Intra- and interspecific tree growth across a long altitudinal gradient in the Peruvian Andes

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Abstract. Tree growth response across environmental gradients is fundamental to understanding species distributional ecology and forest ecosystem ecology and to predict future ecosystem services. Cross-sectional patterns of ecosystem properties with respect to climatic gradients are often used to predict ecosystem responses to global change. Across sites in the tropics, primary productivity increases with temperature, suggesting that forest ecosystems will become more productive as temperature rises. However, this trend is confounded with a shift in species composition and so may not reflect the response of in situ forests to warming. In this study, we simultaneously studied tree diameter growth across the altitudinal ranges of species within a single genus across a geographically compact temperature gradient, to separate the direct effect of temperature on tree growth from that of species compositional turnover. Using a Bayesian state space modeling framework we combined data from repeated diameter censuses and dendrometer measurements from across a 1700-m altitudinal gradient collected over six years on over 2400 trees in *Weinmannia*, a dominant and widespread genus of cloud forest trees in the Andes. Within species, growth showed no consistent trend with altitude, but higher-elevation species had lower growth rates than lower-elevation species, suggesting that species turnover is largely responsible for the positive correlation between productivity and temperature in tropical forests. Our results may indicate a significant difference in how low- and high-latitude forests will respond to climate change, since temperate and boreal tree species are consistently observed to have a positive relationship between growth and temperature. If our results hold for other tropical species, a positive response in ecosystem productivity to increasing temperatures in the Andes will depend on the altitudinal migration of tree species. The rapid pace of climate change, and slow observed rates of migration, suggest a slow, or even initially negative response of ecosystem productivity to warming. Finally, this study shows how the observed scale of biological organization can affect conclusions drawn from studies of ecological phenomena across environmental gradients, and calls into question the common practice in tropical ecology of lumping species at higher taxonomic levels.

Key words: altitudinal gradient; Andes; climate change; species migration; temperature gradient; tree diameter growth; tropical montane cloud forest; Weinmannia *spp.*

Introduction

Tropical forests contain ~25% of the carbon in the terrestrial biosphere, and account for ~33% of global terrestrial net primary productivity (Bonan 2008). Understanding the response of tree diameter growth to temperature is important for predicting forest carbon dynamics under climate change, but studies examining recent trends in tree growth in the tropics have yielded conflicting results (e.g., Phillips et al. 1998, Clark et al. 2003, 2010a, Baker et al. 2004, Feeley et al. 2007, Chave et al. 2008, Lewis et al. 2009). While there are multiple interacting factors that determine tree growth and forest productivity, temperature has a strong influence on tree growth (Clark et al. 2010a), and has been increasing at a rate of 0.26°C per decade in the tropics since the 1960s (Malhi and Wright 2004). As warming is expected to accelerate (Christensen et al. 2007, Urrutia and Vuille 2009), understanding the response of tree growth to temperature will aid in predicting whether tropical forests will be sources or sinks of carbon in the future. In this study of productivity along a tropical altitudinal gradient we examine patterns of tree growth rate at species and genus levels across a mean annual temper-
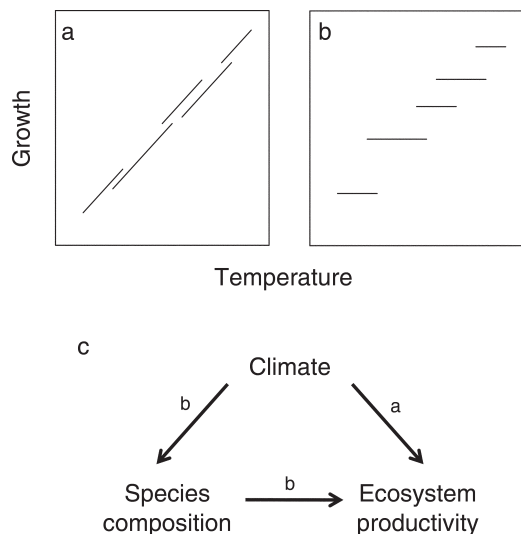
FIG. 1. Two hypotheses relating tropical tree growth to temperature on the eastern slope of the Andes in southern Peru: (a) growth increases within species with temperature, and (b) growth rate is fixed within species, but a trade-off between temperature and growth results in warmer niche species having faster growth. (c) The path through which climate affects ecosystem productivity under scenarios (a) and (b).

ature gradient of ~9°C in the Peruvian Andes. By examining growth both within and among species in the genus *Weinmannia* across the altitudinal gradient, we separate the general physiological response of growth to temperature within species from the effect of species compositional change across the gradient.

Globally, forest ecosystem productivity increases from the poles to the equator (Field et al. 1998, Friend 2010), paralleling an increase in temperature. Across sites and along altitudinal gradients in the tropics, ecosystem productivity also increases with temperature (Kitayama and Mueller-Dombois 1994, Delaney et al. 1997, Kitayama and Aiba 2002, Leuschner et al. 2007, Girardin et al. 2010). While we are aware of no published studies of growth rates for individual tree species across temperature gradients in the tropics, studies at higher latitudes show a similar increase in growth rate within species with temperature across latitudinal and altitudinal gradients (Coomes and Allen 2007, Purves 2009). In contrast, studies from the tropics reporting declines in growth during warm years (Clark et al. 2003, 2010a, Feeley et al. 2007) suggest that for tropical trees the temperature dependence of growth for individuals can be very different than the ecosystem trend taken as a cross section along an environmental gradient (Fig. 1). Clearly it is important to have a better understanding of the temperature dependence of growth across levels of biological organization, to effectively scale from individuals to ecosystems.

