Global Change Biology

Global Change Biology (2011) **17**, 696–708, doi: 10.1111/j.1365-2486.2010.02297.x

The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century

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Abstract

Species distribution models are commonly used to predict species responses to climate change. However, their usefulness in conservation planning and policy is controversial because they are difficult to validate across time and space. Here we capitalize on small mammal surveys repeated over a century in Yosemite National Park, USA, to assess accuracy of model predictions. Historical (1900–1940) climate, vegetation, and species occurrence data were used to develop single- and multi-species multivariate adaptive regression spline distribution models for three species of chipmunk. Models were projected onto the current (1980–2007) environmental surface and then tested against modern field resurveys of each species. We evaluated models both within and between time periods and found that even with the inclusion of biotic predictors, climate alone is the dominant predictor explaining the distribution of the study species within a time period. However, climate was not consistently an adequate predictor of the distributional change observed in all three species across time. For two of the three species, climate alone or climate and vegetation models showed good predictive performance across time. The stability of the distribution from the past to present observed in the third species, however, was not predicted by our modeling approach. Our results demonstrate that correlative distribution models are useful in understanding species' potential responses to environmental change, but also show how changes in species-environment correlations through time can limit the predictive performance of models.

Keywords: climate change, ecological niche models, habitat suitability, multivariate adaptive regression splines, range shifts, species distribution models, *Tamias*

Received 19 April 2010 and accepted 12 July 2010

Introduction

A pressing challenge for biodiversity conservation in the 21st century lies in forecasting species' responses to the direct and indirect effects of climate change (Barnard & Thuiller, 2008). The complexity of these effects and the evidence for the idiosyncratic nature of species' responses to past climate change makes this arguably the most difficult problem confronting biologists today (Brown *et al*., 1997; Jackson & Overpeck, 2000; Walther *et al*., 2002). Novel climates are anticipated in the future (Williams & Jackson, 2007), which further exacerbate our ability to accurately predict how species will respond. Forecasting in the face of this uncertainty requires that we develop a deeper understanding of the ecological and environmental factors that drive changes in distribution at multiple spatiotemporal scales.

Correlative models are widely used to predict the effects of climate change on species' distributions (Thomas *et al*., 2004; Thuiller *et al*., 2005; Lawler *et al*., 2006). These models are based on the observed relationship between a species and its environment (Guisan & Zimmermann, 2000) and when mapped using geographic information systems are referred to as predictive distribution maps (Guisan & Thuiller, 2005). A strong criticism of this approach in predicting species responses to climate change is that they are difficult to validate across time (Araujo *et al*., 2005a; Hijmans & Graham, 2006) so their usefulness as predictive tools remains relatively untested (but see Araujo *et al*., 2005b; Kharouba *et al*., 2009). Another criticism of correlative models is that they tend to rely solely on abiotic variables while excluding biotic factors such as species

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interactions, vegetation and dispersal (Davis *et al*., 1998; Pearson & Dawson, 2003; Hampe, 2004; Araujo & Luoto, 2007; Barnard & Thuiller, 2008; but see Preston *et al*., 2008). In this study, we are in the unique position to address some of these criticisms. Using historical surveys and contemporary resurveys of chipmunks in Yosemite National Park, California, we examine the environmental drivers of changes in distribution over the past century.

The three study species examined in the study, *Tamias alpinus*, *Tamias senex*, and *Tamias speciosus* occupy different elevational zones in Yosemite. Recently, Moritz *et al*. (2008) showed by comparing early 20th century surveys with modern resurveys that these chipmunk species have responded differently to environmental change over the past century. The alpine chipmunk (*T. alpinus*), which occupies the highest elevational zone, retracted its lower elevational range upwards overtime. Meanwhile, the lodgepole chipmunk (*T. speciosus*), which occupies the midelevational zone, did not significantly change its distribution. Finally, the shadow chipmunk (*T. senex*), which occupies the low to mid-elevational zone, experienced massive range collapse and is now extremely rare in the study area. Moritz *et al*. (2008) suggest warmer temperatures as the main driver of the observed shifts for these species and the broader community of small mammals, but did not explicitly test alternative hypotheses or whether climate was acting indirectly on distributions through changes in vegetation or species interactions.

Interspecific competition is likely to be a factor where chipmunk species co-occur (Heller, 1971; Chappell, 1978). However, the study species do differ in their microhabitat preferences (Chappell, 1978; Waters & Zabel, 1998; Waters *et al*., 2001). Laboratory physiological studies of these species suggest they have comparable climatic tolerances (Heller & Gates, 1971; Heller & Poulson, 1972), whereas field based physiological studies suggest that higher altitude chipmunks are slower to recover from heat stress (Chappell *et al*., 1978). Given the previous physiological and behavioral work on *Tamias* species (Heller, 1971; Heller & Gates, 1971; Heller & Poulson, 1972; Chappell, 1978; Chappell *et al*., 1978), we hypothesize that climate, vegetation and species co-occurrence all should be important predictors of the changes in chipmunk distributions observed in Yosemite National Park. However, because of conflicting reports and the dynamic nature of species' geographic boundaries, the relative importance of each of these variables is not easily deciphered.

We use historical (1900–1940) and modern (1980–2007) climate, vegetation, and species presence–absence locality data to 'forecast' changes in chipmunk distributions. Specifically, the objective of this study is to identify drivers of observed distributional changes of three species of chipmunks in Yosemite National Park. Our approach is to include environmental variables both separately (i.e., climate-only and vegetation-only) and together to better understand their relative importance. We examine the roles of climate and vegetation in both single-species models (without congener co-occurrence) and multi-species models (with congener co-occurrence) to determine if accounting for the distribution of potential competitors improves model performance (Fig. 1).

