

Using Herbarium Collections and Plot Data to Track the Effects of Climate Change on Tropical Forests

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Abstract

One of the primary ways that tropical plant species are expected to respond to climate change is through shifts in their geographic distributions (i.e., ‘species migrations’) leading to altered patterns of diversity and community composition. Unfortunately, studies tracking these types of changes are sparse or nonexistent for most of the tropics. One reason for the paucity of tropical studies is a simple lack of data which limits our ability to map species’ ranges and track, or predict, changes in the distributions of species through time. In this paper, I discuss the availability, or lack thereof, of inventory plot and herbarium collections data for tropical plant species. I then review a series of studies using collections data to track changes in the distributions of Amazonian plant species through time, and combinations of collections and plot data to track changes in tree species composition in Peru, Costa Rica and Colombia. These studies show that climate change may potentially be causing changes in species distributions driven mainly by range retractions. The studies also show that the composition of tropical montane forests are changing to include greater relative abundances of lowland thermophilic species and that these changes are likewise being driven primarily by retractions of species’ ranges from hot, lowland areas. These results all suggest that tropical forests are at high risk of species extinctions and biodiversity loss. Finally, I discuss the need for additional high-quality collections and plot data so that we can increase our understanding of the different ways that tropical plant species are responding to climate change and the reasons for their differential responses.

Key Words: biotic attrition, extinction, Global Biodiversity Information Facility, global warming, natural history data, species migrations, thermophilization

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Tropical forests harbor the majority of known and unknown species (Raven 1988; Dirzo & Raven 2003; Joppa *et al.* 2011a) and provide vital ecosystem services such as food production, carbon sequestration, and climate regulation (Costanza *et al.* 1997; Cincotta *et al.* 2000; Fa *et al.* 2002; Milner-Gulland & Bennett 2003; Naidoo *et al.* 2008; Saatchi *et al.* 2011; Baccini *et al.*

2012). Despite their diversity and importance, tropical plants are systematically underrepresented in studies investigating or predicting the impacts of global climate change (Feeley *et al.* 2015; Feeley *et al.* 2017). For example, in their oft-cited study summarizing the predicted effects of climate change on species’ extinction risks, Thomas *et al.* (2004) included studies

of more than 1100 species worldwide but only 172 tropical plant species – 163 from the Brazilian Cerrado and nine from the Amazon (Thomas *et al.* 2004). More recently, Urban (2015) synthesized more than a hundred studies representing many tens of thousands of species to estimate the number of species in different parts of the world that are likely to be driven to extinction by climate change (Urban 2015). Included in the analyses of Urban were data for several thousand species of tropical plants (the exact number of tropical plant species is impossible to discern due to lack of specification of the species' identities or provenances in some of the original datasets). While this is clearly a marked improvement over past syntheses (including that of Thomas *et al.* 2004), it is still just a small fraction of actual tropical plant biodiversity (Joppa *et al.* 2011b), especially considering that the included plant species were meant to represent all possible tropical plant taxa, biogeographic realms, habitat types, and life forms (from Asian cloud-forest bryophytes to Amazon rainforest trees to African savannah grasses). Another important consideration is that none of the studies of tropical plant species included in either Thomas *et al.* (2004) or Urban (2015) looked at how tropical systems are actually responding to climate change but rather were just predictions based on projections of species' estimated ranges (i.e. species distribution models) into the future under different climate change scenarios.

A simple explanation for why tropical plant species are so poorly represented in studies that investigate or predict the impacts of climate change is an extreme paucity of data available for these species. We simply do not have enough data about most tropical plants to map their species distributions or make informed predictions about how they are faring, or will fare, in the face of climate change (Feeley *et al.* 2012; Feeley 2015b).

In this review, I briefly discuss the availability of distribution data for tropical plant species. I then synthesize a series of four recent studies that have used the available herbarium collections and plot data to track changes in the distributions of tropical plant species and the associated changes in forest commu-

nity composition in response to modern anthropogenic climate change. These studies are still just a 'drop in the bucket' compared to the vast diversity of tropical plant species and ecosystems, but they provide examples of the type of analyses that can be conducted using the available data as well as a concrete framework for future research.

