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Regeneration Ecology of Native-Dominated Hawaiian Forests

A dissertation submitted in partial satisfaction of the
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in Biology

by

Faith Marie Inman-Narahari

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ABSTRACT OF THE DISSERTATION

Tree Regeneration Requirements and Physiological Adaptations in Hawaiian Forests

by

Faith Marie Inman-Narahari

Doctor of Philosophy in Biology

University of California, Los Angeles, 2013

Professor Lawren Sack, Co-Chair

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Several hypotheses have been proposed to explain the maintenance of tropical forest diversity. Three frequently investigated hypotheses focus on the seed and seedling stages when plants are most vulnerable to environmental factors. These hypotheses propose that either niche differentiation, negative density dependence, and/or neutral process maintain biodiversity in tropical forests. The niche differentiation hypothesis proposes that plant species are specialized to microhabitats, as evidenced by differential performance (germination, growth, and or survival) of each species. The second, also termed the Janzen-Connell hypothesis, posits that negative density dependence (i.e., higher pathogen- and predator-induced mortality near conspecifics) regulates the density of common species. The neutral theory maintains that stochastic factors and limited seed dispersal contribute to avoidance of competitive interactions by functionally equivalent species. To investigate these hypotheses in low-diversity tropical forest, I measured seed/seedling dynamics and microhabitats (understory irradiance and substrate) in 4-ha plots in Hawaiian wet and dry forests in which all adult trees were mapped. I found evidence in support of all three hypotheses. Overall, recruitment limitation was the strongest driver of seedling dynamics in Hawaiian wet forest. Recruitment limitations and habitat specialization varied more among species within Hawaiian wet forest than among forests with comparable data. In Hawaiian wet forest, I also found evidence of differential performance among species across microhabitats and striking differences in allometric relationships, suggesting the existence of niche differentiation, though some species-pairs appeared to be functionally equivalent and there was substantial niche overlap in seedling distribution across microhabitats. In both wet and dry Hawaiian forest, density dependence was largely positive, thus it does not appear to maintain coexistence. Altogether, these results show that Hawaiian forest recruitment patterns are complex and are more similar than expected to mainland tropical forests. The results of this study will be useful for identifying and predicting the effects of factors that may be important for tree recruitment at the seedling stage and how these factors vary across species and forest types.

The dissertation of Faith Marie Inman-Narahari is approved.

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2013

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PUBLICATIONS

Peer-Reviewed Journal Articles

2013 Murphy, M. J., F. Inman-Narahari, R. Ostertag, and C. M. Litton. Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. *Biological Invasions in press*.

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Manuscripts in Review/Preparation

Inman-Narahari, F., S. Cordell, and L. Sack. Convergence and divergence in woody seedling allometries across species and biogeographic regions: analysis of Hawaiian and global trends. *in prep.*

Inman-Narahari, F., R. Ostertag, G. P. Asner, S. Cordell, S. P. Hubbell, and L. Sack. Niche differentiation of native tree seedlings in Hawaiian wet forest. *in prep.*

Inman-Narahari, F., R. Ostertag, S. P. Hubbell, C. P. Giardina, S. Cordell, and L. Sack. Density-dependent seedling mortality varies with forest type, irradiance and species rarity in wet and dry Hawaiian forests. *in prep.*

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PRESENTATIONS

Invited talks

2012 Density-dependent seedling mortality in Hawaiian dry forest. *Oral presentation*. Hawai'i Conservation Conference, Honolulu, HI.
2011 Natural regeneration in the Pālamanui native-dominated dry forest. *Oral presentation*. Nāhelehele Dry Forest Symposium, Keauhou, HI.

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2013 Niche differentiation of native tree seedlings in Hawaiian wet forest. *Oral presentation*. Association for Tropical Biology and Conservation Annual Meeting, San José, Costa Rica.
2012 Density-dependent seedling mortality varies with light availability and species abundance in wet and dry tropical forests. Poster presentation *Poster presentation*. Ecological Society of America Annual Meeting, Portland, OR.
2011 What's going down and what's coming up: seed rain and seedling establishment of native species in Hawaiian wet forest. *Oral presentation*. Hawai'i Conservation Conference, Honolulu, HI.
2010 Hawaii permanent plot network: first census results and ongoing research. *Oral presentation*. Botanical Society of America Conference, Providence, RI.
2010 Seedling dynamics in native dominated Hawaiian rain forest. *Oral presentation*. Botanical Society of America Conference, Providence, RI.
2009 Regeneration patterns in a native dominated Hawaiian montane wet forest. *Poster presentation*. Annual Meeting of the Ecological Society of America, Albuquerque, NM.
2009 Electronic data collection methods for tree and seedling census data in forest dynamics plots. *Poster presentation*. Ecological Society of America Annual Meeting, Albuquerque, NM.
2008 Using artificial canopy gaps to restore Puerto Rican Parrot (*Amazona vittata*) habitat in tropical timber plantations. Ecological Society of America Annual Meeting, San Jose, CA.
2008 HIPPNET: Hawai‘i's Permanent Plot Network for research, monitoring, and education. Hawai'i Conservation Conference, Honolulu, HI.
2007 Limiting factors of *Portulaca sclerocarpa* (A.Gray) in Hawai‘i Volcanoes National Park.

INTRODUCTION

Tropical forests contain the majority of global terrestrial biodiversity and are increasingly imperiled due to anthropogenic land use and climate changes (Hubbell et al. 2008). To preserve and restore biodiversity, it is essential to have a sound scientific understanding of forest dynamics (Hubbell and Foster 1992), and especially regeneration processes. Seedling recruitment is a key stage of plant establishment (Grubb 1977). Processes that limit seedling recruitment affect future forest composition and diversity (Harms et al. 2000, Uriarte et al. 2005, Wright et al. 2005). Thus, studies of the seedling stage provide insight into long-term forest dynamics. The overall aim of this study was to investigate tree regeneration and community assembly patterns in Hawaiian forests. A secondary goal was to develop the Hawaiian forest as a model system for the study of tropical forests in general. The results of this study will be useful for identifying and predicting the effects of factors that may be important for tree recruitment at the seedling stage and how these factors vary across species and forest types.

