Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences

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Abstract

Climate change effects on biodiversity are already manifested, and yet no predictive knowledge characterizes the likely nature of these effects. Previous studies suggested an influence of topography on these effects, a possibility tested herein. Bird species with distributions restricted to montane (26 species) and Great Plains (19 species) regions of central and western North America were modeled, and climate change effects on their distributions compared: in general, plains species were more heavily influenced by climate change, with drastic area reductions (mode 35% of distributional area lost under assumption of no dispersal) and dramatic spatial movements (0–400 km shift of range centroid under assumption of no dispersal) of appropriate habitats. These results suggest an important generality regarding climate change effects on biodiversity, and provide useful guidelines for conservation planning.

Keywords: biodiversity consequences, birds, climate change, distributions, topography

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Introduction

Changing climates across the Earth are increasingly influencing geographical distributions and natural history of elements of biodiversity (Bethke & Nudds, 1995; Parmesan, 1996; Brown *et al.*, 1997; Visser *et al.*, 1998; Inouye *et al.*, 2000; Xu & Yan, 2001). Model projections predict that these effects will be widespread (Xia, 1995; Gottfried *et al.*, 1999; Price, 2000; Peterson *et al.*, 2001, 2002b). These effects can take the form of change of habitable area, movement of habitable area, effects on phenology, etc.

Generalities regarding climate change effects on biodiversity, however, have proven to be few. Early commentaries on the challenge focused on northward and upward (in elevation) movement of habitable areas (Peters & Darling, 1985; Perry *et al.*, 1990; Peters & Myers, 1991–1992). Further explorations have focused on the area effects of climate change in montane systems (i.e. that movement of a distributional area up the side of a cone should often reduce in area) and subsequent species losses owing to species-area effects (McDonald & Brown, 1992), although not all climatic warming effects in montane systems necessarily involve area reductions (Gottfried

et al., 1999). In general, though, generalities regarding climate change effects in montane systems have focused on the indirect effects of area reduction on species richness.

Translations of these effects on biodiversity into effects of conservation importance are also now being observed (Chapin *et al.*, 2000; Dale *et al.*, 2001; Xu & Yan, 2001). More specifically, climate-driven reorganizations of ecosystems, communities, and individual species' distributions are increasingly impacting elements of biodiversity that are of interest in conservation efforts (Sala *et al.*, 2000). Nevertheless, generalities that predict the behaviour of elements of biodiversity by which conservation planning can be educated have been few.

A recent survey of projected climate change effects across 1870 species of birds, mammals, and butterflies in Mexico (Peterson *et al.*, 2002b) reflected on these issues in two unexpected ways. First, species exhibited idiosyncratic projected responses to climate shifts – although an average tendency was to move poleward or upward in elevation, individual species were projected to move towards the equator, downward, or diverse mixes of them. Second, the spatial foci of the most serious effects of climate change on biodiversity were focused in the Chihuahuan Desert, flatlands areas in northern Mexico, and not in the montane areas that otherwise dominate the country.

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The present contribution is designed to pursue such generalizations in more detail. Specifically, I compare climate change projections for sets of species in adjacent montane and flatlands regions, the Rocky Mountains and the Great Plains of central and western North America. Comparisons are developed in terms of two distinct dimensions of climate change effects: effects on potential distributional area and effects in terms of distance necessary for tracking an ecological niche spatially.

Methods

The general approach to modeling climate change effects on biodiversity used herein is developed in detail elsewhere (Peterson et al., 2001, 2002b), as are the details of the algorithm used for modeling species' ecological niches (Stockwell & Noble, 1992; Stockwell & Peters, 1999; Stockwell, 1999). Previous tests of the predictive ability of this modeling technique for diverse biodiversity phenomena in various regions have been published elsewhere (Peterson & Cohoon, 1999; Peterson, 2001; Peterson & Vieglais, 2001; Feria & Peterson, 2002; Anderson et al., 2002a, b; Peterson et al., 2002a, c, d; Stockwell & Peterson, 2002a, b; Anderson et al., 2003).