The Availability of Collection and Plot Data from Tropical Forests

The most basic information needed to track and predict species' risks of extinction due to climate change are their ranges, which in turn require maps of where the species occur and, ideally, where the species do not occur. Currently, the available data are simply insufficient to make such maps for most tropical plant species (Feeley & Silman 2011a).

For temperate realms, one of the most common sources of data for mapping species ranges and tracking the effects of climate change are plot inventories. In the United States, for example, the national forest service (USFS) maintains a network of over 125,000 permanent forest inventory plots in its Forest Inventory and Analysis (FIA) program. These data are publicly available (<http://www.fia.fs.fed.us/>) and have been used in numerous ecology and biogeography studies (e.g. Iverson & Prasad 1998; Zhu *et al.* 2012; Woodall *et al.* 2013; Fei *et al.* 2017; Janowiak *et al.* 2017). Likewise, many European countries maintain large comprehensive networks of inventory plots that provide detailed data on where species are present and absent (<http://forestportal.efi.int/>). National census plot networks such as these do not exist as of yet in the tropics (although national inventories are planned for several countries).

For an example of how scarce plot data are for tropical plants, one can look to South America, which contains the largest tract of tropical forest (the Amazon), supports the greatest diversity of plant species (Slik *et al.* 2015), and is arguably the best-studied of all tropical realms. Collating data for five of the largest and most prominent tropical plot networks: RAINFOR (<http://www.rainfor.org/>), the Amazon Tree Di-

versity Network (ATDN; <http://web.science.uu.nl/amazon/atdn/>), Forestplots.net (<https://www.forestplots.net/>), the Smithsonian Institute's Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu/>), and the Red de Bosques (<http://www.condesan.org/redbosques/>), there is a combined total of approximately 1500 census plots distributed throughout all of Tropical South America (i.e. just 1% the number of plots maintained by the USFS in the USA, Feeley 2015a). One recent study analyzed tree species occurrences in 1100 (73%) of these plots in the Amazon (ter Steege *et al.* 2013). The included plots contained a total of approximately 5000 distinct tree species. Of these species, more than 1500 were recorded in only one or two plots each; the median number of individuals per species was 18 and the median number of plots per species (i.e. distinct occurrence locations) was seven. Furthermore, there are estimated to be more than 11,000 additional Amazonian tree species that are not included in any of the plots (ter Steege *et al.* 2013). Clearly, it is not possible to map the geographic distributions or estimate the climatic niches for the majority of Amazonian tree species using these plot data alone.

An alternative source of data for mapping the geographic distributions of plant species is herbarium or natural history collections. But here again, data from the tropics are woefully sparse. For tropical South America, there are nearly two million georeferenced plant collection records available for download through the Global Biodiversity Information Facility (<http://www.gbif.org>, accessed on February 1st, 2014). These records include collection coordinates for more than 52,000 valid species names (validity of names determined through <http://tnrs.iplantcollaborative.org/>). Approximately 1/3 of these species are represented by just one or two collections each (Feeley 2015a) and the median number of collections per species is just six. There are likely to be several thousand more species that are not represented by any collections at all or that have yet to be properly identified (Bebber *et al.* 2010). Given that other parts of the tropics, such as Africa and Asia, have even lower collection densities (Feeley & Silman 2011a), the number of

tropical plant species worldwide for which there exist little or no information is truly daunting.

Despite their paucity, the data that are currently available can still provide useful information on the ranges and realized climatic niches for at least a subset of the best-collected tropical plant species. As discussed below, this information can in turn be used alone, or in combination with plot census data, to track how species' ranges and community composition are changing through time in response to climate change or other anthropogenic disturbances.

Tracking the Effects of Climate Change in Tropical Forests

There are only a few possible responses of any species, including tropical plants, to global climate change: (1) species can acclimate or adapt to changes in climate; (2) species can shift their distributions (i.e. 'migrate') to remain at equilibrium with climate; or (3) failing to do either of these two, species will eventually decrease in population size to the point that some will become committed to extinction (Feeley *et al.* 2012). For many tropical plant species there are good reasons to believe that 'migration' is a more viable response than acclimation or adaptation. For example, various constraints (e.g. long-lived individuals, long-generation times, low genetic variation, high levels of habitat/population fragmentation, and accelerating rates of climate change) suggest that most tropical tree species will be unable to adapt to anthropogenic climate change (Feeley *et al.* 2012). In addition, studies show that the composition of paleo-plant-communities in the tropics were tightly linked to temperature and that many plant species shifted their distributions upslope as temperatures increased after the late glacial maximum (Bush *et al.* 2004). As such, we can predict that tropical plant species should likewise be actively migrating upslope due to contemporary warming.

