Compositional shifts in Costa Rican forests due to climate-driven species migrations

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Abstract

Species are predicted to shift their distributions upslope or poleward in response to global warming. This prediction is supported by a growing number of studies documenting species migrations in temperate systems but remains poorly tested for tropical species, and especially for tropical plant species. We analyzed changes in tree species composition in a network of 10 annually censused 1-ha plots spanning an altitudinal gradient of 70–2800 m elevation in Costa Rica. Specifically, we combined plot data with herbarium records (accessed through GBIF) to test if the plots' community temperature scores (CTS, average thermal mean of constituent species weighted by basal area) have increased over the past decade as is predicted by climate-driven species migrations. In addition, we quantified the contributions of stem growth, recruitment, and mortality to the observed patterns. Supporting our *a priori* hypothesis of upward species migrations, we found that there have been consistent directional shifts in the composition of the plots, such that the relative abundance of lowland species, and hence CTS, increased in 90% of plots. The rate of the observed compositional shifts corresponds to a mean thermal migration rate (TMR) of 0.0065 °C yr^{-1} (95% CI = 0.0005–0.0132 °C yr^{-1}). While the overall TMR is slower than predicted based on concurrent regional warming of 0.0167 °C yr^{-1}, migrations were on pace with warming in 4 of the 10 plots. The observed shifts in composition were driven primarily by mortality events (i.e., the disproportionate death of highland vs. lowland species), suggesting that individuals of many tropical tree species will not be able to tolerate future warming and thus their persistence in the face of climate change will depend on successful migrations. Unfortunately, in Costa Rica and elsewhere, land area inevitably decreases at higher elevations; hence, even species that are able to migrate successfully will face heightened risks of extinction.

Keywords: climate change, cloud forest, extinction, forest inventory plots, global warming, species migrations, thermal distributions

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Introduction

As global temperatures rise, climatic conditions suitable to species will be displaced toward higher elevations and latitudes (Loarie *et al.*, 2009). As such, many species are predicted to experience range contractions and elevated extinction risks unless they rapidly shift their distributions poleward and/or upward as required to remain within their thermal niches (Colwell *et al.*, 2008; Feeley & Silman, 2010; Parmesan, 2006; Thomas *et al.*, 2004; Thuiller, 2007; Zhu *et al.*, 2012).

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Indeed, recent studies from an array of ecosystems worldwide have revealed that large numbers of species, and even entire species communities, are already shifting their distributions as expected under climate change (reviewed in Chen *et al.*, 2011; Parmesan & Yohe, 2003; Walther *et al.*, 2002). To highlight a few select examples, comparisons of historical and current distributions indicate that plant species in western Europe have migrated upslope at an average rate of 2.9 m yr^{-1} (Lenoir *et al.*, 2008); plants in California, USA, have migrated upslope at an average rate of 2.2 m yr^{-1} (Kelly & Goulden, 2008); and birds in North America have shifted their breeding distributions northward at an average rate of 2.4 km yr^{-1} (Hitch & Leberg, 2007). More generally, a recent meta-analysis

including 54 studies that represented a combined total of more than 2000 species showed that the majority of species studied did exhibit upward or poleward migrations at average rates of 1.1 m yr^{-1} or 1.7 km yr^{-1}, respectively (Chen *et al.*, 2011).

In contrast to the temperate zones, examples of range shifts from the tropics remain extremely sparse (reviewed in Feeley *et al.*, 2012b). Indeed, in the meta-analysis described above only 2 studies from the tropics were included, representing a combined total of just 160 species [130 species of moths on Mt. Kinabalu, Borneo (Chen *et al.*, 2009), and 30 species of herpetofauna on the Tsaratanana Massif, Madagascar (Raxworthy *et al.*, 2008)]. This despite the fact that the tropics house the majority of Earth's species (Dirzo & Raven, 2003; Joppa *et al.*, 2011; Raven, 1988), many of which are expected to be especially sensitive to climate change due to their narrow climatic tolerances (Huey *et al.*, 2009; Janzen, 1967; McCain, 2009; Sunday *et al.*, 2010). This paucity of studies and data is especially prevalent for tropical plants (Feeley *et al.*, 2012b), highlighted by the complete absence of studies of tropical plants from the meta-analysis mentioned above (Chen *et al.*, 2011). In fact, we know of only two studies documenting range shifts in tropical plant species. In the first study, Feeley *et al.* (2011) analyzed recensus data from a network of forest inventory plots situated along a 3000 m elevational gradient in the southern Peruvian Andes and found that the majority of tree genera had shifted their distributions upslope over the past several years and accordingly that 3/4 of study plots experienced increased abundances of 'lowland' taxa. In a separate second study, Feeley (2012) analyzed temporal changes in the locations from which herbarium specimens have been collected for 239 Amazonian plant species. He found the majority of species exhibited some evidence of 'cold-ward' range shifts as predicted by rising temperatures.

