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- Running head: Tree growth across altitude and species 1 2 Intra- and inter-specific tree growth across a long altitudinal gradient in the Peruvian 3 Andes 4 5 Joshua M. Rapp^{1,2,*}, Miles R. Silman¹, James S. Clark³, Cecile A. J. Girardin⁴, Darcy Galiano⁵, 6 Richard Tito⁵ 7 8 9 ¹: Department of Biology, Wake Forest University, Winston-Salem, NC 27106 USA 10 ²: Present address: Harvard Forest, Harvard University, Petersham, MA 01366 USA 11 ³:Department of Biology and Nicholas School of the Environment, Duke University, Durham, 12 NC 27708 USA 13 ⁴: Environmental Change Institute, School of Geography and the Environment, Oxford 14 15 University, South Parks Road, Oxford, OX1 3QY, England, UK ⁵: Universidad Nacional de San Antonio Abad del Cusco, Perú 16
- ^{*}To whom correspondence should be addressed. Email: <u>rapp.joshua@gmail.com</u>

18 Abstract

19 Tree growth response across environmental gradients is fundamental to understanding species 20 distributional ecology, forest ecosystem ecology, and to predict future ecosystem services. Cross-21 sectional patterns of ecosystem properties with respect to climatic gradients are often used to 22 predict ecosystem responses to global change. Across sites in the tropics, primary productivity 23 increases with temperature, suggesting that forest ecosystems will become more productive as 24 temperature rises. However, this trend is confounded with a shift in species composition, and so 25 may not reflect the response of *in situ* forests to warming. In this study, we simultaneously 26 studied tree diameter growth across the altitudinal ranges of species within a single genus across 27 a geographically compact temperature gradient, to separate the direct effect of temperature on tree growth from that of species compositional turn-over. Using a Bayesian state space modeling 28 29 framework we combined data from repeated diameter censuses and dendrometer measurements 30 from across a ~1700 meter altitudinal gradient collected over six years on over 2400 trees in 31 Weinmannia, a dominant and widespread genus of cloud forest trees in the Andes. Within 32 species, growth showed no consistent trend with altitude, but higher elevation species had lower 33 growth rates than lower elevation species, suggesting that species turn-over is largely responsible 34 for the positive correlation between productivity and temperature in tropical forests. Our results 35 may indicate a significant difference in how low- and high-latitude forests will respond to 36 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 37 38 species, a positive response in ecosystem productivity to increasing temperatures in the Andes 39 will depend on the altitudinal migration of tree species. The rapid pace of climate change, and 40 slow observed rates of migration, suggest a slow, or even initially negative response of

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41 ecosystem productivity to warming. Finally, this study shows how the observed scale of

42 biological organization can affect conclusions drawn from studies of ecological phenomena

43 across environmental gradients, and calls into question the common practice in tropical ecology

44 of lumping species at higher taxonomic levels.

45 Keywords: tropical montane cloud forest, *Weinmannia*, climate change, temperature gradient,

46 tree diameter growth, Andes, altitudinal gradient, species migration

47 Introduction

48 Tropical forests contain ~25% of the carbon in the terrestrial biosphere, and account for ~33% of 49 global terrestrial net primary productivity (Bonan 2008). Understanding the response of tree 50 diameter growth to temperature is important for predicting forest carbon dynamics under climate 51 change, but studies examining recent trends in tree growth in the tropics have vielded conflicting 52 results (e.g. Phillips et al. 1998, Clark et al. 2003, Baker et al. 2004, Feeley et al. 2007, Chave et 53 al. 2008. Lewis et al. 2009. Clark et al. 2010a). While there are multiple interacting factors that 54 determine tree growth and forest productivity, temperature has a strong influence on tree growth 55 (Clark et al. 2010a), and has been increasing at a rate of 0.26°C/decade in the tropics since the 1960's (Malhi and Wright 2004). As warming is expected to accelerate (Christensen 2007, 56 57 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 58 59 of productivity along a tropical altitudinal gradient we examine patterns of tree growth rate at 60 species and genus levels across a mean annual temperature gradient of ~9 °C in the Peruvian Andes. By examining growth both within and among species in the genus *Weinmannia* across 61 62 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. 63

