Projecting the local impacts of climate change on a Central American montane avian community

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ABSTRACT

Significant changes in the climates of Central America are expected over the next century. Lowland rainforests harbor high alpha diversity on local scales (<1 km^2), yet montane landscapes often support higher beta diversity on 10-100 km^2 scales. Climate change will likely disrupt the altitudinal zonation of montane communities that produces such landscape diversity. Projections of biotic response to climate change have often used broad-scale modelling of geographical ranges, but understanding likely impacts on population viability is also necessary for anticipating local and global extinctions. We model species' abundances and estimate range shifts for birds in the Tilarán Mountains of Costa Rica, asking whether projected changes in temperature and rainfall could be sufficient to imperil high-elevation endemics and whether these variables will likely impact communities similarly. We find that nearly half of 77 forest bird species can be expected to decline in the next century. Almost half of species projected to decline are endemic to Central America, and seven of eight species projected to become locally extinct are endemic to the highlands of Costa Rica and Panamá. Logistic-regression modelling of distributions and similarity in projections produced by temperature and rainfall models suggest that changes in both variables will be important. Although these projections are probably conservative because they do not explicitly incorporate biological or climate variable interactions, they provide a starting point for incorporating more realistic biological complexity into community-change models. Prudent conservation planning for tropical mountains should focus on regions with room for altitudinal reorganization of communities comprised of ecological specialists.

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1. Introduction

Global climates are being altered by human activities, and there is increasing evidence that this change often affects species' distributions (Parmesan, 2006). With further change expected, the number of studies projecting biotic response to future climate change has increased. Many of these studies have modelled species' responses to climate change over broad spatial scales, projecting geographical range shifts in response to regional changes (Jetz et al., 2007; Malcolm et al., 2006; Peterson et al., 2002). These approaches often make assumptions about processes operating at local scales (e.g., habitat specialization and dispersal), and it is important to directly study these processes to understand population dynamics that underlie geographical range shifts. It is also important to understand local changes in population size and dis-

tribution on the scale of most conservation efforts, particularly for species that are at greater risk of extinction because of their restricted distributions (Midgley et al., 2002). Tropical mountainsides exemplify the potential impact of climate change on diverse tropical systems in which species are habitat specialists with small geographical ranges (Jankowski and Rabenold, 2007; Jankowski et al., 2009), and some tropical cloud forests appear to be early-warning systems where altitudinal range shifts, population declines, and extinctions have already been found (Pounds et al., 2006).

Central America is expected to experience significant changes in temperature, rainfall, and seasonality (Giorgi, 2006; IPCC, 2007; Neelin et al., 2006; Rauscher et al., 2008) that are likely to seriously impact cloud forests (montane rainforests) dependent on high humidity, cool temperatures and frequent immersion in clouds (Enquist, 2002; Haber, 2000; Jankowski et al., 2009; Karmalkar et al., 2008; Nair et al., 2008). Central America, and the highlands of Costa Rica and Panamá in particular, are also recognized as global conservation priorities because of the concentration of biodiversity and endemism there (Hernández-Baños et al., 1995;

Stattersfield et al., 1998). In this study, we test the hypotheses that projected changes in temperature and rainfall could imperil high-elevation endemic species and that temperature and rainfall effects could each strongly impact avian distribution and abundance in the Monteverde region of Costa Rica.

Our current 32-km² study site surrounding Monteverde harbors 41 bird species narrowly endemic to the cloud forests of Costa Rica and Panamá (Stiles et al., 1989). We employ a data set consisting of systematic point counts over 4 years to describe species' current abundance patterns. We individually shift abundance patterns according to species' associations with local temperature and precipitation gradients to produce estimates of population-level response to climate change. Because each species' distribution may be better predicted by either temperature or precipitation, or both, we used logistic regression to determine the best predictor(s) of species' presence/absence within the study area. Using the logistic models for each species, we then model change in area occupied and use these estimates to assess congruence between distribution and abundance estimates. Finally, depending on which variables are the best predictors of distributions, we produce a best estimate of response to climate change for each species within the study site.

2. Methods

2.1. Study area

The Tilarán range extends 50 km northwest–southeast separating the wet Caribbean slope from the drier Pacific slope of Costa Rica (10°18′N, 84°45′W). When the dominant northeasterly trade-winds are driven up the Caribbean slope, adiabatic cooling relieves air masses of most of their moisture. As winds cross the continental divide, much of the moisture is delivered as mist and cloud water, allowing cloud forests to grow down to 1500 m on the Pacific slope. The forest structure on the Pacific slope demonstrates the impact of aerial moisture and a moderate dry season, particularly the massive epiphyte community at high elevations that nearly disappears below 1400 m (Haber, 2000; Jankowski et al., 2009).

