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Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change

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Several studies have observed that taxa below the level of species can vary in the degree to which they differ from one another in the environmental space they occupy. These patterns of within-species niche variation raise the question of whether these differences should be considered when developing models for predicting the potential effects of climate change on species distributions. We address this question with two divergent datasets, one on sister species and subspecies from the European herpetofauna, the other on subspecies of breeding birds in North America. Atlas and observation data come from the Atlas of Amphibians and Reptiles in Europe and the North American Breeding Bird Survey, respectively. We develop boosted regression tree models of climate-distribution relationships and project the predicted geographic range of each taxon using interpolated weather station data and modeled climate for the year 2080. We find differences between models that distinguish the contributions of subtaxa and those that do not, in terms of prediction of both current and future distributions. In comparison to models that ignore sub-taxon structure, models that incorporate this structure generally predict larger areas of suitable conditions, consistently perform better, if only marginally, as measured by cross-validated AUC, and can reveal divergent potential effects of climate change on subtaxa. Differences in niche occupancy and predicted distribution appear between closely related taxa regardless of their phylogenetic distinctness. For these reasons, information on subtaxon membership and phylogeographic structure should be included in modeling exercises when available, in order to identify both the contribution of these units to the niche occupancy of species and the potentially distinct responses of subtaxa to climate change.

Faced with ongoing anthropogenic climate change (IPCC 2007), accurate prediction of the current and potential future ranges of species is essential for managing biological diversity. One method to predict how species will respond to climate change is ecological niche modeling. Here, a relationship between species occurrence and a series of environmental variables, such as climatic variables and other predictors, is established and then projected onto estimated future values of these variables (Guisan and Thuiller 2005). Occurrence data from a regular or stratified random sampling design (Edwards et al. 2006) or obtained from collections (Graham et al. 2004a) are pooled from the entire range of the species, comprehensively covering the environmental conditions where a species exists (Austin and Gaywood 1994). This practice ignores whether occurrence data represent a single evolutionary entity or a collection of evolutionary lineages that can vary in age, evolutionary independence and genetic distinctiveness.

Populations across the range of a widely distributed species can show persistent morphological differences that are not paralleled by variation at studied loci (Grudzien and Moore 1986) or be locally adapted, suggesting the existence of loci under selection (Maron et al. 2004, Wright et al. 2006). In the extreme, adaptation of populations to local conditions can be accompanied by reciprocal monophyly at additional loci, suggesting complete lineage sorting and continuing reproductive isolation that characterize speciation. The existence of cryptic species and frequent local adaptation suggest that cryptic niche architecture exists within the species-level taxa that are the focus of studies of biogeography, the ecological niche, and biotic responses to climate change.

The implications of ignoring population and phylogeographic structure for modeling species distributions, inferring niche structure or predicting the effects of climate change on species distributions are little studied (Pfenninger et al. 2007). The existence of ecotypes and locally adapted populations suggests genetically-based geographic variation in physiological traits that convey adaptation to climate and other aspects of environment (Savolainen et al. 2007).

Geographic variation in environmental tolerances suggests that regional populations should be modeled to capture these environmental dependencies (Loehle and LeBlanc 1996). In fact, the relationship between distribution and environment varies among subspecies and across the range of species (Mexican birds, Peterson and Holt 2003, a North American tree, Murphy and Lovett-Doust 2007, a colubrid snake, Pyron and Burbrink 2009). This variation can arise from variation among regions in the availability of environments and not genetic adaptation (Choler and Michalet 2002, Murphy and Lovett-Doust 2007). Further, niche similarity among sister species has previously been interpreted as evidence for niche conservatism (Peterson et al. 1999, Kozak et al. 2006). These contrasting views of the significance of geographic structure in the environment-distribution relationships within species and small clades raise the issue of how to model the niche of species that have phylogeographic structure.

Whether a widely distributed species should be modeled with a single comprehensive model or a set of models that represent multiple taxonomic units below the species level is relevant for three reasons. First, distribution models that are developed by pooling across subspecies or lineages within species may obscure the potential that these lineages occupy distinct niches, something that suggests idiosyncratic response of sub-specific lineages to changing climate. This might happen because a comprehensive model could smooth across environmental response curves of specific lineages. Such a model might not describe well the niche of a specific lineage that is adapted to a specific set of climatic conditions (Osborne et al. 2007, Elith and Leathwick 2009). This is analogous to situations in which a response variable, such as species richness, demonstrates a relationship to environmental predictors that varies geographically (Kupfer and Farris 2007, Svenning et al. 2009). Second, a species model could, alternatively, overestimate the species-level response to climate change when, in fact, only a few populations within the species could exhibit such a response. Third, the portion of a species range that is occupied by different subspecies or lineages can vary greatly (e.g. fox sparrow *Passerella iliaca* subspecies, Zink 2008) or be roughly comparable (northern flicker *Colaptes auratus* subspecies, Sibley 2000). Isolated populations that account for a small fraction of species observations might have little influence on a species distribution model when the total number of observations is much larger. However, these isolated populations might contribute disproportionately to the response of species to changing climate, potentially representing the surviving portion of the species.

Here, we explore how taxonomic resolution influences predictions of the extent of suitable climatic conditions for species currently and under future scenarios. We are interested in whether biologically meaningful differences (10% or more) in predicted remaining suitable area arise as a result of the taxonomic resolution that is used in modeling the relationship between climate and distribution. We use data on two sets of vertebrates, a selection of breeding bird species in North America and several species of the European herpetofauna. The chosen taxa, clearly not a random selection from their respective continental faunas, supply examples of either polymorphic species with established subspecies taxonomy or small clades of sister species distinguished based on molecular evidence. We develop ecological niche models using a machine-learning algorithm that implements boosted regression trees. A general circulation model of climate provides data on potential future climatic conditions as may develop under the A2 scenario detailed by the Intergovernmental Panel on Climate Change (IPCC) third assessment.