Temperature is likely to affect productivity both directly and indirectly. Direct metabolic effects have been invoked as a driver for increasing productivity for both individuals and ecosystems, based on kinetic effects of temperature on photosynthetic and respiratory rates (Brown et al. 2004, Allen et al. 2005). Laboratory measurements of photosynthetic carbon assimilation generally show a broad range of increasing assimilation followed by an optimum and then a steep decline as temperature increases (Leuning 2002, Medlyn et al. 2002). Trees may rarely experience conditions near the edges of their metabolic limits (Berry and Bjorkman 1980, Farquhar et al. 1980, Hikosaka et al. 2006), leading to most individuals experiencing increased growth with temperature, particularly in temperate systems. Observations show that the maximum growth rate of many temperate and boreal tree species is near their warm range boundaries (Coomes and Allen 2007, Purves 2009), and they often grow successfully when planted in warmer areas outside their native ranges (Bonan and Sirois 1992, Vetaas 2002). In contrast, a negative growth–temperature relationship seen at some sites in the lowland tropics has been cited as evidence that nighttime respiratory carbon losses have left those trees near their upper metabolic limits (Clark et al. 2003, 2010a).

Indirect effects of environmental temperature regime on ecosystem productivity could occur through growing season length or biotic interactions, which influence growth rates of individuals and are correlated with mean annual temperature. Changes in species composition across temperature gradients could also cause changes in ecosystem productivity if species are distributed across the gradient in relation to their fundamental growth rates. This is likely to occur if there are genetically based trade-offs between growth and persistence such that high growth in warmer conditions is limited by persistence in colder conditions.

Maximum measured assimilation rates are not higher in the tropics than in the temperate zone, so higher annual productivity in the tropics is likely the result of a longer growing season (Huston and Wolverton 2009, Malhi 2012). Likewise, increased growing season length has been proposed as a contributing mechanism for increasing growth in northern high latitude forests during the 20th century (Myneni et al. 1997, McMahon et al. 2010). However, within the tropics growing season is most commonly determined by moisture (Borchert 1999, Worbes 1999, Schongart et al. 2002, Singh and Kushwaha 2005) or radiation seasonality (Rapp 2010) instead of temperature. Because the effect of temperature on growing season length in the tropics is minimal, we will not consider it further here.

Biotic interactions have long been thought to be more intense in the tropics (Dobzhansky 1950, MacArthur 1972), and a recent review supports this view (Schemske et al. 2009). Temperature could be responsible for this gradient by increasing encounter rates of organisms at higher temperatures (Moya-Larano 2010), but other mechanisms not involving temperature per se have also been proposed, such as the greater diversity and more

stable climate of the tropics (Schemske et al. 2009). Across altitudinal gradients there is evidence that negative interactions (i.e., herbivory, seed predation, competition) are more intense at lower altitudes (Coomes and Allen 2007, Hillyer and Silman 2010), while facilitation increases with altitude (Callaway et al. 2002). Studies of fossil leaf assemblages provide evidence for herbivory increasing with temperature independent of altitude or latitude (Wilf and Labandeira 1999, Wilf et al. 2001).

These biotic interactions have the potential to affect the growth rates of individuals, but may also interact with species physiology to create the widely observed trade-off between growth and persistence in trees (reviewed in Stephenson et al. 2011). One such trade-off is that between growth rate and freezing tolerance, mediated by the biotic interaction of competition. North American trees exhibit a growth–cold tolerance trade-off where faster growing trees have lower tolerance to freezing temperatures, so that species (and ecotypes within species) with higher growth rates, and hence a competitive advantage, have more southerly distributions, and species with higher cold tolerance (and lower growth) have more northerly distributions (Loehle 1998). This is true even though there may be several niche axes along which individual species vary such that both fast- and slow-growing tree species exist within a given community. For example, species within a clade of live oaks (Quercus series Virentes) sort out along a latitudinal gradient as predicted by their freezing tolerances and seedling growth rates (Koehler et al. 2012), while these same species exist in communities with both faster and slower growing species. While freezing tolerance per se is unlikely to be important in the tropics except near tree line, trade-offs between growth in favorable environments and persistence in stressful environments are commonly observed (Stephenson et al. 2011).

In summary, the three broad possibilities for the observed positive relationship between ecosystem productivity and temperature (Raich et al. 2006) are a general physiological response of tree growth to temperature, with increasing growth in all species, biotic interactions affecting growth in ways either consistent or not with the physiological effect of temperature, and changes in species composition along temperature gradients, with faster growing species found at warmer sites. The distinction between the pathways is important because of implications for forest response to climate change. If growth within individual species shows a positive relationship to temperature, forests are likely to respond quickly, with an increase in net primary productivity (NPP). If compositional change is driving the positive relationship between temperature and NPP, forest productivity may respond more slowly, as warmer-niche tree species will need to migrate to an area and displace existing individuals before forests show a positive growth response.