A large and growing number of studies have documented upward and poleward shifts in the distributions of various taxa. Most of these studies are from temperate systems and unfortunately, tropical species, and especially tropical plant species, remain

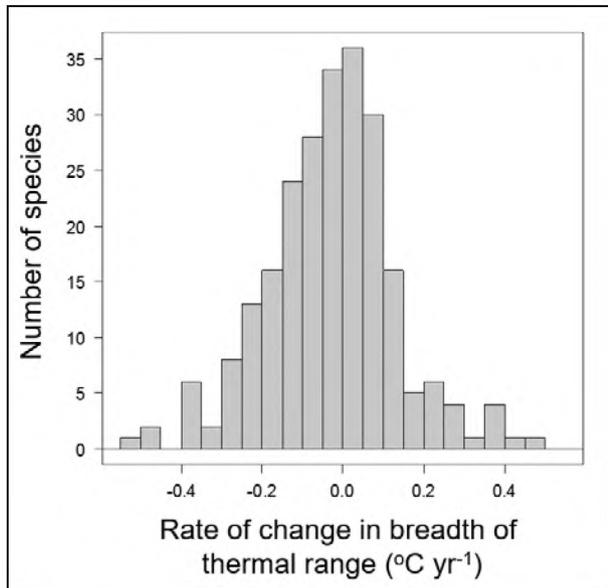


Fig. 1. The annual rate of change in the ranges of mean annual temperatures over which Amazonian plant species were collected between 1970 and 2009 as based on analyses of herbarium records available through GBIF and after correcting for collection biases (Feeley 2012). The average rate of change was -0.029 °C yr⁻¹ (95% CI = -0.047 – -0.009 °C yr⁻¹) indicating that species' realized thermal niches, and hence geographic distributions, are contracting through time.

grossly underrepresented in these studies (Rehm 2014; Feeley *et al.* 2017). For example, a meta-analysis published in 2011 (Chen *et al.* 2011) included over 50 studies representing more than 2000 different plant and animal species. At the time of meta-analysis, no studies were available for any tropical plant species.

Given sufficient data, it should be possible to determine if species are migrating by tracking changes in the locations from which they have been collected through time. Feeley (2012), analyzed thousands of herbarium collection records from tropical South America to test for changes in species distributions. For approximately 240 of the best-collected Amazonian plant species, the changes in the average, maximum and minimum elevations from which they had been collected over the past four decades (1970–2009) was quantified. After correcting for geo-referencing errors and spatiotemporal collection biases (con-

founding factors that need to be accounted for in all studies using natural history records; Schulman *et al.* 2007; Tobler *et al.* 2007; Boakes *et al.* 2010; Feeley & Silman 2010, 2011b), it was found that the majority of species (59%) did in fact show some evidence of distributional shifts towards higher areas that were previously 'too cold'. More specifically, the mean collection location shifted upward in 13% of species, the leading high-elevation range edge shifted upward in 28% of species, and the trailing low-elevation range edge shifted upward in 38% of species (Feeley 2012). The fact that more species shifted their lower trailing range edges upward than shifted their high leading range edges upward suggests that many species are 'migrating' through range retractions rather than range expansions or range 'marches' (Lenoir & Svenning 2015). In fact, a comparison of the leading and trailing edges of the species' ranges shows that the realized thermal niches of Amazonian plant species contracted by an average of 1.13 °C between 1970 and 2009 corresponding to an annual rate of change of -0.03 °C per year (95% CI = -0.05 – -0.01 °C yr⁻¹; Fig. 1). In terms of elevation, this means that the species' ranges shrunk by an average of more than 200 vertical meters over just the past four decades, or in other words, by an average of approximately five vertical meters every year. The fact that thermal ranges are shrinking so rapidly though time certainly does not bode well and suggests a high risk of decreasing population sizes and eventual extinctions.