Data and methods

Study area and species

This study took place in and around Yosemite National Park, California (Fig. 2) and relied on data collected as part of the 'Grinnell Resurvey Project' through the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley (http://mvz.berkeley.edu/Grinnell/index.html). Our study used data from the resurvey of the 'Yosemite transect' published by Moritz *et al*. (2008). Detailed descriptions of the original Grinnell mammal surveys (hereafter historical surveys) from 1914 to 1915 and the modern resurvey of the small mammals in the Yosemite Transect from 2003 to 2006 are given in Moritz *et al*. (2008) (supporting information). For the modern dataset, we expand on the Moritz

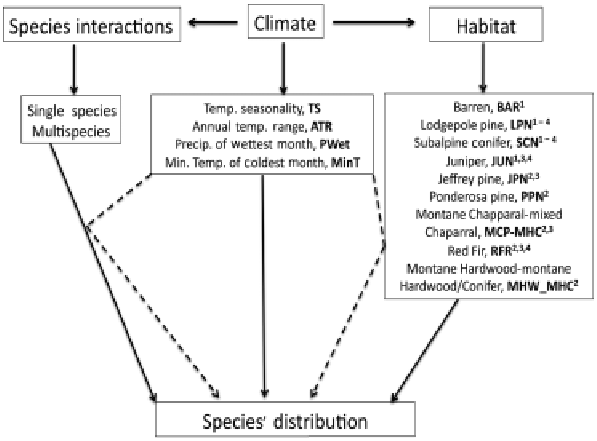

Fig. 1 Conceptual model illustrating modeling framework and the potential direct (black arrows) and indirect (dashed arrows) roles climate can play in species' distributions. Species interactions (in this study, specifically, interspecific competition) and habitat can play a direct or a climate-mediated (indirect) role in limiting distributions. Middle boxes indicate environmental variables and their abbreviations. For the vegetation models, focal vegetation types are coded by species and modeling approach: 1, *Tamias alpinus* single-species models; 2, *Tamias speciosus* single-species models; 3, *Tamias senex* single species models; 4, multi-species models.

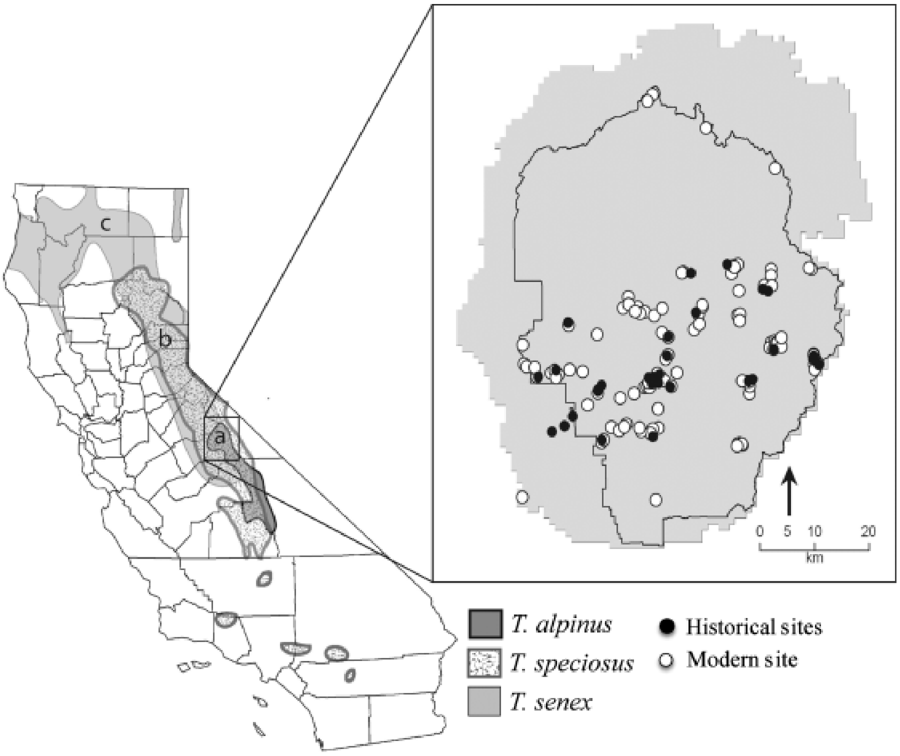

Fig. 2 State of California showing the distribution of (a) *Tamias alpinus*, (b) *Tamias speciosus* and (c) *Tamias senex*. Black rectangle shows blow-up of study area. The gray shaded area is the study area and the black line shows Yosemite National Park boundary. Black dots indicate historical mammal sites (1914–1916, $n = 39$) and white dots show modern mammal sites (2003–2007, $n = 109$).

et al. (2008) data with results from targeted trapping of chipmunks between May and August 2007. Because of the limited availability of comparable vegetation data in both eras, we restricted our study to 39 sites in the historical dataset and 109 sites in the modern dataset. There are more modern than historical sites because the modern surveys were greater in their sampling extent at each general site (i.e., more traplines in the general vicinity of the historical locality) and included new survey sites (i.e., sites not sampled in the past; Fig. 2). The three focal species have overlapping but distinct distributions in California and share several life history traits (Table 1).

Species data

Original Grinnell survey results were georeferenced from detailed field notes and maps (http://bscit.berkeley.edu/mvz/volumes.html?). Traplines within 2 km and 100 m in elevation were aggregated within each era to minimize spatial autocorrelation and account for the uncertainty in the location of historical traplines (hereafter 'aggregated traplines' are referred to as 'sites'). Using detailed field notes on trap captures in the historical and modern surveys, we were able to calculate the probability of detection of each species at each site following the methods of MacKenzie *et al*. (2002), MacKenzie (2006). We did the calculations including the 2007 data following Moritz *et al*. (2008) (supporting information) with one exception, instead of estimating the probability of false absence (PFA) across elevational bands, we calculated PFA for each specific site. We considered a site at which a particular species was not detected to represent a 'true absence' for that species if the PFA was <10%. We used the presence and 'true absence' data when validating the models within and between eras.

