Journal of Biogeography (J. Biogeogr.) (2011) 38, 783–791

ORIGINAL ARTICLE

Upslope migration of Andean trees

Kenneth J. Feeley[1,2]*, Miles R. Silman[3], Mark B. Bush[4], William Farfan[3], Karina Garcia Cabrera[3], Yadvinder Malhi[5], Patrick Meir[6], Norma Salinas Revilla[5,7], Mireya Natividad Raurau Quisiyupanqui[3] and Sassan Saatchi[8,9]

[1]Department of Biological Sciences, Florida International University, Miami, FL, USA, [2]Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, Coral Gables, FL, USA, [3]Department of Biology, Wake Forest University, Winston Salem, NC, USA, [4]Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL, USA, [5]Environmental Change Institute, Oxford University, Oxford, UK, [6]School of GeoSciences, The University of Edinburgh, Edinburgh, UK, [7]Herbario Vargas, Universidad Nacional San Antonio de Abad de Cusco, Cusco, Peru, [8]Jet Propulsion Laboratory, California Institute of Technology, Los Angeles, CA, USA, [9]Institute of the Environment, University of California Los Angeles, Los Angeles, CA, USA

*Correspondence: Kenneth J. Feeley, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA.
E-mail: kfeeley@fiu.edu or kjfeeley@gmail.com

ABSTRACT

Aim Climate change causes shifts in species distributions, or ‘migrations’. Despite the centrality of species distributions to biodiversity conservation, the demonstrated large migration of tropical plant species in response to climate change in the past, and the expected sensitivity of species distributions to modern climate change, no study has tested for modern species migrations in tropical plants. Here we conduct a first test of the hypothesis that increasing temperatures are causing tropical trees to migrate to cooler areas.

Location Tropical Andes biodiversity hotspot, south-eastern Peru, South America.

Methods We use data from repeated (2003/04–2007/08) censuses of 14 1-ha forest inventory plots spanning an elevational gradient from 950 to 3400 m in Manu National Park in south-eastern Peru, to characterize changes in the elevational distributions of 38 Andean tree genera. We also analyse changes in the genus-level composition of the inventory plots through time.

Results We show that most tropical Andean tree genera shifted their mean distributions upslope over the study period and that the mean rate of migration is approximately 2.5–3.5 vertical metres upslope per year. Consistent with upward migrations we also find increasing abundances of tree genera previously distributed at lower elevations in the majority of study plots.

Main conclusions These findings are in accord with the a priori hypothesis of upward shifts in species ranges due to elevated temperatures, and are potentially the first documented evidence of present-day climate-driven migrations in a tropical plant community. The observed mean rate of change is less than predicted from the temperature increases for the region, possibly due to the influence of changes in moisture or non-climatic factors such as substrate, species interactions, lags in tree community response and/or dispersal limitations. Whatever the cause(s), continued slower-than-expected migration of tropical Andean trees would indicate a limited ability to respond to increased temperatures, which may lead to increased extinction risks with further climate change.

Keywords

Andes, climate change, climatic envelope, cloud forest, extinction, forest plots, global warming, monitoring, Peru, species migration.

INTRODUCTION

Species are predicted to shift their distributions, or ‘migrate’, in response to global climate change (Parmesan & Yohe, 2003; Parmesan, 2006; Thuiller, 2007). These distributional shifts have important conservation implications, potentially leading to widespread species extinctions due to reductions in habitat area and population size (Thomas *et al.*, 2004; Feeley & Silman, 2010a) and to local declines in biodiversity due to ‘biotic attrition’ (Colwell *et al.*, 2008; Feeley & Silman, 2010b),

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/j.1365-2699.2010.02444.x

Table 1 The locations, elevations, and census dates of the 14 1-ha Andean forest inventory plots.

Plot no.	UTM E	UTM N	Elevation (m)	First census date	Second census date
1	19S 225215	8567314	950	July 2004	July 2007
2	19S 197947	8582756	1250	Oct 2004	May 2008
3	19S 198534	8582816	1500	Sept 2004	May 2008
4	19S 224863	8556052	1500	Sept 2006	Sept 2008
5	19S 224258	8556260	1750	Aug 2006	Sept 2008
6	19S 222887	8553630	1850	Aug 2003	July 2007
7	19S 222622	8553538	2000	Sept 2003	June 2007
8	19S 221737	8552556	2250	Sept 2003	June 2007
9	19S 220816	8551070	2525	July 2003	June 2007
10	19S 219193	8549686	2750	July 2003	June 2007
11	19S 218992	8549454	3025	Oct 2003	May 2007
12	19S 219595	8540370	3025	Sept 2003	July 2007
13	19S 217594	8549222	3200	June 2003	May 2007
14	19S 217309	8548834	3400	July 2003	June 2007

UTM, Universal Transverse Mercator.

with the potential for consequent alterations of ecosystem services (Bunker *et al.*, 2005).