Several hypotheses have been proposed to explain tropical forest regeneration dynamics, community assembly, and the maintenance of tropical forest diversity. Three of the most frequently investigated hypotheses focus on the seed and seedling stages when plants are most vulnerable to biotic and abiotic factors. According to these hypotheses, niche differentiation, negative density dependence, or neutral process maintain biodiversity in tropical forests (Janzen 1970, Grubb 1977, Hubbell 2001 reviewed in Wright 2002). Some authors have also argued that diversity is maintained by a combination of these processes, with their relative importance dependent on forest characteristics (Gravel et al. 2006). According to the *niche differentiation* hypothesis, plant species are specialized to microhabitats that provide for differential performance (germination, growth, and or survival) of each species and thereby prevent competitive exclusion (Grubb 1977). The second, termed the *Janzen-Connell* hypothesis, posits that negative density dependence (i.e., higher mortality near conspecifics due to more pathogens and predators) contributes to biodiversity by regulating the density of common species (Janzen 1970). The *neutral theory* maintains that stochastic factors such as seed arrival contribute to avoidance of competitive interactions by functionally equivalent species (Hubbell 2001). Although these processes have been extensively studied throughout the tropics, their importance in Hawaiian forests is largely unknown (Cordell et al. 2009).

Hawaiian forests are exceptional as a model system in several ways. Although only covering 10,456 square kilometers, Hawai‘i Island contains 25 of 35 global life zones (Holdridge 1947). Nevertheless, overall tree species diversity is much lower in Hawai‘i than in other tropical forests and 90% of Hawaiian angiosperms are endemic as a result of Hawai‘i's young age, and its being the most remote archipelago in the world (Wagner et al. 1999). Given these unique features, some have suggested that Hawaiian forests are fundamentally different from mainland tropical forests because competition is lower in Hawaiian forests and species can co-exist in smaller areas (e.g., Soulé 2007). However, these statements were not based on direct research. To test these hypotheses for the first time in Hawaiian forest, we collected seed and seedling data within two large scale (4-ha) permanent plots thaat are part of the Hawaii Permanent Plot Network, a member of the Smithsonian Institute Center for Tropical Forest Science (CTFS). By using standard CTFS methodologies, I collected data that could be directly compared with other forest plots globally, providing a means to determine how forests varying in diversity also vary in regeration ecology.

Overview of dissertation chapters

In this dissertation, I present studies that examine data collection methods and test hypotheses of forest regeneration ecology in Hawaiian forest. Testing community ecology hypotheses in natural forests often requires large amounts of data. In chapter one, I present a case study describing how digital data collection was used to improve data collection efficiency for collecting tree data in large-scale permanent forest plots. In chapter two, I compared recruitment limitations (seed, dispersal, and establishment limitation) and habitat associations for Hawaiian forest species with those from other large-scale permanent plots across a diversity gradient. In chapter three, I investigated whether Hawaiian wet forest seedlings show performance trade-offs across microhabitats and the relative importance of understory irradiance, topography, and substrate. Differences in regeneration niches are hypothesized to contribute to species coexistence (Grubb 1977). Niche differentiation may be evidenced by performance trade-offs (growth and survival) between species pairs across microhabitats (Baraloto et al. 2005).

In chapter four, I examined hypotheses for the influence of density dependence on seedling survival in both wet and dry Hawaiian forests and across light gradients within each forest. There is abundant evidence in other tropical forests that negative density dependence is an important biotic factor influencing seedling dynamics and that the interplay between density and environment may also be significant (Harms et al. 2000, Comita and Hubbell 2009, Comita et al. 2009, Metz et al. 2010). This study represents the first test of the Janzen-Connell hypothesis in Hawaiian forest. Janzen-Connell effects are expected to be weaker in Hawaiian forest because of its lower diversity (Janzen 1971). Further, I provide the first examination of density dependent seedling mortality in dry forest and one of few investigations of the interaction between understory irradiance and density dependent seedling mortality.

In chapter five, I used data from seedlings harvested from Hawaiian wet forest to examine how allometric relationships vary among Hawaiian species and between Hawaiian species and species data collected from the literature (global species). I further examined how allometric slopes of both Hawaiian and global species differed from predicted geometric slopes (i.e., isometric slopes). For this chapter, I included size and mass data of woody seedlings (<1 m in height) from 90 studies representing 164 species gathered from the published literature compiled for a global database. I tested 21 different allometric relationships for Hawaiian species and for the global species database with adequate data.

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CHAPTER 1

Digital data collection in forest dynamics plots

co-authored with *Christian Giardina*[1], *Rebecca Ostertag*[2],*Susan Cordell*[1], *Lawren Sack*[3]

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Summary

1. Computers are widely used in all aspects of research but their application to in-field data collection for forest plots has rarely been evaluated.

2. We developed digital data collection methods using ESRI mapping software and ruggedized field computers to map and measure ~30 000 trees in two 4-ha forest dynamics plots in wet and dry tropical forest in Hawaii. We then compared our data collection and entry effort with published values for other forest dynamics plots with the same tree measurement protocols to estimate the efficiency of our methods relative to the more typical use of paper data collection sheets.

3. In-field data collection effort was comparable for all plots. However, use of digital methods resulted in an average 11·8% reduction in total effort due to reduced secondary data entry time.

4. The digital data collection methods described in this article can be applied to a wide range of ecological projects, especially long-term research or monitoring projects where mapping can be integrated into data collection.