Here we test whether the pattern of increasing stem growth with temperature in the wet tropics is due to consistent positive responses of individual species to temperature, or whether the trend is largely due to a change in species composition. We used a ~1700-m altitudinal gradient at a single locale in the Peruvian Andes to study tree growth response to temperature within and between species in the cloud forest tree genus *Weinmannia*. Our study system allowed us to test the effect of temperature independent of those of precipitation and growing season length as precipitation is high across the entire gradient (rainfall > potential evapotranspiration in all months), and growth phenology is similar among altitudes (Rapp 2010). Comparing growth of species within a single genus that differ in altitudinal range made it more likely that differences in growth rates between the species were due to different temperature responses rather than other, phylogenetically confounded traits (Harvey and Pagel 1991). We are aware of no other study in which the relationship between temperature and tree growth has been examined both within and across species in a single study in tropical forest. In doing so, this study improves our understanding of the potential effects of warming on tropical forest productivity.

METHODS

Study site

Data on tree growth were collected along a ~1700-m altitudinal gradient in the Kosñipata Valley (13°6′18″ S, 71°35′21″ W), in and adjacent to Manu National Park, on the eastern slope of the Andes in southern Peru (see Plate 1). Data came from 10 1-ha permanent tree plots located every ~250 m in elevation from 1750 to 3400 m (Appendix A: Table A1), established by the Andes Biodiversity and Ecosystem Research Group (ABERG) in 2003. Eight of the plots are on a single, 8 km long ridge that descends from 3700 to 1700 m, forming the northern margin of the Kosñipata Valley. The other two plots are <10 km from the main ridge, with the plot at 1750 m on a second ridge also along the northern margin of the valley, and the plot at 3025 m on an east facing slope in the southern part of the valley. The substrate of most plots is Ordivician shale and slate, while all or parts of two plots are on Permian granite (Appendix A: Table A1). A cool and wet climate at the study site supports tropical montane cloud forest (TMCF), and temperature decreases with altitude at a measured lapse rate of 5.2°C/km (Rapp 2010). Both aboveground and belowground net primary productivity decrease approximately fourfold between lowland (200 m) and high altitude (3000 m) sites (Girardin et al. 2010), and the wood decomposition rate also decreases with altitude (Meier et al. 2010). A shift in carbon allocation in trees from above ground to below ground contributes to decreasing aboveground biomass and increasing belowground carbon stocks with altitude (Zimmermann et al. 2009, Girardin et al. 2010).

TABLE 1. Number of stems of *Weinmannia* >1 cm dbh (number of stems with dendrometers in parentheses) in 10 1-ha tree plots on the eastern slope of the Andes in southern Peru.

Species	Plot altitude (m)									
	1750	1840	2020	2250	2520	2720	3020	3025	3200	3400
W. lechleriana	22 (4)	35 (2)	52 (7)							
W. pinnata	33 (4)	1	2 (1)							
W. ovata			1 (1)	204 (32)						
W. multijuga				95 (28)		1				
W. reticulata					40 (20)	251 (44)	130 (33)	69 (14)		
W. bangii					70 (38)	56 (38)	6 (3)	101 (4)	194 (40)	
W. mariquitae						25 (11)				
W. crassifolia							17 (12)	794 (43)		
W. microphylla									87 (26)	173 (34)

Weinmannia is the dominant genus in these plots, accounting for 16% of woody stems ≥ 10 cm dbh (diameter at breast height; 0.3–43.5% of stems per plot). Other common genera include *Clusia* (13%) and *Miconia* (8%).

Study species

The genus *Weinmannia* contains ~150 species of cloud forest trees and shrubs, is widespread throughout the tropics, and has a center of diversity in the tropical Andes (Bradford 1998). In general, the environmental niche is conserved across Neotropical members of the genus, which form a monophyletic group (Bradford 1998, 2002). In our study area 17 species of *Weinmannia* were found between 950 to 3800 m in elevation, and they are dominant in the tree community above 2000 m. The nine most abundant species were included in this analysis (Table 1).

Data collection

Tree diameter growth data were derived from repeated diameter measurements on all trees >1 cm diameter at breast height (dbh) in 1-ha permanent tree plots, and yearly diameter increments derived from dendrometer measurements on a subset of the same trees. Individuals with dbh > 10 cm were first censused in 2003 (2005 for the plot at 1750 m), individuals 1–10 cm dbh were first censused in 2006, and all individuals were censused yearly from 2007 to 2009, with a total of 2478 stems included in this analysis (Table 1). At each census, dbh was measured (point of measurement marked by paint and/or located a fixed distance below a tag nailed to the tree), height (in meters) was estimated, and canopy status was scored. Canopy status was scored on a three level scale (1, understory; 2, mid-canopy with some direct light on crown; 3, canopy or emergent tree with >90% direct sunlight on top of crown), modified from Clark and Clark (1992). When multiple estimates (range: 1–7 per stem) for canopy status were available, the median value was used in the analysis.