Past and current changes in climate can provide a guide for improving predictions of species responses to future climate change (Petit *et al.*, 2008). Global land surface temperatures have increased by approximately 0.02 °C year^{-1} over the past several decades (Malhi & Wright, 2004; Hansen *et al.*, 2006). If species are migrating, analyses of repeated censuses will reveal changes in the distributions of individual taxa and/or the composition of ecological communities. Various studies have shown changes in animal and plant distributions consistent with climate-induced migration (e.g. Kalela, 1949; Pauli *et al.*, 1996; Parmesan *et al.*, 1999; Walther *et al.*, 2005; Wilson *et al.*, 2005; Beckage *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008), but only a relatively few migrations have been documented in any tropical species (e.g. Raxworthy *et al.*, 2008; Chen *et al.*, 2009) and no studies have yet demonstrated present-day shifts in the distribution of tropical plant species. This is despite the fact that approximately two-thirds of all plant species on Earth are tropical and that tropical species are hypothesized to be especially sensitive to changes in climate due to low intrinsic climatic variability in the tropics and increased niche specialization (Janzen, 1967; Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; McCain, 2009).

Temperatures in the tropical Andes have increased at a rate of approximately 0.03–0.04 °C year^{-1} since 1975, exceeding the global average (Vuille & Bradley, 2000). Assuming that species distributions are determined at least in part by climate, this warming should have caused upward migrations of species in montane tree communities since temperatures decrease predictably with increasing elevation (Colwell *et al.*, 2008). Given the documented adiabatic lapse rate of −0.0055 °C m^{-1} gain in elevation (Bush *et al.*, 2004), an upslope migration at the pace of approximately 5.5–7.5 vertical m year^{-1} is required for Andean species to remain at equilibrium with the observed temperature increases over the past 30 years.

The migration of species in response to warming can be manifested in several ways. In the simplest of cases, species may show an upward movement of their lower and upper range boundaries. Alternatively, many species may be incapable of responding to climatic changes through rapid migrations because of limited dispersal (Clark, 1998; Clark *et al.*, 1999; Corlett, 2009), long generation times and/or other impediments (Ibáñez *et al.*, 2006). In this case, there may be no or little movement of the upper edge of the species' range but the mean elevation of individuals, or 'centre of gravity', should still shift upwards due to increased performance in the upper/cooler portion of the species' range and reduced performance or dieback in the lower/hotter portion of the species' range (Feeley *et al.*, 2007; Breshears *et al.*, 2008; Lenoir *et al.*, 2008; Chen *et al.*, 2009). Likewise, species may show little or no change in the distribution of individuals, but migrations may still be evident as changes in more labile indicators of abundance, such as percentage cover or basal area in the case of plants (Kelly & Goulden, 2008), or the relative performance of individuals across the species' range.

We investigated the distributional responses of Andean tree genera to increasing regional temperatures by analysing repeat inventory data collected from a series of 14 1-ha tree plots situated in primary tropical montane forest spanning an elevational gradient from 950 to 3400 m a.s.l. in the Kosñipata Valley of Manu National Park in south-eastern Peru (Table 1). The plots were initially censused in 2003–04 and then recensused after an average of 4 years allowing us to analyse changes in floristic composition due to stem growth, mortality and recruitment, and to test how these changes correspond to the predicted upslope distributional shift of Andean trees due to observed warming.

MATERIALS AND METHODS

In 2003–04, we tagged, measured and identified all living woody stems (hereafter, trees) ≥10 cm diameter at breast height (d.b.h.) in 14 1-ha forest inventory plots centred at approximately 950, 1250, 1500, 1500, 1750, 1850, 2000, 2250, 2525, 2750, 3025, 3025, 3200, 3400 m elevation in the Kosñipata Valley at the edge of Manu National Park in south-eastern Peru (Table 1) where temperature increases have averaged approximately 0.03–0.05 °C year^{-1} since climate records were started in the late 1950s (see Appendix S1 in the Supporting Information).

For each tree we calculated the basal area, or cross-sectional area, at breast height (1.3 m above ground measured at the side of the stem) or above buttresses if necessary. If an individual had multiple stems below breast height, basal areas of the stems were combined to give a total basal area for each individual tree. The 14 plots were recensused after an average of 4 years (Table 1) providing data on annual rates of mortality, recruitment and basal area growth for approximately 14,000 individual trees from more than 1000 species of more than 250 genera.

The majority of species were only recorded in a single plot and thus even a large shift in their elevational distribution would not necessarily manifest in the recensus data due to the large elevational interval between plots. We therefore elected to conduct all analyses at the genus level. Conducting the analyses at the genus level is also advantageous in that it helps minimize possible errors due to any individuals that could not be reliably identified to species.

