by the energy budget model (model performance, Manel et al. 2001). All statistical analyses were performed in R ver. 2.10.1.

Results

Our transect counts demonstrate that the number of salamanders observed of *Plethodon jordani* increases with elevation (Fig. 1A), and that the number of surface-active *P. teyahalee* declines with elevation (Fig. 1B). The population-dynamic models fail to predict the empirical trends in the surface activity of both species when we assume this is driven by physiological constraints alone (Fig. 2A), when *P. jordani* and *P. teyahalee* exert equal competitive effects on each other (Fig. 2B), and when *P. teyahalee* is a superior competitor to *P. jordani* (Fig. 2C). However, the empirical trends in surface activity are recovered in models where *P. jordani* activity is governed solely by physiological constraints, and *P. teyahalee* is strongly impacted by competition from *P. jordani* (Fig. 2D, E). Thus, physiological constraints seemingly decrease the abundance of *P. jordani* at lower elevations, whereas competition seems to play the primary role in limiting the presence of *P. teyahalee* at higher elevations.

Predicted variation in the abundance of *P. jordani* and *P. teyahalee* is mapped in Fig. 3B–D. The population-dynamic model based on physiological constraints alone strongly discriminates among presence and absence locations for *P. jordani* (Fig. 3B, AUC = 0.82), but not for *P. teyahalee* (Fig. 3C). Intriguingly, locations at which *P. teyahalee* is absent are generally predicted to have higher abundance than locations where this species is present (Fig. 3C, AUC = 0.19). In order to discriminate among the presence and absence locations of *teyahalee*, a strong competitive effect of *P. jordani* on *P. teyahalee* must be incorporated in the model (Fig. 3D, AUC = 0.80). Predictions from mechanistic models can be sensitive to parameterization. The most influential parameter in our population dynamic model is prey abundance, *a*. We therefore explored the impact of varying this parameter on predicted elevational patterns of salamander abundance by parameterizing the model with the 95% quantiles of the prey abundance frequency distribution (Table 1). Consistent with other studies utilizing a similar mechanistic model (Buckley and Roughgarden 2006), predictions are qualitatively unaltered by changing prey abundance (Fig. 4). The empirical elevational trends in salamander surface counts are only recovered when a strong competitive impact of *P. jordani* on *P. teyahalee* is imposed. Thus, the predicted elevational trends in abundance appear robust to model parameterization.

The energy budget models are mapped in Fig. 3E–F. The distribution of climatically suitable locations for *P. jordani* generally parallels its geographic distribution (Fig. 3E, sensitivity = 0.85, specificity = 0.64, model performance = 0.76). As suggested by the population-dynamic models, the range limit of *P. teyahalee* cannot be explained by physiological and climatic constraints alone; the energy budget model predicts highly suitable locations for *P. teyahalee*