Globally, forest ecosystem productivity increases from the poles to the equator (Field et al. 1998, 64 Friend 2010), paralleling an increase in temperature. Across sites and along altitudinal gradients 65 66 in the tropics, ecosystem productivity also increases with temperature (Kitayama and Mueller-67 Dombois 1994, Delaney et al. 1997, Kitayama and Aiba 2002, Leuschner et al. 2007, Girardin et 68 al. 2010). While we are aware of no published studies of growth rates for individual tree species 69 across temperature gradients in the tropics, studies at higher latitudes show a similar increase in 70 growth rate within species with temperature across latitudinal and altitudinal gradients (Coomes 71 and Allen 2007, Purves 2009). In contrast, studies from the tropics reporting declines in growth 72 during warm years (Clark et al. 2003, Feeley et al. 2007, Clark et al. 2010a), suggest that for 73 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 74 is important to have a better understanding of the temperature dependence of growth across 75 levels of biological organization, to effectively scale from individuals to ecosystems. 76

Temperature is likely to affect productivity both directly and indirectly. Direct metabolic effects 77 78 have been invoked as a driver for increasing productivity for both individuals and ecosystems, 79 based on kinetic effects of temperature on photosynthetic and respiratory rates (Brown et al. 80 2004, Allen et al. 2005). Laboratory measurements of photosynthetic carbon assimilation 81 generally show a broad range of increasing assimilation followed by an optimum and then a 82 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, 83 84 Farguhar et al. 1980, Hikosaka et al. 2006), leading to most individuals experiencing increased growth with temperature, particularly in temperate systems. Observations show that the 85 86 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 night time respiratory carbon losses have left those trees are near their
upper metabolic limits (Clark et al. 2003, Clark et al. 2010a).

92 Indirect effects of environmental temperature regime on ecosystem productivity could occur 93 through growing season length or biotic interactions, which influence growth rates of individuals 94 and are correlated with mean annual temperature. Changes in species composition across 95 temperature gradients could also cause changes in ecosystem productivity if species are 96 distributed across the gradient in relation to their fundamental growth rates. This is likely to 97 occur if there are genetically based trade-offs between growth and persistence such that high 98 growth in warmer conditions is limited by persistence in colder conditions.

99 Maximum measured assimilation rates are not higher in the tropics than in the temperate zone, so 100 higher annual productivity in the tropics is likely the result of a longer growing season (Huston 101 and Wolverton 2009, Malhi 2012). Likewise, increased growing season length has been 102 proposed as a contributing mechanism for increasing growth in northern high latitude forests 103 during the 20th century (Myneni et al. 1997, McMahon et al. 2010). However, within the tropics 104 growing season is most commonly determined by moisture (Borchert 1999, Worbes 1999, 105 Schongart et al. 2002, Singh and Kushwaha 2005) or radiation seasonality (Rapp 2010) instead 106 of temperature. Since the effect of temperature on growing season length in the tropics is 107 minimal, we will not consider it further here.

108 Biotic interactions have long been thought to be more intense in the tropics (Dobzhansky 1950, 109 MacArthur 1972), and a recent review supports this view (Schemske et al. 2009). Temperature 110 could be responsible for this gradient by increasing encounter rates of organisms at higher 111 temperatures (Moya-Larano 2010), but other mechanisms not involving temperature per se have 112 also been proposed, such as the greater diversity and more stable climate of the tropics 113 (Schemske et al. 2009). Across altitudinal gradients there is evidence that negative interactions 114 (i.e. herbivory, seed predation, competition) are more intense at lower altitudes (Coomes and 115 Allen 2007, Hillyer and Silman 2010), while facilitation increases with altitude (Callaway et al. 116 2002). Studies of fossil leaf assemblages provide evidence for herbivory increasing with 117 temperature independent of altitude or latitude (Wilf and Labandeira 1999, Wilf et al. 2001). 118 These biotic interactions have the potential to affect the growth rates of individuals, but may also 119 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 120 121 growth rate and freezing tolerance, mediated by the biotic interaction of competition. North 122 American trees exhibit a growth – cold tolerance trade-off where faster growing trees have lower 123 tolerance to freezing temperatures, so that species (and ecotypes within species) with higher 124 growth rates, and hence a competitive advantage, have more southerly distributions, and species 125 with higher cold-tolerance (and lower growth) have more northerly distributions (Loehle 1998). 126 This is true even though there may be several niche axes along which individual species vary 127 such that both fast and slow growing tree species exist within a given community. For example, 128 species within a clade of live oaks (*Ouercus* series Virentes) sort out along a latitudinal gradient 129 as predicted by their freezing tolerances and seedling growth rates (Koehler et al. 2012), while 130 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).