Data from conventional gauges and windscreens suggest that moisture in the ridge-top cloud forests averages 4000–6000 mm annually, and declines to 2000 mm within 4–5 km toward the Pacific (below 1000 m), where there is a pronounced dry season (Bolaños and Watson, 1993; Haber, 2000; Häger, 2006). These drier lowlands are considerably warmer (6 °C/1000 m altitude), further increasing potential evapotranspiration and reducing soil moisture (Clark et al., 2000). Moisture declines approximately 1000 mm/km moving horizontally away from the continental divide on the Pacific slope. Corresponding changes in plant communities show complete turnover in tree species composition within 3 km of the divide (Haber, 2000). Similar rates of turnover have been documented in birds, and distance to the continental divide (DTD) and altitude are the two variables that best predict species' local distributions (Jankowski and Rabenold, 2007).

2.2. Estimating current populations

We sampled bird communities in primary forests during the peak of the breeding season (May–July) in 2003, 2006, 2007, and 2008 at 82, 135, 95 and 97 points each year, respectively, across the Pacific slope of the Monteverde region (most points overlapped across years; maximum altitude 1850 m). Sampling points were separated by ⩾200 m and were revisited four times within each season. Two observers mapped sightings and songs for all bird species within a 100 m radius for 10 min (Jankowski and Rabenold, 2007). Within each year, we estimated density for each species

at each point as the maximum number of individuals detected during any one of the four visits. As some species were detected only at short distances, we adjusted density estimates using the equation: $N = C/\beta$ where N is the estimate of true density, C is the maximum recorded abundance at a point, and β is an index of detectability (representing the probability that individuals are detected within a 100-m radius; Williams et al., 2002). We pooled data from the first 3 years and modelled detectability using program DISTANCE (Thomas et al., 2006) for species with >20 detections following procedures recommended by Buckland et al. (2001) (for further details on the above methods see Jankowski et al. (2009)).

We organized data from all 4 years of sampling at each point into bands of 100 m altitude or 300 m DTD according to measurements of altitude using hand-held altimeter–barometers (calibrated daily to local reference sites) and Euclidean distance measures to the continental divide in ArcGIS 9.2 (ESRI, 2007). We calculated the mean number of individuals occurring per 3.14 hectares (the area sampled at each point) in each band and used this density value to calculate total population size based on the forest area available (measured at 30 m resolution from 2001 Landsat 7 images; NASA, 2001).

2.3. Single-climate-variable models of species' abundances

Our approach for shifting species distributions follows the methods of Shoo et al. (2005), that project species' population responses to climate change by shifting current abundance patterns up mountain slopes, assuming that species' densities would remain constant within zones and would track their associated climate "envelopes" (Pearson and Dawson, 2003). We used two single-climate-variable models to project species distributions and abundances in response to different environmental changes: the altitude model, using temperature change only (and an adiabatic lapse rate of 6 °C/km of elevation; Raxworthy et al., 2008), and the distance-to-divide model using precipitation change only (DTD; observed 1000 mm/km moisture gradient from the ridge separating the Atlantic and Pacific drainages; Figs. 1 and 2; Jankowski et al., 2009; Haber, 2000). In the altitude model, we shifted each species upslope by 500 m altitude based on a digital elevation model, representing moderate A1B or B2 climate projections of 3 °C warming in 100 years (IPCC, 2007; Ruosteenoja et al., 2003). In the DTD model, we shifted species 600 m toward the continental divide, also representing projections with a moderate A1B projection of 15% drying effect (based on average of Central American region models; Rauscher et al., 2008). We recalculated expected abundance within available forest of each 100 m altitude or 300 m DTD band and combined values across bands to project future total populations for each model (Fig. 1).

Because the study site did not extend below 1000 m altitude and many dry forest species detected at those altitudes have populations extending into the Pacific lowlands (Stiles et al., 1989), we assumed that the densities observed in the lowest altitudinal and farthest DTD bands were representative of densities for these species in lowland areas below our study site. When abundance patterns were shifted, we reapplied the current density values in those bands to the forest area available to create a more realistic model of expansion of lowland species into the study site.