Data on distributions and ecological dimensions

For the analyses developed herein, I sought species that had geographical distributions exclusively in mountain systems, or exclusively in plains. Specifically, I identified species occurring only in the Great Plains, or only in the 'mountain west' of the United States and Canada (i.e. occurring in the Rocky Mountains, and possibly also in the mountains of California, the Great Basin, western Canada, and Alaska). The idea throughout was to have two sets of species occurring in adjacent regions (Rocky Mountains vs Great Plains) that contrast sharply in their landforms (mountains vs plains). To maximize the number of species available for analysis, I identified all species fitting the above descriptions for which ≥5 unique occurrence records were available in the US Breeding Bird Survey data set.

Distributional data representing 9439 records (i.e. unique species × latitude–longitude combinations) for 19 Great Plains species and 26 Rocky Mountain species meeting the criteria listed above (Table 1; 8286 and 1253 unique occurrence records, respectively) were drawn from the results of the US Breeding Bird Survey[1]. Environmental data included 8 electronic map layers summarizing slope and aspect (from the US Geological Survey's[2] Hydro-1K data set), and aspects of climate

[1]http://www.mbr-pwrc.usgs.gov/bbs/bbs.htm.
[2]http://edcdaac.usgs.gov/gtopo30/hydro/.

Table 1 Summary of 19 Great Plains and 26 Rocky Mountains bird species and sample sizes of unique localities available for each

Species	Sample size
Mountains	
Aeronautes saxatilis	73
Aphelocoma californica	46
Carpodacus cassinii	43
Cinclus mexicanus	81
Cyanocitta stelleri	94
Dendroica auduboni	174
Dendroica graciae	7
Dendroica nigrescens	57
Empidonax hammondii	463
Empidonax oberholseri	524
Empidonax occidentalis	275
Empidonax wrightii	210
Gymnorhinus cyanocephalus	33
Melanerpes lewis	19
Myadestes townsendi	61
Nucifraga columbiana	36
Oporornis tolmiei	66
Piranga ludoviciana	110
Poecile gambeli	59
Selasphorus platycercus	31
Siala currucoides	96
Sialia mexicana	42
Sitta pygmaea	34
Sphyrapicus nuchalis	27
Sphyrapicus thyroideus	51
Vermivora virginiae	12
Flatlands	
Aimophila cassinii	297
Ammodramus bairdii	184
Ammodramus leconteii	301
Anthus spragueii	185
Bartramia longicauda	903
Buteo regalis	410
Buteo swainsoni	971
Calamospiza melanocorys	514
Calcarius mccownii	96
Calcarius ornatus	201
Centrocercus urophasianus	148
Charadrius montanus	70
Petrochelidon fulva	55
Quiscalus mexicanus	375
Spiza americana	1089
Spizella pallida	686
Tympanuchus cupido	72
Tympanuchus pallidicinctus	13
Tympanuchus phasianellus	244

including daily temperature range; mean annual precipitation; maximum, minimum, and mean annual temperatures; and vapour pressure (annual means

1960–1990; from the Intergovernmental Panel on Climate Change[3]).

Scenarios of climate change

The general circulation model used (Carson, 1999) (HadCM2) includes several scenarios. We assessed both a conservative and a less conservative view of how climates could change over the next 50 years using the HHGSDX50 and HHGGAX50 scenarios[4]. The HHGSDX50 scenario assumes $0.5\% \, yr^{-1}$ CO_2 increase (IS92d), and incorporates sulphate aerosol forcing, making it a relatively conservative estimate of climate change. The HHGGAX50 scenario assumes a $1\% \, yr^{-1}$ CO_2 increase (IS92a) and does not allow for the effects of sulphate aerosols, and so is more liberal. Results are based on a 30-year average around 2055 (2040–2069), and therefore our models do not take into account the potential effects of increased climate variability (El Niño events, in particular) on species' distributions. Climate data are provided at a spatial resolution of $2.5 \times 3.75°$. Expected changes in temperature (°C) and precipitation (mm) under each scenario were extracted from the relatively coarse raw model results. These expected changes were applied to the IPCC current climate data layers ($0.5 \times 0.5°$ cells).

Ecological niche modeling and dispersal assumptions

The ecological niche of a species can be defined as the conjunction of ecological conditions within which it is able to maintain populations without immigration (Grinnell, 1917; Holt & Gaines, 1992); as such, it is defined in multidimensional ecological-environmental space (MacArthur, 1972). Several approaches have been used to approximate species' ecological niches (Austin *et al.*, 1990); of these, the most robust appears to be the *Genetic Algorithm for Rule-set Prediction* (GARP), which includes several inferential approaches in an iterative, artificial-intelligence-based approach (Stockwell & Peters, 1999).