Key-words

Center for Tropical Forest Science; digital data collection; ecology methods; forest dynamics plots; Hawaii

Introduction

Considerable amounts of money and time are often invested in data collection and entry, and data quality can affect the analysis and conclusions of a study. Thus, it is worthwhile to explore options that may increase efficiency and accuracy. The use of digital methods is well described in the medical literature (Abernethy *et al.* 2008; Hayrinen, Saranto, & Nykanen 2008; Borycki *et al.* 2009; Fonseca, Ribeiro, & Granja 2009; Mador & Shaw 2009; Ohmann & Kuchinke 2009), but there are relatively few studies that discuss these methods for ecological research projects (Logan & Smith 1997; Elzinga *et al.* 2001; Southwell *et al.* 2002; Waddle, Rice, & Percival 2003; Stoleson *et al.* 2004; van Tamelen 2004). Digital data collection has become standard in national vegetation monitoring networks, such as the USDA Forest Service's Forest Inventory and Analysis Program (http://fia.fs.fed.us/; Forest Inventory and Analysis National Core Field Guide, Volume I: Field Data Collection Procedures for Phase 2 Plots, Version 4.0, 2007). However, most forest plot studies use written methods and we are not aware of studies that have shown the efficiency of electronic data collection methods as an alternative to paper-based data collection methods in forest plots. Indeed, a Web of Science search on ‘digital data collection’ returned over 1500 citations of which more than 60% were related to medical research and most of the remainder discussed applications for climate and remote sensing research. Of the few articles that discussed ecological research, most focused on wildlife research (Logan & Smith 1997; Elzinga *et al.* 2001; Southwell *et al.* 2002; Waddle, Rice, & Percival 2003; Stoleson *et al.* 2004; van Tamelen 2004). For example, Waddle, Rice & Percival (2003) and Elzinga *et al.* (2001) outlined the qualitative benefits and concerns associated with digital data collection. Others have described methods to integrate the collection of location, audio, and other types of data by using Personal Digital Assistants (Logan & Smith 1997; Southwell *et al.* 2002; Stoleson *et al.* 2004; Travaini *et al.* 2007). All concluded that these systems were cost-effective and increased data collection efficiency. However, to our knowledge, only one article directly compared efficiency of digital vs. written methods for collecting ecological data; in this study, digital vs. standard calipers were compared for measuring crabs and found that digital methods were three times faster than written methods and that data quality was comparable (van Tamelen 2004).

Electronic data collection holds great promise for enhancing ecological research capacity, yet researchers may be reluctant to adopt digital methods for many reasons including concerns of losing large amounts of data, the money and time needed to buy and implement a new system, the weather-resistance of electronic devices, and lack of familiarity with digital options. Some would question any investment in additional training once a field crew is trained and familiar with a written system. However, digital technology has improved greatly in recent years to become more secure, rugged, economical and user-friendly. These new systems have the potential to improve efficiency and increase data accuracy for vegetation monitoring and ecological studies.

We quantified the increase in efficiency resulting from digital collection methods for mapping and measuring trees in large-scale permanent forest dynamics plots (FDPs). We describe the digital data collection methods we developed for the first census; we anticipate efficiency and time savings to increase with each re-census. We then compared data collection and data entry time estimates in this case study with those for other FDPs that followed the same tree measurement protocols, but used written data collection methods. We calculated approximate savings realized from the implementation of digital methods. In addition, we analysed plot data to test for possible factors underlying the variation in data collection rates (i.e., tree density and number of species). The information presented here is broadly applicable to ecological research, especially when location data are recorded.

Materials and methods

Plots —. In 2007–2009, the Hawaii Permanent Plot Network (HIPPNET) established two 4-ha plots on the Island of Hawaii at Laupahoehoe and Palamanui. The Laupahoehoe plot is located in mid-elevation wet forest and the Palamanui plot is located in low-elevation dry forest (http://www.hippnet.hawaii.edu). HIPPNET is part of a global network of 34 FDPs affiliated with the Smithsonian Tropical Research Institute, Center for Tropical Forest Science (CTFS; http://www.ctfs.si.edu, accessed on 14 January 2010). In each FDP, all trees ≥1-cm d.b.h. (i.e., at 1·3-m from tree base) are identified, permanently tagged and measured according to standard protocols developed for the first plot on Barro Colorado Island, Panama (BCI). In addition, each tree is mapped relative to a precisely installed grid system of 20 × 20-m quadrats. CTFS plot sizes range from 2-ha to 52-ha and have from 15 to 1182 species represented by 11 900 to 360 000 stems per plot. Plots are re-censused every 5 years. In all of the plots, trees are measured and mapped using standard protocols (Condit 1998). Most CTFS plots continue to use written data collection methods. To date, we are aware of only two locations, Hawaii and Wabikon Lake Forest in Wisconsin, that have adopted a digital system (Robert Howe, *pers. comm.*).

Description of HIPPNET data collection methods

Hardware and software. — Tree location and attribute data were collected data using ArcPad (version 7.0.1.53 copyright ©1995–2006; ESRI, Redlands, CA, USA) installed on Allegro field computers (Allegro CX, Juniper Systems Inc., Campbell Scientific, Utah, USA; cost = ~$1600–3000 per unit); Allegro field computers are currently used by the USDA Forest Service's Forest Inventory and Analysis Program to monitor permanent vegetation plots across the United States (http://fia.fs.fed.us/). These field computers are completely waterproof and shock-resistant, with data entry by alphabetic and numeric keypads and touch screens. The rechargeable battery lasts all day (10 h) and can be re-charged in a vehicle as necessary. Data and programmes can be stored without battery power in the built-in flash memory drive and removable memory cards can be purchased. If data are saved into stable memory, the data should be extractable even if the field computer were to crash. Thus, as long as data files are backed up at the end of each field day, no more than 1 day of work would be lost due to system failure. The HIPPNET project has used three units continuously for 2 years and we expect them to be usable for several more years. To create and edit maps on field computers, we used ArcPad, a simplified mobile version of ArcMap (ArcGIS Desktop 9·2 Copyright © 1999–2006; ESRI). Its functions are similar to ArcMap without many of the more advanced features. We used ArcPad Application Builder (v. 7·0·1·2OU Copyright © 2002–2006; ESRI) to create custom data collection forms for ArcPad. ArcPad data were downloaded/uploaded to/from PC's using Microsoft® Active-Sync® (v. 4·5·0 Copyright © 1996–2006; Microsoft Corporation, Seattle, WA, USA). On the PC, we used built-in ArcGIS tools to update data stored in ArcGIS geodatabases. Data can then be opened in data base format (including Microsoft® Office Access®, Copyright © 2007; Microsoft Corporation) to generate error reports and export to other formats for analysis.