Climate data

We used a climate dataset generated with the Anusplin interpolation algorithm on weather station data at 1 km^2 spatial resolution (Parra & Monahan, 2008). A comparison of these interpolated layers of historical and present climate indicated that our study area has become drier and on average, the minimum monthly temperature has increased by about 1°C. However, warming is not consistent across sites; low elevation sites have warmed from 0.8 to 2.9 °C and certain high elevation sites have remained stable or become slightly cooler.

Table 1 Elevational zone, observed distributional change (as recorded by Moritz *et al*., 2008), prevalence and habitat description of study species in and around Yosemite National Park

Species	Elevational zone in study area	Elevation shift reported in Moritz *et al*. (2008)	Prevalence in historical era (# detected/# sites)	Prevalence in modern era (# detected/# sites)	Habitat in study area*
Tamias alpinus	Above 3000 m	Retracted 628 m up	10/39 (0.26)	18/109 (0.17)	Mainly above treeline in open granite slab areas, talus slopes and at meadow edges
Tamias speciosus	2000–3000 m	Expanded 128 m down and 65 m up	12/39 (0.31)	48/109 (0.44)	Open lodgepole forest stands; present at treeline but rarely above
Tamias senex	1800–2300 m	Retracted 1007 m up and 334 m down	7/39 (0.18)	1/109 (0.01)	Dense canopy old-growth forests; Jeffrey Pine & Red Fir; riparian vegetation

*Grinnell & Storer (1924), Johnson (1943), Waters & Zabel (1998), Waters *et al*. (2001).

This variation is not unexpected given the topological complexity of the area. The Anusplin interpolation is consistent with the available climate station data from each time period (National Climate Data Center, 2003; see Appendix S1 for more details). Nineteen bioclimatic variables were derived for each time period. We removed variables that were highly correlated (cut-off Pearson's $r < 0.85$, Elith *et al*., 2006) and selected a final set of variables that were biologically relevant to the study species. From previous research, we know that winter temperatures and timing of spring snowmelt are important factors for the survival and reproduction of alpine plants (e.g., Dunne *et al*., 2003), nonhibernating boreal mammals (e.g., pika: Smith & Ivins, 1983; Morrison & Hik, 2007; snowshoe hares: Odonoghue & Krebs, 1992) and hibernating sciurid mammals (marmots: Inouye *et al*., 2000, red squirrels: Réale *et al*., 2003). Therefore, we selected climatic variables based on the life history of the study species and the resources upon which they depend at emergence. Four biologically relevant variables were considered in our models: TS, temperature seasonality (standard deviation of mean monthly temperature); ATR, annual temperature range (maximum temperature of warmest month minus minimum temperature of coldest month); PWe, precipitation of wettest month; MinT, minimum temperature of coldest month.

Vegetation data

The vegetation dataset used for this study was derived from two vegetation maps of the area representing both eras (historical: Wieslander, 1935 and modern: NatureServe, 2003). The Wieslander Vegetation Type Map (VTM) collection consists of plot data, plot maps and vegetation maps which show hand drawn polygons of forest type and their associated species across California. The VTM collection has been digitized and is available online (Kelly *et al*., 2005; Thorne *et al*., 2008) and a recent analysis of spatial uncertainties in this dataset suggest that the use of these data in environmental niche modeling or multivariate analyses, such as this study, alleviate spatial error concerns (Kelly *et al*., 2008).

S. Cameron, P. Moore, & J. Thorne (unpublished results) reclassified both the historical and modern vegetation maps into a matching classification scheme (i.e., developed a vegetation 'crosswalk') using the California Wildlife Habitat Relationship database (California Department of Fish and Game & California Interagency Wildlife Task Group, 2008). Twelve vegetation categories were recorded in the Yosemite area in both time periods. From these 12, we chose four to six vegetation types for each species using the habitat associations recorded in the CWHR database and representing habitats that each species is known from field observation to inhabit. Multi-species vegetation models included four vegetation types that are overlapping between at least two of the three species (Fig. 1).

Model development and evaluation

We developed correlative distribution models using both single- and multi-species multivariate adaptive regression splines (Friedman, 1991). We constructed single- and multi-species models with different combinations of predictor variables according to the following framework: climate-only, vegetation-only and climate + vegetation. All models were run in the statistical package R 2.9.0 (R Development Core Team, 2009) using the *mda* library and custom code written by Elith

& Leathwick (2007). We developed 18 historical models and 12 modern models. We have a reduced set of modern models because the prevalence of *T. senex* dropped from 0.18 in the historical survey to <0.01 in the modern resurvey with comparable detectability (Moritz *et al.*, 2008, this study). Hence, modern models were run for only *T. alpinus* and *T. speciosus*.

We evaluated the accuracy of the models both within- and between-eras. For the within-era scenario we projected the model onto the environmental landscape from the era in which it was built. In the between-era evaluation we projected models built in one era onto the environmental landscape of the modern or past era and then used the species data from the era into which it was projected to evaluate the accuracy of the model. Sites where focal species exhibited low detectability or a PFA >0.1 were removed from the historical and modern test data sets.