2.4. Evaluating climate variables using logistic models

The above methods produced two abundance projections for each species modelled, one based on climatic warming, with species shifting along the altitudinal gradient, and the other based on reduced precipitation, with species shifting along the moisture gradient. As our goal was to offer a "best" estimate of each species'
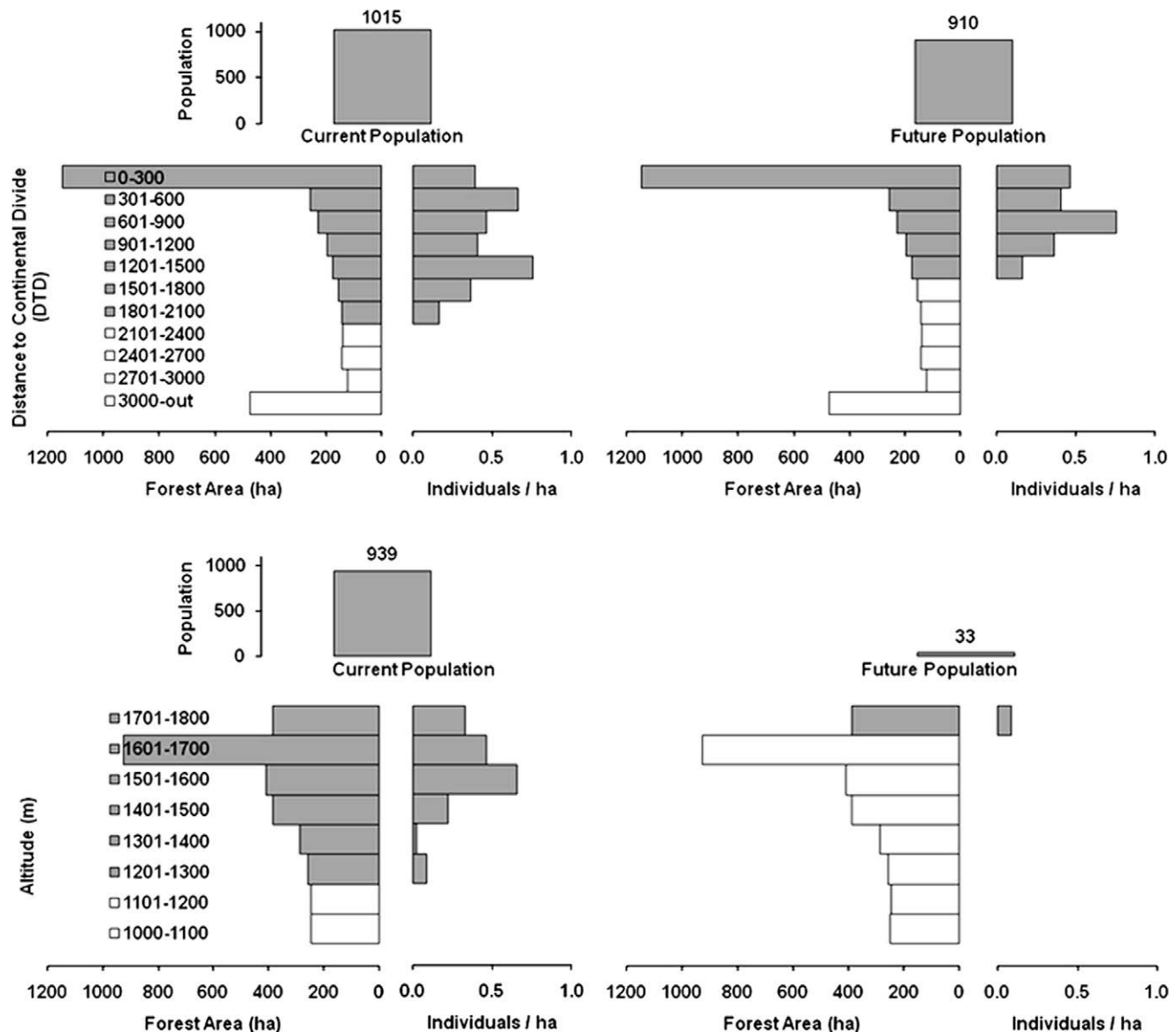
Fig. 1. Current and future abundance patterns for the Resplendent Quetzal. Projected change in local population resulting from shifting current abundance patterns 600 m closer to the continental divide to simulate a 15% decrease in precipitation (upper panel). Projected population change when abundance patterns are shifted upward 500 m in altitude to simulate 3 °C warming (lower panel). Left and right halves within panels demonstrate current and projected abundance patterns, respectively.

response to climate change, we used logistic regression to identify which climate variables (temperature or precipitation) were the best predictors of distribution. We used step-wise model selection with the Logistic procedure in SAS Version 9.1 (SAS Institute Inc., 2007) to fit each species to a logistic equation using presence/absence data from the first 3 years and the variables altitude and DTD. We then used the relationships identified between climate variables and distribution to project future distributions, and compared the magnitudes of projected changes in distribution to those produced by single-variable projections of abundance. For species whose logistic models retained both variables, we used distribution projections instead of abundance projections because simultaneous shifts of abundance patterns according to both expected change in temperature and precipitation were not possible.

2.5. Logistic distribution modelling

Using the Raster Calculator feature in ArcMap (ESRI, 2007), we applied the logistic equation of each species to the appropriate

set of 30-m resolution raster files, including forested habitat and one of the following representing altitude, DTD, and/or an altitude * DTD interaction, to produce a map depicting the probabilities of a species' occurrence in each pixel. The performance of logistic equations in predicting distributions was evaluated using the area under the receiver operating characteristic curve (ROC), also known as AUC (Fielding and Bell, 1997), by testing probability maps against data from the 2008 dataset. Despite recent criticism of AUC analysis in distribution modelling (Lobo et al., 2008), its use is acceptable because our models were trained using true absences, which prevents the potential upward bias imposed on AUC scores when pseudo-absences are used to train models. Logistic models producing AUC values >0.7 (probability that the model assigns higher probability of occurrence to a randomly chosen occupied pixel than to a randomly chosen unoccupied pixel) were considered informative (Fielding and Bell, 1997).