Following the protocol of Chen *et al.* (2009), who investigated elevational range shifts of moth species on Mount Kinabalu, Borneo, we calculated the centre of the elevational distribution of each genus, or its 'centre of gravity', as the mean elevation weighted by number of individuals per elevation and also weighted by relative basal area per elevation (basal area relativized within genera across plots).

We tested for changes in the mean elevation between censuses for all tree genera that occurred in at least two plots. Thirty-eight genera met this criterion (Table 2) representing 20% of all genera recorded in the plots but accounting for >80% of all individuals and >75% of total basal area. For each of these genera we estimated the migration rate as the annualized change in the centre of gravity of a genus based on first the distribution of individuals and second the distribution of basal area (Chen *et al.*, 2009).

In addition to testing for changes in the mean elevation of individual tree genera, we also tested for directional changes in the floristic composition of each study plot, specifically testing the hypothesis that if trees are migrating upslope through time there will be a corresponding increase in the abundance of tree genera from lower elevations. For each of the 14 plots we calculated the 'community elevation score' at the time of the first and second census. The community elevation score is the mean centre of gravity of all genera found in the plot (i.e. including some genera that were excluded from the genus-level analyses due to small sample sizes) as estimated from the initial round of censuses and weighted by their relative abundances in the plot during either the first or second census as measured by number of individuals or basal area. A decrease in community elevation score indicates an increase in the relative abundance or basal area of tree genera from lower elevations consistent with upward migrations (Chen *et al.*, 2009); however, for consistency with genus-level migration rates, we present our estimates of community-level migration rates such that positive values indicate upslope migrations.

Since inventory plots sample individuals only within portions of the distributional ranges, we also calculated the community elevation score for each plot using an independent measure of centres of gravity for each genus based on the distribution of the elevations from which herbarium samples have been collected in Peru, excluding samples from our study plots and correcting for biases in sampling intensity across elevation (Feeley & Silman, 2010a). We downloaded all available herbarium records for plants collected in Peru through the Global Biodiversity Information Facility (GBIF; http://www.gbif.org; Appendix S2). We screened to eliminate obvious georeferencing errors and duplicate records and excluded any collections from the study plots, resulting in a database of more than 125,000 unique records (Feeley & Silman, 2011). For 147 genera (58%) occurring in the study plots and represented by ≥30 records including elevational information, we estimated mean elevation by counting the number of specimens collected within elevational bands spanning 250 vertical metres (the width of elevational bands chosen to approximate the resolution of plot data). In our analyses we used only elevational data recorded with the collections themselves rather than elevations extracted on the basis of geographic coordinates in order to minimize the potential influence of georeferencing errors, which can be severe and problematic especially in mountainous areas (Feeley & Silman, 2010c). Collection intensity may be biased by elevation, for example due to differential access and/or proximity to field stations and population centres (Kadmon *et al.*, 2004; Moerman & Estabrook, 2006). We corrected for potential biases in collection intensity by standardizing over the total number of records available across all species (including samples of non-study species and samples not identified to species) from the corresponding elevational band (Feeley & Silman, 2010a).

RESULTS

Overall, during the period of 2003–04 to 2007–08 more Andean genera migrated upslope than downslope; 62% of genera increased in mean elevation of individuals and 87% increased in mean elevation of basal area (Table 2, Fig. 1a,b). The contrast in the number of upslope- versus downslope-migrating genera is more pronounced in more abundant genera (Table 2, Appendix S3). For example, of the 12 genera with ≥200 individuals, 75% increased their mean elevation of individuals and 100% increased their mean elevation of basal area (see insets in Fig. 1a,b).

We estimate that the mean migration rate of the Andean tree genera, in terms of distribution of individuals, was

Table 2 'Centres of gravity', or mean elevations, and annual migration rates estimated for 38 tree genera occurring in at least 2 of the 14 forest inventory plots in the south-eastern Peruvian Andes (genera ordered by abundance). Positive migration rates (bold) indicate upslope migration.