Another approach that holds great potential for tracking the effects of climate change is to combine the data from herbarium collections with plot census data and test for directional changes in community composition. This type of analysis involves three general steps: (1) use the location of herbarium collections to estimate the preferred or optimum temperature (or other environmental condition of interest) for each species represented in the plots; (2) calculate the Community Temperature Score (CTS) of each study plot during an initial and subsequent census based on the relative abundance of species and their optimum temperatures, and (3) calculate the annualized differences of each plot's Community Temperature Score

Table 1. Community Temperature Scores (CTS; °C) and Thermal Migration Rates (TMR; °C century⁻¹) and their 95% confidence intervals (CI) calculated from recensuses of neotropical forest inventory plots. Data for Peru from Feeley *et al.* (2011), for Costa Rica from Feeley *et al.* (2013), and for Colombia from Duque *et al.* (2015)

Country	CTS	(95% CI)	TMR	(95% CI)	% plots with positive TMR
Peru	-2.7	(-3.1 - -2.2)	1.12	(0.29 - 2.1)	0.79
Costa Rica	-4.8	(-5.6 - -4.0)	0.6	(-0.10 - 1.11)	0.90
Colombia	-4.3	(-3.5 - -5.0)	1.04	(0.19 - 2.13)	0.81
Combined	-3.5	(-3.9 - -3.1)	0.95	(0.48 - 1.53)	0.83

to characterize the rate and direction of compositional change.

To date, this approach has been applied to analyze compositional changes in three different systems of forest inventory plots in the tropics, each containing many hundreds of tree species: the Kosñipata valley transect in Southern Peru (14 1-ha plots spanning 950–3400 m asl), the Volcan Barva transect in Costa Rica (10 1-ha plots spanning 70–2800 m asl), and a network of plots in Antioquia, Colombia (16 1-ha plots spanning 40–2950 m a.s.l.). While these three studies were conducted independently, there was enough overlap in methods and analyses that we can now combine the results to get a larger-scale picture of how species composition relates to temperature and how climate change is influencing the composition of species in these tropical forests (Feeley *et al.* 2011; Feeley *et al.* 2013; Duque *et al.* 2015).

According to the steps 1 and 2 listed above, in all three studies, the optimum temperature (or elevation which can then be translated to temperature on the basis of an adiabatic lapse rate) was calculated for each species represented in the plots. The optimum temperature was estimated as the average of the mean annual temperatures occurring at all locations from which the species had been collected according to available records in the Global Biodiversity Information Facility after correcting for collection biases. The CTS of each plot was subsequently estimated in the initial and all subsequent censuses as the mean of the