For species with informative models, we recalibrated logistic equations by combining all 4 years of presence/absence data, assuming this would improve model accuracy. The recalibrated lo-
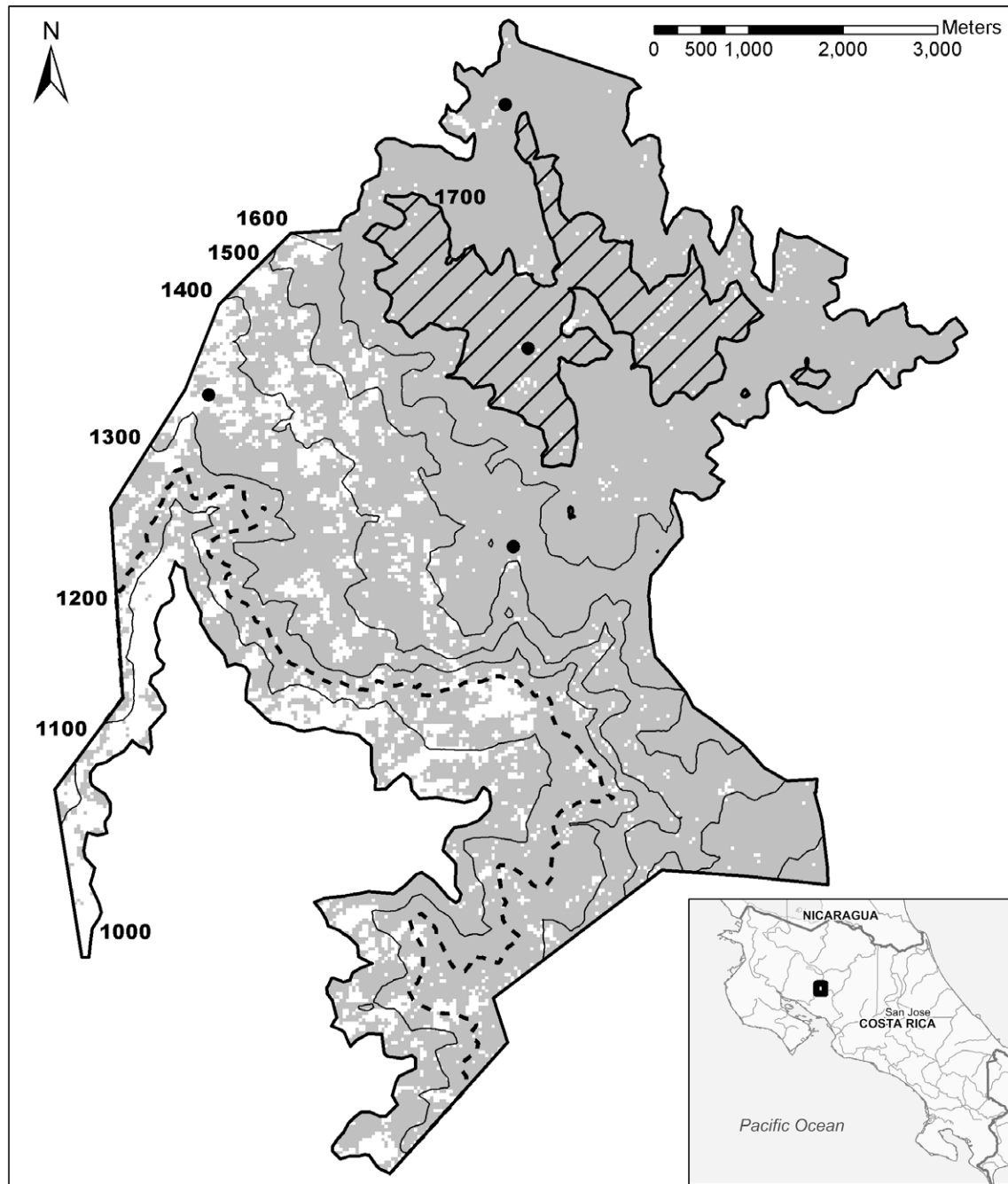
Fig. 2. Projected altitudinal distribution change for the Resplendent Quetzal. The polygon of the study site includes all sites where abundance data were collected. Gray shading represents existing forest. Contour lines represent 100 m altitudinal bands. Areas higher in altitude than the dotted line indicate the Resplendent Quetzal's current distribution, compared to crosshatched areas above 1700 m representing 100-year distribution projection. Such a 500 m shift toward higher altitudes corresponds to the 3 °C increase expected for the region. Location dots moving clockwise from left represent Santa Elena, the Santa Elena Cloud Forest Reserve entrance, communication towers, and the Monteverde Cloud Forest Reserve entrance.

gistic models were reapplied to forested habitat, DTD and/or altitude raster datasets (derived from a NASA shuttle radar topographic mission digital elevation model; USGS, 2006) to produce new probability maps that were transformed into current presence/absence distribution maps for each species based on each species' optimal probability-threshold value (selected by minimizing the difference between sensitivity and specificity; Lobo et al., 2008; Supplementary Table S1). We then applied these logistic models to adjusted altitude and DTD rasters (simulating range shifts) to produce maps of species' future distributions. The total number of pixels occupied in current versus future distribution maps was used to estimate the proportionate change caused by changes in climate.