Genus	No. of individuals	Initial centre of gravity (m)*	Migration rate (m year^{-1})*	Initial centre of gravity (m)†	Migration rate (m year^{-1})†	Centre of gravity (m)‡
Cyathea	1689	2210.8	**5.4**	2252.4	**5.7**	1473.4
Weinmannia	1129	2903.5	**2.4**	2926.2	**3.4**	2591.2
Clusia	724	2662.9	**5.7**	2708.4	**4.5**	1992.3
Miconia	594	2689.4	**8.1**	2825.8	**9.5**	1886.6
Clethra	296	2369.3	**7.7**	2575.7	**4.9**	2363.5
Alchornea	287	1976.0	−1.9	2051.5	**6.6**	1622.7
Ocotea	284	2096.0	−0.2	2163.4	**3.5**	1431.4
Myrsine	268	2860.3	**5.4**	2854.2	**4.1**	2611.9
Ilex	263	2414.3	−0.1	2543.5	**2.6**	2423.1
Nectandra	242	1824.9	**3.5**	1772.1	**7.7**	1433.6
Hedyosmum	235	2262.0	**24.9**	2259.8	**15.8**	2200.3
Prunus	227	2681.8	**9.4**	2788.9	**6.5**	2463.7
Tapirira	190	1690.3	−0.3	1653.4	**0.9**	725.8
Myrcia	187	1845.7	**0.2**	1827.8	−0.7	1449.8
Symplocos	180	3157.2	−0.5	3239.2	**2.9**	2821.4
Ficus	179	1383.2	**1.7**	1449.1	−0.5	1365.3
Persea	154	2319.6	**5.5**	2505.1	**8.0**	2084.9
Cecropia	122	1637.1	**0.8**	1670.9	**3.9**	1519.5
Alzatea	118	1986.9	−1.3	1980.3	−1.5	n.a.
Mollinedia	117	1787.8	−6.2	1764.2	−6.4	1354.1
Axinaea	115	3160.4	−1.0	3160.0	**0.3**	n.a.
Guatteria	110	1712.7	**0.2**	1692.2	**4.2**	946.4
Inga	109	1431.7	**0.8**	1406.8	**3.6**	1044.1
Hieronyma	104	1889.9	−1.3	1852.1	**0.1**	n.a.
Ladenbergia	101	1275.7	**0.0**	1209.7	**0.8**	1192.4
Virola	100	1249.0	**3.7**	1212.7	**3.6**	578.7
Freziera	98	2713.0	**1.7**	2747.7	**2.8**	n.a.
Elaegia	95	1485.3	**2.4**	1551.9	−1.2	n.a.
Meliosma	89	2285.7	−5.3	2083.6	**0.8**	1674.6
Dendropanax	84	1616.1	−1.1	1586.2	**1.1**	1281.4
Clarisia	79	1334.8	−1.3	1313.3	**0.1**	908.1
Schefflera	78	2540.1	**30.0**	2668.0	**20.6**	1830.8
Cinchona	72	2406.3	**2.2**	2358.9	**4.4**	2252.2
Pseudolmedia	69	1615.9	**0.5**	1540.9	**0.2**	752.3
Brunellia	61	2815.6	−0.2	2787.8	**2.8**	2541.2
Protium	57	1724.6	**0.6**	1703.8	**1.0**	521.9
Tachigali	56	1460.7	**0.3**	1338.0	**4.3**	496.8
Palicourea	51	2034.8	−4.4	2036.3	**1.8**	1735.6

n.a., not applicable (i.e., could not be calculated from herbarium records due to insufficient collections).

*As estimated from the distribution, or change in distribution, of individuals across elevation.

†As estimated from the distribution, or change in distribution, of basal area across elevation.

‡As estimated from the elevational distribution of herbarium collection records from Peru correcting for sampling biases (accessed through the Global Biodiversity Information Facility, GBIF).

+2.5 m year^{-1} [95% confidence interval (CI) = +0.6 to +4.9 m year^{-1}; Table 2, Fig. 1a], and the mean migration rate in terms of basal area was +3.5 m year^{-1} (95% CI = +2.2 to +5.1 m year^{-1}; Table 2, Fig. 1b). As with the number of migrating genera, the mean rate of migration increased with increasing abundance of the genus (Fig. 1, Appendix S4). For example, for genera with ≥200 individuals the mean migration rate of individuals was +5.7 m year^{-1} (95% CI = +2.6 to +9.9 m year^{-1}) and the mean migration rate of basal area was +6.2 m year^{-1} (95% CI = +4.5 to +8.4 m year^{-1}; insets in Fig. 1a,b).

Migration rate in terms of basal area increased in relation to the initial centre of gravity of a genus, or mean elevation, such that basal area migration rates increased by an average of +2.8 m year^{-1} per 1000 m increase in a species' initial mean elevation ($F_{1,36} = 5.1$, $R^2 = 0.12$, $P = 0.03$).

When using the centre of gravity scores calculated from the initial plot censuses, we found that the community elevation