Band dendrometers were installed in October 2003 and January 2007, for a total of 441 individual stems (Table 1). The bands installed in 2003 were on stems randomly selected across all species (100 dendrometers per plot; see Girardin et al. [2010] and Rapp [2010]). In 2007 additional bands were installed on up to 50 randomly selected *Weinmannia* stems per plot. Stems with deformities that would prevent accurate increment readings (split stems, cavities, and other deformities) were avoided. After each installation, bands were allowed to settle on the stem, and the first (baseline) measurement was made 5–8 months after installation. Dendrometers were measured in June 2004, July 2006, and three times a year between June 2007 and August 2009. Diameter growth for each measurement interval was calculated as $d_i = C_i/\pi$, where d_i is the diameter growth for the interval and C_i is the measured circumferential growth from dendrometer bands. Growth of all measurement intervals within a study year was summed to calculate annual diameter increment. For growth intervals that overlapped study years, growth within the study year was prorated by the number of days of that interval contained within that year. A study year was defined as beginning on 16 July, and ending on 15 July of the next calendar year, and labeled as the first calendar year. We define it this way for three reasons: to correspond to the diameter censuses, which were typically done June–August of each year; to make the greatest use of the dendrometer data; and because the dry season (June–August) is a period of relatively low tree growth (Rapp 2010), so that defining a year in this way is comparable to north temperate zone studies where the growing season is within one calendar year.

Analysis

Our sampling scheme provided us with two types of data typically used in analysis of tree growth: diameter data from repeated censuses using measuring tapes and diameter increments based on high-precision dendrometers, each of which have strengths and weaknesses. The diameter censuses provided good coverage of individuals since we measured every stem with dbh >1 cm, but trees were not measured every year. Also, because cloud forest trees grow slowly and often have irregular trunks, measurement errors were relatively large compared with diameter growth rates.

PLATE 1. View, from 3500 m, looking east over the study area in the Kosñipata Valley, Peru. Eight of the ten tree plots in this study are located along the prominent ridge in the center of the photograph. The emergent tree on the left is a *Weinmannia microphylla*. Photo credit: J. M. Rapp.

Dendrometers provided much more accurate measurements and were measured frequently to provide sub-yearly measurements on growth. However, dendrometer data were available on fewer stems because accurate measurements are only obtained on trees with fairly round, damage-free stems with dbh >10 cm, and dendrometers are expensive in terms of materials and installation effort.

To make use of both data sets while accounting for the unrealistic negative growth estimates from census data (see Appendix B for a discussion of comparing data from these two sources), we used a Bayesian state space modeling approach that uses both dbh and dendrometer increments, and constrains growth rates to be positive using informative priors. The Bayesian model combines data from several sources while accommodating their dependence structure, that between different types of observations, between and among individuals, and over years. The Bayesian state-space model used here was presented in Clark et al. (2007) and extended in Clark et al. (2010b). Here we give a description of only the most relevant features, including the addition of covariates for altitude, canopy status, and diameter. These covariates were identified as important predictors in an exploratory analysis using a generalized linear model (GLM) framework with the dendrometer data alone (Appendix C).

Different information was available for each tree, because censuses began in different years for different plots and sets of trees (i.e., stems > 10 cm dbh vs. stems 1–10 cm dbh), and dendrometers were installed at different times on different trees. Thus, we needed to combine different data sources and make a probability statement about growth in years for which data were missing. The model was structured to emphasize the blending of data, and for "borrowing strength" across the full data set (Clark et al. 2007). We therefore estimated growth for each individual tree and year (tree-year), and fitted confidence envelopes reflecting information about how the different sources of variation affected each tree-year (Appendix D: Fig. D2). The model partitioned the measurement error of each data source (diameter census and dendrometer data), and included a term for process error, i.e., variation in growth not taken up by covariates (canopy status, diameter, and altitude), and fixed year and random individual effects. While plots differ for reasons other than altitude, we could not reliably estimate the variability associated with plot-to-plot differences independent of altitude because there was only one plot at each altitude in most cases. An earlier version of the model included a random plot effect but no altitude effect, to account for the possibility of climatic optima in growth. Monotonic altitudinal trends in growth were seen for all species, so the final version included altitude as a covariate but no plot effect.