All modeling in this study was carried out on a desktop implementation of GARP now available publicly for download[5]. Available occurrence points are divided evenly into training and test data sets. Genetic algorithm for rule-set prediction (GARP) is designed to work based on presence-only data; absences are included in the modeling exercise via sampling of pseudoabsence points from the set of pixels where the species has not been detected. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection: first,

a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules), and then is applied to the training data and a rule developed; rules may evolve by a number of means (e.g. truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive accuracy is then evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence.

Ecological niche models developed with GARP can be projected onto both current and modeled future landscapes. Projection onto the current landscape provides an estimate of present-day geographical distribution of suitable conditions. Because species' distributions are limited by combined effects of ecological and historical factors (e.g. barriers to dispersal) (MacArthur, 1972), for the contiguous and no dispersal assumptions, I restricted predicted distributions to those ecoregions[6] in which the species has actually been recorded; in this way, I approximated the actual area of distribution of the species. GARP models consist of an ordered series of if-then statements that predict either presence or absence; these statements can be applied to the transformed landscapes to identify areas of potential distribution for a species after the modeled sequences of environmental change.

I thus synthesized the pre-change and two post-change maps (liberal and conservative scenarios averaged) for each species by measuring potential distributional area under each of three sets of assumptions regarding dispersal ability. An unrealistic assumption was that species could disperse to any site at which conditions were favourable for population persistence ('universal dispersal') (i.e. raw, uncut niche distributions were compared before and after change). More realistic for some species was the assumption that species would be able to disperse through continuous habitat but not jump over barriers ('contiguous dispersal') (i.e. the modeled actual distribution was overlapped with the post-change prediction, and areas of continuous habitable environments that touch the present distribution were identified; discontinuities of one pixel or greater (~10 km) were considered barriers to dispersal), or that species were simply unable to disperse and would inhabit only those portions of present distributional areas that remain habitable ('no dispersal') (i.e. the modeled actual distribution was reduced to those areas predicted to be habitable post-change). Centroids of each of the three maps were calculated using ArcView (version 3.2), and geographical distances among centroids calculated using great-circle distance formulas. Overall, these analyses

assume no evolution in niche characteristics (Peterson *et al.*, 1999), and do not take into account interactions among species such as competition, predation, etc.

Results

Predictions of climate change effects on individual species' potential geographical distributions varied from subtle adjustments to dramatic rearrangements of potential distributional areas (Fig. 1). For example,