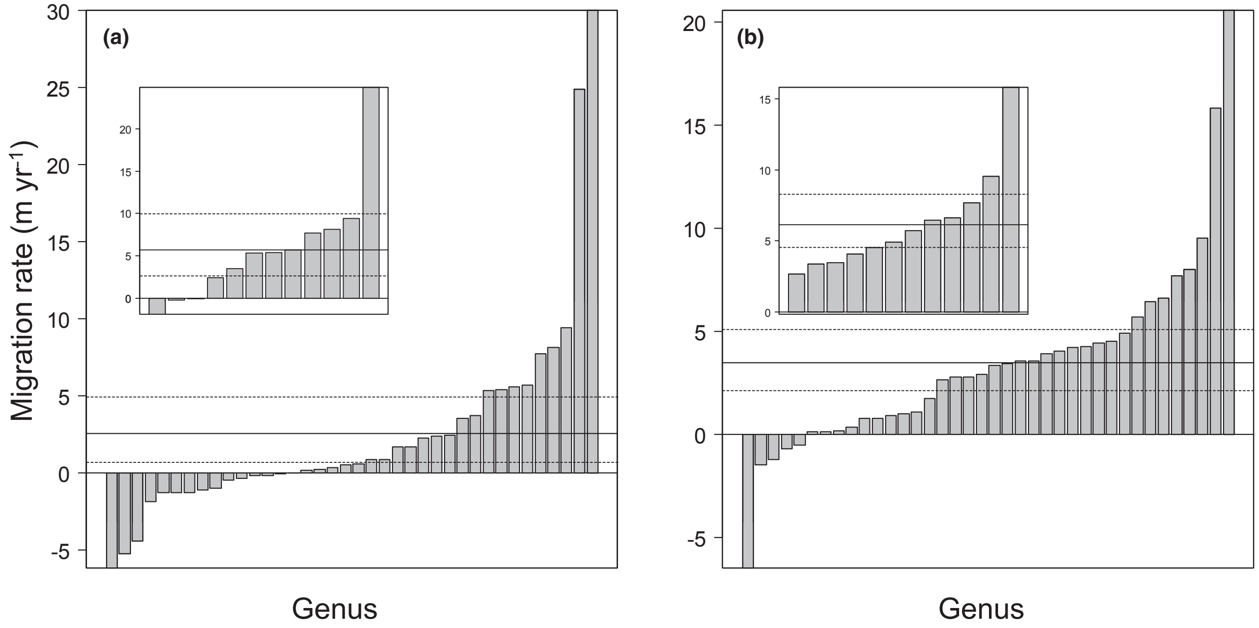

Figure 1 Migration rates estimated for each tree genus occurring in at least 2 of the 14 study plots in south-eastern Peru. Migration rates were estimated as the annualized changes in the 'centre of gravity' of the genus as weighted by (a) the number of individuals per elevation or (b) the relative basal area per elevation. Horizontal lines show the mean rate of change and 95% confidence intervals. Positive values indicate upslope migrations. Insets show the results if analyses are restricted to genera with ≥200 individuals.

score increased in 11 of the 14 plots if abundances were weighted by number of individuals, and in 12 plots if abundances were weighted by relative basal area (Table 3, Fig. 2a,b). The mean rate of change in community elevation scores corresponds to an upward migration of individuals at the rate of +1.1 m year^{-1} (95% CI = +0.4 to +1.9 m year^{-1}; Fig. 2a) and an upward migration of basal area at a rate of +2.0 m year^{-1} (95% CI = +1.1 to +2.8 m year^{-1}; Fig. 2b).

When using centre of gravity scores based on the distributions of herbarium collection records, we found that community elevation scores increased in 12 plots if weighted by number of individuals and in 11 plots if weighted by relative basal area (Table 3), with corresponding migration rates of +2.1 m year^{-1} (95% CI = +1.1 to +3.4 m year^{-1}; Fig. 2c) and +2.4 m year^{-1} (95% CI = +0.8 to +4.2 m year^{-1}; Fig. 2d), respectively. There was no relationship between change in community elevation score and plot elevation.

DISCUSSION

These results provide the first demonstration that tropical trees may respond to climate change through distributional migrations over short (subdecadal) time-scales. We show that there have been directional shifts in the distributions of tree genera in the Peruvian Andes such that the mean elevations of most genera increased from 2003–04 to 2007–08 and accordingly at any given elevation the abundance of genera centred at lower elevations has also increased.

The number of Andean genera migrating upslope and the rate of migration was greater when estimated based on changes in the distribution of basal area versus changes in the

Table 3 The estimated community-level migration rates of the 14 1-ha Andean forest inventory plots. Positive migration rates (bold) indicate upslope shifts.

Plot no.	Migration rate (m year^{-1})*	Migration rate (m year^{-1})†	Migration rate (m year^{-1})‡	Migration rate (m year^{-1})§
1	−3.16	**6.31**	**5.79**	**5.52**
2	**4.33**	**12.97**	**12.13**	**17.30**
3	**3.16**	**12.14**	**6.07**	**6.44**
4	**1.67**	**6.01**	**4.28**	**12.52**
5	**3.56**	**5.29**	**8.55**	**3.20**
6	**8.38**	**12.56**	**13.52**	**13.70**
7	**2.48**	**3.75**	−5.54	−8.52
8	**2.35**	**11.23**	**9.97**	**34.01**
9	−1.81	−1.17	**6.73**	**2.12**
10	**19.70**	**19.93**	**30.83**	**27.24**
11	**5.33**	**0.01**	**2.68**	−3.73
12	**1.97**	**1.95**	−1.76	**3.87**
13	−1.84	−2.29	**2.56**	−5.67
14	**7.61**	**5.70**	**7.29**	**6.54**

*As estimated from the change in the individual-based community elevation score calculated using centres of gravity for genera based on the distribution of individuals across study plots.