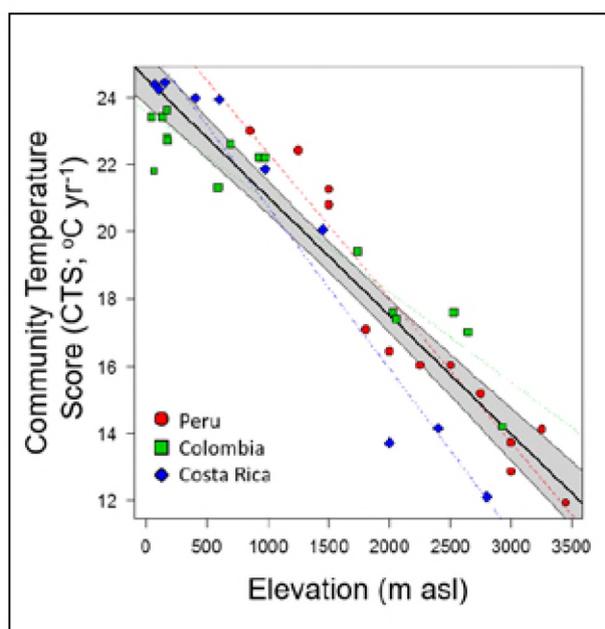


Fig. 2. The Community Temperature Scores (CTS = mean of the constituent species’ optimum temperatures weighted by relative abundance) of plots in Peru, Colombia, and Costa Rica vs. plot elevation. CTS decreases significantly with elevation within each system and for all three systems combined. The gray shading indicates the overall relationship between CTS and elevation with 95% confidence interval (lapse rate = -3.5 °C km⁻¹ [95% CI = -3.9 - -3.1 °C km⁻¹], R² = 0.89. The individual relationships for Peru, Colombia and Costa Rica are shown in red, green, and blue lines, respectively (Peru: lapse rate = -2.7 °C km⁻¹ [-3.1 - -2.2 °C km⁻¹], R² = 0.91; Colombia: lapse rate = -4.3 °C km⁻¹ [-3.5 - -5.0 °C km⁻¹], R² = 0.92; Costa Rica: lapse rate = -4.8 °C km⁻¹ [-5.6 - -4.0 °C km⁻¹], R² = 0.95).

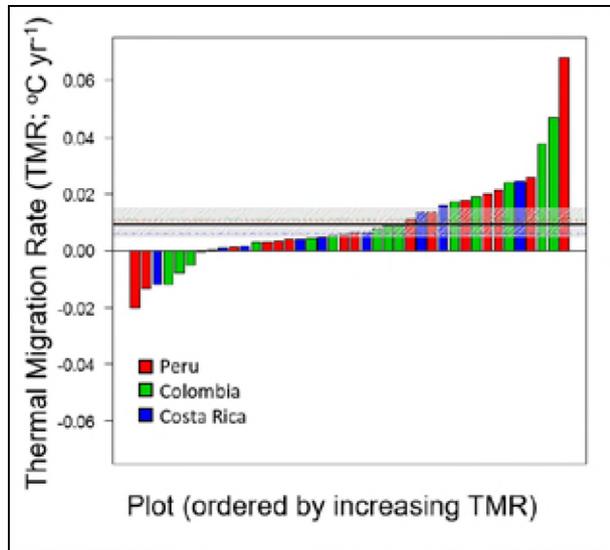


Fig. 3. The Thermal Migration Rates (TMR = annualized change in Community Temperature Scores) of plots in Peru, Colombia and Costa Rica. Combining systems, the overall thermal migration rate is $0.95 \text{ }^{\circ}\text{C century}^{-1}$ (95% CI = $0.48\text{--}1.53 \text{ }^{\circ}\text{C century}^{-1}$; black line and gray shading). The thermal migration rate does not vary significantly between the different plot networks (95% CIs = Peru: $0.29\text{--}2.1 \text{ }^{\circ}\text{C century}^{-1}$; Colombia: $0.19\text{--}2.13 \text{ }^{\circ}\text{C century}^{-1}$; Costa Rica: $-0.10\text{--}1.11 \text{ }^{\circ}\text{C century}^{-1}$). The mean TMR for Peru, Colombia, and Costa Rica are indicated with red, green, and blue lines, respectively.

optimum temperatures of all represented species with the species weighted based on their relative basal areas.

For each system independently and for all plots combined, CTS was very strongly correlated with plot elevation with slopes corresponding to lapse rates between $-2.7 \text{ }^{\circ}\text{C}$ and $-4.8 \text{ }^{\circ}\text{C km}^{-1}$ (Table 1; Figure 2). As discussed in Feeley *et al.* (2013), the relationship of CTS vs. elevation tends to have a lapse rate that is shallower than the true adiabatic rate ($-5.5 \text{ }^{\circ}\text{C km}^{-1}$) due to niche truncation at high and low elevations (cold and hot temperatures, respectively).

The decrease in CTS with elevation indicates that cold, highland plots tend to have greater relative abundances of species that are most often collected from the highlands while hot, low-elevation plots tend to have greater relative abundances of the more-thermophilic species typically collected from

the lowlands. While this result appears obvious, it is actually extremely informative and important. The strength of the relationship confirms that a species' optimum temperature as estimated from collection records is in fact a meaningful measure of the species' niches and that community composition is strongly determined by temperature vs. by other environmental factors (for example, in Colombia it was found that there is no significant relationship between the plots' Community Precipitation Scores [analogous to CTS but based on the total annual precipitation at collection locations rather than the mean annual temperatures] and actual rainfall; Duque *et al.* 2015). As such, we can predict that even fairly minor changes in temperature should lead to observable directional changes in composition. Specially, we can predict that increases in temperature should lead to a thermophilization of community composition which will be evidenced by increases in the CTS of plots.