2.6. Selection of best models

We selected a "best" projection for each species based on the climate variable(s) retained in its logistic equation. For those containing both variables, we used the distribution projection. For species that did not have a significant predictor in their logistic equation, we used projections of change in abundance from the DTD model as the "best" projection because DTD was most fre-

Table 1
Projected changes in abundance for 77 Central American cloud forest species.

	DTD			Altitude		
	All Species	Endemic to…		All Species	Endemic to…	
		Central America	Costa Rica/ Panamá		Central America	Costa Rica/ Panamá
>+25%	23	5	1	34	6	3
0% to +25%	20	2	2	0	0	0
0% to −25%	21	2	8	3	0	0
−25% to −50%	8	1	3	4	0	0
−50% to −75%	3	1	2	6	0	1
>−75%	1	0	2	18	3	7
Extinction	1	0	1	12	2	8

Table 2
Ranks of the 25 largest projected declines for the DTD model compared to rankings based on the altitude model.

Species	DTD		Altitude	
	Rank	% Change	Rank	% Change
Pselliophorus tibialis[b]	1	−100.0	1	−100.0
Geotrygon costaricensis[b]	2	−86.6	24	−84.4
Thripadectes rufobrunneus[b]	3	−81.8	2	−100.0
Scytalopus argentifrons[b]	4	−54.3	14	−97.4
Veniliornis fumigatus	5	−53.5	22	−88.7
Nothocercus bonapartei	6	−52.3	33	−62.4
Catharus frantzii[a]	7	−51.5	3	−100.0
Myioborus torquatus[b]	8	−50.5	4	−100.0
Phainoptila melanoxantha[b]	9	−46.9	5	−100.0
Turdus plebejus[a]	10	−42.2	6	−100.0
Cranioleuca erythrops	11	−40.8	7	−100.0
Margarornis rubiginosus[b]	12	−29.1	8	−100.0
Semnornis frantzii[b]	13	−28.1	21	−90.7
Syndactyla subalaris	14	−25.3	13	−97.5
Pheucticus tibialis[b]	15	−23.2	9	−100.0
Myadestes melanops[b]	16	−22.5	15	−97.1
Henicorhina leucophrys	17	−18.9	35	−56.2
Vireo leucophrys	18	−12.1	10	−100.0
Chlorospingus ophthalmicus	19	−10.8	23	−87.9
Zimmerius vilissimus	20	−10.8	42	−14.4
Pharomachrus mocinno[a]	21	−10.3	16	−96.5
Troglodytes ochraceus[b]	22	−10.0	19	−93.6
Catharus fuscater	23	−9.8	37	−44.7
Chamaepetes unicolor[b]	24	−9.3	28	−81.8
Arremon brunneinucha	25	−9.0	41	−17.3

[a] Endemic to Central America.
[b] Endemic to highlands of Costa Rica and Panamá.

quently included in the logistic equations of other species and tended to give more conservative estimates (see Section 3.2).

3. Results

3.1. Single-climate-variable models

Through four breeding seasons, we accumulated 17 823 detections of 127 bird species representing 28 families on the Pacific slope of the Tilarán Mountains. We excluded from analyses 44 species that were detected on fewer than 20 occasions, as well as six species whose seasonal and daily movements made density estimates problematic. Of the 77 species used to model response to climate change, 30 species' ranges are limited to Central America, and 19 of these are endemic to the highlands of Costa Rica and Panamá (Stiles et al., 1989; Table 3).

The altitude model projected drastic changes in individual species' abundances and in the avian community. Nearly half of the species were projected to decline in abundance, and 12 were

Table 3
Projected population changes from each single-variable model and the distribution model (% change in distribution). Missing values indicate either failure to produce a logistic model or a model that failed to successfully test against excluded data. Bold values represent the best projection for each species and were selected based on which variables were included in a species' logistic equation (DTD, altitude, or distribution model using both). DTD was used as the default best model for species lacking a significant predictor variable in their logistic equation because DTD was most often the lone predictor variable in other species' models and frequently represented more conservative projected change. Species taxonomically organized to the AOU's *Check-list of North American Birds, 7th Edition* and its 50th supplement.