†As estimated from the change in the basal area-based community elevation score calculated using centres of gravity for genera based on the distribution of basal area across study plot.

‡As estimated from the change in the individual-based community elevation score calculated using centres of gravity for genera based on the distribution of herbarium collection records from Peru.

§As estimated from the change in the basal area-based community elevation score calculated using centres of gravity for genera based on the distribution of herbarium collection records from Peru.

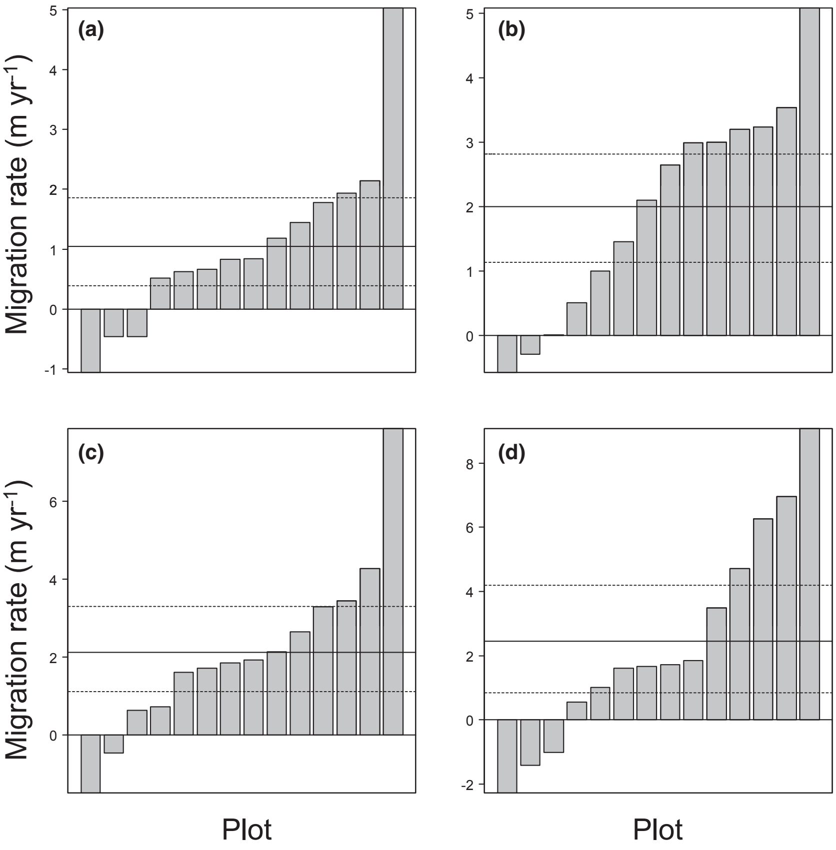

Figure 2 Migration rates as estimated from the annualized changes in community elevation scores of each of 14 1-ha tropical Andean forest inventory plots. In (a) and (b), community elevation scores are based on the average initial 'centre of gravity' for all represented genera as calculated from the plot censuses and weighted by (a) the number of individuals or (b) the relative basal area in the first versus second census. In (c) and (d), the centres of gravity were calculated from the distribution of herbarium collections for each genus available through the Global Biodiversity Information Facility (GBIF) from Peru and weighted by (c) the number of individuals and (d) the relative basal area. Horizontal lines show the mean rate of change and 95% confidence intervals. Positive values indicate upslope migrations.

distribution of individuals. This is not surprising given the duration of the study in relation to the long life span of trees. In contrast to the distribution of individuals, changes in distribution of basal area are influenced not only by mortality and recruitment events but also by changes in relative tree growth rates that can occur over shorter time-scales.

Basal area migration rates were positively correlated with mean elevation. This may be indicative of the fact that in the tropical Andes temperature increases have generally been greater at higher elevations (Vuille & Bradley, 2000). Alternatively, this pattern may in part be an artefact of the fact that diversity is lower in higher-elevation plots, leading to increased sample sizes within genera (173.4 more individuals per genus for each 1000 m gain in initial elevation; $F_{1,36} = 4.0$, $R^2 = 0.10$, $P = 0.05$). However, if abundance is accounted for, the relationship between basal area migration rates and initial mean elevation remains significant ($P = 0.05$).