Data flow process: Step 1. Create and export data collection files.— Our data were stored within geodatabases to be easily exported to ArcPad for data collection and imported back to ArcMap for storage and analysis (Fig. S5-1, Supporting information, software templates and code available from authors upon request). Prior to data collection, an ArcMap geodatabase was created containing all the data collection fields. It was added to a GIS map along with additional layers as needed for reference. In our case, we added a grid-point layer we created to represent all the grid points in the plot and a polygon grid layer to represent each 20 × 20 quadrat. We exported our map in 20 × 20-m quadrat sections (about a day's work). To do this, we zoomed into the selected area and used the Export Data to ArcPad tool to create a new folder containing an ArcPad map referencing the map layers. Then, we copied our custom data collection form and any lists used by the form (e.g., species list for drop-down menu) into this ArcPad folder. In an additional step, we opened our form in ArcPad Application Builder and added the quadrat number to the 'quad' field as a default value to obviate repeatedly entering that value in the field. Finally, the ArcPad folders were uploaded to the field computer and taken to the field for data collection. Once the geodatabase, map layers, and custom forms were created, the entire data export process, including adding and editing form files, took less than an hour per hectare and could be done by assistants with only minimal instruction.

Data flow process: Step 2. In-field data collection.— In our plots, one crew member measured trees while another crew member entered the data into a field computer. To add a tree to the data set, the mapper opened the appropriate file for editing, zoomed into the correct location (usually the 5 × 5-m subquadrat) and tapped on the map to draw the tree at a location relative to the grid points on the map and on the ground. This action opened the custom data collection form in which tree identification, measurement and other attribute data were entered. Our data collection forms included drop-down menus for species names and notes, automatic date entry and required fields (e.g., must enter number ≥1 in tag field). We used one field-computer per mapping/measuring team and typically had 2–3 teams measuring at any one time.

Data flow process: Step 3. Download data and update map data base.— Following collection, data were copied from the field computer to a PC. We then used the 'Check in Data From ArcPad' tool in ArcMap to upload data to the map data base. This tool used a change-code generated in ArcPad to look for new and changed values and used this to update the geodatabase.

The seamless integration of mapping and tree data collection removed the need to enter data and digitize maps from paper copies.

Methods comparisons among forest dynamics plots. — We constructed a data-flow model to graphically illustrate and compare processes and potential sources of error for digital and written methods. This allowed clarification of the number of steps required by the different methods and identification of those steps in which errors were likely to be propagated.

We compared in-field data collection rates among FDPs in the CTFS network based on published rates and our own estimates from the Hawaii plots. In-field data collection rates for the initial census of six FDPs (BCI, Panama; Luquillo, Puerto Rico; Yasuni, Ecuador; Korup, Cameroon; Ituri, Dem. Rep. Congo) are available in Condit (1998) as trees per person per day; we did not include the Sri Lanka plot in our comparison of data collection rates as trees in that plot were identified and specimens were collected at the time of measurement, making their rate much slower and not comparable with the other plots, in which trees were identified separately. We calculated in-field data collection effort in person months per hectare by dividing the number of trees per plot by the product of the number of days worked per month and the number of trees measured per day over hectares per plot. To understand the variability in field data collection rate among FDPs (from 40 to 80 trees per day per person), we analysed the relationship between data collection rates and plot variables that may affect data collection rate, i.e., tree density (which varied from 3026 to 7200 trees/ha) and number of species (which varied from 35 to 1114 species) using ordinary linear regression (R language; *lm* function;R Development Core Team 2009).

To estimate the data entry effort from paper forms onto computers for plots other than BCI, we calculated the per tree data entry effort for BCI (28 person months for 208 400 trees = 0·000134 person months per tree; approximately 1·35 minutes per tree; Condit 1998, p. 98). We multiplied the BCI value by the number of trees per hectare in the given plot to determine the data entry effort in persion months per hectare. We estimated digital data entry rates (digitally uploading field computer data to a computer data base) from our own records.

We compared estimates of the total effort required for collecting field data manually, that is, writing tree locations and measurements on paper forms and then later manually entering the paper form data into a computer data base, with total effort for digital methods. Total effort required for data collection was calculated as the sum of in-field data collection plus data entry efforts. We also calculated data entry effort as a percent of total effort (data entry effort (person months plot^{-1})/total effort (person months plot^{-1}) × 100%).

Results

Data flow model. — In a comparison of the data collection, entry and checking steps of digital and written methods (Fig. 5-1), we identified similarities and differences in the overall process and the potential sources of error. The first difference is the possibility of improved data quality during field data collection (*process 1*). In the field, data can be entered or written incorrectly or forgotten entirely for either method. However, with digital forms, it is possible to programme data validation to remind the user to enter data or check suspect values while in the field, potentially reducing overall error rates in the data. Second, and most importantly, digital data are uploaded from the field computer to a desktop computer instead of entered from paper data sheets thus saving effort and eliminating transcription errors (*process 2*). Our digital approach eliminates the need to re-check paper data sheets and to revise incorrectly entered data (*process 4*). The field error check step is similar for both methods except that digital, instead of printed, maps and data sheets may be used with digital methods (*process 5*). Finally, corrected values from field checks are entered by hand for paper methods while for digital methods they are uploaded and the data base may be automatically updated (*process 6*).

Methods comparisons among forest dynamics plots. — In our analysis of data collection rates and tree density and species per plot, we found that tree data collection rate was independent of the number of species represented in a plot ($r^2 = 0{\cdot}05$; $P = 0{\cdot}66$) but increased with stem density ($r^2 = 0{\cdot}79$; $P = 0{\cdot}017$). Given the high variation in number of trees per hectare and number of species, the data collection effort in person months per hectare was relatively conservative across sites, ranging from 2·8 person months ha^{-1} for Yasuni to 5·1 person months ha^{-1} for Korup (Fig. 5-2). Hawaii's value (4·6 person months ha^{-1}) fell close to the average for all the other five plots (4·2 person months ha^{-1}).