Species	DTD % Change	Altitude % Change	Distribution model % Change
Nothocercus bonapartei	−52.3	−62.4	
Chamaepetes unicolor[b]	−9.3	**−81.8**	
Odontophorus leucolaemus[b]	**107.9**	126.5	
Geotrygon chiriquensis[b]	103.9	**128.5**	
Geotrygon costaricensis[b]	−86.6	−84.4	
Piaya cayana	**137.6**	183.8	
Trogon aurantiiventris[b]	**−1.9**	153.5	
Pharomachrus mocinno[a]	−10.3	**−96.5**	
Momotus momota	128.1	316.3	
Semnornis frantzii[b]	−28.1	**−90.7**	
Aulacorhynchus prasinus	**118.8**	154.0	132.6
Veniliornis fumigatus	**−53.5**	−88.7	
Cranioleuca erythrops	−40.8	−100.0	
Premnoplex brunnescens	**−0.7**	−95.3	
Margarornis rubiginosus[b]	**−29.1**	−100.0	
Syndactyla subalaris	**−25.3**	−97.5	
Sclerurus mexicanus	**−7.2**	−92.9	
Sclerurus albigularis	105.8	−74.2	
Thripadectes rufobrunneus[b]	−81.8	**−100.0**	
Dendrocincla homochroa	134.3	256.0	
Sittasomus griseicapillus	**130.0**	212.2	132.8
Xiphorhynchus erythropygius	120.0	−29.7	
Lepidocolaptes souleyetii	**121.3**	226.9	164.0
Dysithamnus mentalis	105.1	**219.8**	
Myrmotherula schisticolor	153.2	**178.5**	
Myrmeciza immaculata	124.3	**202.3**	
Scytalopus argentifrons[b]	−54.3	−97.4	**−100.0**
Elaenia frantzii	−1.8	**−51.9**	
Mionectes olivaceus	140.0	−73.3	
Mionectes oleagineus	111.1	**550.1**	
Zimmerius vilissimus	−10.8	−14.4	
Lophotriccus pileatus	130.1	**239.4**	
Rhynchocyclus brevirostris	145.4	149.2	
Platyrinchus mystaceus	**106.8**	−28.7	
Mitrephanes phaeocercus	**132.9**	−82.9	
Empidonax flavescens[a]	**101.9**	−80.8	−23.1
Attila spadiceus	123.3	197.0	
Rhytipterna holerythra	−8.5	136.5	
Myiarchus tuberculifer	**132.1**	251.1	145.3
Myiodynastes hemichrysus[b]	**133.1**	−95.1	
Chiroxiphia linearis[a]	**134.5**	326.2	132.3
Vireo leucophrys	−12.1	−100.0	
Hylophilus ochraceiceps	110.2	**339.2**	
Hylophilus decurtatus	128.7	255.2	**131.9**
Cyanocorax morio[a]	**129.9**	295.4	147.5
Cyanolyca cucullata[a]	−3.7	−75.7	
Thryothorus rutilus	131.4	367.3	
Thryothorus rufalbus	138.0	273.2	**164.9**
Thryothorus modestus[a]	130.2	325.8	**177.8**
Troglodytes ochraceus[b]	−10.0	−93.6	**−14.7**
Henicorhina leucosticta	131.5	417.8	
Henicorhina leucophrys	**−18.9**	−56.2	−12.7
Myadestes melanops[b]	−22.5	−97.1	**−33.1**
Catharus aurantiirostris	**134.2**	328.0	133.5
Catharus fuscater	−9.8	−44.7	−13.5
Catharus frantzii[a]	**−51.5**	100.0	
Catharus mexicanus[a]	122.7	**287.1**	476.6
Turdus plebejus[a]	−42.2	−100.0	**−100.0**
Turdus assimilis	112.4	**−12.8**	
Phainoptila melanoxantha[b]	−46.9	**−100.0**	
Myioborus miniatus	119.4	−26.8	
Myioborus torquatus[b]	−50.5	−100.0	**−100.0**
Basileuterus culicivorus	**129.0**	213.0	132.4
Basileuterus rufifrons	121.0	339.1	**148.0**
Basileuterus tristriatus	**106.7**	−82.7	
Zeledonia coronata[b]	−6.8	**−100.0**	

Table 3 (*continued*)

Species	DTD % Change	Altitude % Change	Distribution model % Change
Chlorospingus ophthalmicus	−**10.8**	−87.9	−13.1
Tangara dowii[b]	−**7.1**	−100.0	
Tangara icterocephala	143.6	−83.6	
Pselliophorus tibialis[b]	−100.0	−100.0	
Arremon brunneinucha	−**9.0**	−17.3	
Melozone leucotis[a]	**132.6**	256.1	138.3
Piranga flava	113.4	235.7	
Habia rubica	119.0	**546.7**	
Pheucticus tibialis[b]	−23.2	−**100.0**	−100.0
Euphonia hirundinacea[a]	128.4	302.3	**132.9**
Chlorophonia callophrys[b]	−4.8	−**56.8**	−72.5

[a] Endemic to Central America.
[b] Endemic to Costa Rica and Panamá.

projected to become locally extinct on the Pacific slope of the Tilarán range within the next century following altitudinal shifts corresponding to 3 °C warming; 24 additional species were projected to decline by more than 50% (Table 1). In contrast, 34 species' populations were projected to increase by more than one quarter, as their ranges shift upward into higher elevations where forests are better protected. The DTD model projected only one species' local extinction in response to a 15% decrease in precipitation, while four were projected to decline by more than 50%, and 23 were projected to increase by one quarter or more (Table 1).