American Dippers (*Cinclus mexicanus*) are projected to retain the broad-brush form of their distribution, but with subtle retractions around much of the range periphery, and expansion along the northwestern border. Baird's Sparrow (*Ammodramus bairdi*), in contrast, is projected to retract from much of its geographical distribution, retaining significant distributional areas only in the south-central portion of its distribution, and with minor expansion in one sector of its northern border. Overall, the idiosyncratic nature of projected changes
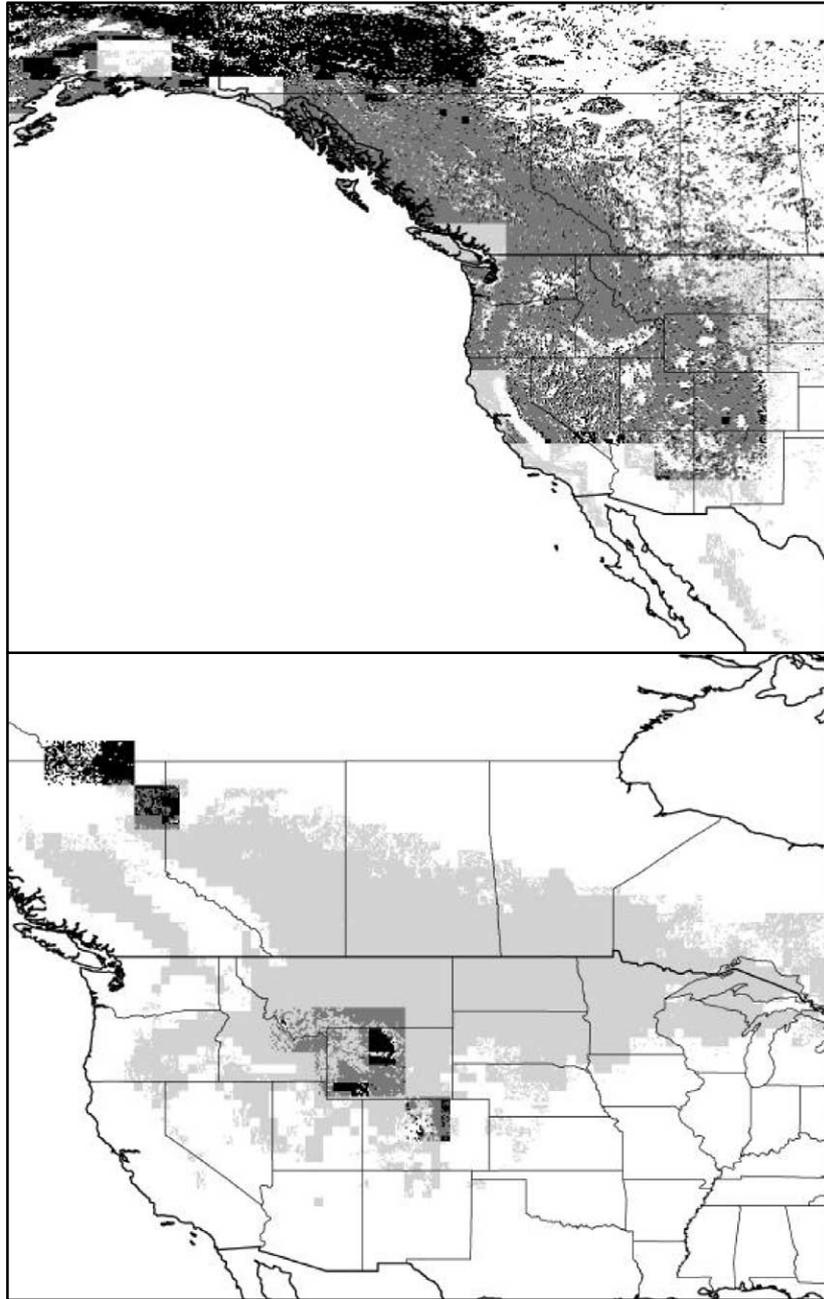

Fig. 1 Two exemplar future projections of effects of climate change (HHGGAX50 climate change scenario) on species' geographical distributions. (Top) American Dipper (*Cinclus mexicanus*) (Bottom) Baird's Sparrow (*Ammodramus bairdi*). Light gray = areas presently habitable but not predicted to remain habitable, dark gray = areas presently habitable that are projected to remain habitable, and black = areas not presently habitable that are projected to become habitable.

on species' distributions is again illustrated: distributional expansions tend to take place along northern borders, and retractions along southern borders, but many significant variations on these themes were also observed.

Overall projected effects of climate changes on species' geographical distributional areas differed between montane and flatlands species (Fig. 2). Montane species invariably either retained more of present-day distributional areas or even increased in distributional area, depending on the dispersal assumption employed. Comparisons of montane and flatlands species indicated that

area effects on flatlands species were highly statistically significantly more severe than those on montane species (Mann–Whitney U-tests, all $P < 0.0001$).