We analyzed growth separately for the nine most common species, which differed in altitudinal range but taken together were widely distributed across the gradient. An altitude effect was estimated only for the four species which had at least 20 stems at multiple elevations (Table 1). We then analyzed the effect of species median altitude on growth rate across species
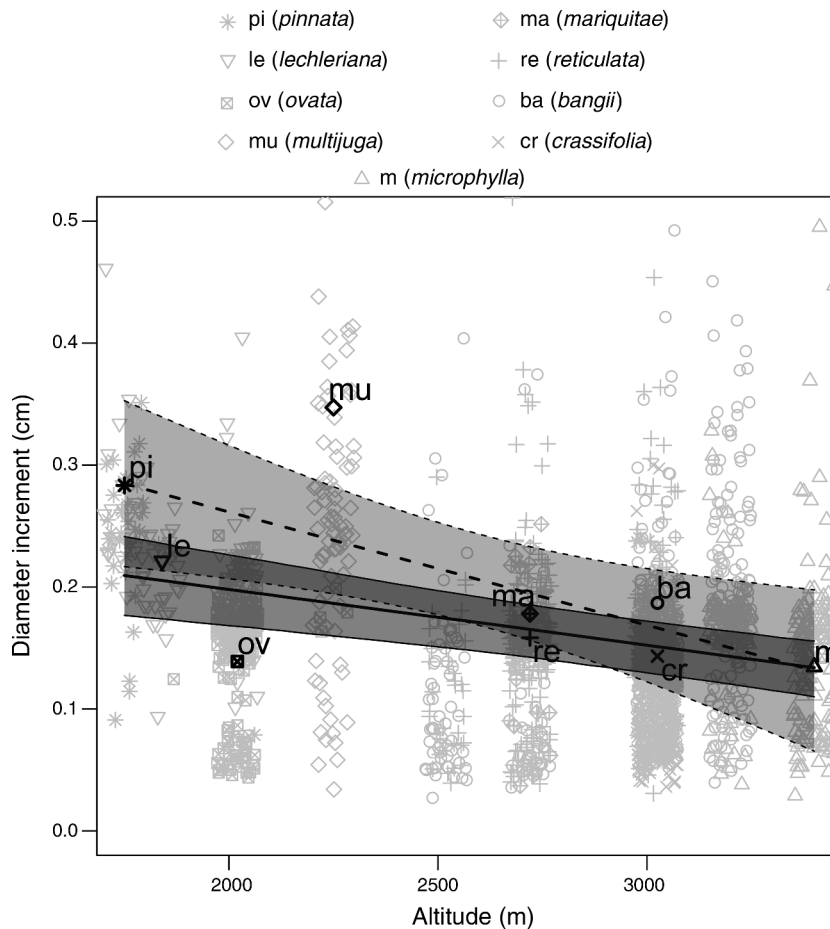
Fig. 2. Modeled diameter increment vs. altitude for adult canopy *Weinmannia* trees of all species. Gray points indicate the growth of individual stems, while black points show the predicted growth rate of a canopy tree at the species' median altitude. Different symbols demark species, and the black points are labeled with the first two letters of the species epithet. Lines (thick line is mean; shaded areas show 95% credible interval) depict the trend in diameter increment of a canopy tree vs. species median altitude. Solid lines show the predicted diameter increment from the Bayesian model of all species combined, while the dashed lines show the regression through the predicted growth rate of a canopy tree at the species' median altitude. In calculating both lines, data for *W. ovata* were omitted (for justification see *Results: Altitudinal trends across species*).

by combining data from all species and parameterizing the model with a random effect of species and assigning the mean species altitude, instead of stem altitude, to all stems of a given species. Each model was analyzed using Gibbs sampling (Gelfand and Smith 1990) implemented in R (version 2.11; R Development Core Team 2010). Detailed diagnostics for this Markov chain Monte Carlo (MCMC) model are described in Clark et al. (2010b). The model was run for 50 000 steps (burn in period 10 000 steps), and visual inspection showed rapid convergence of the MCMC chains (Appendix D: Fig. D1). R scripts are included as a Supplement.

Evaluating growth trends with altitude

To evaluate trends in tree growth with altitude both within and across species, we compared growth among trees of a standardized size in a consistent