To test for thermophilization, changes in CTS are tracked through time within each plot to provide an estimate of the constituent species' mean Thermal Migration Rate (TMR). Based on this analysis it was found that the vast majority of the plots (33 of 40 plots [83%], binomial probability <0.0005) did increase in CTS through time (i.e. had positive TMR; Fig. 3). The average TMR was $0.95 \text{ }^{\circ}\text{C century}^{-1}$ (95% CI = $0.48\text{--}1.53 \text{ }^{\circ}\text{C century}^{-1}$) and does not vary significantly between the different plot networks (Table 1).

It was previously argued that the thermal migrations rates in Peru and Costa Rica were slower than required to keep pace with concurrent warming (Feeley *et al.* 2011; Feeley *et al.* 2013). However, updated estimates of regional warming rates indicate that while TMRs are in fact slower than the rate of warming in Costa Rica, average TMRs are not significantly slower than the rates of warming in Peru (or Colombia; rates of warming since 1960s in the nearest major cities of Cusco, Peru; San Jose, Costa Rica; and Medellin, Colombia; have been 0.63 ± 0.31 , 1.60 ± 0.47 , $1.45\pm 0.17 \text{ }^{\circ}\text{C century}^{-1}$, respectively; <http://berkeleyearth.org/>). Across all systems, TMRs were sufficient to keep up with warming in 47.5% of the study plots (Peru: 71.4%; Costa Rica: 30.0%; Colombia: 37.5%). That said, in

agreement with the herbarium-based study described above, it appears that most of the observed changes in species composition were due to range contractions (Feeley *et al.* 2013; Duque *et al.* 2015). In other words, the relative abundance of highland tree species is decreasing in the plots through time not due to the incursion or increased abundances of lowland thermophilic species but instead due to dieback of the highland species. As above, this suggests a high risk of extinction for many species as well as a high risk of biodiversity loss and biotic attrition (Colwell *et al.* 2008; Lenoir & Svenning 2015). Adding to this risk is the fact that rates of warming are accelerating. It is generally accepted that global temperatures will increase by at least 2 °C by the end of this century (IPCC 2013). This will require that species not only continue to migrate but that they more than double their current rate of migration. For many species, this simply may not be possible.

Summary and Prospects

Taken together, the studies described above provide compelling evidence that many plant species from several sites throughout the neotropics are migrating upslope potentially in response to warming. These migrations are in turn causing changes in species composition towards increasing relative abundances of thermophilic species. Worrisome is the fact that the observed species migrations appear to be occurring primarily as a consequence of range retractions rather than range expansions or range shifts/marches. Indeed, the herbarium-based study (Feeley 2012) indicates that species' geographic and thermal ranges are shrinking rapidly through time. If this continues, range retractions will eventually lead to local and possibly global extinctions.

These analyses and their results, which are only possible because of the public availability of collections data and information online, provide us with a 'first run' understanding of how some tropical forests are responding to global warming and can be used to help guide future conservation efforts. However, many important questions remain to be addressed.

For example, how are other species and other tropical systems responding? How are individual species migrating and what factors determine the sensitivity of plant species to environmental change and their ability to migrate? Are migration rates determined by dispersal, by phenology, by specialization on factors other than climate, or other life history traits yet to be considered?

To answer these and other questions, more and better data are required (Feeley 2015b). Ideally we would like to know where species occur and why they do not occur elsewhere so that we can better predict how individual species are responding to environmental change. This requires higher-resolution data than what is currently available. Specifically, we need enough plots or collections to characterize the ranges, and especially the range edges, of tens of thousands of species and how these range edges relate to various environmental factors. Alternatively, physiological studies and experiments can be used to determine the tolerances of select species for different factors (Feeley 2015b). Given the pending impacts of climate change on the megadiverse forests of the tropics (Perez *et al.* 2016), we must strive to rapidly increase the amount and quality of data. Towards this end, herbarium, natural history collections, and census plot networks all serve vital roles. Indeed, we must push for increased public access of existing data at the same time that we support ongoing inventories, collections, and research.

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