134 In summary, the three broad possibilities for the observed positive relationship between 135 ecosystem productivity and temperature (Raich et al. 2006) are a general physiological response 136 of tree growth to temperature, with increasing growth in all species, biotic interactions affecting 137 growth in ways either consistent or not with the physiological effect of temperature, and changes 138 in species composition along temperature gradients, with faster growing species found at warmer 139 sites. The distinction between the pathways is important because of implications for forest 140 response to climate change. If growth within individual species shows a positive relationship to 141 temperature, forests are likely to respond quickly, with an increase in net primary productivity 142 (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 143 144 migrate to an area and displace existing individuals before forests show a positive growth 145 response.

146 Here we test whether the pattern of increasing stem growth with temperature in the wet tropics is 147 due to consistent positive responses of individual species to temperature, or whether the trend is 148 largely due to a change in species composition. We used a ~1700 meter altitudinal gradient at a 149 single locale in the Peruvian Andes to study tree growth response to temperature within and 150 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 151 152 precipitation is high across the entire gradient (rainfall > PET in all months), and growth 153 phenology is similar among altitudes (Rapp 2010). Comparing growth of species within a single

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154 genus that differ in altitudinal range made it more likely that differences in growth rates between 155 the species were due to different temperature responses rather than other, phylogeneticly 156 confounded traits (Harvey and Pagel 1991). We are aware of no other study in which the 157 relationship between temperature and tree growth has been examined both within and across 158 species in a single study in tropical forest. In doing so, this study improves our understanding of 159 the potential effects of warming on tropical forest productivity.

160 Methods

161 *Study site*

Data on tree growth were collected along a ~1700 meter altitudinal gradient in the Kosñipata 162 Valley (-13° 6' 18'' latitude, -71° 35' 21" longitude), in and adjacent to Manu National Park, on 163 164 the eastern slope of the Andes in southern Peru. Data came from ten 1 ha permanent tree plots 165 located every ~250 m in elevation from 1750 m to 3400 m (Table A1), established by the Andes Biodiversity and Ecosystem Research Group (ABERG) in 2003. Eight of the plots are on a 166 single, 8 km long ridge that descends from 3700 m to 1700 m, forming the northern margin of 167 168 the Kosñipata Valley. The other two plots are <10 km from the main ridge, with the plot at 1750 169 m on a second ridge also along the northern margin of the valley, and the plot at 3025 m on an 170 east facing slope in the southern part of the valley. The substrate of most plots is Ordivician shale 171 and slate, while all or parts of two plots are on Permian granite (Table A1). A cool and wet 172 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⁻¹ (Rapp 2010). Both aboveground 173 174 and belowground net primary productivity decrease approximately 4-fold between lowland (200 175 m) and high altitude (3000 m) sites (Girardin et al. 2010), and the wood decomposition rate also 176 decreases with altitude (Meier et al. 2010). A shift in carbon allocation in trees from above- to

below-ground contributes to decreasing above-ground biomass and increasing below-ground carbon stocks with altitude (Zimmermann et al. 2009, Girardin et al. 2010). *Weinmannia* is the dominant genus in these plots, accounting for 16% of woody stems \geq 10 cm DBH (0.3 – 43.5% of stems per plot). Other common genera include *Clusia* (13%) and *Miconia* (8%).

181 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 m to 3800 m in elevation, and they are dominant in the tree community above 2000 meters. The nine most abundant species were included in this analysis (Table 1).

188 Data collection

189 Tree diameter growth data were derived from repeated diameter measurements on all trees 190 greater than 1 cm diameter at breast height (DBH) in one hectare permanent tree plots, and 191 vearly diameter increments derived from dendrometer measurements on a subset of the same 192 trees. Individuals greater than 10 cm DBH were first censused in 2003 (2005 for the plot at 1750 193 m), individuals 1-10 cm DBH were first censused in 2006, and all individuals were censused 194 yearly from 2007 to 2009, with a total of 2478 stems included in this analysis (Table 1). At each 195 census, DBH was measured (point of measurement marked by paint and/or located a fixed 196 distance below a tag nailed to the tree), height (in meters) was estimated, and canopy status was 197 scored. Canopy status was scored on a three level scale (1 = understory; 2 = mid-canopy with198 some direct light on crown; 3 = canopy or emergent tree with greater than 90% direct sunlight on

top of crown), modified from Clark and Clark (1992). When multiple estimates (range: 1 - 7 per
stem) for canopy status was available, the median value was used in the analysis.