light environment. The use of scenarios enabled us to make realistic comparisons within and between species, whereas comparing mean growth rates could be misleading if, as is the case here, size distribution and light environment varies between plots and species (J. M. Rapp, *unpublished data*). We compared three scenarios: (1) sapling (dbh = 10 cm) in the understory (canopy status, 1); (2) sapling in a gap (canopy status, 3); and (3) adult (dbh, 80th percentile for that species) canopy tree (canopy status, 3). We used the 80th percentile of dbh for each because species vary in maximum size such that choosing an arbitrary dbh would not be representative of a mature tree for all species. We chose 10 cm dbh for saplings so that dendrometer data would inform these estimates because growth estimates for trees with dendrometers were better than those without.
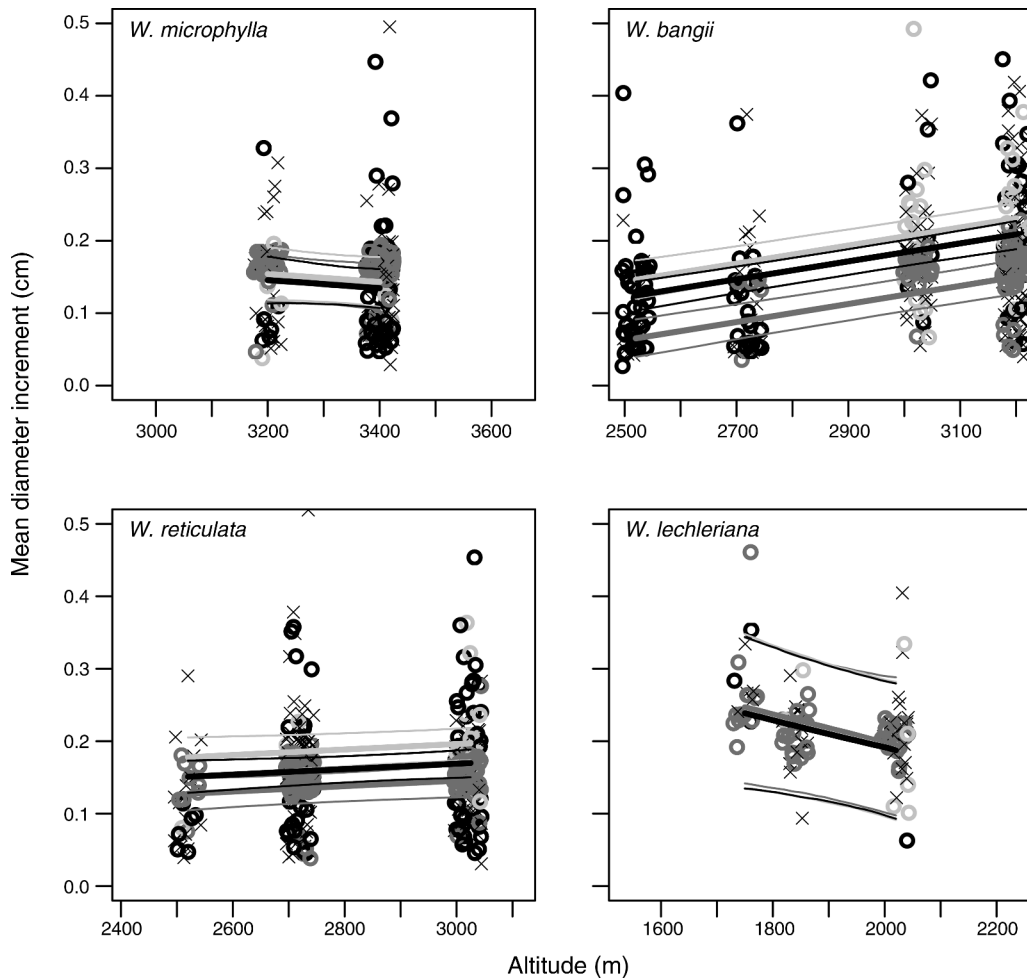
FIG. 3. Mean diameter increment vs. stem altitude for four common *Weinmannia* species. Points are modeled mean diameter increment for each tree, while lines (thick line is mean, thin lines are the 95% credible interval) depict predicted growth for three different scenarios: saplings in the understory (dark gray; dbh 10 cm; canopy status 1); saplings in gaps (light gray; dbh 10 cm; canopy status 3); and canopy trees (black; dbh 80th percentile of dbh distribution for each species; canopy status 3). Points have the same grayscale as lines, with stems < 15 cm dbh considered saplings and stems in the 70th percentile or above considered canopy trees. Stems indicated by an "×" do not fit into any of the three scenarios.

RESULTS

Species growing at high altitude (low mean annual temperature) grew more slowly than species growing at lower altitude (high mean annual temperature) (Fig. 2; Appendix C: Fig. C2), but within species the growth response to altitude was species specific.

Diameter growth within species

For no species was there a statistically significant positive correlation between growth and mean annual temperature. Of the four species with at least 20 individuals at multiple elevations (*W. microphylla*, *W. bangii*, *W. reticulata*, and *W. lechleriana*), two showed a trend of decreasing growth with altitude, and two showed an increasing trend (Fig. 3). For only one of these species (*W. bangii*), was the trend statistically significant (95% credible interval for altitude effect =

0.97–1.51 mm/km; Appendix D: Table D3), and this trend was for higher growth at higher altitude (lower temperature), the opposite of what would be predicted if a direct physiological effect of temperature on growth was a dominant driver of the ecosystem pattern.

While the effect of altitude within species varied in magnitude and direction across species, canopy status had a consistently positive effect, and dbh had a consistently negative effect on growth within species, although the magnitude of each effect varied by species (Fig. 4; Appendix D: Tables D1–D9). Comparing the growth trends of saplings in gaps, saplings in the understory, and canopy trees showed that growth in *W. bangii* and *W. reticulata* responded strongly to light environment and diameter, while in *W. lechleriana* and
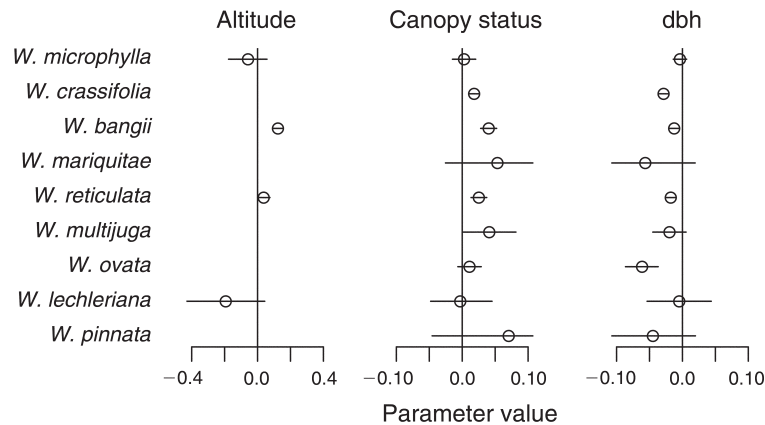
FIG. 4. Parameter values for three covariates included in the Bayesian model. Points represent the mean posterior parameter value, while lines depict the 95% credible interval of the parameter. Parameter estimates greater (less) than zero indicate that the parameter had a positive (negative) effect on growth. Note that the credible intervals for *W. mariquitae* and *W. pinnata* are truncated.