We are primarily interested in determining whether the taxonomic resolution of lineages influences predictions of climate change impacts on the future distributions of these lineages. We investigate three conflicting hypotheses: first, we might expect species pairs in the European herpetofauna to show little niche overlap because of the accumulated ecological differences that may accompany speciation. In contrast and second, we expect subspecies to show great niche similarity because the taxonomic standing of subspecies suggests that they are genetically and ecologically less differentiated than bone fide species. Third, we could conjecture that there should be little niche differentiation among sibling species and subspecies because of the coarse resolution of the European dataset and the observation that sister species generally show little niche differentiation (Peterson et al. 1999). Our results suggest that an understanding of the phylogeographic structure within small clades or among closely related lineages provides an alternative perspective on potential responses of taxa to climate change. This can help reduce uncertainty when predicting climate change impacts on species potential distributions.

Methods

Terminology, study taxa and distribution data

We address the relationship between taxonomic resolution and predictive species distribution modeling using sister species and groups of subspecies. Sister species are dichotomous clades while the designation of subspecies within species defines groups that can vary greatly in both morphological and genetic distinctiveness. To avoid proliferation of terminology, we refer to models derived from observations pooled from various taxa, which may be across sister species or subspecies, as ‘‘clade models’’. We refer to models that are derived from single taxa, either single species or single subspecies, as subclade models.

Herpetofauna of Europe

The herpetofauna of Europe provided a well-studied group of vertebrates, here referred to as herptiles. We primarily considered taxa for which taxonomic revision has upgraded sub-species to sister species based on molecular phylogenetic analysis (Table, Supplementary material Appendix S1). We extracted published distribution data from the Atlas of Amphibians and Reptiles in Europe (Gasc et al. 1997). This large-scale atlas summarized, in a standardized way, data from national atlas projects, from the literature and from museum collections. Species presence in this atlas was reported within the 3869 50 × 50 km Universal Transverse Mercator (UTM) cells that intersected Europe. Because of changes in taxonomic status of several taxa occurred after publication of the Atlas, we updated the distribution information for the newly recognized species using national atlases (Pleguezuelos et al. 2002, Loureiro et al. 2008), published papers (Arntzen et al. 2007) and unpublished government reports, while maintaining the atlas resolution. We assumed that atlas cells where species were not noted as present represent true absences. While this likely introduced a small amount of error into the models, it was unlikely that these errors varied systematically between sister species or subspecies.

Breeding Birds in North America

The assemblage of breeding birds in North America provided several cases in which widely distributed species demonstrated well-developed population structure or geographically structured morphological variation. This included cases where: 1) subspecies were recognized based on stable color polymorphisms and/or morphological variation or 2) subspecies were recognized based on regional to continental patterns of genetic and morphological characteristics (Table, Supplementary material Appendix S1). Data on the distribution of these taxa in the United States and Canada came from the download web site of the North American Breeding Bird Survey (BBS, USGS Patuxent Wildlife Research Center 2009). We selected three of four taxa because they were formerly recognized as species that were subsequently downgraded to subspecies in order to form one polytypic species. These included *Junco hyemalis* (dark-eyed junco), *Colaptes auratus* (northern flicker) and *Dendroica coronata* (yellow-rumped

Table 1. Persistence of suitable climatic conditions in initially occupied cells, according to models trained with a pooled set of occurrences of two or more species or subspecies (denoted "clade") and models trained on the occurrences of individual taxa.

Perdicting models		Sub-clade models			
Predicted taxa	Occurences	2000		2080	
		predicted	% (sensitivity)**	predicted	%
European Herpetofauna subspecies and sister species					
Bombina variegata (clade)	577	565	97.92	354	61.35
Bombina pachypus	43	43	100	7	16.28
Bombina variegata	534	522	97.75	347	64.98
Lacerta viridis (clade)	722	707	97.92	227	31.44
Lacerta viridis	345	335	97.10	164	47.54
Lacerta bilineata	377	372	98.67	63	16.71
Pelodytes punctatus (clade)	325	323	99.38	66	20.31
Pelodytes punctatus	273	271	99.27	35	12.82
Pelodytes ibericus	52	52	100.00	31	59.62
Testudo hermanni (clade)	208	207	99.52	149	71.63
Testudo hermanni hermanni	59	59	100.00	27	45.76
Testudo hermanni boettgeri	149	148	99.33	122	81.88
Triturus carnifex (clade)	169	168	99.41	61	36.09
Triturus carnifex	125	124	99.20	44	35.20
Triturus macedonicus	44	44	100.00	17	38.64
Triturus marmoratus (clade)	294	293	99.66	97	32.99
Triturus marmoratus	212	211	99.53	34	16.04
Triturus pygmaeus	82	82	100.00	63	76.83
Mean across herpetofauna taxa, excluding clade values	252.17	188.58	99.24	79.50	42.69
Standard error	46.17	45.08	0.28	27.61	7.05
North American bird subspecies					
Colaptes auratus (clade)	3501	3181	90.86	2053	58.64
Colaptes auratus auratus	2507	2250	89.75	1430	57.04
Colaptes auratus cafer	994	931	93.66	623	62.68
Dendroica coronata (clade)	1409	1297	92.05	534	37.90
Dendroica coronata auduboni	571	533	93.35	442	77.40
Dendroica coronata coronata	838	764	91.17	92	10.98
Junco hyemalis (clade)*	1568	1479	94.32	659	42.03
Junco hyemalis caniceps	161	154	95.65	105	65.22
Junco hyemalis hyemalis	876	820	93.61	186	21.23
Junco hyemalis oreganus	531	505	95.10	368	69.30
Passerella iliaca (clade)	408	393	96.32	149	36.52
Red group	148	139	93.92	36	24.32
Slate group	157	152	96.82	51	32.48
Sooty group	38	37	97.37	9	23.68
Thickbill group	65	65	100.00	53	81.54
Mean across bird taxa, excluding clade values	683.47	577.27	94.58	308.64	47.81
Standard error	253.72	193.78	0.86	127.10	7.70

Table 1. Extended.