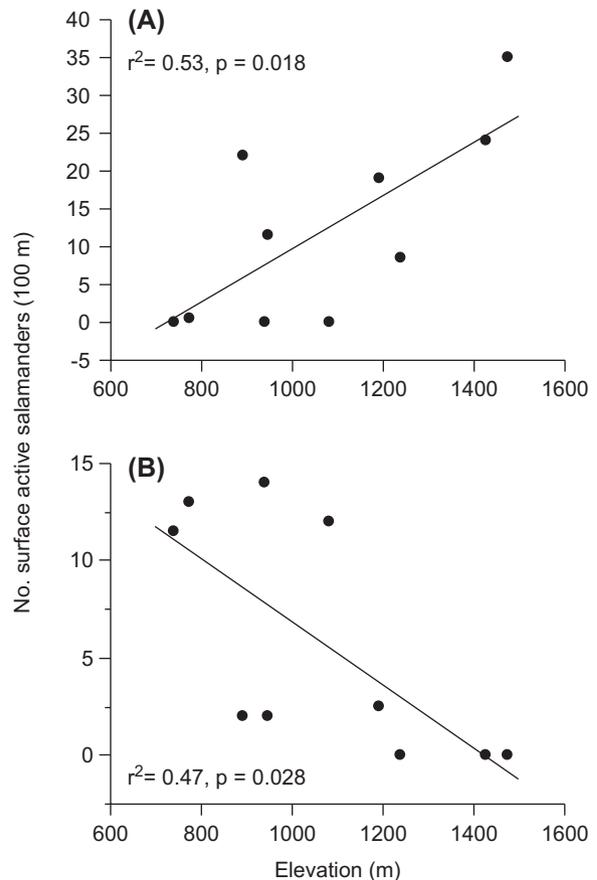


Figure 1. Surface active salamanders along 100 m transect as a function of elevation. Elevational trends are shown for the high elevation species, *P. jordani*, in (A) and for the low elevation species, *P. teyahalee*, in (B).

that extend well beyond its current range into the distribution of *P. jordani* (Fig. 3F, sensitivity = 0.93, specificity = 0.003; model performance = 0.52).

Discussion

A fundamental question in ecology is ‘What limits the distributions of species along elevational gradients?’ Given that many hotspots of endemism and species richness are associated with montane regions, the study of elevational range limits is central to explaining large-scale variation in biodiversity. Understanding the factors that restrict the elevational distributions of species also has important implications for conservation. Many of the species in montane regions have narrow elevational distributions, and therefore, could be particularly susceptible to rapid changes in climate. Yet, the ecological mechanisms that drive the elevational range limits of species are understudied and poorly understood.

In this study, we used a mechanistic approach to dissect the ecological factors that underlie the elevational zonation of woodland salamander distributions in the southern Appalachian Highlands. Parapatric species distributions that are not associated with steep climatic transitions are often thought to be a consequence of interspecific competition