Discussion

We found that the implemention of digital data collection methods in forest plots was practical and resulted in high efficiency. Comparison with estimates for the global network of CTFS plots shows a reduction in data entry effort resulting from use of digital methods and potentially a lower total effort. In all plots using written methods, data entry effort is a substantial proportion of the total effort; the minimized data entry time for digital methods would result in an 11·8% average reduction of total effort. Thus, eliminating data entry time would enable savings of 9–35 person months per census depending on the size of the plot (mean = 25 person months). Such a saving in human effort translates into a savings of $18 000–$70 000 USD (mean $50 000), assuming an average salary of $2000 per month for data entry personnel. We note that salaries can be widely different, and the cost-savings may also vary across plots, but would be expected to always be important given that data entry from paper forms was always a substantial percent of total effort when using manual methods. Thus, even for small plots, the savings in effort of using digital data collection would more than compensate for the expense of field computers and software. This is important because forest dynamics data are proving essential for understanding ecological processes and an increasing number of FDPs are currently being developed. The ability to maximize limited resources can therefore increase the potential to further expand research agendas.

Based on our analysis of the variation of rates of in-field data collection among plots, the Hawaii rate is about what is expected for a plot with our tree density, suggesting that our digital data collection methods did not have a strong effect on field data collection rate. Instead, the field data collection effort (person months ha^{-1}) for Hawaii plots was close to the average for other plots we examined. Although digital methods allow features such as default values and drop-down menus that may presumably increase the speed of data collection, we found no savings in data collection time in Hawaii as compared with other CTFS plots. This may be because the digital data collection features that may speed up data collection are compensated by the necessity of collecting data for only one tree at a time per measurement crew. Interestingly, across FDPs the per tree data collection rate increased with tree density, presumably because of the more limited travelling time between trees when they are closely spaced; this relationship explains the relatively conservative (less than twofold) range in field data collection effort across plots despite the wide range of species diversity and tree density among plots. Indeed, we had expected that plots with high species diversity might have slower data collection rates, but that was not the case, probably because most plots do not identify species when they are measured. Although in Hawaii we did identify trees while mapping and measuring, we did not collect specimens, so this probably did not strongly affect our data collection rate.

Understanding the effects of digital methods on in-field data collection rate is important because the majority of effort is in the field; if digital methods made data collection slower, then the time savings of data entry may be negated. Our finding of similar in-field data collection effort is subject to uncertainty because we compared across multiple plot projects; a clearer estimate would require comparing paper and digital methods using both methods within a given plot which is outside the scope of this case study. However, beyond the question of in-field data collection, based on the data flow model comparing of paper and digital methods, it is clear that digital data collection methods could drastically reduce data entry time and eliminate transcription errors. In addition, the fewer steps required for digital data collection can make these systems easier to manage. Further, because there are no data entry errors caused by transcription from paper to digital, it is not necessary to recheck the paper forms, thereby also saving time in data checking. An additional advantage is that measurements can be immediately uploaded and analysed thereby increasing the ability to rapidly compare and standardize data across plots.

Digital data collection methods have additional advantages for collection of spatially explicit field data. The seamless integration of mapping and data collection removes the need to enter data and digitize maps from paper copies. Instead, data collected on field computers can be automatically incorporated into the main data base from the field copies. Lists of errors, such as suspect and missing values, can be quickly generated along with maps to locate problem trees. Finally, our field crews typically found the Allegro field computers easy to use and simpler than switching between separate paper data sheets needed for mapping and recording data. Allegro field computers are ruggedized and waterproof and can be less problematic than paper data sheets in inclement weather. Our results are consistent with previous publications on digital data collection methods that found large increases in efficiency from the application of digital methods in other project designs (Waddle, Rice, & Percival 2003; van Tamelen 2004). Indeed, digital methods have been used extensively for the past several years to collect vegetation data (e.g., the Forest Inventory and Analysis Program of the U.S. Forest Service), and our study supports that practice, given the efficiency of digital methods as compared with that of paper-based methods.

Potential reservations to using digital data collection. — During the development and practice of our digital approach, and in numerous discussions with field ecologists, several concerns were raised pertaining to plots converting to a digital data collection approach. These are described and the ways in which potential problems might be addressed are listed below, with the clear proviso that further development of digital methods will likely increase efficiency and decrease costs for many similar large-scale projects.

The potential for system crashes that can result in losses of data is a primary concern for field ecologists. That problem can be minimized by: (i) saving files on stable drives that are not erased if the battery dies or the programme crashes; (ii) daily downloading of collected data; and (iii) regular backup to onsite and offsite storage. These precautions are simple, take just a few minutes per day, and should prevent the loss of more than a day of work – and this would be only if the system were to fail. Indeed, with regular offsite data storage, the risk of data loss due to catastrophic events may less than paper-based methods, because paper data collection methods are not immune to data loss (e.g., due to lost or damaged data sheets).

The cost of hardware and software is another major concern. These problems are especially acute for researchers in developing countries, graduate students with little funding, and small, short-term projects. For these projects, digital methods may still be useful given that less expensive hardware and software options are available, although not explored in this study. However, for larger projects, the savings in data entry time should more than compensate for the cost of equipment purchased, as described above.

We note that there may be a large initial time investment to set up a new system and create customized forms. Of course, to create a well-designed paper datasheet also takes time. We have found that simple digital forms made in spreadsheet programmes can actually be much faster and easier to create than paper forms given that fields can be created or edited in the field as needed. Using off-the-shelf instead of custom programmes also saves time and makes it easier to adapt methods to other projects. These programmes are typically user-friendly and do not require programming skills, and allow modifications to ensure high quality data collection.