Clade level model				clade 2080/subclade 2080†	Model AUC††
2000		2080			
predicted	% (sensitivity)	predicted	%		
563	97.57	354	61.35	1.00	0.971
42	97.67	37	86.05	5.29	0.984
521	97.57	317	59.36	0.91	0.978
697	96.54	459	63.57	2.02	0.96
326	94.49	150	43.38	0.91	0.965
371	98.41	309	81.96	4.90	0.987
323	99.38	130	40.00	1.97	0.983
271	99.27	88	32.23	2.51	0.981
52	100.00	42	80.77	1.35	0.976
206	99.04	163	78.37	1.09	0.975
59	100.00	55	93.22	2.04	0.978
147	98.66	108	72.48	0.89	0.976
168	99.41	91	53.85	1.49	0.976
124	99.20	67	53.60	1.52	0.978
44	100.00	24	54.55	1.41	0.988
293	99.66	137	46.60	1.41	0.993
211	99.53	82	38.68	2.41	0.993
82	100.00	55	67.07	0.87	0.996
187.50	98.73	111.17	63.62		
44.81	0.46	28.94	5.72		
2839	81.09	1758	50.21	0.86	0.821
2105	83.96	1299	51.81	0.91	0.932
734	73.84	459	46.18	0.74	0.959
1241	88.08	442	31.37	0.83	0.912
483	84.59	244	42.73	0.55	0.954
758	90.45	198	23.63	2.15	0.948
1423	90.75	479	30.55	0.73	0.932
136	84.47	76	47.20	0.72	0.944
785	89.61	164	18.72	0.88	0.948
502	94.54	239	45.01	0.65	0.981
391	95.83	206	50.49	1.38	0.938
146	98.65	82	55.41	2.28	0.971
145	92.36	60	38.22	1.18	0.943
38	100.00	27	71.05	3.00	0.947
62	95.38	37	56.92	0.70	0.979
535.82	89.81	262.27	45.17		
179.74	2.31	110.47	4.45		

Notes: *the designation of species as a clade assumes that the group of subspecies shown here, and potentially other subspecies that were not modeled, form a monophyletic group. This is likely, but this but has not been with molecular data, *Junco hyemalis* subspecies. Means and standard errors were calculated before rounding values to two decimal places.

** Sensitivity is the proportion (or present) of occurrence points that are correctly predicted.

† This number is the ratio of the number of map cells that still have suitable climate for the taxon in the year 2080, as predicted by clade models and sub-clade models.

††Model AUC was calculated by evaluating clade models on all observations. AUC for subclade models was calculated using presences of the subclade group and considering all other cells as absences.

warbler, Table 1). We excluded *Junco hyemalis* subspecies *J. h. aikeni* and *J. h. mearnsi* because of the small number of occurrences that they presented, six and twenty-two respectively. Workers who survey BBS routes were encouraged to report to which archaic species the observed forms of these species belong (D. Ziolkowski pers. comm.). We also elected to analyze BBS occurrence data on *Passerella iliaca* (fox sparrow) because recent work showed marked geographic structure in mtDNA variability in this species (Zink 1994, 2008, Supplementary material Appendix S2). We assembled species observation data from 4514 BBS routes that were surveyed at least once between and including the years 1997–2008. We used the available route coordinates as the location for all observations associated with any particular survey route.

Climate data

All data for current conditions and potential future climates were obtained from the WorldClim website (<www.worldclim.org/download>, Hijmans et al. 2005). We used climate data from the HadCM3 general circulation model for the A2a future scenario. Climate data layers at 10-min resolution were trimmed to the extent of North America and then re-projected in the Albers equal area projection with ArcInfo and ArcMap 9.3 (ESRI 1999–2008), using bilinear interpolation to produce a final resolution of 18.8 km. At this resolution, the coordinates for neighboring BBS transects only rarely occur in the same pixel. We used the time slices for 2020, 2050, and 2080 that were available on the WorldClim website, but because trends in predicted extent of suitable climate were temporally consistent, we only present analyses for current conditions and 2080. Current and future climates of Europe were estimated as for North America, except that the working resolution was 50 × 50 km to coincide with atlas data on the European herpetofauna.

Ecological niche modeling

Niche models were developed using the algorithm for generalized boosted regression trees in the R statistical package "gbm", available at <www.cran.r-project.org>. We chose this method because it 1) can fit non-linear models to complex data, 2) performed comparatively well when models were used to predict species distributions as functions of independent datasets (Elith et al. 2006), 3) had been shown to model species-environment relationships accurately (Elith and Graham 2009) and 4) avoided over-fitting through use of additional functions, available in the gbm package (R Development Core Team 2009). In building gbm models, one generally develops a model object using a large number (several thousands) of regression trees. Subsequently, we determined an optimal number of these trees to use in projecting the model into geographic space, using ("cv") in the R functions gbm() and gbm.perf() to avoid over-fitting.

Climate variables and model development

Nineteen bioclimatic variables were available as part of the WorldClim datasets (Hijmans et al. 2005). From these variables we calculated growing degree days above 0.5°C and second quarter precipitation. These 21 variables can demonstrate substantial correlation, depending on the geographical location and extent of the area under consideration. We avoided using correlated variables for calibrating gbm models by defining multiple alternate sets of variables that displayed mutual correlations of < 0.7. There were six alternative parameterizations for fitting models to breeding bird data and four for fitting data on European reptiles and amphibians (Supplementary material Appendix S3). For each subspecies, species and clade we chose the model with the highest ten-fold, cross-validated AUC value for further analysis (Supplementary material Appendix S4). For each species and clade we compared the geographic distribution of suitable climate resulting from both the clade model and the union of the corresponding subclade models. We examined these patterns using several criteria for establishing a threshold value for constructing a binary prediction of taxon distribution (Liu et al. 2005). We tabulated the number of currently occupied sites that are predicted to retain suitable climatic conditions in the future under the models. We also examined the degree to which predicted range for one taxon, developed as one subclade model, coincided with predicted range for a related taxon, developed as another subclade model, i.e. "cross-prediction". Finally, we considered the area that was predicted by one or more subclade models to have suitable climatic conditions to be an 'aggregate' model for the distribution of the clade (or species in the case that subclade models represent subspecies).

Niche occupancy

We examined graphically the niche for each taxon, as estimated by clade and subclade models, along each of the environmental variables. Our objective here was to compare probabilities of occurrence of related taxa, including clades, species and subspecies. We focused on the distribution of the niche along the environmental variables that most influenced the gbm models for each taxon to help us understand potential differences in the predicted distributions that were generated by clade and subclade models, (Supplementary material Appendix S5). But because each taxon also varied in prevalence in the training datasets, we compared species probabilities of occurrence along environmental gradients in a way that would not be biased by differences in prevalence, as follows.