W. microphylla growth was relatively insensitive to these variables (Fig. 3).

Altitudinal trends across species

Lower altitude species grew faster, with the effect robust to the method of analysis and the species included. Including all *Weinmannia* species, the effect of species median altitude was −0.195 mm/km (95% CI = −0.363 to −0.0275 mm/km). One of the species, *W. ovata* often exhibits a shrub-like growth form distinct from the other species included in this analysis, and its low growth rate may be related to this uncommon life form rather than its altitudinal niche. Excluding *W. ovata* from the analysis resulted in a stronger effect of species median altitude of −0.459 mm/km (95% CI = −0.67 to −0.251 mm/km; Fig. 2; Appendix D: Table D10). This study, like most tree growth studies, sampled trees in plots on a per area basis. Because tree diversity declines with altitude, more individuals per species were sampled with increasing altitude, so higher altitude species had a greater influence on the across species analysis. We therefore also calculated the regression through the predicted growth of adult canopy trees growing at the median altitude of each species (excluding *W. ovata*), which predicted a stronger trend of −0.929 mm/km ($r^2 = 0.47$, $P = 0.0358$; Fig. 2). While this regression provides a useful bound on the effect of altitude across species, inference is limited because it assumes growth rate is predicted perfectly for each species, and does not account for important variability either in growth within species or in the sample size used to make each estimate.

Model output and parameter estimates

The Bayesian state space model also estimated variability associated with fixed year effects, measurement error, random individual effects, and process error (variability not associated with other parameters). For all species, diameter measurement error and individual effects were larger than "process" error and increment measurement error (Appendix D: Fig. D3, Tables D1–D9). While there was a trend toward higher growth in the last three years of the study, there was very little year-to-year variation in growth rates (Appendix D: Fig. D4, Tables D1–D9).

DISCUSSION

This study illustrates how biotic responses to an environmental gradient can change across scales of biological organization. The growth response to altitude of individual species differed from that seen at the genus level, supporting the hypothesis that species compositional change is largely responsible for the positive relationship between ecosystem productivity (NPP) and temperature observed in the tropics and at this study site (Raich et al. 2006, Girardin et al. 2010). Diameter growth response to the temperature gradient was species specific, with one species showing a negative response of growth to temperature, while the growth responses of three other species were not statistically different from zero (Figs. 1b and 3). At the genus-level growth was positively correlated with temperature (Fig. 2). Our results imply that temperature acts indirectly to cause the observed altitudinal gradient in ecosystem productivity, by determining the altitudinal niche and mean growth rates of individual species, while species compositional change drives increasing ecosystem productivity with temperature (Fig. 1b, c, path b).

Altitudinal growth trends within species

A direct metabolic effect of temperature on growth is inconsistent with the constant or declining growth with altitude observed for the four *Weinmannia* species examined. It appears likely that another factor in the biotic or abiotic environment has a stronger effect than the metabolic effect of temperature on growth. One alternative explanation is that genetic variation across

the altitudinal gradient causes the observed pattern because genetic variation associated with climatic variation across species ranges is commonly observed (Eckert et al. 2010, Sork et al. 2010). However, this seems unlikely because the entire altitudinal ranges of these *Weinmannia* species are contained within a few kilometers, and good dispersal potential of the small (~0.0001-g) wind-dispersed seeds should lead to genetically well-mixed populations, although we have no data to confirm this.

An abiotic cause for the constant or increasing growth within species with altitude seems unlikely in this system as well. While in many mountain systems drought is common at lower altitudes and constrains growth (e.g., Jump et al. 2006), in our study system rainfall is higher at lower altitude and rainfall is greater than potential evapotranspiration on a monthly scale at all elevations (Rapp 2010). Likewise, growing season length, soils, and topography are all relatively consistent across the study site.

Biotic interactions are more likely to have produced the within-species altitudinal patterns of growth observed here. Competition for light is asymmetric and dependent on the height of the tree canopy (Weiner 1990). Because canopy height declines with altitude in our system (Girardin et al. 2010), we expect that lower light competition could lead to greater growth at higher altitude. Other biotic interactions such as seed predation (Hillyer and Silman 2010) and herbivory (R. Tito, *unpublished data*) also decline with altitude at the study site, and increased herbivory in particular can lower growth through direct loss of photosynthate to herbivores and costs associated with increased investment in plant defenses. There are no data on pathogen prevalence or the effect of mycorrhizae or endophyte mutualists on growth in this system, although the taxonomic composition but not the diversity of microbes living on *Weinmannia* leaf surfaces changes with altitude (Fierer et al. 2011).