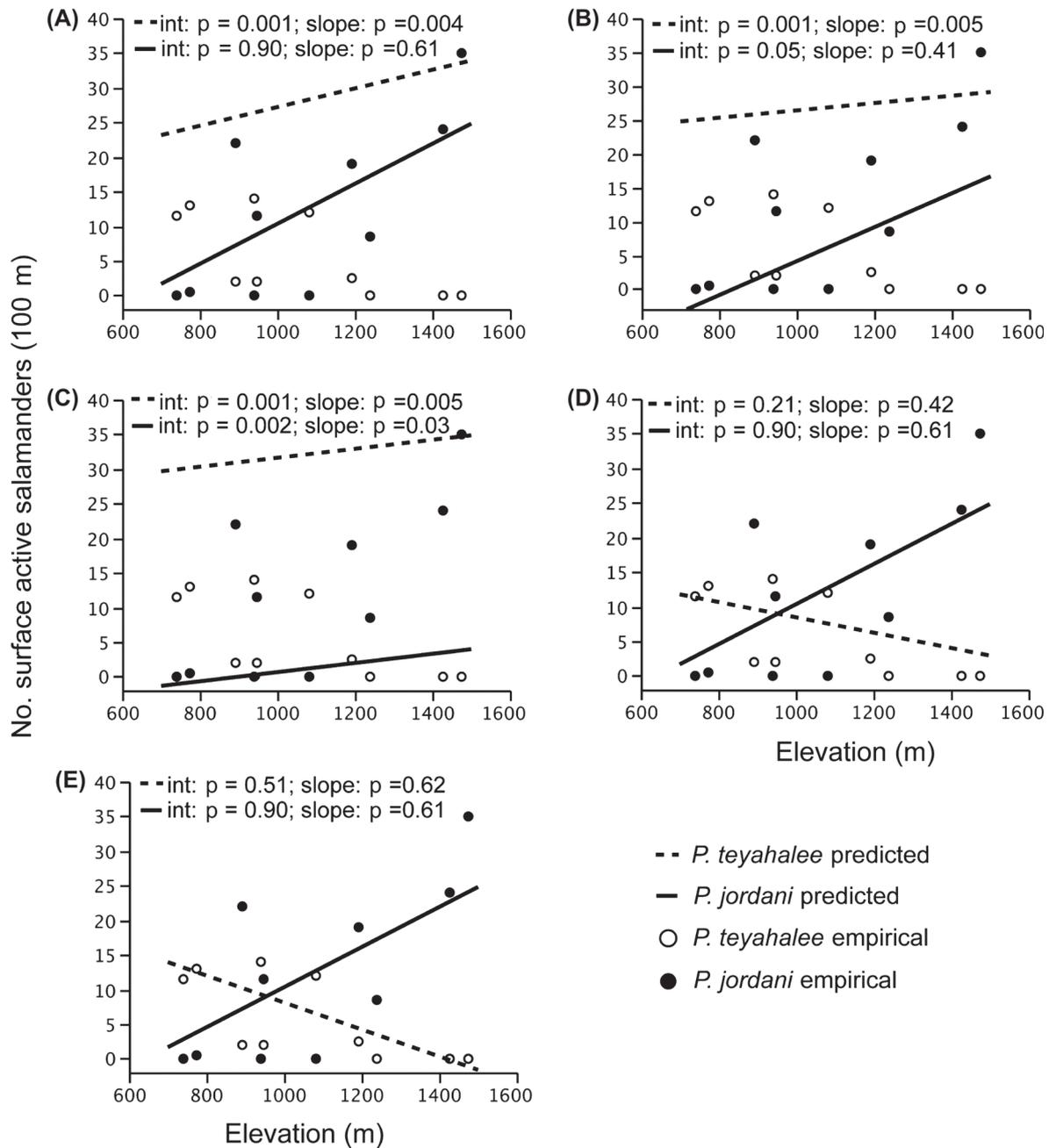


Figure 2. The fit of modeled salamander abundance (assuming varying patterns of competition) to surface counts as a function of elevation (x): (A) no competition; (B) equal competition: $a_{jt} = 0.3$, $a_{jt} = 0.3$; (C) *P. teyahalee* superior: $a_{jt} = 0.8$, $a_{jt} = 0.3$; (D) *P. jordani* superior [constant competition]: $a_{jt} = 0$, $a_{jt} = 2.5$; and (E) *P. jordani* superior [linearly varying competition]: $a_{jt} = 0$, $a_{jt} = 0.004x - 0.89$. Open and filled circles represent surface counts for *P. teyahalee* and *P. jordani*, respectively. Dashed and solid lines indicate least-squares fits to the predicted abundance for *P. teyahalee* and *P. jordani*, respectively. ANCOVA results testing whether the modeled abundance differs in intercept and slope from the empirical surface counts are shown at the top of each panel.

(Sexton et al. 2009). However, our analyses demonstrate that biotic interactions alone cannot explain the elevational replacement of *P. teyahalee* and *P. jordani* along the slopes of the Great Smoky Mountains. We found that a physiological model incorporating energetic constraints alone predicts the lower elevational range limit of *P. jordani* better than a model incorporating competition. Our population-dynamic and energy-budget models (which are based on thermal constraints on energy intake and consumption) strongly predict

the patterns of surface activity and distribution of this species. We interpret this result to indicate that physiological constraints drive the lower elevational range limit of *P. jordani*. Conversely, unfavorable climatic conditions do not prevent *P. teyahalee* from colonizing high-elevation habitats. In fact, the climatic suitability for this species is predicted to increase with elevation, the exact opposite of its empirical distribution and our counts of surface active salamanders. Consequently, only models in which *P. jordani* outcompetes *P. teyahalee* at