The two models differed in the magnitude of changes in abundance predicted in part because of the way biological reserves at higher elevations fall into the bands of DTD and altitude (Fig. 1), but they projected the same direction of change for 64 of 77 species. Among the 25 species projected to decline most sharply by each model, 19 were common to both lists (Table 2). Seven of the 11 species projected to decline by 40% or more in the DTD model were projected to become locally extinct in the altitude model. The total number of endemic species (limited to either Central America or to Costa Rica and Panamá) projected to decline or increase in abundance was nearly equal in the two models, but both endemic classes experienced more drastic abundance changes when shifted by altitude than when shifted by DTD (Table 1). Of the 25 species projected to decline most using either model, three were endemic to Central America and 15 were endemic to the highlands of Costa Rica and Panamá (Table 3).

3.2. Logistic distribution modelling

Fifty-eight of the 77 species' distributions were significantly related to at least one of the climate variables in the logistic models (28 DTD, 20 altitude, 10 both). Twenty-six of those 58 species' models were reasonably accurate in predicting distributions (AUC >0.7; Supplementary Table S1) and were used to create a projection of change in species' distributions (Table 3). Projected changes for 20 of the 26 distribution projections were within the range of estimates produced from the DTD or altitude single-climate-variable models (Table 3).

3.3. Best estimate summary

Using the best projection for each species, results suggest that nearly half of the species (*N* = 35) were projected to decline, and nearly two thirds of those were endemic. Eight species restricted to Central America (seven of those restricted to Costa Rica and Panamá) were projected to become locally extinct (Table 3).

4. Discussion and conclusions

4.1. Climate change impacts

Estimates of response to climate change have been produced for species in other Neotropical regions, but such estimates have been confined to projections of changes in species distributions over large geographical areas (e.g. Mexico; Peterson et al., 2001, 2002). We present the first projections of local community changes in Neotropical species' abundances (30-m resolution) in response to climate change. Expectations were upheld that projected climate changes could imperil mountaintop endemics and that both temperature and rainfall could be important. Our models indicate that reorganization of the Monteverde bird community should be expected, but the extent of change projected depends upon which climate variable is most strongly associated with species' distributions. Logistic regression suggests that future changes in both temperature and precipitation will influence the redistribution of species across the mountainside, since both variables were significant predictors of distribution. Logistic regression also enabled selection of the most appropriate projection for each species and comparisons of the extent of change projected by distribution and abundance models. Our work suggests that future change in the community will consist of lowland species expanding upward into protected areas near the top of the mountains while species currently near the top of the mountains will either experience drastic declines in abundance or local extinction. Many of the species we studied are habitat specialists and narrow endemics, so these changes, extrapolated to other mountain ranges, would threaten their global populations. Because many tropical species also have limited geographical ranges (most in our study have ranges much smaller than temperate counterparts (Jankowski and Rabenold, 2007), and 30 have ranges <200,000 km^2), these communities will be particularly vulnerable to local and regional environmental change.

4.2. Assumptions and limitations

Although we have used local abundance estimates and fine-resolution climate data as an alternative approach to assess potential response to climate change, there remain many assumptions and limitations of these methods. The accuracy of results produced from climate-envelope models like these relies on several key assumptions. The first, and likely the most important for this type of modelling, is that species distributions are regulated by climate variables, implying that species are physiologically restricted to a set range of abiotic conditions (Ghalambor et al., 2006; Janzen, 1967; McCain, 2009; Pearson and Dawson, 2003). In the context of this study, we assume that species' altitude or DTD abundance patterns will follow their temperature or precipitation optima as these abiotic conditions shift over the landscape. However, this assumption may not be correct (e.g. Archaux, 2004) since few studies have demonstrated how a particular abiotic condition can directly influence the location of individuals. Instead, the correlation between abiotic conditions and a species' distribution may actually be a result of abiotic regulation of resources (e.g. primary producers) important to species survival (Williams and Middleton, 2008). For example, climate change could affect the local phenology of fruiting Lauraceae trees that are main food sources for frugivorous species such as the Resplendent Quetzal (*Pharomachrus mocinno*). These trees could track favorable climates upward along mountain slopes, but it is not yet possible to predict which plant species will be able to successfully shift their distributions and it is reasonable to assume that colonization will prove difficult as species will face competition from other plant species

(Foster, 2001). Furthermore, complete establishment of mature cloud forests has been found to take up to 200–300 years, which may not be fast enough to track rapidly changing climates (Foster, 2001). Animal species that rely on insects and/or plant resources unique to mature cloud forests may then lack adequate resources to persist (Benzing, 1998).

Climate-envelope models also do not incorporate the possible effects of biotic interactions, rapid evolutionary adaptation, or species dispersal (Pearson and Dawson, 2003). Biotic interactions, such as competition, predation and parasitism, may strongly influence species distributions, although evidence of such features being strong regulators of bird distributions remains limited (but see Terborgh and Weske, 1975). Similarly, species may persist by adapting to novel environments (West-Eberhard, 2005), but this remains debated as evidence of adaptation is limited (Charmantier et al., 2008; Franks et al., 2007; Jiguet et al., 2007; Teplitsky et al., 2008) and such a response is expected to be limited in long-lived species and small populations (Parmesan, 2006; Pearson and Dawson, 2003; Willi et al., 2006).