The 'best' models were defined using two approaches. First, we calculated Akaike Information Criterion (AIC, Burnham & Anderson, 2002) to select the top model from three candidate models (i.e., climate-only, vegetation-only, and climate + vegetation). Models were ranked based on the lowest AIC score for a given species and modeling technique (single- vs. multi-species). Second, we assessed model prediction accuracy by examining the area under the receiver–operating characteristic curve (AUC), and the true skill statistic (TSS). AUC varies from 0 to 1: a score of 1 is perfect discrimination and a score of 0.5 is no different from random. TSS is defined as sensitivity (correctly classified presences) + specificity (correctly classified absences) – 1 (Allouche *et al.*, 2006). We set the threshold for calculating TSS to the prevalence (# of presences/# of sites) in the training dataset (Liu *et al.*, 2005). The values of the thresholds to calculate TSS for each species are shown in Table 1.

We determined the top performing model by examining its predictive power as measured by AUC and TSS. An AUC >0.8 and TSS >0.50 suggest strong predictive power (Swets, 1988; Allouche *et al.*, 2006). The model for each species with the highest AUC and the highest TSS (i.e., highest cumulative accuracy score) was considered the most accurate at predicting the species' distribution either within or between eras. AUC or TSS values that differed by 0.05 or less between competing models were considered to have similar predictive performance and in these cases the model with the lowest AIC score was used to determine the top model. All models with an AUC <0.70 and TSS <0.40 were considered poor. For specific details of the model settings, please refer to the supporting information (Appendix S2, S3).

Results

Based on AIC scores alone, the historical single- and multi-species climate-only models were ranked as the best models for all three species (Table 2a and b). The same was true for the modern models with the exception of *T. speciosus* for which the climate + vegetation model was ranked highest based on AIC for both single- and multi-species models. For all species, across eras and modeling approaches, the vegetation-only models were ranked lowest by AIC. However, models with high AIC rankings were not always the most accurate as measured by AUC and TSS (Table 2a–d, Fig. 3). The historical multi-species models did not greatly improve the between era accuracy of models, but the inclusion of co-occurrence did improve the ability of modern models to predict distributions in the past.

Within-era model accuracy

Results for the single-species models show that historical models with the top AIC score (climate-only models) have high accuracy (Table 2a). The historical climate + vegetation model was ranked second best by AIC for all species and also did a good job of recovering the input data. The lowest AIC-ranked model (vegetation-only) exhibited high accuracy for *T. alpinus* and *T. speciosus*, but not for *T. senex*.

The modern climate-only model for *T. alpinus* had high accuracy (Table 2c) whereas the highest AIC-ranked climate + vegetation modern model for *T. speciosus* had low accuracy (Table 2c). In fact, all three modern within-era models for *T. speciosus* performed poorly indicating a weak model fit between the input data and the predictor variables. The addition of species co-occurrence in the multi-species models did not significantly improve model performance within eras (Table 2b and c).

Between-era model accuracy

Historical to modern. The historical single-species climate-only model accurately predicted the elevational shift observed in *T. alpinus* (Fig. 3b). All three historical *T. alpinus* models had high discriminatory power when predicting this species' distribution to the present, but only the climate-only model had high accuracy with both AUC and TSS. Predictive performance was not improved by adding co-occurrence into the historical *T. alpinus* models (Table 2b), but overall, the multi-species climate-only model had higher accuracy than either of the other two single-species models (climate + vegetation and vegetation-only).

Table 2 AIC model selection and performance statistics (AUC and TSS)

Model	AIC	ΔAIC	Predictor variables	AUC (within era)	TSS (within era)	AUC (between era)	TSS (between era)
(a)							
Tamias alpinus							
Climate-only	−22.9	0.0	TS, MinT	1.0	1.0	0.92	0.72
Climate + vegetation	−21.3	1.6	PWet, SCN, JUN, BAR, LPN	1.0	1.0	0.81	0.47
Vegetation-only	−17.1	5.8	SCN, JUN, BAR, LPN	0.97	0.93	0.81	0.40
Tamias speciosus							
Climate-only	−11.2		MinT, ATR, PWet	1.0	1.0	0.60	0.13
Climate + vegetation	−9.5	1.6	LPN, MinT, ATR, PWet	1.0	0.92	0.62	0.08
Vegetation-only	−2.9	8.3	LPN, RFR, MCP_MCH	0.9	0.83	0.61	0.19
Tamias senex							
Climate-only	−15.3		TS, MinT, PWet	0.98	0.77	0.68	0.68
Climate + vegetation	−8.0	7.3	TS, MinT, PWet, RFR, JUN	0.93	0.70	1	0.52
Vegetation-only	−2.7	12.7	JUN, RFR, MCP_MCH	0.69	0.34	1	0.69
(b)							
T. alpinus							
Climate-only	−25.2	0.0	TS, MinT, ATR	1.0	1.0	0.83	0.65
Climate + vegetation	−25.2*	0.0	TS, MinT, ATR	1.0	1.0	0.83	0.65
Vegetation-only	−9.7	15.5	RFR, JUN	0.92	0.84	0.75	0.35
T. speciosus							
Climate-only	−7.8	0.0	TS, MinT, ATR	1.0	1.0	0.68	0.14
Climate + vegetation	−7.8*	0.0	TS, MinT, ATR	1.0	1.0	0.68	0.14
Vegetation-only	−5.1	2.7	RFR, JUN	0.9	0.83	0.65	0.22
T. senex							
Climate-only	−6.0		TS, MinT, ATR	0.89	0.67	0.89	0.0
Climate + vegetation	−6.0*		TS, MinT, ATR	0.89	0.67	0.89	0.0
Vegetation-only	0.6	5.4	RFR, JUN	0.68	0.26	1	0.71
(c)							
T. alpinus							
Climate-only	−50.6	0.0	TS, MinT, ATR	0.93	0.72	0.88	0.0
Climate + vegetation	−50.6*	0.0	TS, MinT, ATR	0.93	0.72	0.88	0.0
Vegetation-only	−15.6	35	BAR, SCN	0.73	0.43	0.77	0.5
T. speciosus							
Climate + vegetation	15.2	0.0	TS, PWet, LPN	0.79	0.42	0.62	0.06
Climate-only	19.4	4.2	TS, MinT	0.76	0.34	0.92	0.43
Vegetation-only	27.4	12.2	PPN, MHW_MHC	0.62	0.25	0.79	0.57