While it may be surprising that the distributional shifts of Andean trees are in fact measurable over a census interval of 4 years, it should be noted that the observed migration rates are in line with the mean upslope range shifts observed for tropical Lepidoptera (1.6 m year^{-1}) (Chen *et al.*, 2009) and reptiles (2.2 m year^{-1}) (Raxworthy *et al.*, 2008) but slower than those observed for tropical amphibians (9.0 m year^{-1}) (Raxworthy *et al.*, 2008). It is also significantly slower than the 5.5–7.5 m year^{-1} expected based on the recorded 0.03–0.05 °C year^{-1} increase in temperature for the region and is markedly slower than the >9 m year^{-1} migration that will be required to remain in equilibrium with climate if temperatures increase by >5 °C over the next century as generally predicted under high-range greenhouse gas emissions scenarios (Malhi *et al.*, 2009; Urrutia & Vuille, 2009). The migration rates estimated here are consistent with past rates of change as estimated through palaeoecological records of Andean tree communities during the Ice Age to Holocene transition (Bush *et al.*, 2004; Urrego *et al.*, 2010) and thus may approximate the maximum migration rate for this system. Alternatively, species migrations may be punctuated by rapid periods of spread due to rare, long-distance dispersal events (Clark *et al.*, 1999; Nathan, 2006), emphasizing the need for longer-term studies.

The observed changes in tree distributions are clearly non-random and the direction of change is consistent with a priori expectations of upslope migrations under rising temperatures. However, we cannot exclude the possibility that these changes are due to factors other than long-term warming. For example, given the relatively short duration of the study and the possibility of delayed responses in the dynamics of long-lived trees, the observed range shifts may be in response to an isolated climatic event such as the 2005 Amazonian drought (Phillips *et al.*, 2009; Allen *et al.*, 2010) in which temperatures were elevated throughout much of the south-west Amazon, or other past climatic events such as El Niños. The difficulty in distinguishing between the effects of climatic events, climate trends and other possible drivers further emphasizes the need for additional longer-term studies.

Longer-term and larger-scale studies will also hopefully allow for additional analyses to be conducted at the species level. At the current taxonomic resolution, the observed upslope shifts in mean elevations of genera may possibly reflect changes in the relative abundances of species rather than actual migrations (i.e. the mean elevation of a genus will shift upslope if species centred at higher elevations are increasing in abundance/basal area relative to congeners centred at lower elevations, even in the absence of range shifts). While this is certainly a possibility that warrants further exploration, in preliminary analyses of the 50 most abundant species we find that mean elevations of the majority of species have in fact shifted upslope and that the mean migration rate is significantly upslope at the rate of +1.1 m elevation year^{-1} (95% CI = +0.4 to +1.8 m year^{-1}).

CONCLUSIONS

While the underlying causes and mechanisms need further elucidation, these results provide valuable evidence that tropical trees may potentially respond to environmental changes through distributional shifts. In addition, these results provide estimates of the speed at which modern tropical tree communities can potentially migrate. These data can be incorporated into models and used to better predict changes in species future population sizes under various climate change scenarios and the associated risks of extinction (Feeley & Silman, 2010a). In general, we predict that if tropical species continue to migrate at the rates observed here and are incapable of tolerating and/or adapting to rising temperatures, they will fail to keep pace with future climate changes, resulting in rapid losses of habitat area and high risks of extinction (Thomas *et al.*, 2004; Feeley & Silman, 2010a).

ACKNOWLEDGEMENTS

This paper is a product of the Andes Biodiversity and Ecosystems Research Group consortium (ABERG; http://www.andesconservation.org). The data presented here represent an exceptional effort on the part of botanists and field assistants in Peru, particularly those from the Universidad Nacional San Antonio de Abad, Cusco, and Luis Imunda Gonzales. Identifications for the species were aided by more than 20 specialists, and we particularly thank the Universidad Mayor de San Marcos, the Missouri Botanical Garden, the Field Museum of Natural History, and the New York Botanical Garden. Support came from the Gordon and Betty Moore Foundation's Andes to Amazon initiative, NSF DEB-0237684 and NSF BCS-0216607, the Blue Moon Fund, the Amazon Conservation Association, and the FTBG's Center for Tropical Plant Conservation. We thank the GBIF and all contributing institutions for making collection data publicly available. We especially thank INRENA and the personnel of Manu National Park, Peru, for their gracious help in logistics and permission to work in the protected area. The Amazon Conservation Association and the Cock-of-the-Rock Lodge provided logistical support throughout the project.

REFERENCES

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259,** 660–684.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T. & Perkins, T. (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the green mountains of Vermont. *Proceedings of the National Academy of Sciences USA*, **105,** 4197–4202.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B. & Davison, J.E. (2008) Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences USA*, **105,** 11591–11592.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M. & Naeem, S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310,** 1029–1031.

Bush, M.B., Silman, M.R. & Urrego, D.H. (2004) 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303,** 827–829.

Chen, I.C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences USA*, **106,** 1479–1483.

Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, **152,** 204–224.

Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80,** 1475–1494.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C. & Longino, J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322,** 258–261.

Corlett, R.T. (2009) Seed dispersal distances and plant migration potential in tropical east Asia. *Biotropica*, **41,** 592–598.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, **105,** 6668–6672.