One area of the tropics that has been the focus of considerable research on the effects of global change is Costa Rica. Results of studies from Costa Rica include the prediction of future climates under various scenarios of warming (Bradley *et al.*, 2008; Karmalkar *et al.*, 2008; Still *et al.*, 1999), shifts in the abundance and distributions of life zones (Enquist, 2002; Foster, 2001) and species (Nadkarni & Solano, 2002; Pounds *et al.*, 2006, 1999) in response to past and future changes in climate, and the development of the 'Biotic Attrition' hypothesis (Colwell *et al.*, 2008). Despite this progress, we still have only a rudimentary understanding of the effects of climate change on the tree species themselves, and thus our ability to predict how tropical lowland and montane forest ecosystems will respond to future climate change remains extremely limited.

Here, we test the species migration hypothesis (i.e., the geographic distributions of species will shift through time to remain at equilibrium with climate) using annual recensus data from a network of 10 1-ha forest inventory plots spanning a ca. 3000 m elevational gradient along the flanks of the Volcán Barva in central Costa Rica. Specifically, we analyze temporal changes in the composition of tree species within each of the plots to test if the abundance of taxa with distributions centered on hotter climates (species distributions based on analyses of herbarium records) has increased in the higher elevation plots through time, as is predicted to occur under climate change-driven species migrations. We further break down the contributions of range shifts into differential growth, recruitment, and mortality. As far as we are aware, this study constitutes the first test of the species migration hypothesis to be conducted for tropical plants outside of South America and is also the first study to analyze the contributions of different demographic processes (growth, recruitment, mortality) to the migrations of any tropical plant species.

Materials and methods

Plot surveys

The study was conducted along an elevational gradient running from <100 m elevation at the La Selva Biological Station to >2800 m elevation in Braulio Carrillo National Park on the Caribbean slopes of Volcán Barva in northeastern Costa Rica (at ca. 84.034°W, 10.303°N; Fig. S1). The study area is covered mostly with wet old-growth tropical forests with annual precipitation being one of the highest in the neotropics ranging from ca. 4000 mm in low elevation plots to ca. 9000 mm at intermediate elevations and reducing to ca. 3000 mm at the summit of Volcán Barva. The elevational transect begins in lowland tropical wet forest, then rises through tropical premontane, tropical montane, to a small area of tropical cloudforest at the summit (Hartshorn & Peralta, 1988; Heaney & Proctor, 1990; Lieberman *et al.*, 1996). Soil parent materials are Plio-Pleistocene basaltic and andesitic lavas; nutrient availability generally increase with elevation while decomposition and mineralization rates decrease with elevation (Heaney & Proctor, 1990; Lieberman *et al.*, 1996; Marrs *et al.*, 1988). Current mean annual temperatures average >26 °C in the lowlands and decrease to ca. 10 °C at the summit. Since 1950, mean annual temperatures in the region have increased at a rate of 0.017 °C yr^{-1} and mean minimum and maximum temperatures have increased at similar rates of 0.018 and 0.015 °C yr^{-1}, respectively (Fig. S2; Harris *et al.*, 2013).

A network of 10 annually censused 1-ha forest inventory plots was established between 70 and 2800 m elevation along this elevational transect through collaborative efforts of Conservational International's TEAM Project (http://www.team-network.org) and NASA's Jet Propulsion Laboratory. The 1-ha inventory plots were designed to provide representative

samples of old-growth forest to enable long-term studies of forest composition and performance stratified across the gradients of interest in the larger landscape, which in this case were primarily elevation, local topography, and stand history. Written protocols were developed *a priori* to select, in a stratified random design, relatively flat old-growth sites with no signs of recent human disturbance and that contained no large stands of bamboo or permanent rivers or streams.