Projected effects of climate changes on spatial position of geographical distributions also depended on dispersal assumptions (Fig. 2). If species were largely sedentary (no dispersal assumption), montane species experienced no or minimal net movement in their geographical distributions, but flatlands species saw dramatic net movement of the potential distribution (Mann–Whitney U-test, $P < 0.0001$). Under contiguous dispersal assumptions, ranges for the two sets of species were completely
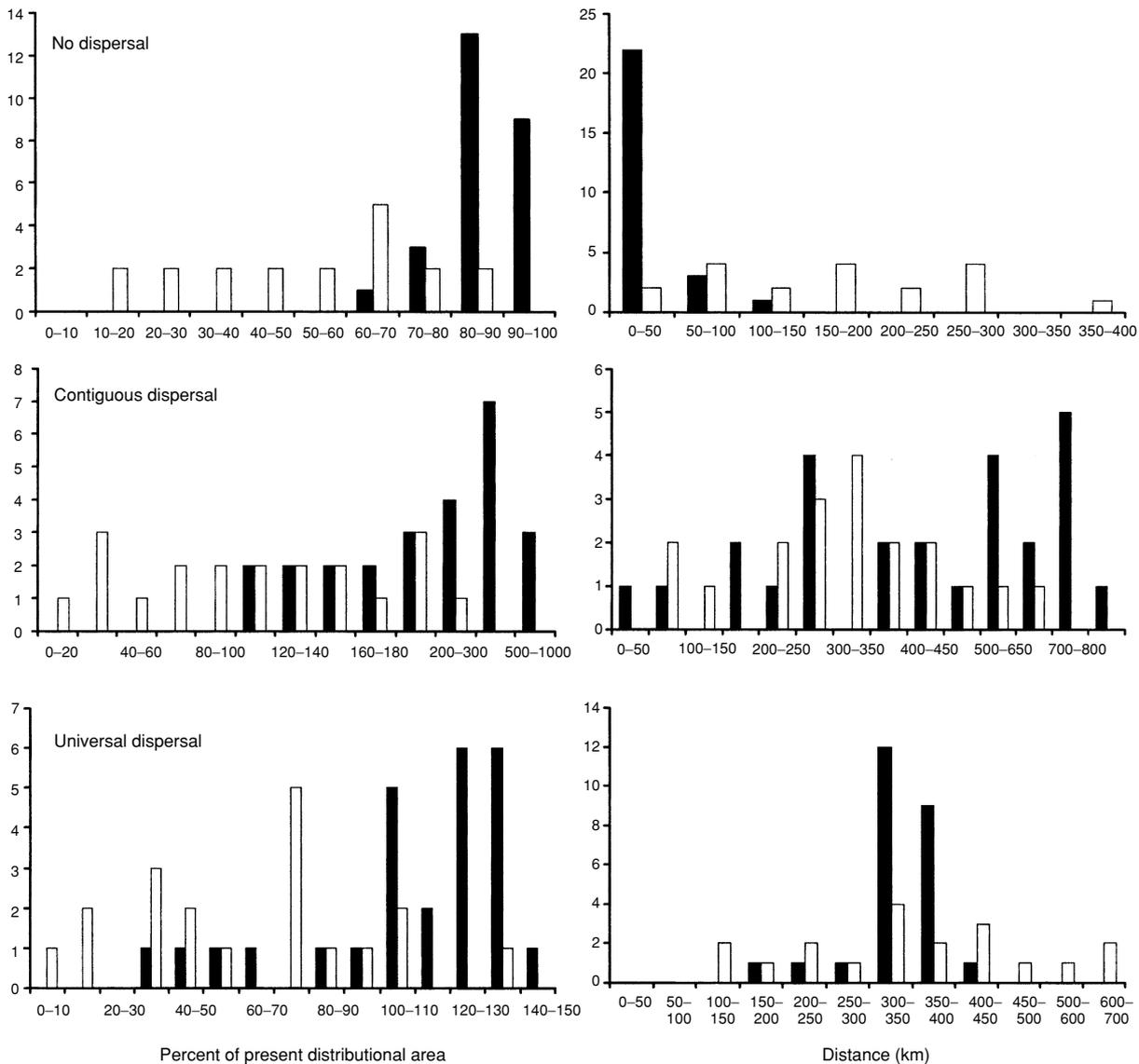
Fig. 2 Projected change in potential distributional areas (left column, expressed as percent of present distributional area), and projected distance that range centroids would shift, as a result of modelled climate change processes. Results are separated for montane (black) and flatlands (white) species, and for three assumptions regarding dispersal ability (no dispersal, contiguous dispersal, universal dispersal).

overlapping, and montane species saw somewhat greater distance effects (Mann–Whitney U-test, $P \sim 0.05$); under the universal dispersal assumption, no significant difference was observed between montane and flatlands species (Mann–Whitney U-test, $P > 0.35$).

Discussion

Limitations

The methodology employed herein depends critically on the modeled ecological niche as a stable constraint on species' geographical distributional potential. The stability of ecological niches in short-to-moderate periods of evolutionary time has been explored extensively. (1) Ecological niches modeled on native distributional areas provide excellent predictivity for potential invaded ranges in other regions (Peterson et al., 2001; Peterson & Vieglais, 2003). Over longer time periods, mammal species surviving the end of the Pleistocene in North America followed predictable climate regimes in their range shifts over this dramatic climate change event (E. Martínez-Meyer, unpublished data). Finally, comparisons of sister species pairs and comparisons across broader clades indicate that closely related species often share highly similar ecological niches, suggesting evolutionary conservatism of ecological niche characters, which breaks down when comparisons are made deeper in clades (Peterson et al., 1999). This growing body of evidence speaks to the evolutionary stability of modeled niches, which (by definition) constitute distributional constraints.