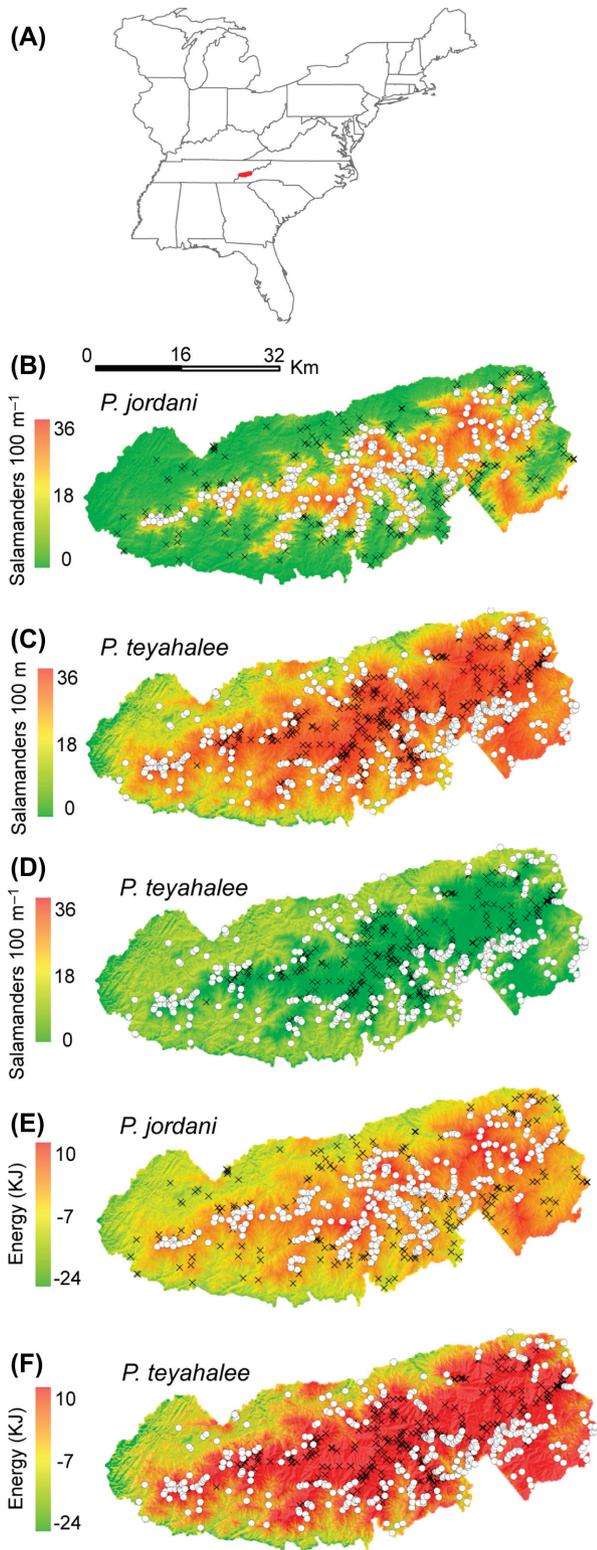


Figure 3. (A) Map of the eastern United State showing outline of Great Smoky Mountains National Park in red. Predicted spatial variation in salamander abundance (number of salamanders predicted 100 m^{-1}) for *Plethodon jordani* (B) and *P. teyahalee*. (C) and (D) show the predicted abundance of *P. teyahalee*, with and without competition from *P. jordani*, respectively. Discretionary energy budgets of *Plethodon jordani* (E) and *P. teyahalee* (F). White dots illustrate presence localities for *P. jordani* in (B) and (E), and for *P. teyahalee* in (C), (D), and (F). Similarly, bold crosses show known absence localities for *P. jordani* (B, E) and for *P. teyahalee* (C, D, F).