For each taxon, we considered the best-performing gbm model and projected it to climate values across the same map from which the training data came. We then standardized the probabilities of occurrence by dividing the probability value associated with each map cell by the sum of probabilities of across the entire map. This allowed construction of a density function for each taxon, the area under which sums to unity (Warren et al. 2008), as

$$1 = \sum\nolimits_{j=1}^{M} p_j, \qquad (1)$$

where M is the number of map cells and p_j is the probability of occurrence of the species in the particular map cell j. These standardized values represented the modeled probability that an occurrence actually coincides with a particular cell and are dependent on the total number of map cells and the frequency distribution of the values of predictor variables. Because the density function of each taxon is standardized to sum to unity, these standardized distributions were comparable across taxa. The validity of these relationships depended on the assumption that the prevalences of the species in the data with which the model was trained and across the cells of the map are identical, i.e. that the training data came from a random sample taken from the area represented by the map.

We assigned the standardized map cell values to 100 uniform-width bins that spanned the range of values of each environmental variable that was used in the models. The total probability density corresponding to the map cells that were assigned to a particular bin equaled:

$$d_i = \sum_{j=1}^{m_b} p_j, \qquad (2)$$

where d_i is the proportion of probability density that is contributed by the map cells, numbering m_b, that have values of the environmental variable that fall within the interval corresponding to bin b.

We divided the accumulated density within each bin (the d_i's) by the corresponding number of map cells assigned to the bin to remove the dependence of accumulated bin density on the frequency of the corresponding map cells. We used a Gaussian kernel (Mouillot et al. 2005) to produce for each taxon and variable a smoothed distribution of mean probabilities of occurrence along the 100 intervals. Thus standardized, the distribution of average probability of occurrence along an environmental gradient is comparable among species and lineages that vary in prevalence.

Composite clade models

We used the standardized bin values to compare niche estimates that were produced by subclade and clade models. We also produced a model that summarized the niche across all subclade models. To do this, we first observed that each subclade model was developed independently of other subclade models. Thus, the standardized probabilities of occurrence of subclades in each map cell were statistically independent. We further assumed that no other biologically relevant processes influenced the probability of co-occurrence of related taxa. We then took advantage of the fact that the standardized bin values represent the mean probability that the species in question will be found in each map cell within a bin. The quantity one minus this probability is the probability that the species will be found in map cells corresponding to other bins. To construct an analog of the clade model from the subclade models, we calculated the mean probability of occurrence of at least one of the related taxa for the map cells represented by each bin as:

$$P_b(x) = 1 - \prod_{i=1}^{N}(1 - P(x_i)), \tag{3}$$

where $P_b(x)$ is the average probability of the clade occurring in the sites represented in bin b, N is the number of taxa (and subclade models) and $P(x_i)$ is the mean probability of occurrence of taxon i across the map cells represented by bin b. We call this model the "composite" model, either for a clade of two sister species or for a species with multiple subspecies.

Results

Models of the distributions of birds and herptiles displayed AUC values consistently above 0.9 (Table 1). In both the bird and herptile datasets, AUC values were marginally higher for subclade models (0.97 ± 0.005; mean ± std. error) than they were for models that were trained on data pooled across taxa (clade models 0.95 ± 0.02), but the average magnitude of the difference was not significant (Pairwise Wilcoxon test, $n = 10$, $p = 0.24$). Nonetheless, it was unusual that AUC was higher for subclade models for 9 of the 10 species (Bionomial Test, $p = 0.01$). For herptiles, we found no evidence of a correlation between model fit (measured by cross-validated AUC) and taxon prevalence ($r_s = -0.34$, $n = 18$, $p = 0.16$). For birds, there was a weak correlation between model fit and taxon prevalence ($r_s = -0.56$, $n = 15$, $p = 0.03$). However, this correlation became non-significant when the observation for *Colaptes auratus* (clade model) was omitted from the analysis. As a clade, *C. auratus* demonstrated the greatest prevalence and the lowest AUC value of all clade models for birds.

Current predicted geographic distributions

Several of the clades of both European herptiles and North American birds demonstrated notable differentiation at the subclade level in the current geographic location of modeled suitable climate. For the herptiles, subclade models for each of the sister species showed little or no cross-prediction (Supplementary material Appendix S6b, S7b, S8). Thus, there was substantial difference in niche occupancy among sister species.

In North American birds, models for subspecies of *Colaptes auratus* and *Dendroica coronata* did not substantially cross-predict the range of the other subspecies of the same species (Supplementary material Appendix S9b, S10b). In contrast, models of the subspecies of *Passerella iliaca* cross-predicted extensively (results not shown), as did the models of the subspecies of *Junco hyemalis* (Supplementary material Appendix S11). Results on cross-prediction by subclade models were largely robust to choice of threshold for converting probability values into binomial (presence-absence) maps of predicted distributions, both for birds and herptiles species. Because of this general consistency among threshold criteria, we further consider and report only distributions based on the maximized True Skill Statistic (TSS) criterion (Allouche et al. 2006).

Predictions of clade models versus aggregated subclade models

The predicted distributions from clade models and aggregated (i.e. geographic union of) subclade models coincide to varying degrees. Aggregated subclade models predict larger suitable areas for European herptile taxa under current climatic conditions than do clade models in all but *Pelodytes punctatus* and *Triturus carnifex* clades (Fig. 1a, 2a). In all cases, the extents of these differences are small, $<9\%$ (Supplementary material Appendix S12 and S13). The extent of suitable area predicted by aggregated subclade and clade models for species in the *T. carnifex* clade are nearly identical (difference of 0.55%; Fig. 2a and Supplementary material Appendix S12). In North American birds, the aggregated subclade models predict larger areas of currently suitable climatic conditions than do the clade models. For example, much of the area around the hybrid zone between the two subspecies of *C. auratus* is predicted habitable by one or the other subclade models, but not by the clade model (Fig. 3a). For *C. auratus*, as well as for the other avian species, the subclade models predict suitable climate in areas that extend beyond and peripheral to the area that is predicted suitable by the clade model (Fig. 3a, 4a and Supplementary material Appendix S14).