The need for electricity may be a drawback to using digital methods in situations where it might not be available in remote field sites. The battery in the Allegro field computer lasts about 16 h and can be charged using a vehicle outlet, but greater difficulty may arise for plots sited far from any roads. Field computers can lose their charge in the middle of a field day if not charged properly. In this case, back-up datasheets or a plan for another activity will ensure that the time spent travelling to and from the field site is not wasted.

The small screen size of the Allegro may make some types of data collection awkward. However, in ArcPad, it is possible to zoom in or out to any scale to see larger or smaller areas. For example, it is possible to zoom in and see closely spaced trees that may be hard to visualize on paper forms.

These principal reservations can thus likely be overcome and digital collection systems can be further improved by implementing several principles. Most importantly, it is ideal to create data collection forms to work with the natural flow of data collection and the preferences of the field crew. It is easier to adjust the system to work with the people than trying to adjust the people to the system. Fine-tuning the system to work with the natural flow of data collection will add speed and probably result in fewer errors. For example, in our plots, the crew first read the tag number, so in the data entry form this field comes first. Then, the person collecting data can tab through each field in the order they are customarily measured in the field. Developing a system that works smoothly with the field crew requires that the project manager solicit and implement feedback from the field crew on a regular basis.

The findings of our case study pointed to substantial efficiency of digital methods that should be applicable to many other studies and opens up further questions for study. Further research should quantify the difference in in-field data collection accuracy between digital and paper methods given that these methods allow the incorporation of pre-set default field values, required fields, automated in-field data checking and drop-down menus. These comparisons would be valuable for evaluating the utility of digital methods. Further estimation of savings in data entry would also be beneficial. Finally, we note that it is important for plot managers to carefully evaluate all options to choose the system that best fits their needs and available resources. We hope this article will aid in that evaluation process.

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Figure captions

Figure 1. Data flow models for paper and digital data collection, entry and checking processes; numbers indicate steps in the data collection and entry process (*process 1*: in-field data collection with overall effort similar between methods but errors possibly reduced in digital method due to data validation;*process 2*: data are entered manually for written methods and data are uploaded for digital methods, transcription errors may occur with written method; *process 3*: automated error checks occur once the data are in the data base similarly for both methods; *process 4*: errors are checked against paper data sheets for paper but not digital methods; *process 5*: field error checks are similar except that digital maps and data sheets may be used with digital methods; *process 6*: for paper methods, corrected values from field checks are entered by hand and for digital methods, they are uploaded and the data base is automatically updated).

Figure 2. Total effort in person months per hectare (data collection effort + data entry effort) for six Forest Dynamics Plots; data entry values for all plots except Hawaii based on published values (Condit 1998; http://www.ctfs.si.edu).

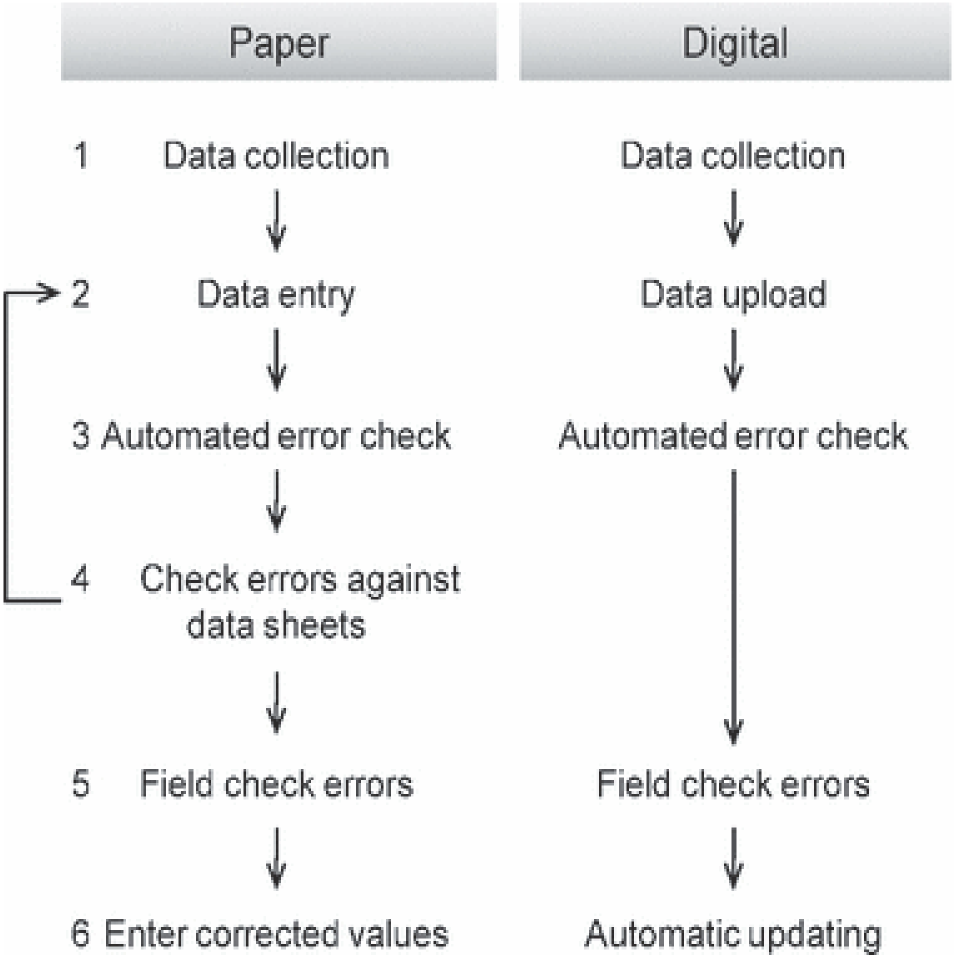

Paper
Digital
1 Data collection
Data collection
2 Data entry
Data upload
3 Automated error check
Automated error check
4 Check errors against data sheets
5 Field check errors
Field check errors
6 Enter corrected values
Automatic updating