Band dendrometers were installed in October 2003 and January 2007, for a total of 441

202 individual stems (Table 1). The bands installed in 2003 were on stems randomly selected across 203 all species (100 dendrometers per plot; see Girardin et al. (2010) and Rapp (2010)). In 2007 204 additional bands were installed on up to 50 randomly selected Weinmannia stems per plot. Stems 205 with deformities that would prevent accurate increment readings (split stems, cavities, etc.) were 206 avoided. After each installation, bands were allowed to settle on the stem, and the first (baseline) 207 measurement was made 5-8 months after installation. Dendrometers were measured in June 208 2004, July 2006 and three times a year between June 2007 and August 2009. Diameter growth 209 for each measurement interval was calculated as $d_i = C_i / \pi$, where d_i is the diameter growth for the 210 interval and C_i is the measured circumferential growth from dendrometer bands. Growth of all 211 measurement intervals within a study year was summed to calculate annual diameter increment. 212 For growth intervals that overlapped study years, growth within the study year was pro-rated by 213 the number of days of that interval contained within that year. A study year was defined as beginning on July 16th, and ending on July 15th of the next calendar year, and labeled as the first 214 calendar vear. We define it this way for three reasons: to correspond to the diameter censuses, 215 216 which were typically done June-August of each year; to make the greatest use of the 217 dendrometer data; and because the dry season (June-August) is a period of relatively low tree 218 growth (Rapp 2010), so that defining a year in this way is comparable to north temperate zone 219 studies where the growing season is within one calendar year.

220 Analysis

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221 Our sampling scheme provided us with two types of data typically used in analysis of tree 222 growth: diameter data from repeated censuses using measuring tapes and diameter increments 223 based on high-precision dendrometers, each which have strengths and weaknesses. The diameter 224 censuses provided good coverage of individuals since we measured every stem greater than 1 cm 225 DBH, but trees were not measured every year. Also, because cloud forest trees grow slowly and 226 often have irregular trunks, measurement errors were relatively large compared with diameter 227 growth rates. Dendrometers provided much more accurate measurements and were measured 228 frequently to provide sub-yearly measurements on growth. However, dendrometer data were 229 available on fewer stems since accurate measurements are only obtained on trees with fairly 230 round, damage-free stems greater than 10 cm DBH, and dendrometers are expensive in terms of materials and installation effort. 231

232 To make use of both datasets while accounting for the unrealistic negative growth estimates from 233 census data (see Appendix B for a discussion of comparing data from these two sources), we 234 used a Bayesian state space modeling approach that uses both DBH and dendrometer increments. 235 and constrains growth rates to be positive using informative priors. The Bayesian model 236 combines data from several sources while accommodating their dependence structure, that 237 between different types of observations, between and among individuals, and over years. The 238 Bayesian state space model used here was presented in Clark et al. (2007) and extended in Clark 239 et al. (2010b). Here we give a description of only the most relevant features, including the 240 addition of covariates for altitude, canopy status, and diameter. These covariates were identified 241 as important predictors in an exploratory analysis using a generalized linear model (GLM) framework with the dendrometer data alone (Appendix C). 242

Different information was available for each tree, because censuses began in different years for 243 244 different plots and sets of trees (i.e. stems > 10 cm DBH vs. stems 1-10 cm DBH), and 245 dendrometers were installed at different times on different trees. Thus, we needed to combine 246 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 247 248 strength" across the full dataset (Clark et al. 2007). We therefore estimated growth for each 249 individual tree and year (tree-year), and fitted confidence envelopes reflecting information about 250 how the different sources of variation affected each tree-year (Fig. D2). The model partitioned 251 the measurement error of each data source (diameter census and dendrometer data), and included 252 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 253 254 reasons other than altitude, we could not reliably estimate the variability associated with plot-to-255 plot differences independent of altitude since there was only one plot at each altitude in most 256 cases. An earlier version of the model included a random plot effect but no altitude effect, to 257 account for the possibility of climatic optima in growth. Monotonic altitudinal trends in growth 258 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 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

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266 (Version 2.11; R Development Core Team 2010). Detailed diagnostics for this Markov Chain

- 267 Monte Carlo model are described in Clark *et al.* (2010b). The model was run for 50,000 steps
- 268 (burn in period 10,000 steps), and visual inspection showed rapid convergence of the MCMC
- chains (Fig. D1). R scripts are included as a supplement (Supplement 1).