Continued

Table 2. (*Contd.*)

Model	AIC	ΔAIC	Predictor variables	AUC (within era)	TSS (within era)	AUC (between era)	TSS (between era)
(d)							
T. alpinus							
Climate-only	−52.5	0.0	MinT	0.92	0.72	1	0.55
Climate + vegetation	−43.5	9.0	TS, MinT, ATR, PWet, Jun	0.93	0.73	0.61	0.0
Vegetation-only	−17.0	35.5	RFR, JUN	0.67	0.35	0.53	0.05
T. speciosus							
Climate + vegetation	15.8	0.0	TS, MinT, ATR, PWet, Jun	0.8	0.48	0.57	0.13
Climate-only	18.6	3.2	MinT	0.75	0.33	1	0.86
Vegetation-only	41.0	25.2	RFR, JUN	0.59	0.18	0.62	0.25

(a) Single-species historical models projected onto historical (within era) and modern (between era) environmental data; (b) multi-species historical models projected onto historical (within era) and modern (between era) environmental data; (c) single-species modern models when projected onto modern (within era) and historical (between era) environmental data; (d) multi-species modern models projected onto modern (within era) and historical (between era) environmental data.

*Even with the inclusion of vegetation variables, model result is the identical to climate-only model.

AIC, Akaike Information Criterion; AUC, area under the receiver–operating characteristic curve; TSS, true skill statistic.

In contrast to the high accuracy of the *T. alpinus* models, all three historical *T. speciosus* models performed poorly in predicting the stability of this species' distribution to the present (Table 2b; Fig. 3e–h) and in all cases an upwards shift in distribution was predicted. For *T. speciosus*, the multi-species models had slightly greater discriminatory power (AUC) but the distribution of this species was still grossly underpredicted, as reflected in the low TSS scores. All six historical models for *T. speciosus* predicted a modern shift upwards in elevation that was not empirically observed.

The third AIC-ranked vegetation-only model more accurately predicted the range collapse of *T. senex* than the top AIC-ranked climate-only model (Table 2a, Fig. 3j). In fact, both the single-species and the multi-species vegetation-only models are most accurate at predicting the observed range collapse of *T. senex*. The single-species climate + vegetation and the multi-species climate-only models do have high discriminatory power (AUC = 1.0 and 0.89, respectively), but these models do not perform well when examining the threshold-dependent TSS. However, the low TSS score is likely an artifact of the testing data, which includes only one presence point. The incorrect classification of this single point results in a sensitivity of zero. Nonetheless, the predictive maps of these models both indicate a northward contraction of *T. senex*, suggesting that both climate and vegetation are related to the range collapse of this species.

Modern to historic. The single-species modern climate-only model for *T. alpinus* did not accurately predict the species' historical distribution (Table 2c). Although it had a high discriminatory power (AUC), the model underpredicted the true historical range of *T. alpinus* based on TSS. The single-species model that showed the highest accuracy in predicting the distribution back in time was the vegetation-only model, a model that did poorly at predicting the distribution within era (Table 2c). Overall, the best performing modern *T. alpinus* model at predicting the species' distribution in the past was the multi-species modern climate-only model (Table 2c, Fig. 3c).

The best modern single-species model based on AIC for *T. speciosus* was the climate + vegetation model, but this model showed lower overall accuracy at predicting the historical range of *T. speciosus* in the past than both the vegetation-only and the climate-only models (Table 2c). The most accurate modern model was the multi-species climate-only model. The climate + vegetation multi-species model, which was ranked as best in terms of AIC, did an inadequate job at predicting the historical range. In general, the best modern *T. speciosus* models did a better job at predicting historical distribu-