Plots were surveyed using slope-corrected distances and a surveying transit and plot corners were geolocated with differential GPS. Within each plot, all woody stems ≥10 cm diameter at breast height (dbh) were mapped and tagged, identified to species (or to morphospecies in the case of <5% of stems) and censused annually for stem diameter growth, mortality and recruitment using the vegetation monitoring protocols of the TEAM Project (http://www.teamnetwork.org/protocols/bio/vegetation). Plots were initiated in different years between 2003 and 2010 and thus the duration of the data available varied between plots from 1 to 8 census intervals (Table 1; Table S1).

Species thermal distributions

Using protocol similar to those of Feeley *et al.* (2011), we estimated the thermal distributions of all tree species occurring in the Volcán Barva Transect plots based on the locations in Costa Rica from which their herbarium specimens had been collected. Specifically, all the available data records of herbarium specimens that had been collected from Costa Rica were downloaded through the Global Biodiversity Information Facility data portal (GBIF; http://www.gbif.org/; accessed in November 2012; Table S2). Records that were missing collection coordinates, that had been tagged by GBIF as having possible coordinate issues, and records that had obvious georeferencing errors (i.e., coordinates occurring over the ocean or in other countries) were discarded. Duplicate records were also discarded.

The mean annual temperatures (hereafter temperatures) at the collection locations of all specimen were estimated by extracting the temperature values from the WorldClim extrapolated climate map (http://www.worldclim.org/; Hijmans *et al.*, 2005) downscaled to a horizontal resolution of 90 m.

Spatial downscaling was based on the differences in elevations as mapped according to a 90 m resolution Shuttle Radar Topography Mission Digital Elevation Model (SRTM DEM; http://www2.jpl.nasa.gov/srtm/) vs. the mean elevation of the encompassing 30 arc second WorldClim climate cell and assuming an adiabatic lapse rate of 5.5 °C km^{-1} elevation.

For each of the tree species recorded in the Volcán Barva Transect plots that were represented by ≥10 herbarium collection records from Costa Rica ($n = 315$ species), the mean temperature (°C) of the herbarium collection locations were calculated [analogous to Lenoir *et al.*'s (2008) 'optimum elevation' and Chen *et al.*'s (2009) 'center of gravity'; Table S3]. In calculating the mean temperature per species, values were weighted by the inverse distribution of land area across temperatures in Costa Rica to help account for differences in the numbers of collections per temperature due to differences in available land area and sampling efforts as opposed to the underlying biological responses of the species to temperature.

For species with <10 available records ($n = 69$ species), we used the average collection temperature as calculated from all available records of congeneric individuals collected from Costa Rica. We were unable to estimate a mean temperature due to a lack of sufficient specimens (i.e., $n < 10$ herbarium specimen) at either the species or generic level for only one species, *Rnodostemomodaphne kunthiana* (Lauraceae) that was represented by 2 individuals (both in the plot at 960 m elevation). In addition, 115 individuals remain unidentified at the genus level. Unidentified individuals and individuals of *R. kunthiana* were excluded from all subsequent analyses (Table S3).

Community temperature scores and thermal migration rates

For each plot census, we calculated a community temperature score (CTS; °C) as the average of the mean temperatures for the constituent species weighted by the relative basal area of the species at that census [analogous to the 'community elevation score' of Chen *et al.* (2009) and Feeley *et al.* (2011)]. The annual changes in the CTS values were then calculated for each plot over all possible consecutive censuses as estimates

Table 1 Characteristics of study plots in the Volcán Barva Transect (averages calculated across census years)

Plot name	Elevation (m asl)	Year established	Average number of species	Average number of individuals	Average basal area (m^2 ha^{-1})	Average community temperature score (CTS; °C)
VG-VB-9	70	2010	90.5	373.5	24.7	24.4
VG-VB-1	100	2003	93.7	425.7	22.0	24.2
VG-VB-2	150	2004	88.3	447.6	24.3	24.4
VG-VB-4	400	2006	143.3	640.5	26.4	24.0
VG-VB-3	600	2006	162.0	593.0	27.1	23.9
VG-VB-7	975	2009	69.0	429.0	20.2	21.9
VG-VB-8	1450	2009	58.7	405.0	23.9	20.2
VG-VB-5	2000	2008	47.3	522.5	26.7	15.9
VG-VB-10	2400	2010	37.0	577.5	35.7	14.6
VG-VB-6	2800	2008	16.8	1222.3	65.5	15.0

of each plot's annual thermal migration rate (TMR; $°C\ yr^{-1}$). The mean TMR (TMR_{mean}) was then calculated as the average of all TMRs across all census intervals available for each plot.