Fig. 1

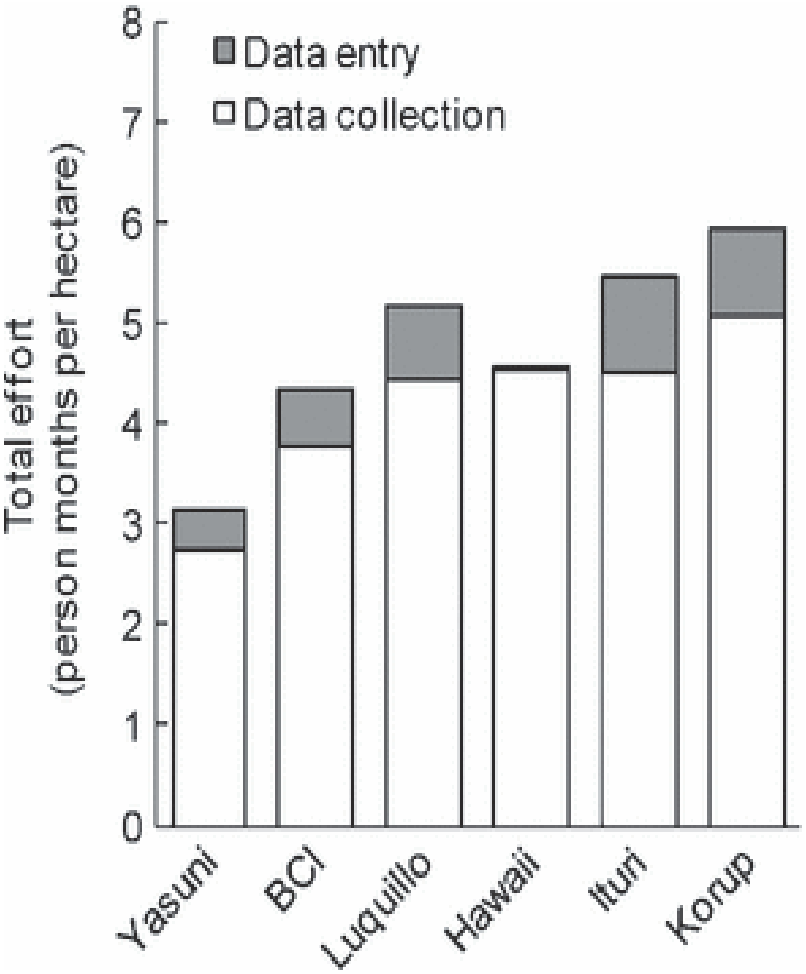
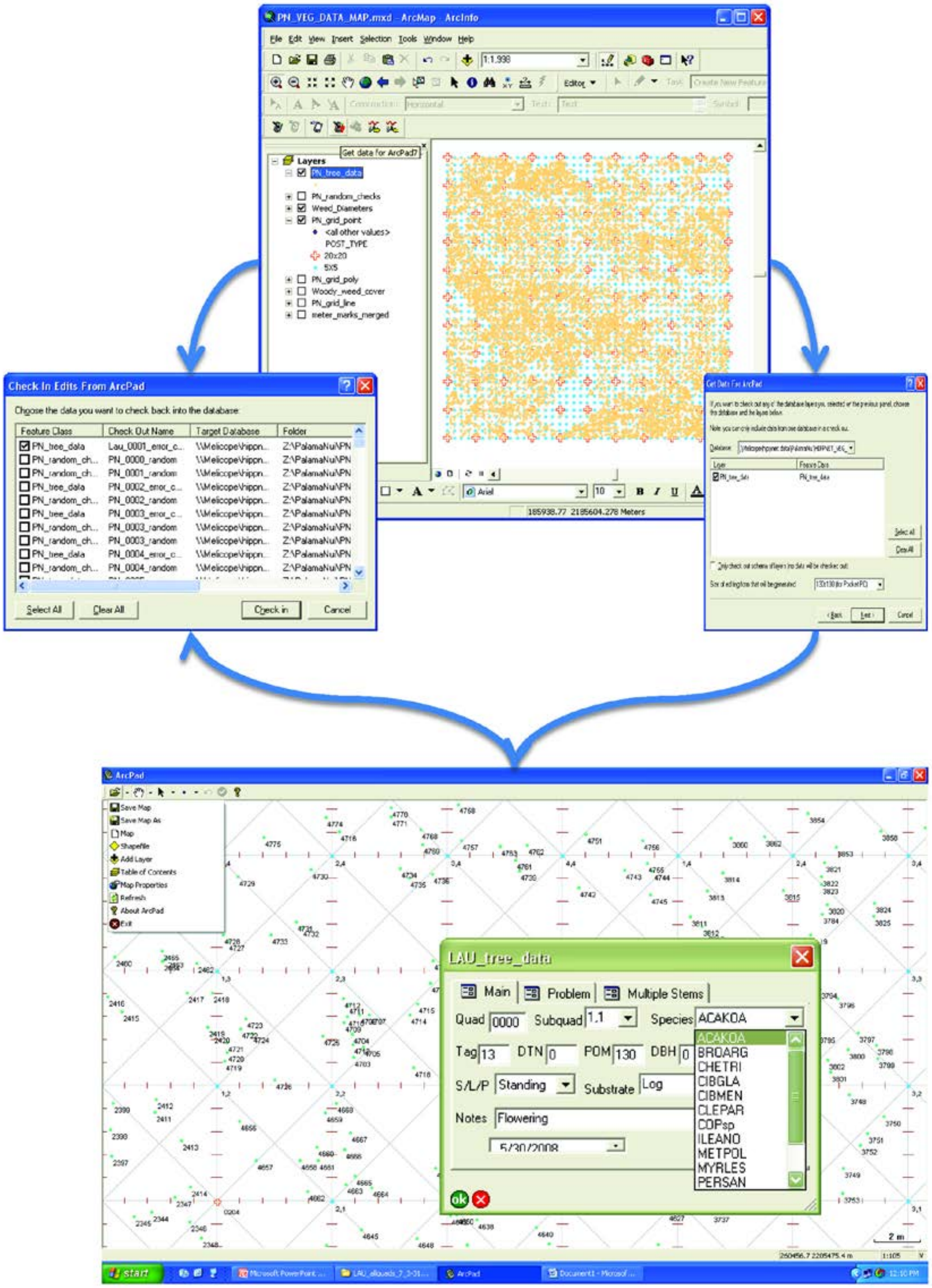

Data entry
Data collection
Total effort
(person months per hectare)
0
1
2
3
4
5
6
7
8
Yasuni
BCI
Luquillo
Hawaii
Ituri
Korup

Fig 2.