270 Evaluating growth trends with altitude

271 To evaluate trends in tree growth with altitude both within and across species, we compared 272 growth among trees of a standardized size in a consistent light environment. The use of scenarios 273 enabled us to make realistic comparisons within and between species, whereas comparing mean 274 growth rates could be misleading if, as is the case here, size distribution and light environment 275 varies between plots and species (J.M. Rapp, *unpublished data*). We compared three scenarios: 276 1) sapling (DBH = 10 cm) in the understory (Canopy Status = 1); 2) sapling in a gap (Canopy Status = 3); and 3) adult (DBH = 80^{th} percentile for that species) canopy tree (Canopy Status = 277 278 3). We used the 80th percentile of DBH for each because species vary in maximum size such that 279 choosing an arbitrary DBH would not be representative of a mature tree for all species. We chose 280 10 cm DBH for saplings so that dendrometer data would inform these estimates since growth 281 estimates for trees with dendrometers were better than those without.

282 **Results**

Species growing at high altitude (low mean annual temperature) grew more slowly than species growing at lower altitude (high mean annual temperature) (Figs. 2 and C2), but within species the growth response to altitude was species-specific.

286 Diameter growth within species

For no species was there a statistically significant positive correlation between growth and mean 287 288 annual temperature. Of the four species with at least 20 individuals at multiple elevations (W. 289 *microphylla*, *W. bangii*, *W. reticulata*, and *W. lechleriana*), two showed a trend of decreasing 290 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 = 291 0.97-1.51 mm km⁻¹; Table D3), and this trend was for higher growth at higher altitude (lower 292 293 temperature), the opposite of what would be predicted if a direct physiological effect of 294 temperature on growth was a dominant driver of the ecosystem pattern. 295 While the effect of altitude within species varied in magnitude and direction across species, 296 canopy status had a consistently positive effect, and DBH had a consistently negative effect on 297 growth within species, although the magnitude of each effect varied by species (Fig. 4, Tables 298 D1-D9). Comparing the growth trends of saplings in gaps, saplings in the understory, and canopy 299 trees showed that growth in W. bangii and W. reticulata responded strongly to light environment 300 and diameter, while in W. lechleriana and W. microphylla growth was relatively insensitive to 301 these variables (Fig. 3).

302 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 -

 $305 \quad 0.195 \text{ mm km}^{-1} (95\% \text{ CI} = -0.363 \text{ to } -0.0275 \text{ mm km}^{-1})$. One of the species, *W. ovata* often

306 exhibits a shrub-like growth form distinct from the other species included in this analysis, and its

- 307 low growth rate may be related to this uncommon life form rather than its altitudinal niche.
- 308 Excluding W. ovata from the analysis resulted in a stronger effect of species median altitude of -
- $309 \quad 0.459 \text{ mm km}^{-1} (95\% \text{ CI} = -0.67 \text{ to} 0.251 \text{ mm km}^{-1}; \text{ Fig. 2, Table D10}).$ This study, like most

310 tree growth studies, sampled trees in plots – on a per area basis. Since tree diversity declines with 311 altitude, more individuals per species were sampled with increasing altitude, so higher altitude 312 species had a greater influence on the across species analysis. We therefore also calculated the 313 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⁻¹ ($r^2 =$ 314 0.47, p = 0.0358; Fig. 2). While this regression provides a useful bound on the effect of altitude 315 316 across species, inference is limited because it assumes growth rate is predicted perfectly for each 317 species, and does not account for important variability either in growth within species or in the 318 sample size used to make each estimate.

319 *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 (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 (Fig. D4, Tables D1-D9).

326 **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 the 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 (Fig 1b, Fig. 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 and 1c, path b).