We also calculated the TMR for each plot over each census interval due solely to stem growth (TMR_{growth}), tree recruitment (TMR_{rec}), and tree mortality (TMR_{mort}). For each census interval, the TMR_{grow} of a plot is the difference in the plot's CTS as calculated using the initial vs. final basal areas of just the trees surviving through the census period. For each census interval, the TMR_{rec} of a plot is the difference in its CTS as calculated using the final basal areas of all stems recorded at the end of the census interval vs. its CTS as calculated using the final basal areas of just the stems that survived through the census interval. Finally, for each census interval, a plot's TMR_{mort} is the difference in its CTS as calculated using the initial basal areas of all stems recorded in the first census vs. its CTS as calculated using the initial basal areas of just the stems that survived through the census interval.

Results

A total of 386 tree species were recorded across all censuses of the 10 forest plots in the Volcán Barva elevational transect. The number of species per plot varied from less than 40 at the two highest elevations (2400 and 2800 m) to ca. 150 at the mid-elevations (400 and 600 m). The number of stems per plot ranged from less than 400 at the lowest elevation (70 m) to over 1200 the highest elevation (2800 m). Stand level basal area varied from ca. 20 $m^2\ ha^{-1}$ at 900 m elevation to a maximum of >65 $m^2\ ha^{-1}$ at 2850 m (Table 1).

The average community temperature scores (CTSs) of the plots ranged from 12.10 to 24.42 °C and was strongly negatively correlated with plot elevation ($r = -0.97$, $P < 0.0001$) with a slope of -4.8 $°C\ km^{-1}$ elevation gain (Fig. 1).

Thermal migration rates (TMRs) were positive in 26 of the 37 possible plot census intervals (binomial probability = 0.010; Figs 2 and 3) and averaged 0.0065 $°C\ yr^{-1}$ (95% CI based on nonparametric bootstrapping with 5000 resamples = 0.0005–0.0132 $°C\ yr^{-1}$). This is equivalent to an upward migration of 1.18 $m\ yr^{-1}$ (95% CI = 0.09–2.40 m^{-1} assuming an adiabatic lapse rate of 5.5 $°C\ km^{-1}$). TMR_{mean} values were positive (i.e. CTSs increased through time) in 9 of the 10 plots (binomial probability = 0.011 if plots are weighted equally; binomial probability <0.001 if plots are weighted by number of censuses; Fig. 3a). Across plots, TMRs were positive on average in 6 of 8 possible census intervals (significantly so in 2004–2005, 2006–2007, and 2010–2011; Fig. 3b).

The largest changes in CTSs were due to tree mortality events (TMR_{mort}; Fig. 4). In most cases (60% of plot census intervals), TMR_{mort} was positive. Likewise, in most cases (70% of plot census intervals), changes due
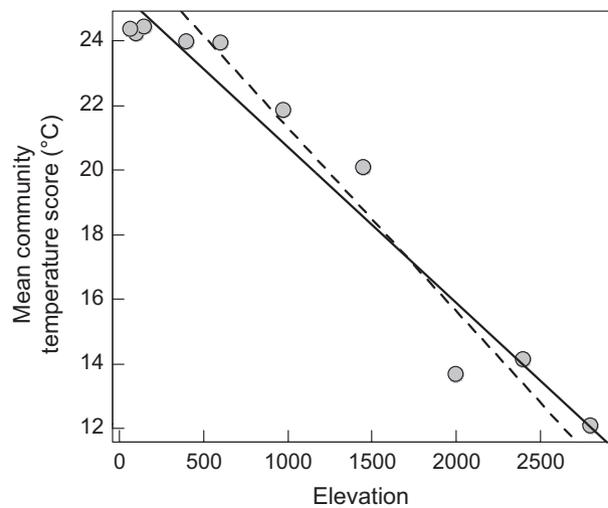