Climate change and the persistence of suitable conditions

For amphibians and reptiles, clade models predict that more currently occupied sites will remain suitable in the future

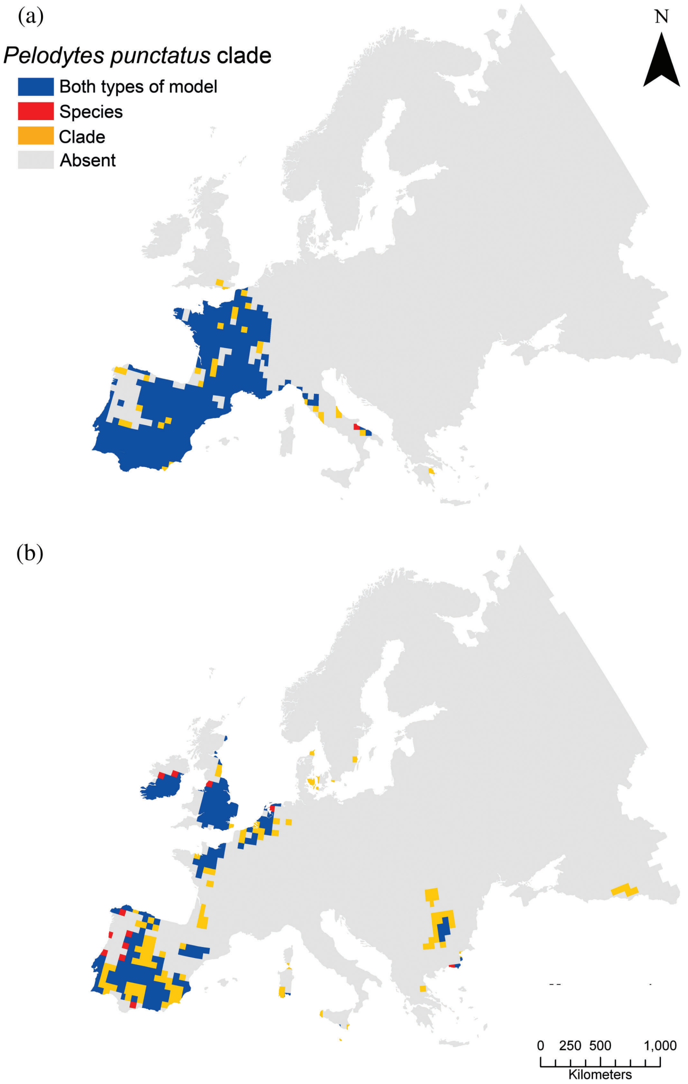

Figure 1. Predicted geographic distribution of suitable climatic conditions for the *Pelodytes punctatus*. Discrepancies between the clade model and the union of the two subclade models (for *Pelodytes punctatus* and *P. ibericus*) are shown in orange and red, respectively for the years (a) 2000 and (b) 2080. Areas predicted habitable by the clade model and either of the subclade models are shown in blue.

than does the aggregate of subclade models, sometimes by up to a factor of two (Table 1). Within clades, however, taxa often differ in the degree to which the predictions of persistent suitable conditions made by aggregated subclade models differ from the predictions of the corresponding clade model. For example, the clade model for *Testudo hermanni* predicts more than twice the number of sites remain climatically suitable for *T. hermanii hermanni* than does the subclade model for this subspecies itself (Table 1). Further, all clade models for herptiles predict the persistence of suitable conditions at as many or more sites, for all subclades collectively, than do the corresponding aggregated subclade models. For example, the clade model for *Lacerta viridis* predicts twice as many sites remain suitable than does the aggregate of subclade models (Table 1). In contrast, three out of four clade models for the North American birds predict the persistence of suitable climatic conditions at fewer sites than does the aggregate of subclade models (Table 1).

Total predicted suitable area

The aggregate of subclade models predicts more extensive areas of suitable climate currently than the clade models for four of six herptile clades (Supplementary material Appendix S12). Under modeled climate at 2080, aggregates of subclade models predict greater suitable area than clade models for three of six herptile clades (Fig. 1b, 2b, Supplementary material Appendix S12 and S13). In comparison, for three of the four species of North American birds we studied, subclade models predict greater extent of suitable area at year 2000, compared to the predictions of clade models (Fig. 3, 4, Supplementary material Appendix S12 and S14). For the year 2080, aggregate models predicted greater extent of suitable habitat for all four avian species than do clade models. For example, in *Passerella iliaca* subclade models predict greater habitat suitability in the southern portion of the range by 2080 than does the clade model (Supplementary material Appendix S14).