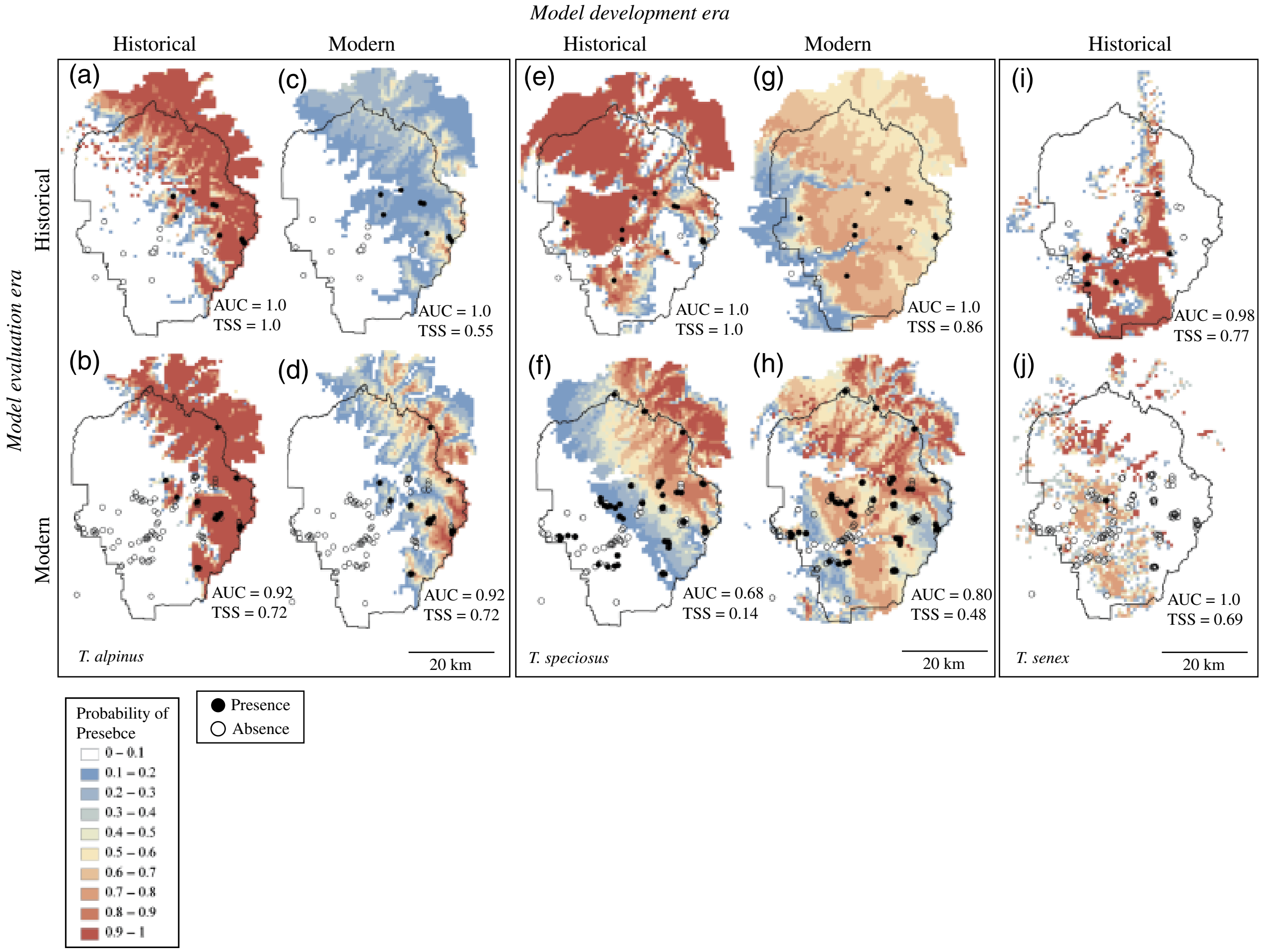

Fig. 3 Predictive distribution maps of most accurate models [based on area under the receiver–-operating characteristic curve (AUC) and true skill statistic (TSS)] for *Tamias alpinus* (a–d), *Tamias speciosus* (e–h) and *Tamias senex* (i–j). The 'model development era' along the horizontal axis of the figure refers to the timeframe in which the model was built; the 'model evaluation era' along the vertical axis refers to the timeframe in which the model was tested. All models evaluated in the historical era were tested with the historical P/A points. All models evaluated in the modern era were tested with modern P/A points. Black dots represent presences and open circles represent absences. Mapped top models are as follows: *T. alpinus* (a) historical single-species climate-only on historical environment; (b) historical single-species climate-only on modern environment; (c) modern multi-species climate-only on historical environment; (d) modern multi-species climate-only on modern environment; *T. speciosus* (e) historical single-species climate-only on historical environment; (f) historical multi-species climate-only on modern environment; (g) modern multi-species climate-only on historical environment (h) modern multi-species climate + vegetation on modern environment; *T. senex* (i) historical single-species climate-only on historical environment; (ii) historical single-species vegetation-only on modern environment.

tions than the historical models did at predicting into the present (Table 2c, Fig. 3e–h).

Predictor variables

The variables included in the best models for predicting species' distributions varied by species, modeling approach (single- vs. multi-species) and era (Table 2a–d). The most common climate variables selected for the historical single-species models were 'minimum temperature of coldest month' (MinT) and 'precipitation of wettest month' (PWet). The climate variables selected for the historical multi-species models were 'TS', MinT, and 'ATR' and this did not change when vegetation was included in the model (Table 2b).

The most common climate variables selected for the modern single-species models were ATR and MinT. The set of predictor variables for each species in the historical era was not the same set of variables that were selected by the models for the modern era. For example, the *T. alpinus* historical single-species climate-only model included TS and MinT but the modern model of the same type included TS, MinT and ATR. Overall, TS appears to be a more important predictor of species' distributions in the present than in the past and MinT maintained its importance as a predictor in both eras.

Model results suggested that a minimum temperature of approximately −10 °C during the coldest month of the year is required for *T. alpinus* to occupy an area (Fig. 4a). Sites that did not exhibit this threshold had low probability of presence. This threshold temperature was present in both the historical and modern model results. The modeled probability of presence for *T. speciosus* shows a unimodal pattern in both eras, suggesting that there are lower and upper thresholds for critical temperatures; however, these limits were not constant over time (Fig. 4b). Currently, *T. speciosus* occupies both warmer and colder environments than it did in the past.

The vegetation variables included in models were different for each species as described in the methods. There were two cases where vegetation-only models outperformed or were comparable to climate models between eras. One was in predicting the range collapse observed in *T. senex*. The historical single- and multi-species vegetation-only models for *T. senex* selected red fir (RFR), Juniper (JUN) and Montane Chapparal-Mixed Chaparral (MCP_MHC), and RFR and JUN respectively. The other case is the single-species modern vegetation-only model for *T. alpinus*. When projected back in time, this model performed nearly as well as the multi-species modern climate-only model. The vegetation variables in this model were barren (BAR) and Subalpine Conifer (SCN).