Fig. 1 The mean community temperature scores (CTSs) of plots in the Volcán Barva Transect, Costa Rica, vs. their elevation. The CTS values were strongly negatively correlated with plot elevation ($r = -0.98$, $P < 0.0001$) with a slope corresponding to a thermal lapse rate of -4.0 $°C\ km^{-1}$ elevation gain (solid line). If only the plots located 600–2400 m are included, the thermal lapse late of CTS vs. elevation (dashed line) is 5.4 $°C\ km^{-1}$ ($r = -0.99$, $P < 0.01$).
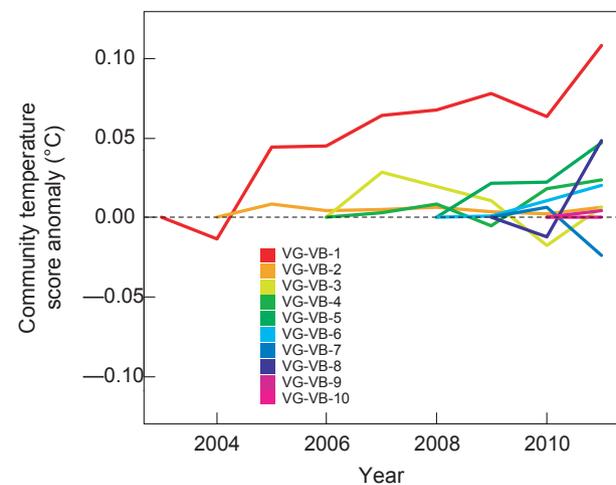

Fig. 2 The estimated community temperature score (CTS) anomalies of plots in the Volcán Barva Transect, Costa Rica. Anomalies are calculated as the absolute difference between a plot's CTS in year i and the plot's initial CTS. Positive anomalies indicate increased abundances of lowland taxa consistent with upward range shifts. The plot names in the legend correspond to information provided in Table 1.

to stem growth (TMR_{grow}) were positive. In contrast, changes due to recruitment of new individuals into the plots (TMR_{rec}) did not show any strong consistency in directionally but were negative in most (55%) of the plot census intervals (Fig. 4). TMR_{grow} and TMR_{rec} values were generally lower in magnitude than TMR_{mort}.
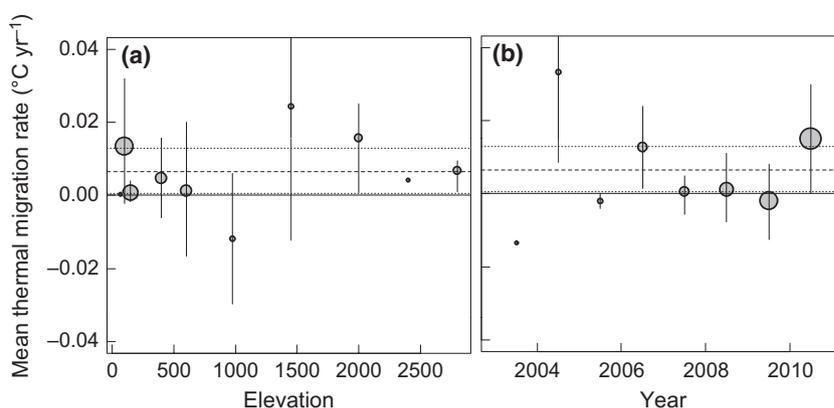
Fig. 3 The estimated community thermal migration rates (TMR = mean annual change in community temperature scores; °C yr^{-1}) per (a) plot and (b) census interval in the Volcán Barva Transect, Costa Rica. The sizes of the points are proportional to the number of census years per plot in panel (a), or the number of plots per census interval in panel (b). Vertical bars indicate 95 CIs (based on bootstrapping with 5000 resamples) and the dashed horizontal lines indicate the overall TMR (and 95% CIs) across all years and plots. Positive TMRs indicate increased abundances of species with hotter affinities (i.e., lowland species), consistent with upward range shifts.