339 *Altitudinal growth trends within species*

340 A direct metabolic effect of temperature on growth is inconsistent with the constant or declining 341 growth with altitude observed for the four *Weinmannia* species examined. It appears likely that 342 another factor in the biotic or abiotic environment has a stronger effect than the metabolic effect 343 of temperature on growth. One alternative explanation is that genetic variation across the 344 altitudinal gradient causes the observed pattern, since genetic variation associated with climatic 345 variation across species ranges is commonly observed (Eckert et al. 2010, Sork et al. 2010). 346 However, this seems unlikely since the entire altitudinal ranges of these *Weinmannia* species are 347 contained within a few kilometers, and good dispersal potential of the small (~0.0001 g) wind-348 dispersed seeds should lead to genetically well mixed populations, although we have no data to 349 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

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elevations (Rapp 2010). Likewise, growing season length, soils, and topography are all relatively
consistent across the study site.

356 Biotic interactions are more likely to have produced the within species altitudinal patterns of 357 growth observed here. Competition for light is asymmetric and dependent on the height of the 358 tree canopy (Weiner 1990). Since canopy height declines with altitude in our system (Girardin et 359 al. 2010), we expect that lower light competition could lead to greater growth at higher altitude. 360 Other biotic interactions such as seed predation (Hillyer and Silman 2010) and herbivory (R. 361 Tito, *unpublished data*) also decline with altitude at the study site, and increased herbivory in 362 particular can lower growth through direct loss of photosynthate to herbivores and costs 363 associated with increased investment in plant defenses. There is no data on pathogen prevalence 364 or the effect of mycorrhizae or endophyte mutualists on growth in this system, although the 365 taxonomic composition but not the diversity of microbes living on Weinmannia leaf-surfaces 366 changes with altitude (Fierer et al. 2011).

367 Species composition and ecosystem productivity

368 If the divergent patterns seen here for growth within and between *Weinmannia* species across a 369 temperature gradient hold for other tropical tree taxa, the pattern of increasing NPP with 370 temperature in the wet tropics (Raich et al. 2006) may largely be due to species compositional 371 change. Understanding the effects of species composition may be particularly important when 372 projecting future patterns of ecosystem productivity based on projected climate changes. Model 373 predictions suggest a lag between climate change and species migrations (Iverson et al. 2004, 374 Morin et al. 2008), and observed tree species migration rates lag behind historical rates of 375 climate change and are slower than needed to keep pace with predicted climate change (Feeley et 376 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 377 378 increases if most Andean tree species respond similarly to Weinmannia. Only once species 379 migrations have equilibrated with climate will ecosystem productivity increase. This response 380 could be moderated by adaptation of growth to new climate conditions, but because trees are 381 long-lived it is unlikely that tree populations will be able to adapt fast enough to keep track with 382 rising temperatures (Kuparinen et al. 2010). Temperatures are predicted to continue to rise given 383 current projections of anthropogenic greenhouse gas emissions (Meehl 2007), so ecosystems are 384 likely to be in disequilibrium with climate for decades or longer. In addition, species migrate at 385 different rates and novel combinations of tree species ("no-analog" communities sensu Williams 386 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 387 388 difficult.

389 Differences between tropical and temperate forests

390 The results shown here differ from results for temperate areas where productivity increases with 391 temperature within species across latitudinal and altitudinal gradients (Loehle 1998, Coomes and 392 Allen 2007, Purves 2009). This inconsistency may be the result of a shift in the primary drivers 393 of tree growth rate with latitude. For instance, since biotic interactions generally increase in 394 importance towards the tropics (Schemske et al. 2009), these may mask the positive metabolic 395 effect of temperature on growth in the tropics, but not in temperate areas. However, biotic 396 interactions have the potential to have both positive and negative effects on growth, and not all 397 relevant interactions show a latitudinal trend (e.g. herbivory; Moles et al. 2011a, Moles et al. 398 2011b), so it is unclear whether this would be a general mechanism. On the other hand, a 399 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).

406 Growth rate variability among individuals

407 Altitudinal growth trends were only revealed after properly attributing errors and disaggregating 408 the overall data into meaningful scenarios for comparison because of the high growth rate 409 variability among individuals in this study (Figs. 2 and 3). High and low growth rates were 410 observed at all altitudes, with predicted variability within species often exceeding the predicted 411 change in growth rate across species for canopy adults. However, by effectively attributing 412 variation between measurement error, 'process' error, and fixed and random effects, and by using 413 scenarios to compare trees of similar life-stage and microenvironment across the gradient (e.g. 414 using conditional rather than marginal distributions; Clark et al. 2011), ecological meaning was 415 extracted from a highly variable system. For example, ignoring canopy status (positive effect on 416 growth) and diameter (negative effect on growth), would have obscured important patterns since 417 the size distribution of individuals and stand structure vary across sites (J.M. Rapp, unpublished 418 data).