Discussion

This study evaluated the role of climate, habitat and occurrence of congeners in predicting known changes in chipmunk distributions over the past century. Overall, we found that even with the inclusion of biotic predictors, climate alone is the dominant predictor explaining the distribution of the study species within a time period, and this was particularly true for the historical era. However, climate was not consistently an adequate predictor of changes in all three species' distributions across time. The top model accurately predicted the observed elevational shift upslope for *T. alpinus*, but also predicted a similar upslope shift in *T. speciosus* that was not observed. Climate alone did an adequate job of explaining the distribution of *T. senex* in the historical era but it did not predict its collapse as accurately as models including vegetation.

Direct vs. indirect effects of climate on chipmunk distributions

Animals and plants that live on mountaintops are thought to be especially vulnerable to climate change for two reasons: they are more extinction prone due to limited dispersal options (McDonald & Brown, 1992), and often have relatively narrow tolerances to temperature (e.g., pika, Macarthur & Wang, 1973). *T. alpinus* is an example of an alpine animal that has retracted its distribution upwards in elevation over the past century. Our results strongly support the hypothesis that a warmer modern climate is the major driver of this elevational shift rather than factors such as vegetation and competition with other chipmunk species. In particular, our results show that a minimum winter temperature, approximately −10 °C during the coldest month of the year, is an important limiting factor for *T. alpinus* within the study area. The elevation at which this minimum temperature occurs appears to have moved upslope over the past century and this species has tracked it through time. Recently, as part of the Grinnellian resurvey of Californian birds, Tingley *et al.*

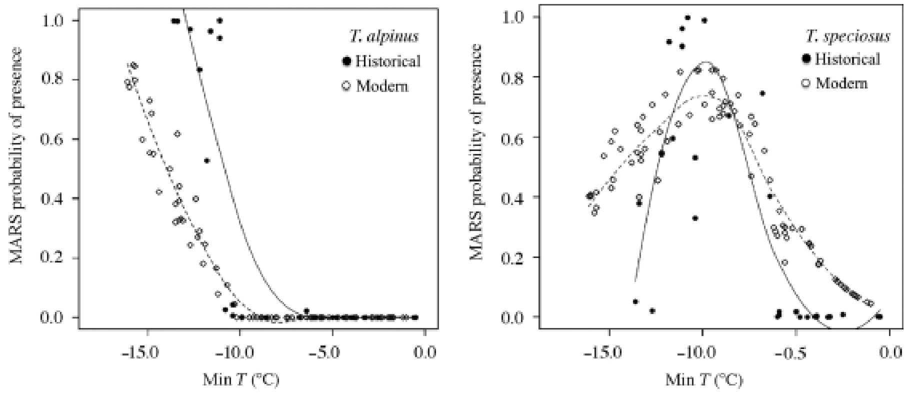

Fig. 4 The multivariate adaptive regression spline (MARS) predicted probability of presence of *Tamias alpinus* (left), and *Tamias speciosus* (right), across minimum monthly temperatures (MinT) in the historical (black circles), and modern (open circles) models. MARS probabilities generated from historical and modern single-species climate-only models.

(2009) found that several species of birds have also tracked their 'climatic niche' over the past century.

It is important to note, however, that although it appears that MinT is a limiting factor in *T. alpinus*' distribution, our approach cannot determine causation. Our climate data estimate air temperatures, which are known to be important cues for hibernating sciurid mammals, particularly for springtime arousal (Inouye *et al.*, 2000), but other biologically important factors related to climate were not directly measured in this study and also vary with elevation, such as snowpack. Snowpack provides a critical insulating layer for small mammals and is an important factor for overwinter survival (Vaughan *et al.*, 2000). Our results suggest that *T. alpinus* inhabits some colder areas now than it did in the past (Fig. 4). One explanation of this is that the higher the elevation the lower the MinT, but the temperature inside the hibernacula during the winter is likely warmer at higher elevations with deep snowpack, than lower elevations with less snowpack. This example demonstrates the multidimensional nature of climate-species interactions but also stresses the potential limitations of using interpolated bioclimatic variables as biologically relevant proxies.

Interestingly, the modern multi-species climate-only model is more accurate at predicting the historical distribution of *T. alpinus* than the equivalent single-species model. The multi-species model is based solely on MinT, further supporting evidence that minimum temperature is an important factor delimiting the elevational zonation of these species, and *T. alpinus* in particular. This result also suggests that perhaps simpler models with few biologically relevant predictor variables are more accurate at predicting across time than more complex models (the single-species modern climate-only model selected three: TS, MinT, and PWet). It is also possible that single-species within era models are subject to model-overfitting and therefore suffer reduced performance when projected between eras.

A key weakness of species distribution models is their high prediction error rate when projecting into novel environments and/or non-analog climates (Fitzpatrick & Hargrove, 2009). This occurs because the correlations between the environmental variables and species data in the training model may not exist in those combinations in the new environmental space (Thuiller *et al.*, 2004). An alternative hypothesis for the large prediction error when predicting a distribution across time is that the predictor variables selected by the model in one era are not tracked by the species across time and space (Broennimann *et al.*, 2008). In other words, what limits a species distribution in one era may be different than what limits its distribution in another (e.g., Monahan & Hijmans, 2008). This appears to be the case for *T. speciosus*. The single-species historical climate-only model did an adequate job of recovering the species distribution within the historical era, but the climate-only model did not perform well when forecasting the current distribution or simply recovering the modern distribution from the modern input data. However, both the single- and multi-species modern climate-only models accurately predicted the historical distribution of *T. speciosus*. These results suggest that the historical distribution of *T. speciosus* in the study area was delineated by climate, primarily by minimum winter temperature and secondarily by seasonality. However, this correlative relationship between temperature and the species' distributional limit no longer exists. *T. speciosus* appears to now occupy both warmer and colder habitats than it did in the past. Perhaps this suggests that it is no longer limited by temperature; however, a more likely explanation is that it was not and is not in a stable equilibrium state with respect to these environmental variables, a simplifying assumption of most distribution models.