Discussion

The CTSs of plots along the Volcán Barva Transect were strongly negatively correlated with elevation indicting that tree species composition changes predictably across the elevational/temperature gradient. The fact that the lapse rate of CTS was depressed relative to the expected adiabatic lapse rate (4.0 vs. ca. 5.5 °C km^{-1}) was to be anticipated. This is because plots at the thermal extremes (i.e., at very low or high elevations) will tend to be composed of species whose thermal means are displaced toward more moderate temperatures. For example, a plot at the alpine timberline will invariably be composed of species whose thermal ranges include hotter but not colder temperatures. If only the 6 midelevation (400–2400 m) plots are included, the slope of the CTS vs. plot elevation relationship increases to 5.6 °C km^{-1} ($r = -0.97$, $P = 0.002$) and is not significantly from the expected adiabatic lapse rate.

The CTS of most plots (9 of 10) have increased since their initial establishment 2–9 years ago (i.e., plots had positive TMR$_{mean}$). In the absence of climate change, we would expect that approximately half the plots would have positive TMR$_{mean}$ and the other half would have negative TMR$_{mean}$. The consistency of migrations combined with the fact that the mean rate of migration was significantly faster than the null expectation is strong evidence that species ranges are shifting directionally upslope, supporting the hypothesis of climate-driven species migrations.

The only plot that exhibited a decrease in its CTS (i.e., had a negative TMR$_{mean}$) was located at 975 m elevation and was established in 2009 (Table 1). The decrease in CTS at this plot was mortality-driven (Fig. 4) and is largely attributable to the death of a single large

Vochysia allenii (Vochysiaceae) tree (dbh = 62.2 cm) between the 2010 and 2011 censuses. *V. allenii* is generally found at lower hotter elevations (mean herbarium collection temperature = 23.51 °C) and thus its loss helped to cause a decrease in the plot's CTS from 21.86 to 21.83 °C.

Since 1950, mean annual temperatures in the region encompassing the Volcán Barva Transect have increased at a rate of ca. 0.017 °C yr^{-1} (Harris *et al.*, 2013). While this is significantly faster than the overall average TMR observed across the ten Volcán Barva Transect plots (mean TMR = 0.0065 °C yr^{-1}; 95% CI = 0.0005–0.0132 °C yr^{-1}), it is not significantly faster than the migration rates observed in 4 of the 10 individual plots (100, 600, 1450, and 2000 m elevation). In other words, the composition of species in approximately half (40%) of the Volcán Barva Transect plots is changing roughly on pace with what is required to remain at equilibrium with concurrent temperature changes.