419 Species versus 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,

423 and ecosystem patterns and processes (e.g. Feeley et al. 2011). Indeed, the results from 424 Weinmannia suggest the practice could lead to qualitatively different conclusions about the 425 processes in question, whether the lumping is to increase sample sizes to calculate growth or 426 vital rates, or to deal with taxonomic uncertainty in highly diverse or poorly sampled systems. 427 We expect this to be a concern any time congeneric species sort out along an environmental 428 gradient, whether it be temperature as in this study, or soil nutrients, moisture, or rain fall 429 seasonality which are common determinants of species distributions in the lowland tropics 430 (Toledo et al. 2012). Lumping species at higher taxanomic levels may be appropriate depending 431 on the purpose and scale of the comparison. For instance, combining species in the largely 432 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 433 434 and the lowland taxa.

435 Conclusions

436 In this study we showed that species differed in growth rate across their altitudinal ranges, and 437 that these differences were idiosyncratic among species, such that genus-level patterns did not 438 mimic species-level patterns. Instead, novel patterns of ecosystem productivity emerged at 439 higher levels of biological organization. These results highlight the importance of considering 440 community species composition when interpreting studies of ecosystem productivity across 441 temperature gradients in the tropics, especially when considering the response of ecosystems to 442 climate change. While this study reveals intriguing patterns, future studies are needed to 443 determine how well these results generalize to other species, and to identify the specific 444 temperature-driven trade-off(s) in the tropics hypothesized to set species growth rates. In 445 addition, differences between drivers of tree growth patterns across tropical and temperate

climate gradients should be explored to understand whether we should expect a fundamentallydifferent response to climate change between the tropics and higher latitudes.

448 Acknowledgements

- 449 This paper is a product of the Andes Biodiversity and Ecosystem Research Group (ABERG;
- 450 http:/andesconservation.org). Data included here are the result of an exceptional effort by
- 451 botanists and field assistants in Peru, most from the Universidad Nacional de San Antonio Abad
- 452 de Cusco, Peru. Special thanks go to Prof. Norma Salinas Revilla. Support came from the
- 453 Gordon and Betty Moore Foundation's Andes to Amazon initiative, NSF DEB-0237684, and
- 454 NSF EAR-0711414. INRENA, SERNANP, and personnel of Manu National Park, Peru,
- 455 provided gracious assistance with logistics and permission to work in the protected area, while
- 456 the Amazon Conservation Association and the Cock-of-the-Rock Lodge provided logistical
- 457 support. We thank E.K. Faison and two anonymous reviewers for their valuable comments.

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- 683 Ecological Archives
- 684 Appendix A: Study plot locations and characteristics.
- 685 **Appendix B:** Issues in comparing growth rates derived from census and dendrometer data.
- 686 Appendix C: Generalized linear model analysis of tree growth rate using dendrometer data only.
- 687 **Appendix D:** Parameter estimates from the Bayesian analysis of tree growth.
- 688 Supplement: R code and example dataset for fitting the Bayesian model of tree growth.

Table 1. Number of stems of Weinmannia greater than 1 cm DBH (stems with dendrometers installed in parentheses) in each plot.

	Plot altitude (meters)									
Species	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)	4(1)			-	-	-	-
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)
	I									

Figure legends

Figure 1. Two hypotheses relating tree growth to temperature: 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).

Figure 2. Modeled diameter increment versus altitude for adult canopy 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 versus 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* was omitted (for justification see main text).

Figure 3. Mean diameter increment versus stem altitude for four common 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 = 80^{th} percentile of dbh distribution for each species, canopy status = 3). Points have the same color scheme as lines, with stems < 15 cm dbh considered saplings and stems in the 70^{th} percentile or above considered canopy trees. Stems indicated by an 'x' do not fit into any of the three scenarios.

Figure 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 parameter had a positive (negative) effect on growth. Note that the credible intervals for *W. mariquitae* and *W. pinnata* are truncated.



Figure 1



Figure 2









Figure 4