It is possible that the historical distribution of *T. speciosus* was in fact limited indirectly by interspecific competition and not by climate as the models suggest. It meets two congeners at both distributional boundaries: *T. senex* at the lower elevational boundary and *T. alpinus* at the upper boundary. Our results provide strong evidence that *T. alpinus* is limited by climate and moderate evidence that both climate and vegetation have played a role in the range collapse of *T. senex*. With the retraction of both of these species, *T. speciosus* may have been released from competition and responded by filling the space left following the contraction of the other two species, hence moving into both cooler and warmer areas. In addition, there was greater opportunity for interspecific interactions in the past, because the species' distributions had greater geographic overlap.

Using the historical surveys, we calculated that *T. senex* and *T. speciosus* were found together at 27% of sites out of all sites where at least one of the species was found. Currently, both species were only detected at one site (2%), the single site where we detected *T. senex*. There was a similar trend with *T. alpinus*. In the past, *T. alpinus* and *T. speciosus* were caught at the same site 35% of the time whereas today, we only caught both species at 18% of sites out of all sites where at least one was captured. Interestingly, in the past there was one site (elevation 2455 m) where all three species were detected whereas currently, only *T. speciosus* was detected at that site. Although *T. speciosus*' distribution has generally remained stable overtime, Moritz *et al.* (2008) did report an elevational expansion up by 65 m and down by 128 m, which provides some evidence consistent with competitive release of this species at its elevational boundaries. *T. speciosus* was 'likely the most common chipmunk' in Yosemite National Park during Grinnell surveys (Grinnell & Storer, 1924) and today, trap captures corrected for effort suggest that it has increased in relative abundance since the original surveys across the park (Rubidge, unpublished data). Based on this evidence and our results, it is possible that *T. speciosus*' distribution in the study area is not limited by climate but by interspecific interactions with the other two chipmunk species. However, the environmental change in the study area appears to have had an indirect and positive effect on *T. speciosus* by removing its competitors at its distributional limits.

Our study area captures the southern-most tip of the *T. senex* range. Local populations at range edges are expected to experience higher extinction rates and possess lower genetic diversity than those at the center because they tend to occur in less favorable habitats (Lawton, 1993). The local populations at the rear edge are at particular extinction risk under climate change scenarios because they already represent the warmest conditions a species inhabits (e.g., Parmesan, 1996), and perhaps do not possess the genetic variation required for adaptation to a change in conditions (Kirkpatrick & Barton, 1997; Case & Taper, 2000). Grinnell & Storer (1924) describe *T. senex* as a 'common resident' in Yosemite National Park; today, *T. senex* has virtually disappeared from the area. The collapse of *T. senex's* distribution in Yosemite is likely another example of a poleward range shift in response to warming that has been observed in other taxa (reviewed in Parmesan & Yohe, 2003). Resurvey efforts in other parts of California including a site just 190 km north of our study area report capture rates of *T. senex* similar to the historical surveys in the same area (Chris Conroy, pers. comm.). *T. senex* is the largest of the three study chipmunks and previous studies suggest that it selects dense closed-canopy old growth Jeffrey pine and Red Fir forests (Sharples, 1983; Coppeto *et al.*, 2006) and riparian habitat (Waters & Zabel, 1998). A recent study reported that between 1930 and 1990, large diameter tree density in Yosemite declined by 24% (Lutz *et al.*, 2009). Jeffrey Pine (*Pinus jeffreyi*), in particular, suffered disproportionately greater losses of large-diameter trees in the lower-elevation portions of their range. Lutz *et al.* (2009) attribute the death of old growth trees in Yosemite to increased water stress. The direct impact of climate change on vegetation has indirect effects on the species that depend upon these habitats. According to our model results, the documented change in the vegetation structure of the forests of Yosemite, as well as warming, have likely played a role in the northward retraction of the *T. senex* range. However, because this species has become so rare in the study area our power to validate the model is low.

Conclusions

Species are responding to climate change by shifting their distributions both by latitude and elevation (Parmesan, 2006). Correlative distribution models can be useful for predicting where species will occur under future climates, but the correlations do not necessarily hold through time. This study was able to assess the predictive accuracy of correlative species distribution models over a century of climate change, but we were also able to include habitat and species co-occurrence predictors to determine their relative importance. Our results demonstrate that correlative distribution models are useful in understanding species' potential responses to environmental change, but also show how changes in species-environment correlations through time can limit the predictive performance of models. With recent developments in biodiversity informatics and the increasing availability of spatiotemporally explicit data (Graham *et al.*, 2004), studies like this that are able to validate models in a projection environment, and include both abiotic and biotic predictor variables, will allow us to develop a more complete mechanistic understanding of which species respond directly or indirectly to climate change.

Acknowledgements

We are grateful to J. L. Patton, C. Conroy, the YNP resurvey field team, C. Patton and L. Chow for their role in collecting the modern field data. Thank you to J. Thorne and the Wieslander Working Group for access to historical vegetation data and to P. Moore for access to contemporary vegetation data. Early drafts of this manuscript were greatly improved by C. Moritz, the Grinnell Resurvey Group, C. Burton, L. Prugh and other members of the Brashares Lab Group, and N. M. Kelly. E. M. Rubidge was supported by a National Science & Engineering Research Council PGS D award, the Museum of Vertebrate Zoology, and the Environmental Science, Policy and Management Department at UC Berkeley, during this research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Climate comparison.
Appendix S2. Detailed description of model development and evaluation.
Appendix S3. Sampling and Sample size effects on modeling results.