The results of this study make an interesting comparison to those of a similar study of range shifts previously conducted by Feeley *et al.* (2011) in the southern Peruvian Andes. When Feeley *et al.* calculated their CTS estimates using methods comparable to those used here, (i.e., thermal means of taxa calculated from the distributions of herbarium records and CTS values calculated by weighting by the relative basal area of stems per plot), they found 11 of 14 plots in the Andes (79%) to have positive TMRs vs. 9 of 10 plots (90%) observed to have positive TMRs in Costa Rica. Under a lapse rate of 5.5 °C km^{-1}, the upward migrations observed in the Andes corresponds to a mean TMR of 0.0132 °C yr^{-1} (95% CI = 0.0044–0.0231 °C yr^{-1}) which is not significantly different from the rate that we observed at Volcán Barva. Also, like in Costa Rica, the average
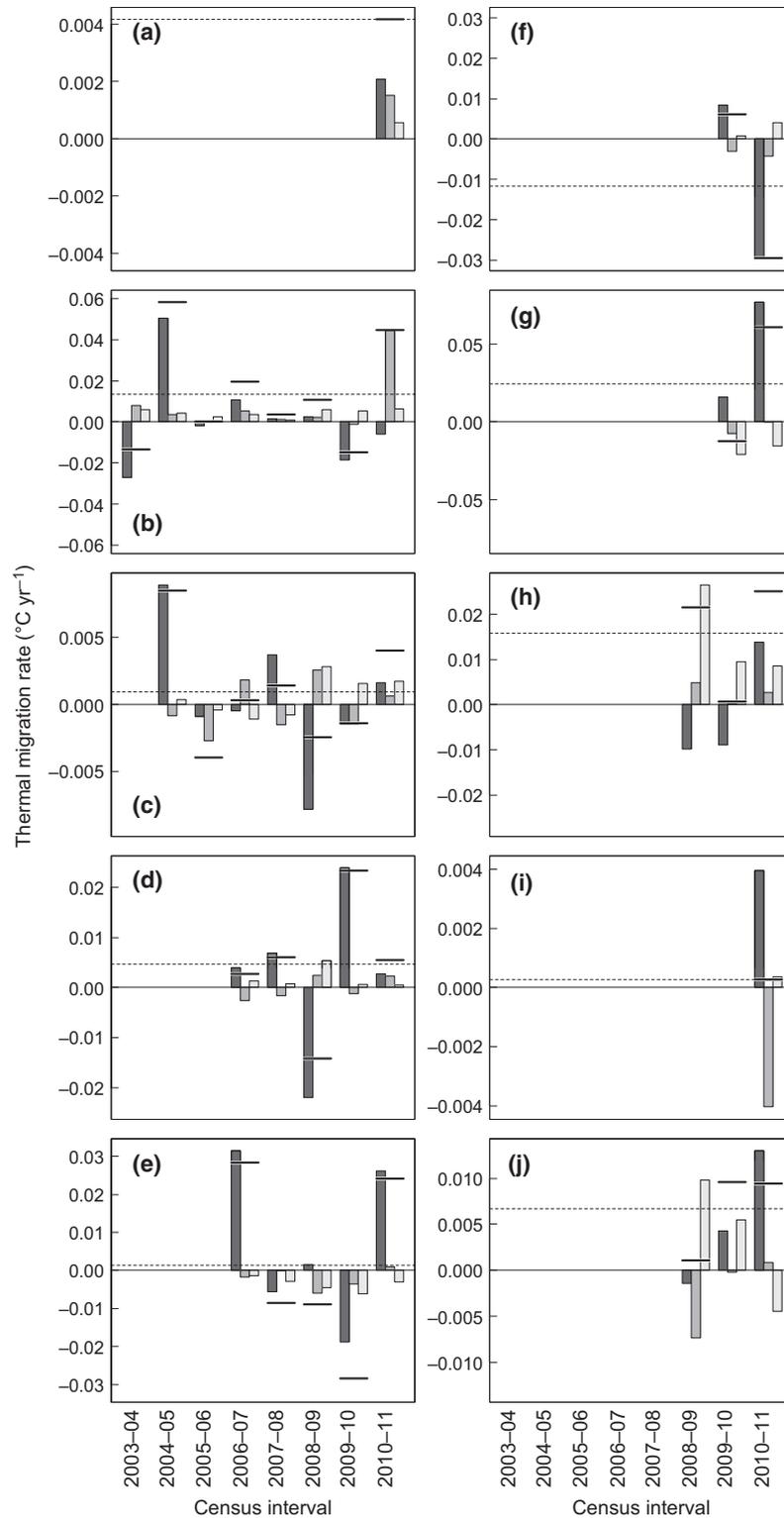
Fig. 4 The estimated changes in community temperature scores due to mortality thermal migration rate (TMR$_{mort}$; black), recruitment (TMR$_{rec}$; dark gray), and stem growth (TMR$_{grow}$; light gray) of trees between censuses within plots in the Volcán Barva Transect, Costa Rica. Plots were located at (a) 70 m, (b) 100 m, (c) 150 m, (d) 400 m, (e) 600 m, (f) 975 m, (g) 1450 m, (h) 2000 m, (i) 2400 m, and (j) 2800 m elevation. The horizontal line segments show the cumulative changes in the plots' CTSs and the dashed horizontal lines show the mean changes the plots' CTSs across all census intervals (i.e., the TMR$_{mean}$). Positive changes indicate increased abundances of lowland taxa consistent with upward range shifts. Note that the scale of the vertical axis differs between panels.

migration rate in the Andes was slower than required to keep pace with the rapid warming that has occurred there over the past several decades (ca. 0.03–0.05 °C yr^{-1}) but migration rates appear to have been sufficiently fast in at least 5 (36%) of the individual plots (Feeley et al., 2011).