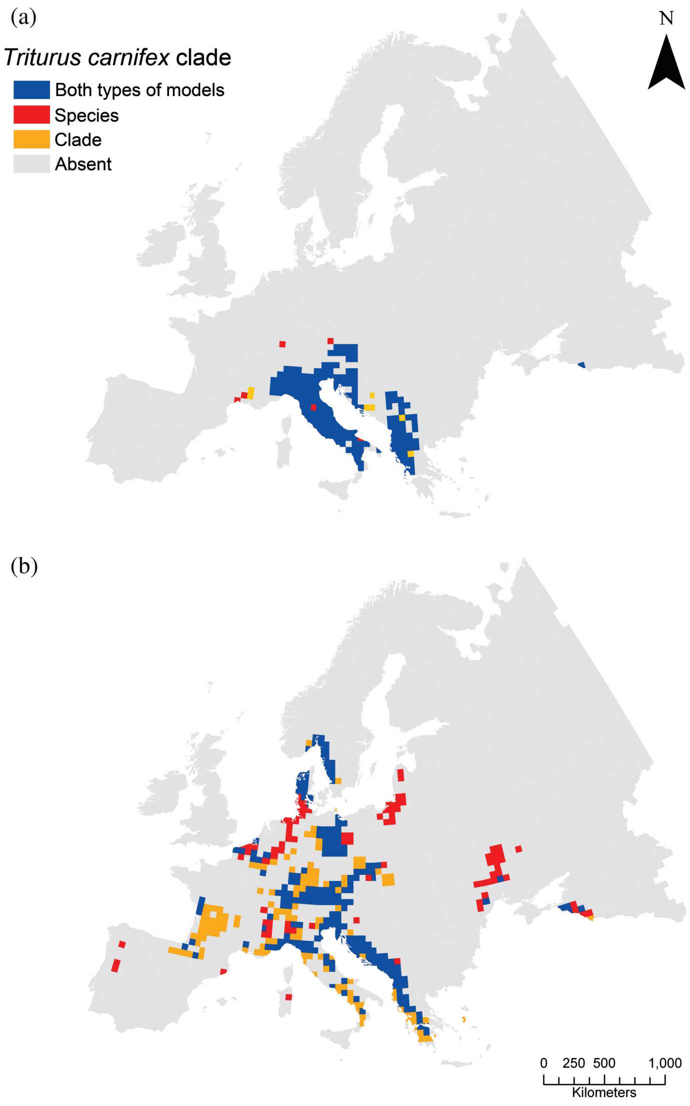

Figure 2. Predicted geographic distribution of suitable climatic conditions for the *Triturus carnifex* clade. Discrepancies between the clade model and the union of the two subclade models (for *Triturus carnifex* and *T. macedonicus*) are shown in orange and red, respectively for the years (a) 2000 and (b) 2080.

Clade and aggregated subclade models for herptiles agree in predicting the trend (i.e. increase or decrease) of change of potential habitat by 2080 (Supplementary material Appendix S15). However, subclade models for four of six herptile clades show contrasting responses to shifting climatic conditions. For example, the clade model of *Triturus marmoratus* clade and the aggregated subclade model both predict a reduction of habitat suitability by 2080 for the entire clade (Supplementary material Appendix S15). Nonetheless, the subclade model for the species *Triturus pygmaeus*, one of the two clade members, forecasts an increase in suitable area for this species (Supplementary material Appendix S8.4d, S13.4b, and S15), while the extent of suitable habitat of the clade as a whole decreases. Similarly, clade and aggregate models agree on the trend in extent of suitable habitat for three of the four bird clades. However, within each clade, subclade models predict that taxa will experience opposite trends in extent of suitable climate by the year 2080 (Supplementary material Appendix S15).

Niche differences within clades and species

The trend for subclade models to predict greater climatic suitability of peripheral geographic areas, mainly under current conditions, was also reflected in the probability of map cell occupancy as a function of climatic gradients. In our data, subclade models sometimes predict greater probability of occurrence towards the extremes of environmental gradients than do clade models. This pattern is exemplified by *Lacerta viridis* and *L. bilineata*, which have higher probability of occurrence at greater and smaller current temperature seasonality values, respectively, than the corresponding clade model (Supplementary material Appendix S16). Similarly, in North American birds, the subclade model of *Colaptes auratus auratus* demonstrates greater probability of occurrence at both low and high extremes of growing degree-days than does the clade model (Supplementary material Appendix S17). In contrast, the great proportion of probability density of the subclade model for *Dendroica coronata auduboni* is found at higher

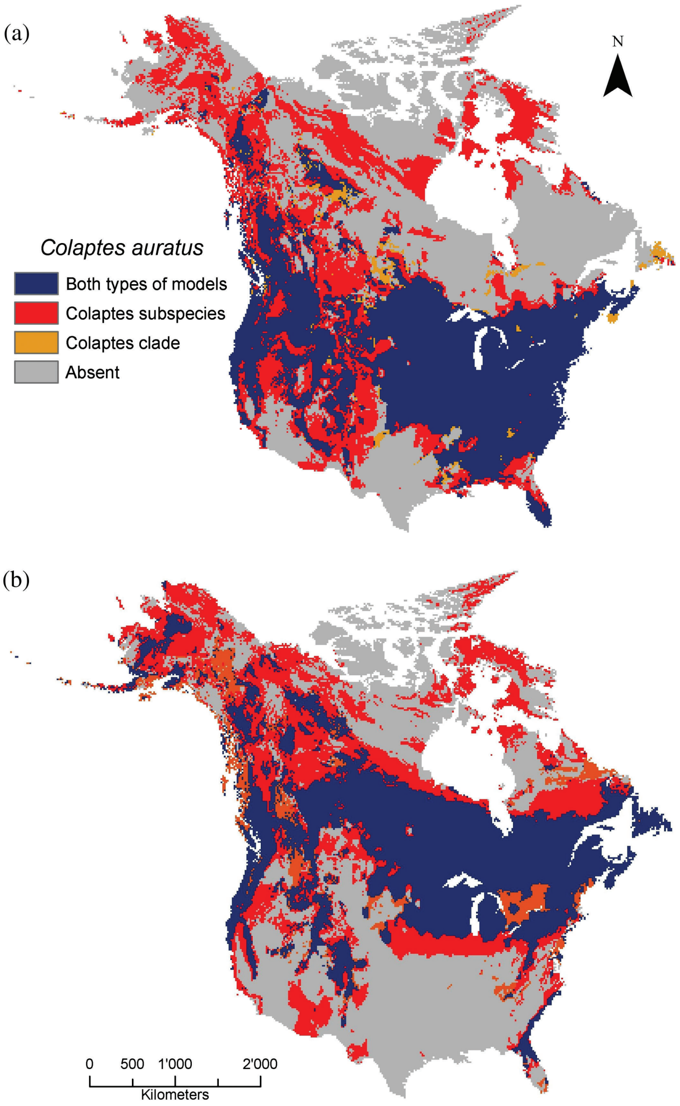

Figure 3. Predicted geographic distribution of suitable climatic conditions for *Colaptes auratus* (northern flicker). Discrepancies between the single clade model and the union of the two subclade models (*Colaptes auratus auratus* and *C. a.cafer*) are shown in orange and red, respectively, for the years (a) 2000 and (b) 2080.

values of mean temperature of the driest quarter than indicated for the clade model of *Dendroica coronata* (Supplementary material Appendix S18).

The niches modeled by clade models and the composite models are similar across herptile species (Supplementary material Appendix S19). Often, the peak of probability of occurrence is slightly higher for the clade model than for the composite model (Supplementary material Appendix S20). On the contrary, in birds the niche as determined from clade models often differs from the niche as determined from the subclade-based composite models. For instance, the composite model for the entire species for *Colaptes auratus*, indicates that subclade models overall predict marginally greater probability of occurrence at lower values of growing degree-days than does the clade model (Supplementary material Appendix S21). In contrast, the composite subclade-based model for *Dendroica coronata* (Supplementary material Appendix S22) shows higher probability of occurrence at high values of the mean temperature of the driest quarter of the year than does the clade model.