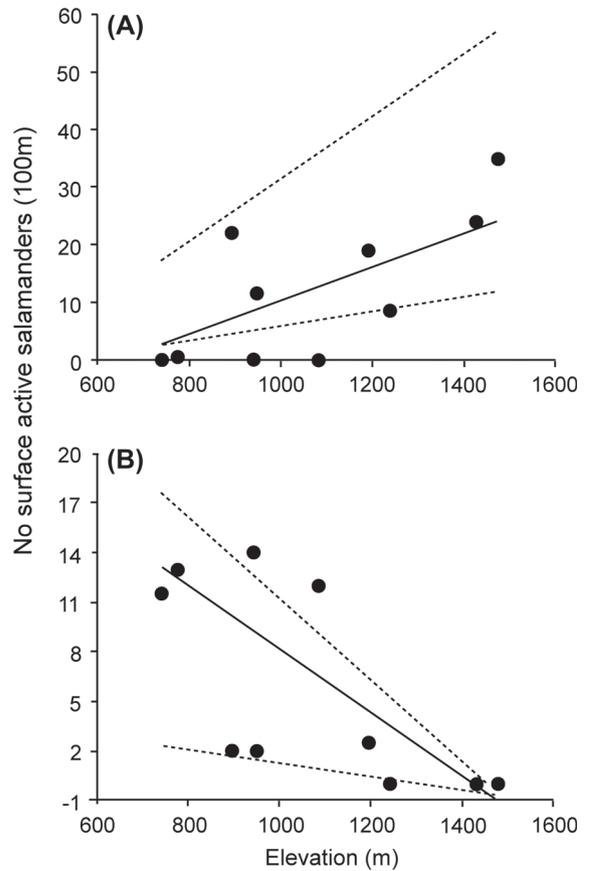


Figure 4. Sensitivity of population dynamic model predictions to prey abundance. Solid symbols show number of salamanders observed during transect counts for *P. jordani* (A) and *P. teyahalee* (B). Dashed lines in each graph represent best-fit (from Fig. 3) model predictions while varying prey abundance (95% quantiles for the frequency distribution, $a = 0.023$ and $a = 0.046$ for the top and bottom dashed lines, respectively in each graph).

higher elevations received any support. This interpretation also appears robust to model parameterization; elevational trends in abundance are qualitatively unchanged by varying the most sensitive parameter in the model (i.e. prey abundance, Buckley and Roughgarden 2006).

These results challenge the long-held idea that competition with lowland species drives the elevational distributions of montane plethodontids (Hairston 1951), and the lower elevational limits of montane species in general (reviewed in Lenoir et al. 2010). In a seminal study, Hairston (1980) performed reciprocal removal experiments of *P. jordani* and *P. teyahalee* where they coexist in the Great Smoky Mountains. Based on his results, he concluded that *P. teyahalee* is a superior competitor and prevents *P. jordani* from colonizing adjacent, low-elevation habitats. Our mechanistic models permit a rigorous comparison of Hairston's hypothesis and the alternative hypothesis that climatic factors alone limit the range of *P. jordani*. Employing the competition coefficients estimated from his study, our population-dynamic model predicts that *P. teyahalee* should exclude *P. jordani* across the entire elevational gradient. This outcome seems unlikely given our results (Fig. 2) and ecological and evolutionary studies that demonstrate long-term stability in the abundance and

elevational distribution of *P. jordani* (Hairston et al. 1992, Hairston and Wiley 1993, Chatfield et al. 2010).

Several independent lines of evidence corroborate the elevational-range dynamics predicted by our models. First, as would be predicted for a montane species that is restricted to high elevations by climatic factors, populations of *P. jordani* are found at lower elevations on north- than on south-facing slopes (Hairston 1949, 1980). Second, interference competition via aggressive interactions is common among coexisting species of *Plethodon* (Adams 2004, 2007), including *P. jordani* and *P. teyahalee*. Behavioral studies demonstrate that *P. jordani* is more aggressive towards *P. teyahalee* than the reverse (Nishikawa 1985, 1987), a finding that is consistent with our models that predict the former species excludes the latter species from climatically suitable habitats at high elevations. Finally, *P. teyahalee* expands its range to higher elevations (>1500 m) where *P. jordani* and other montane endemic species of *Plethodon* are absent (Hairston 1951), a classic biogeographic signature of competitive release (Daimond 1970, 1973; but see Cadena 2007, Cadena and Loiselle 2007).

Here, we have focused on the ecological mechanisms that drive the elevational zonation of two species in a single region of the world. Additional mechanistic studies are needed to further test the generality of our results. Nevertheless, studies on other montane endemics and in other montane regions support our findings. For example, montane endemic plethodontid salamanders in the Ouachita Mountains and the Ridge and Valley of eastern North America are more aggressive than their widespread congeners that inhabit the adjacent, lowland habitats (Anthony et al. 1997, Arif et al. 2007). The question of whether climatic constraints drive the elevational ranges of these montane endemics has yet to be addressed mechanistically. However, distribution-based niche models are consistent with the hypothesis that climatic factors set the lower elevational range limits of the montane endemics, and that the lowland species are competitively excluded from higher elevations (Kozak and Wiens 2006, Arif et al. 2007). Similarly, in the Sierra Nevada Mountains, the lower elevational range limits of montane chipmunks are set by climatic constraints, and the upper limits of species that inhabit lower elevations are set by aggressive interactions with their high-elevation relatives (Chappell 1978).