While the finding that at least some of the forest communities in Costa Rica (and the Andes) are migrating on pace with regional warming is perhaps heartening, there is reason to expect that even these forests will not be able to continue to keep pace with future climate change. This supposition is due to the predicted acceleration in climate change velocities over the current and coming centuries (especially if other climatic factors such as precipitation and seasonality are considered in conjunction with temperature changes; Feeley & Rehm, 2012; McCain & Colwell, 2011) as well as the fact that land area inevitably decreases at higher elevations. For example, in Costa Rica there is over 6.5 times as much land area between 1800 m and the highest plot at 2800 m as between 2800 m and the highest point in Costa Rica at 3820 m elevation (ca. 3340 vs. 500 km^2; as derived from the SRTM DEM data). The negative effects of decreasing land area at higher elevations will be compounded by the large distances between highland habitats (Forero-Medina et al., 2011; La Sorte & Jetz, 2010), as well as the potential inability of forest species to cross the timberline (at ca. 3400 m in Costa Rica; Friedrich-Karl, 2009) to invade high elevation grassland and alpine habitats (Feeley & Silman, 2010; Rehm & Feeley, 2013).

It is also important to note that the largest driver of changes in the CTSs of plots in the Volcán Barva Transect was tree mortality events (TMR$_{mort}$; Fig. 4). In most cases, TMR$_{mort}$ was positive, indicating that there tended to be greater losses of basal area due to mortality in species with colder affinities as opposed to species with hotter affinities. This is consistent with dieback due to temperatures exceeding species' thermal tolerances (Allen & Breshears, 1998). In a previous modeling study, Feeley et al. (2012a) estimated the potential losses of habitat area for Amazonian and Andean species, and the associated spatial patterns of biotic attrition, that may occur under several scenarios of future warming. This study indicated that rates of habitat loss will be relatively minor if species are capable of persisting in areas where temperatures increase to levels outside of the species' current thermal 'envelopes'. However, if species are incapable of persisting in these 'hot' areas and experience dieback along the trailing portions of their ranges, then rates of habitat loss are expected to dramatically increase, with the ranges of most species contracting by a median of 81.5 or 98.7% under 2 or 4 °C global warming scenarios,

respectively, and most areas experiencing massive attrition (Feeley et al., 2012a). The results from Volcán Barva suggest that the species there will not be capable of persisting in their current habitats as global warming proceeds. If this result is generalizable to other tropical plant species and other regions of the tropics, we predict that large numbers of species will become committed to extinction in the very near future.

Coda

The methods presented here and in Feeley et al. (2011) provide a relatively simple yet powerful tool for testing for changes in species composition in relation to species niches. This method does not require large numbers of plots or large numbers of recensuses (minimum of one recensus of one plot) to estimate TMRs. That said, the power in analyses such as these come from the temporal and spatial consistency of the observed changes between censuses periods and between plots, respectively. We therefore encourage other researchers to consider applying these methods to their own data to help paint a more complete and larger scale picture of how species composition may or may not be changing in response to climate change throughout the tropics and throughout the globe. One possible limitation that will need to be overcome is the 'void' of collection records from many parts of the tropics (Feeley & Silman, 2011). This study was based on forest inventory plots in Costa Rica; Costa Rica is one of the most densely collected areas in the world. Other parts of the tropics are represented by much fewer collection records which will hamper the ability of researchers to estimate the thermal distributions of species, providing yet another motivation to increase botanical exploration, records management, and data distribution efforts.

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Supporting Information

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

Figure S1. Map of study area and plots in the Volcán Barva Transect, Costa Rica.
Figure S2. Average daily (a) maximum, (b) mean, and (c) minimum temperatures 1950–2009 in the area around the Volcán Barva Transect, Costa Rica (84.75 to 83.75°W and 9.75 to 10.75°N) as extracted from the CRU high resolution climatology (Harris *et al.*, in press). Since 1950, temperatures in the area have increased at a rate of ca. 0.015–0.017 °C yr^{-1}.
Table S1. Species identifications and basal areas of trees censused in the Volcán Barva Transect plots, Costa Rica.
Table S2. List of herbaria providing collections data from Costa Rica used in the analyses. All collections were accessed through the Global Biodiversity Information Facility (GBIF) data portal (http://www.gbif.org/) in November 2012.
Table S3. Mean temperature of herbarium collection locations within Costa Rica for species occurring in the Volcán Barva Transect plots.