Species composition and ecosystem productivity

If the divergent patterns seen here for growth within and between *Weinmannia* species across a temperature gradient hold for other tropical tree taxa, the pattern of increasing NPP with temperature in the wet tropics (Raich et al. 2006) may largely be due to species compositional change. Understanding the effects of species composition may be particularly important when projecting future patterns of ecosystem productivity based on projected climate changes. Model predictions suggest a lag between climate change and species migrations (Iverson et al. 2004, Morin et al. 2008), and observed tree species migration rates lag behind historical rates of climate change and are slower than needed to keep pace with predicted climate change (Feeley et al. 2011). Given this lag, our results suggest initial ecosystem-level productivity responses to climate change are likely to be small, with flat or possibly decreasing productivity as temperature increases if most Andean tree species respond similarly to *Weinmannia*. Only once species migrations have equilibrated with climate will ecosystem productivity increase. This response could be moderated by adaptation of growth to new climate conditions, but because trees are long-lived it is unlikely that tree populations will be able to adapt fast enough to keep track with rising temperatures (Kuparinen et al. 2010). Temperatures are predicted to continue to rise given current projections of anthropogenic greenhouse gas emissions (Meehl et al. 2007), so ecosystems are likely to be in disequilibrium with climate for decades or longer. In addition, species migrate at different rates and novel combinations of tree species ("no-analog" communities sensu Williams and Jackson 2007) are likely to be common. Given the dependence of ecosystem productivity on species composition, predicting the ecosystem properties of no-analog communities will be difficult.

Differences between tropical and temperate forests

The results shown here differ from results for temperate areas where productivity increases with temperature within species across latitudinal and altitudinal gradients (Loehle 1998, Coomes and Allen 2007, Purves 2009). This inconsistency may be the result of a shift in the primary drivers of tree growth rate with latitude. For instance, because biotic interactions generally increase in importance toward the tropics (Schemske et al. 2009), these may mask the positive metabolic effect of temperature on growth in the tropics, but not in temperate areas. However, biotic interactions have the potential to have both positive and negative effects on growth, and not all relevant interactions show a latitudinal trend (e.g., herbivory; Moles et al. 2011*a*, *b*), so it is unclear whether this would be a general mechanism. On the other hand, a temperature-dependent growing season is a common feature of higher latitudes and can have a strong influence on tree growth (Myneni et al. 1997, McMahon et al. 2010), and we suspect that the observed positive relationship between tree growth and temperature at higher latitudes may be due to growing season length rather than temperature per se. This is supported by observations of decreased growth and higher mortality as temperatures warm in temperate systems where growing season is limited by summer drought rather than temperature (e.g., Jump et al. 2006).

Growth rate variability among individuals

Altitudinal growth trends were only revealed after properly attributing errors and disaggregating the overall data into meaningful scenarios for comparison because of the high growth rate variability among individuals in this study (Figs. 2 and 3). High and low growth rates were observed at all altitudes, with predicted variability within species often exceeding the predicted change in growth rate across species for

canopy adults. However, by effectively attributing variation between measurement error, process error, and fixed and random effects, and by using scenarios to compare trees of similar life stage and microenvironment across the gradient (e.g., using conditional rather than marginal distributions; Clark et al. 2011), ecological meaning was extracted from a highly variable system. For example, ignoring canopy status (positive effect on growth) and diameter (negative effect on growth), would have obscured important patterns because the size distribution of individuals and stand structure vary across sites (J. M. Rapp, *unpublished data*).

Species vs. genus in ecological analysis

That responses measured at the genus level are not the same as responses measured on species within the genus calls into question the widespread practice in the tropical forest ecology literature of lumping species together at the genus level to measure distributional, community, and ecosystem patterns and processes (e.g., Feeley et al. 2011). Indeed, the results from *Weinmannia* suggest the practice could lead to qualitatively different conclusions about the processes in question, whether the lumping is to increase sample sizes to calculate growth or vital rates, or to deal with taxonomic uncertainty in highly diverse or poorly sampled systems. We expect this to be a concern any time congeneric species sort out along an environmental gradient, whether it be temperature as in this study, or soil nutrients, moisture, or rain fall seasonality which are common determinants of species distributions in the lowland tropics (Toledo et al. 2012). Lumping species at higher taxonomic levels may be appropriate depending on the purpose and scale of the comparison. For instance, combining species in the largely montane genus *Weinmannia* in a comparison of montane and lowland taxa could be permissible if the variation in the trait measured was less within the genus than that between *Weinmannia* and the lowland taxa.

CONCLUSIONS

In this study we showed that species differed in growth rate across their altitudinal ranges, and that these differences were idiosyncratic among species, such that genus-level patterns did not mimic species-level patterns. Instead, novel patterns of ecosystem productivity emerged at higher levels of biological organization. These results highlight the importance of considering community species composition when interpreting studies of ecosystem productivity across temperature gradients in the tropics, especially when considering the response of ecosystems to climate change. While this study reveals intriguing patterns, future studies are needed to determine how well these results generalize to other species, and to identify the specific temperature-driven trade-off(s) in the tropics hypothesized to set species growth rates. In addition, differences between drivers of tree growth patterns across tropical and temperate climate gradients should be explored to understand whether we should expect a fundamentally different response to climate change between the tropics and higher latitudes.

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Supplemental Material

Appendix A

Study plot locations and characteristics (*Ecological Archives* E093-197-A1).

Appendix B

Issues in comparing growth rates derived from census and dendrometer data (*Ecological Archives* E093-197-A2).

Appendix C

Generalized linear model analysis of tree growth rate using dendrometer data only (*Ecological Archives* E093-197-A3).

Appendix D

Parameter estimates from the Bayesian analysis of tree growth (*Ecological Archives* E093-197-A4).

Supplement

R code and example data set for fitting the Bayesian model of tree growth (*Ecological Archives* E093-197-S1).