Feeley, K.J. & Silman, M.R. (2010a) Land-use and climate change effects on population size and extinction risk of Andean plants. *Global Change Biology*, **16,** 3215–3222.

Feeley, K.J. & Silman, M.R. (2010b) Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology*, **16,** 1830–1836.

Feeley, K.J. & Silman, M.R. (2010c) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of geo-referencing errors and the importance of data filtering. *Journal of Biogeography*, **37,** 733–740.

Feeley, K.J. & Silman, M.R. (2011) The data void in modeling current and future distributions of tropical species. *Global Change Biology*, **17,** 626–630.

Feeley, K.J., Wright, S.J., Supardi, M.N.N., Kassim, A.R. & Davies, S.J. (2007) Decelerating growth in tropical forest trees. *Ecology Letters*, **10,** 461–469.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46,** 5–17.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W. & Medina-Elizade, M. (2006) Global temperature change. *Proceedings of the National Academy of Sciences USA*, **103,** 14288–14293.

Ibáñez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., Ladeau, S., McBride, A., Welch, N.E. & Wolosin, M.S. (2006) Predicting biodiversity change: outside the climate envelope, beyond the species–area curve. *Ecology*, **87,** 1896–1906.

Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101,** 233–249.

Kadmon, R., Farber, O. & Danin, A. (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, **14,** 401–413.

Kalela, O. (1949) Changes in geographic ranges in the avifauna of Northern and Central Europe in response to recent changes in climate. *Bird Banding*, **20,** 77–103.

Kelly, A.E. & Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences USA*, **105,** 11823–11826.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320,** 1768–1771.

Malhi, Y. & Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,** 311–329.

Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C. & Meir, P. (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences USA*, **106,** 20610–20615.

McCain, C.M. (2009) Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters*, **12,** 550–560.

Moerman, D.E. & Estabrook, G.F. (2006) The botanist effect: counties with maximal species richness tend to be home to universities and botanists. *Journal of Biogeography*, **33,** 1969–1974.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313,** 786–788.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37,** 637–669.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421,** 37–42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399,** 579–583.

Pauli, H., Gottfried, M. & Grabherr, G. (1996) Effects of climate change on mountain ecosystems: upward shifting of mountain plants. *World Resource Review*, **8,** 382.

Petit, R.J., Hu, F.S. & Dick, C.W. (2008) Forests of the past: a window to future changes. *Science*, **320,** 1450–1452.

Phillips, O.L., Arãgao, L.E.O.C., Lewis, S.L. *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323,** 1344–1347.

Raxworthy, C.J., Pearson, R.G., Rabibiso, N., Rakotondrazafy, A.M., Ramanamanjato, J., Raselimanana, A.P., Wu, S., Nussbaum, R.A. & Stone, D.A. (2008) Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology*, **14,** 1703–1720.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427,** 145–148.

Thuiller, W. (2007) Biodiversity: climate change and the ecologist. *Nature*, **448,** 550–552.

Urrego, D.H., Bush, M.B. & Silman, M.R. (2010) A long history of cloud and forest migration from Lake Consuelo, Perú. *Quaternary Research*, **73,** 364–373.

Urrutia, R. & Vuille, M. (2009) Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research*, **114,** D02108.

Vuille, M. & Bradley, R.S. (2000) Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical Research Letters*, **27,** 3885–3888.

Walther, G.-R., Beiner, S. & Burga, C.A. (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16,** 541–548.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8,** 1138–1146.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Mean annual temperatures recorded at climate stations in Cusco and in Puerto Maldonado.

Appendix S2 Herbaria contributing data to this study and accessed through the Global Biodiversity Information Facility.

Appendix S3 Percentage of Andean tree genera showing upward migrations as indicated by a positive change in the centre of gravity weighted by number of individuals or basal area versus the minimum abundance criteria to be included in the analyses.

Appendix S4 The annualized migration rate for Andean tree genera as weighted by the distribution of individuals or basal area versus the minimum abundance criteria to be included in the analyses.

BIOSKETCH

Kenneth J. Feeley is an Assistant Professor in the Department of Biological Sciences at Florida International University and a Conservation Biologist in the Fairchild Tropical Botanic Garden's Center for Tropical Plant Conservation. His research focuses on understanding the responses of tropical forest ecosystems to large-scale anthropogenic disturbances such as deforestation, fragmentation and climate change. This study was conducted through the Andes Biodiversity and Ecosystem Research Group (ABERG; http://www.andesconservation.org).

Author contributions: K.J.F. designed the study, collected data, analysed the data and wrote the paper; M.R.S. designed the study, collected data and wrote the paper; M.B.B., Y.M., P.M. and S.S. designed the study; W.F., K.G.C., N.S.R. and M.N.R.Q. collected data. All authors helped to revise and edit the paper.

Editor: Miguel Araújo