The suggestion that predictivity of niche models is limited by confounding effects of species' interactions (Davis et al., 1998) is not supported by this series of studies. If shifting interactions are as pervasive a process as these authors suggest, predictivity across more immediate shifts in community context (species' invasions) or longer-term phenomena (Pleistocene-to-recent comparisons, phylogenetic comparisons) would not be likely. Hence, the drastic shifts in observed niche characteristics anticipated based on experimental situations (Davis et al., 1998) appear to result more from the restrictive nature of those experiments than from general shifts to be expected over climate change events.

Limitations of more serious concern for the outcome of these modeling exercises are those of full estimation of dimensions of the ecological niche: with estimation of these dimensions in one time period, and projection to another, complications arise. First, projection onto a future surface presenting conditions outside of the present-day range of conditions involves necessary assumptions about translation of rules into those unsampled conditions. Second, to the degree that species'

interactions may limit present-day ecological distributions across broad spatial scales, such interactions could cause underprediction of future distributional potential. In sum, predictions among time periods can be complex, but are feasible under certain assumptions.

Finally, and perhaps most seriously, the utility of the model predictions developed herein is limited by the accuracy and resolution of the general circulation models upon which they are based. The Hadley models, although improved markedly in latest versions (Pope et al., 2002), are global in coverage, and thus perforce must be coarse to permit multidimensional simulations. Such global models will invariably be limited in their spatial resolution, so eventually shifting to more detailed regional climate scenarios will be necessary, and will constitute an important improvement to model quality.

Dispersal scenarios

In this study and in past studies (Peterson et al., 2001, 2002b), I have developed climate change projections across 3 dispersal scenarios: universal dispersal, contiguous dispersal, and no dispersal. These scenarios are simultaneously useful and enormously frustrating – on the positive side, they certainly bracket the universe of possible effects of climate change on species, and they are applicable without requiring specific information about particular species. At the same time, on the negative side, they differ dramatically in the magnitude of effects predicted for species, and particular species are generally difficult to place as pertaining to one dispersal scenario or another.

The species treated in this paper are relatively mobile, and may come out as fairly good dispersers, at least as compared with other taxa (e.g. trees). All the same, given well-documented phenomenon of philopatry, even in migratory birds (Gill, 1994), the species considered herein are unlikely even to approach the 'universal dispersal' assumption. Rather, most likely, the nonmigratory forms considered herein (e.g. *Cyanocitta stelleri*, *Tympanuchus cupido*) are likely to fall in between 'no dispersal' and 'contiguous dispersal', whereas migratory species (e.g. *Dendroica auduboni*, *Bartramia longicauda*) may fall into a more mobile category closer to 'contiguous dispersal'. My results are more or less consistent across these different assumption sets, with the exception of range centroid distance calculations for contiguous dispersal, the reasons for which are unclear. These rough guesses regarding dispersal capacity, nevertheless, are too crude to permit confidence in further detail of interpretation, such as calculating average range loss with each species placed under the appropriate dispersal assumption.

Mountains vs flatlands

In general, this study suggests that the idea that montane areas will be foci of negative climate change effects on biodiversity is not well-founded. Whereas area effects will influence montane areas, area reductions predicted in this study were actually more intense in flatlands. Moreover, concerns with tracking habitable conditions spatially were essentially nil in montane areas, but potentially quite serious in flatlands areas.

A general idea of climate change effects on species' ranges can be developed from the very simple framework developed in Fig. 3. In terms of area, montane distributions will almost always see area reductions if warming trends push life zones upward in elevation (Fig. 3a); such area effects are not necessarily expected in flatlands systems (Fig. 3b). The horizontal implications of these shifts, however, contrast sharply between montane (Fig. 3c) and flatlands (Fig. 3d) landscapes: much more dramatic horizontal shifts would be expected in flatlands systems simply because of the geometry of the two landscapes, given the same intensity of temperature shifts. These general expectations, although reasonable in theory, need to be reexamined in light of actual empirical data regarding climate change across real, complex landscapes.

The montane area effects are clear (Fig. 3c), although exceptions are possible given the particulars of local topography (Gottfried et al., 1999). Although the general conclusion of this study was of relatively subtle area effects, it is worthy of note that no highest-montane species (e.g. rosy-finches, Leucosticte spp., which are restricted to tundra habitats) were included. For those species inhabiting mountaintop habitats, area effects can be absolute, with the climate regime literally disappearing off the top of the mountains.