Discussion

We chose two datasets for analysis because of our familiarity with them and the intuition that, because of their differences in geographic location, spatial resolution, taxonomic focus, and the evolutionary distinctness of the taxa, they could display distinct tendencies in terms of the degree of niche differentiation among taxa and potential impacts for predicting the effects of climate change. Further, the results of previous studies have demonstrated that closely related taxa can show a range of degrees of niche divergence and that this is to be expected given the diversity of species and their ecologies (Wiens and Graham 2005). For example, niche models of closely related species can show substantial similarity, to such a degree that closely related

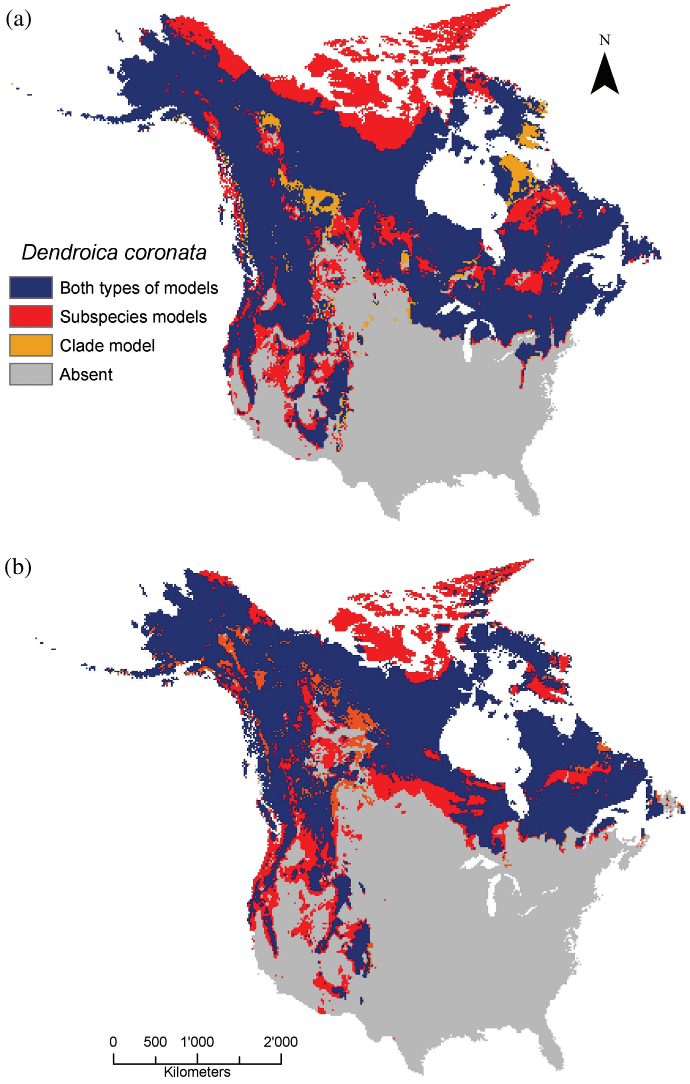

Figure 4. Predicted geographic distribution of suitable climatic conditions for *Dendroica coronata* (yellow-rumped warbler). Discrepancies between the single clade model and the union of the two subclade models (*D. c. coronata and D. c. auduboni*) are shown in orange and red, respectively, for the years (a) 2000 and (b) 2080.

species pairs from diverse taxa can sometimes mutually predict distribution limits of putative sister species (Peterson et al. 1999). In other cases, niche modeling has revealed divergent climatic affinities among very closely related species (Rice et al. 2003, Graham et al. 2004b, Knouft et al. 2006). In general, our data support the existence of a broad range in the degree of similarity in the niche characteristics of closely related taxa. The niche differences we identify here between closely related taxa substantially influence predictions of climate change impacts on species future potential distributions.

Clade and subclade models can differ in their portrayal of the potential effects of climate change. This occurs when subclades occupy different niches and is well exemplified by *Colaptes auratus* (Fig. 3, Supplementary material Appendix S9). Clade models can smooth across the climate-distribution relationships that are identified by subclade models (e.g. *Lacerta* clade, Supplementary material Appendix S16; *Dendroica* clade, Supplementary material Appendix S18). Further, subclade models can predict suitable areas that are geographically peripheral to areas predicted suitable by clade models (e.g. *Junco* clade, Supplementary material Appendix S14). When a taxon has strong phylogeographic structure, models can underestimate climate tolerances and overestimate effects of climate change on taxon range size, as shown for seven of the 10 study taxa (Supplementary material Appendix S12). On the other hand, subclade models can detect lineage-specific effects of climate change that are absent in clade models. For example, distinguishing between two *Bombina* species suggests that some lineages are likely more threatened by climate change than are others, and that this is not detected by clade models (Supplementary material Appendix S6, see also *Testudo*, Supplementary material Appendix S8). Together, these results suggest that models that integrate phylogeographic and subspecies structure can provide an important additional perspective on the potential effects of climate change on species distribution.

Our results support the hypothesis that sister species can show marked niche differentiation. For example, models of the sister species *Triturus carnifex* and *T. macedonicus* show no geographical overlap in the distribution of suitable climatic conditions. Similarly, models of *Lacerta viridis* and *L. bilineata,* and *Bombina variagata* and *B. pachypus* show little overlap in the distribution of suitable climate. We also found substantial niche differences for the subspecies of the woodpecker, *Colaptes auratus*, and the warbler *Dendroica coronata.* However, models for three broadly distributed subspecies of *Junco hyemalis* demonstrated cross-prediction for their geographic ranges, which is in conflict with their generally exclusive distributions (Supplementary material Appendix S11). This variability is in agreement with Peterson and Holt (2003), who found variation among subspecies in the degree to which models of one subspecies cross predicted the distribution of other subspecies. Substantial differences in the niches occupied by subspecies may occur without strong reproductive isolation, as in the case of *Colaptes auratus* (Moore 1987, Moore et al. 1991). Deep and persistent phylogeographic divisions and accompanying differences in niche occupancy suggest that ecological niche models should take these biological characteristics into account. This paper has demonstrated two ways to approach the construction of niche models and predicted distributions when such divisions exist.