Together these results suggest that competitive ability may be inversely related to climatic tolerance-breadth. However, exactly why climatically-restricted montane endemics should be better competitors than their wider-ranging relatives is unclear. One possible explanation is that given their narrower climatic tolerances, the fundamental niches of montane endemics are often nested within those of their wider-ranging relatives. Under this scenario, parapatric boundaries between montane endemics and their widespread relatives will only be maintained if the species with the 'included niche' is a superior competitor (Hutchinson 1957, Miller 1967). An alternative, non-exclusive explanation is that species may sacrifice (i.e. tradeoff) competitive ability for the evolution of broad climatic tolerances (Huey and Slatkin 1976, Gilchrist 1995).

Many of the species that inhabit montane biodiversity hotspots are endemic to a single mountain, or limited number of adjacent mountains. Thus, a key question to address for understanding the causes of high montane diversity is

'What prevents montane species from dispersing into lowland habitats?' Given that their lower elevational range limits often coincide with the distributions of lowland species rather than abrupt changes in climate, a classic explanation for the restricted elevational distributions of montane endemics is competitive exclusion (Hairston 1951, 1980, Jaeger 1970). However, our results demonstrate that even subtle elevational gradients in climate can generate and maintain montane endemics. For example, in the southern Appalachians, high- and low-elevation habitats are generally quite similar (both consist primarily of temperate, deciduous forests). Nevertheless, our results demonstrate that small differences in microclimate may ultimately lead to energetic constraints that prevent montane species like *P. jordani* from successfully colonizing lower-elevation habitats.

Given that at least some species of *Plethodon* thrive in the lowlands, why have so many of the species in this clade (most species are found at high elevations) failed to become more widespread in low-elevation habitats? A recent study across all species of eastern North American plethodontids suggests that the ancestor of the group was restricted to a montane climate and that phylogenetic conservatism of the climatic-niche has constrained the dispersal of lineages to low-elevation environments (Kozak and Wiens 2010). Our study provides some insight on the traits that may underlie this long-term conservation of the ancestral climatic niche. We speculate that evolutionary stasis in desiccation and metabolic rates (which are both positively associated with temperature, and therefore inversely correlated with elevation [$r^2 = 0.87$, $p < 0.0001$], Supplementary material Appendix 1, Fig. A1) may have played a role in generating and maintaining the disparity in species richness between montane and lowland habitats. A fruitful avenue for future research will be to explicitly quantify the relationship between these and other functional traits in a phylogenetic context across many montane and lowland taxa.

Our results have important implications for understanding recent and future range shifts of montane taxa, and raise the sobering possibility that even small changes in climate might cause erosion of the ranges of many high-elevation species. Recent studies attempting to explain whether species will move upslope, downslope, or maintain their elevational range limits in the face of climate change have operated under the assumption that lower elevational limits of montane taxa are set by competition and that that physiological stress increases with elevation (Lenoir et al. 2010). Our findings suggest that this long-held idea is no longer tenable, and challenge the idea that competitive release at species' lower elevational range limits are driving the downslope range shifts exhibit by some montane taxa (Lenoir 2010, but see Crimmins et al. 2011). We hypothesize that there is no universal relationship between physiological stress and elevation across the tree-of-life. Instead, we anticipate that the factors driving species' elevational range limits will be explained by the principle of phylogenetic niche conservatism and the evolutionary history of the taxon in question (Crisp et al. 2009, Wiens et al. 2010). Species that belong to clades that originated in cool climates will have their lower elevational range margins set by physiological stress. Conversely, species in clades that diversified in association with warm climates (e.g. tropical or subtropical conditions) should generally follow the

predictions of the classic lower-margin-competition/higher-margin-stress hypothesis (McArthur 1972).

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Supplementary material (Appendix E6866 at <www.oikosoffice.lu.se/appendix>). Appendix 1.