Flatlands will see an alarming combination of area effects and niche-tracking challenges. Somewhat surprisingly, area effects assessed in this study proved more severe in flatlands systems than in montane areas. However, at least under some dispersal assumptions, in tandem with area effects are dramatic spatial movements of appropriate conditions. Hence, species restricted to flatlands areas are presented with a doubly difficult situation in the face of climate change. These effects are compounded if the area is at all bounded – low, flat islands, high plateaus, poleward coastal areas, and other bounded flatlands areas would be particularly vulnerable.

Conclusions and implications for conservation

An important challenge for coming years in understanding and anticipating climate change effects on biodiversity is that of arriving at a generalizable and predictive understanding of those effects. This study represents a second step towards such an understanding, following initial broad surveys that documented the idiosyncratic nature of expected responses by species (Peterson et al., 2001, 2002b). Here, I have explored the effects of general landform on expectations for climate change effects.
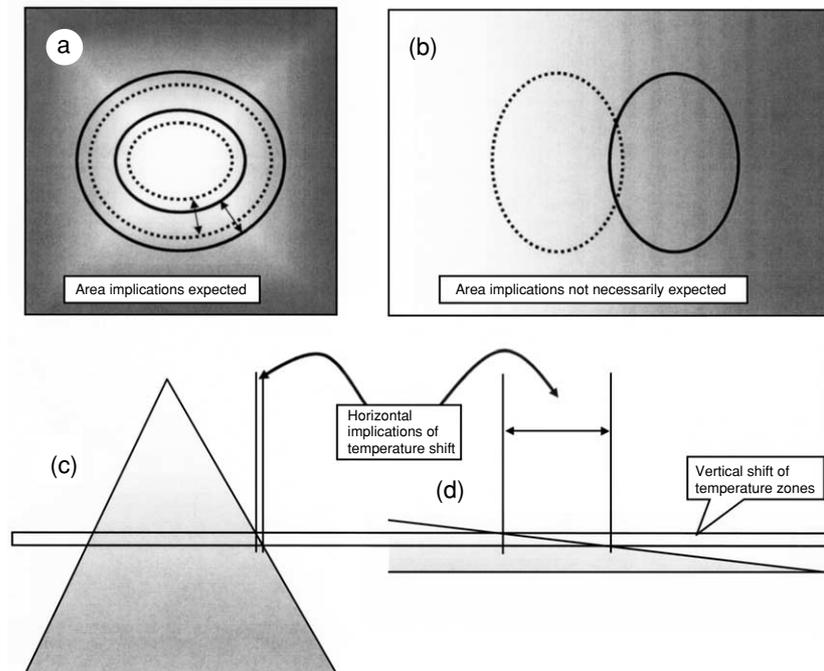
Fig. 3 Diagram illustrating potential effects of topography (dark-to-light shading indicates increasing elevation) on species' ranges during climate change: (a) mountain area effects, (b) flatlands area effects, (c) mountain range shifts and (d) flatlands range shifts. See text for detailed explanation.

Studies that have modeled and predicted climate change effects on species' distributions (Perry *et al.*, 1990; Johnston & Schmitz, 1997; Kadmon & Heller, 1998; Price, 2000; Peterson *et al.*, 2001, 2002b) have noted the idiosyncratic and individualistic nature of species' expected responses to climate change. In this sense, a best solution to conservation planning would thus be development of species–specific models across a region to permit effective planning – in this way, the idiosyncratic nature of species' responses to climate change would be taken into consideration in as detailed a manner as modelling techniques permit.

All the same, many conservation planning decisions must be made sooner rather than later, and often cannot await detailed modeling exercises. In such situations, the generalizations that are beginning to emerge, from this study and others (Peterson *et al.*, 2001, 2002b), indicate a critical role of topography in determining the success or failure of a particular conservation strategy. Certainly, linkage of montane and flatlands systems will provide some buffer to the flatlands in the form of marginal relief. Flatlands systems will require north–south corridors to accommodate the broad movements that are expected. These patterns, although noted in Mexico (Peterson *et al.*, 2001, 2002b) and tested herein and in preliminary analyses of Canadian butterflies, would benefit from further testing, and additional details and generalities will doubtless emerge.

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