It remains unclear whether intra-specific variation in niche occupancy is due to differences in the "available" environmental variation among regions, adaptation to local conditions with concomitant maladaptation to foreign conditions, or other causes. Murphy and Lovett-Doust (2007) conclude that niche occupancy varies among regions in the broadly distributed tree *Gleditsia triacanthos* (Fabaceae), but that this is primarily due to regional differences in the availability of environments. In contrast, experimental studies have repeatedly found differences in performance among populations of trees grown in differing environments. These differences suggest that populations are often best adapted to the local environment (Rehfeldt et al. 1999, Rweyongeza et al. 2007, Savolainen et al. 2007) and that genotype-by-environment interactions are common in widespread species. While ecological correlates of intraspecific niche differentiation may be elusive (McPherson and Jetz 2007), deep phylogeographic divisions within species indicate the potential for intraspecific niche differentiation and suggest the need for definitive field experiments.

Biotic interactions

Another factor that could potentially influence niche occupancy of phylogeographic lineages of a species or clade is geographic variation in the strength of biotic interactions. Incorporation of variables to represent the distribution of potential competing or facilitating species frequently leads to improvement in the performance of species distribution models (Elith and Leathwick 2009, Meier et al. 2010). This suggests that niche differences among subspecies or sister species might arise in part through the differential interaction of these taxa with additional species. In this case, studies that take advantage of phylogeographic structure to construct subclade models can examine benefits in the form of improved model fit that could arise from incorporating information on the distribution of potentially interacting species. An approach that models subclade distributions, as we have done here, allows for the possibility that biotic interactions could affect subclades to different degrees.

Composite niche models and climate change

Models to describe the relationship of climate to the distribution of subspecies and regional portions of widely distributed species could make sense if three conditions were met: 1) a biological basis for regionalization, such as distinct geographic lineages and population genetic subdivision, 2) evidence for local or regional adaptation, and 3) evidence for geographic structure in tradeoffs that result from local adaptation to environment. Some of these conditions, although time consuming and expensive to evaluate, have been reported for species in a variety of unrelated higher taxa. Dozens of experimental studies of the effect of provenance on tree growth, survival and reproduction suggest geographic variation in traits that might be important to mediating population response to climate change (reviewed in Savolainen et al. 2007). Variation in timing of reproduction among populations of bird species in regions with distinct climates and habitats can be genetically based (Blondel et al. 1990, Lambrechts and Dias 1993), respond to selection (Bradshaw and Holzapfel 2006, 2008) and can create fitness costs in newly established populations (Van Der Jeugd et al. 2009). Similarly in larval anurans, variation in season length can select for divergent growth curves as a function of temperature (Berven et al. 1979, Berven 1982). Further, when some geographically-restricted taxa (subspecies or lineages) below the species level have low prevalence, relative to other related taxa, these narrowly distributed taxa can contribute little to modeled distribution at the level of the species. Development of predicted distribution based on a composite niche model gives greater weight to the contribution of these taxa to the niche occupancy displayed by a species. This approach deserves closer inspection and further development.

Data limitation and potential bias

A number of potential sources of spurious influence and bias deserve recognition. We recognize that one aspect of several models of avian distribution in North America is predicted presence in the high arctic, something that is unrealistic for these species. This likely occurs in part because we used only climate data and no land cover variables. Further, despite being the best available data, the BBS dataset includes few survey routes in the high arctic, so that there may be insufficient absence data to constrain distribution in this extremely cold environment. This artifact would likely have been lessened had we additionally constrained the models by the presence of forest vegetation, but this would have been arbitrary had not a full range of land cover data been comprehensively included in the study. In any case, each modeling exercise is limited to a finite number of variables. The results of comparisons, such as those reported here, could potentially be limited to the variables that we used, as in any correlative analysis. Subsequent research can examine an extended set of environmental and landcover variables, but limitations in the northern extent of BBS data will likely remain.

We summarized the geographic location of each 39.4 km BBS route by using a single geographic location to locate the species occurrences found along the entire BBS route. Through much of the North American Midwest, northern Canada, coastal regions and eastern provinces and states, the error that this introduces into the occurrence-climate relationships is surely minimal. Climate variation along survey routes in these areas is small in comparison to the climate gradients that exist over the continental extent of the entire collection of survey routes. In areas of greater topographical diversity, our practice may have introduced error. This is unlikely to have influenced our results substantially for two reasons. First, we used climate estimates with a cell size of 10 min, or roughly 20 km at the temperate latitudes of our study. Climate averaging within these cells is roughly at the same resolution as the location data for survey routes. Secondly, BBS survey routes are almost exclusively along roads and thus are biased against extremes of high elevation. The climatic conditions of topographically diverse areas may be poorly represented in climate data that have a resolution of multiple kilometers. In the herptile dataset, it is unlikely that all atlas cells have been equally well surveyed. Habitat affinities of herptiles likely guide surveys, however, and we assume that inaccuracies are not critical to our interpretation of the patterns we have elucidated.

Conclusion

The analyses that we present demonstrate that subclade models, here representing either species or subspecies, can consistently, if only marginally, outperform clade models as measured by 10-fold cross-validated AUC values. More importantly, subclade models capture the climate-distribution relationship for groups of populations with similar evolutionary histories and shared selective regimes (Avise 2000). Incorporation of this information when modeling species can substantially alter the predicted effects of climate change on the potential distribution of species. We have shown that there are a number of ways to combine subclade models to reflect on the distributions of entire species and that these methods can vary substantially in their predictions for future species distributions. Modeling of species distribution sometimes involves pooling data from groups of populations with very different demographic and evolutionary history. Although this has been advocated as a method for dealing with populations with divergent demographic and evolutionary histories (Broennimann and Guisan 2008), this practice needs further study and refinement. Differential representation of segments of subspecies or phylogeographic lineages in species occurrence data sets can lead to some lineages having little representation in the resulting species model unless appropriate measures are taken.

Unlinked References

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