It is also important to recognize that the projections presented here apply only to a portion of these species' global distributions. We have projected change for a portion of the Pacific slope of the Tilarán range, yet many species have distributions extending over a broader area on the Caribbean slope (Jankowski et al., 2009; Young et al., 1998) and are often found in even larger areas on the neighboring Cordilleras Central and Talamanca, and sometimes in other Central American mountain ranges (Hernández-Baños et al., 1995; Stiles et al., 1989). If conditions create population sinks within our study site, some species may persist if immigration comes from these potential neighboring source populations. It seems likely; however, that immigration would come only from the Caribbean slope of Tilarán because movement from neighboring mountain ranges is inhibited by intervening low-altitude habitat that is also largely deforested. If precipitation is the most important variable regulating species' local distributions, species with populations extending downward on the Caribbean slope may persist even if annual rainfall was reduced by 15% because rainfall occurs year-round due to prevailing winds and reaches an annual total as high as 8 m there (Haber, 2000). Such a constant input of rain should be well beyond water-stress levels for plants on the Caribbean slope, leading to possibly greater stability of bird communities than projected for the Pacific slope.

Though it is possible some species could persist on the Caribbean slope of the Tilarán range, this is less likely to occur for the species we have identified to be the most sensitive to both changes in precipitation and/or temperature because they are habitat specialists. A majority of these species are Central American and/or Costa Rica–Panamá endemics restricted to peak and ridge-line habitats that are unique because of their cool temperatures and high humidity. These habitats remain water-saturated even during the dry season because current climate conditions permit cloud formation at lower altitudes where clouds immerse terrestrial habitats. However, recent research suggests that deforestation in the Caribbean lowlands and further regional climate change will lift the level of cloud formation, which would in turn decrease the current pattern of cloud immersion throughout the Tilarán range (Lawton et al., 2001; Ray et al., 2006; Still et al., 1999). The resulting loss of moisture from cool, high-altitude locations could then eliminate current patches of that unique habitat and would result in local extinctions as severe as those projected in our altitude model.

4.3. Future modelling of local abundance

Beyond producing quantitative estimates of response to climate change, our results demonstrate the importance of using projec-

tions from multiple models if modelling employs single climate variables. We found, for instance, that estimates produced from the altitude model would lead us to expect twelve local extinctions within the Monteverde region rather than the one projected based on the DTD model. By using relatively simple methods (here logistic regression), reliance on results from a single model were avoided and replaced by informed choice from multiple models when multiple predictors of distribution pertained.

We used a moderate 100-year climate scenario to develop our projections assuming stable patterns of land use; however, continuing deforestation could also influence climate (Lawton et al., 2001; Ray et al., 2006), and future climate modelling should be fine-tuned to include such regional effects. Though more complex modelling methods can offer a more statistically sophisticated approach for modelling response to climate change (Hilbert et al., 2004; Li et al., 2009), implementation of such techniques in most tropical areas is not possible because these methods require fine-scale data on distribution, abundance, and environmental variables that are not currently available (Li et al., 2009; Raxworthy et al., 2008; Sekercioglu et al., 2008). Similarly, as climate models can vary considerably, studies should produce projections for a range of potential future climate scenarios so that the range of estimates will be more likely to include the actual response.

4.4. Conservation implications

In spite of the limitations of our single-factor analyses, these analyses can serve as a starting point for understanding the possible impacts of climate change on tropical montane forest communities. It seems likely that our estimates are conservative since our models do not include environmental changes that may result from increased evapotranspiration rates caused by the combination of decreased precipitation and increased temperature (Still et al., 1999). Such an interaction between these climate variables may increase stress on plant communities (Foster, 2001), resulting in decreased productivity or increased mortality among plants that provide resources for birds. Fine-tuned species interactions could magnify effects beyond those envisioned for single species in isolation, but it is also possible that species will be able to adapt to changing conditions (Bradshaw and Holzapfel, 2006), thereby buffering potential population losses. Because of the uncertainty in modelling the impacts of climate change, along with the consensus that significant changes are possible (Parmesan, 2006), it would be prudent to develop strategies for the maintenance of viable populations of high-altitude endemic species that were identified by our models to be the most likely species to be threatened by climate change. Principal among these strategies would be improved protection of cloud forests in larger mountain ranges, such as the neighboring Cordillera Central and Talamanca. These ranges are currently well-protected in Costa Rica, at least at the highest altitudes, yet areas such as the Chiriqui highlands in western Panamá remain less secure (Oostra et al., 2008). Furthermore, in both Costa Rica and Panamá, these mountain ranges have been substantially deforested in the middle altitudes on the Pacific slope. Such areas represent current strongholds for the high-altitude species our models have identified to be most threatened in the Tilarán range. Increased protection of middle-altitude sites in Costa Rica and both middle- and high-altitude forests in Panamá would offer further refuge for the species most likely to disappear from cloud forests in the Tilarán range (Jankowski et al., 2009; Oostra et al., 2008).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.02.034.

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