Supporting Information



Check In Edits From ArcPad

Choose the data you want to check back into the database

Feature Class	Check Out Name	Target Database	Folder
☑ PN_tree_data	Lau_0001_error_c...	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0000_random	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0001_random	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_tree_data	PN_0002_error_c...	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0002_random	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_tree_data	PN_0003_error_c...	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0003_random	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0003_random	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_tree_data	PN_0004_error_c...	\\Melicope\hippn...	Z:\PalamaNui\PN
☐ PN_random_ch...	PN_0004_random	\\Melicope\hippn...	Z:\PalamaNui\PN

Select All | Clear All | Check in | Cancel

LAU_tree_data

Main | Problem | Multiple Stems

Quad: 0000
Subquad: 1.1
Species: ACAKOA
Tag: 13
DTN: 0
POM: 130
DBH: 0
S/L/P: Standing
Substrate: Log
Notes: Flowering
5/30/2008

Species list: ACAKOA, BROARG, CHETRI, CIBGLA, CIBMEN, CLEPAR, COPsp, ILEANO, METPOL, MYRLES, PERSAN

Figure S1. HIPPNET data flow process: data from ArcMap are exported to ArcPad, data are collected on custom forms, then data are imported to the map and the underlying geodatabase is automatically updated.

CHAPTER 2

Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests

co-authored with *Rebecca Ostertag*[1] *Susan Cordell*[2] *Christian P. Giardina*[2]
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Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests

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Abstract. Recruitment limitations determine forest community regeneration patterns. Source limitation and dispersal limitation contribute to overall seed limitation, while environmental conditions and habitat associations influence establishment limitation. Several hypotheses have made contradictory predictions for how the relative importance of these limitations should vary with diversity. However, comparative data have not been available for low-diversity tropical forests. We quantified recruitment limitations using 2.5 yrs of seed rain and seedling distribution data collected within a 4 ha forest dynamics plot in low-diversity native-dominated Hawaiian wet forest. We further quantified seedling irradiance and substrate habitat associations and niche overlap (using Pianka's niche overlap index). Additionally, we compared recruitment limitations and the frequency of seedling habitat associations across forests using the few available published data from sites employing similar field and analytical methods. In Hawaiian wet forest, seed dispersal more strongly limited recruitment than did establishment limitation across species, with 11 of 18 species completely seed limited (i.e., no seeds found). However, the relative importance of limitations varied greatly among species. For the three most abundant species, habitat conditions more strongly limited regeneration than did seed arrival, especially for the dominant canopy species, *Metrosideros polymorpha*, which was not seed limited. Most species were significantly associated with specific ranges of irradiance and/or substrates. Although habitat associations may indicate niche differentiation, Hawaiian species also showed significant niche overlap. Across the three forests compared, community-wide mean seed and establishment limitation values were similar, despite wide variation in diversity. However, recruitment limitations differed strongly among species within forests due to species' life-history differences. While seed limitation in Hawaiian forest was as high as in high-diversity forests, mechanisms may differ; seed limitation in Hawaii may arise from loss of pollinators and dispersers rather than from a high proportion of rare species as occurs in high-diversity forests. The strong habitat associations in Hawaiian forest relative to high-diversity forests supported theoretical expectations that lower species diversity should increase the importance of habitat associations. However, these habitat associations were not linked to niche differentiation in Hawaii. Our findings suggest that high recruitment limitation may facilitate coexistence despite niche overlap in low-diversity Hawaiian forest.

Key words: Center for Tropical Forest Science; *Cheirodendron trigynum*; *Coprosma rhynchocarpa*; dispersal limitation; establishment limitation; habitat association; Hawaii, USA; *Metrosideros polymorpha*; Pianka's niche overlap; regeneration ecology; seed limitation.

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INTRODUCTION

A key objective of ecology is to understand the factors that determine the distributions and abundances of plant species within and across ecosystems. Thus, the relative importance of recruitment limitations is an increasing focus of ecological research (Grubb 1977, Tilman 1994, Hubbell et al. 1999, Chesson 2000, Nathan and Muller-Landau 2000, Muller-Landau et al. 2002, Adler et al. 2007, Clark et al. 2007, Poorter 2007, Myers and Harms 2010). Seedling abundance across the landscape (and its opposite, "seedling limitation") is determined by seed limitation and establishment limitation; in turn, seed limitation arises from source limitation and is determined by adult seed production and dispersal limitation (quantitative definitions in Fig. 1; Nathan and Muller-Landau 2000, Muller-Landau et al. 2002, Terborgh et al. 2011). The relative importance of seed and establishment limitations highlights the fundamental ecology and the general mechanisms for species coexistence within given ecosystems. For example, high seed limitation is an "equalizing" mechanism that may promote species coexistence by allowing species to avoid hierarchical interspecific competition (i.e., "winning-by-forfeit"; Hurtt and Pacala 1995). Alternatively, high establishment limitation reflects niche differentiation and habitat specificity which are "stabilizing" mechanisms for species coexistence (Tilman 1994, Chesson 2000, Muller-Landau et al. 2002, Gravel et al. 2006, Adler et al. 2007, Paine and Harms 2009, Mutshinda and O'Hara 2011).

Ecologists have proposed multiple hypotheses to explain how equalizing and stabilizing mechanisms may differ across ecosystems varying in structure and diversity (summarized in Table 1). However, these hypotheses sometimes lead to contradictory predictions, and their ability to account for patterns across forests have not been examined simultaneously. The paucity of data, especially for low-diversity forest, impedes this work. We considered all the available hypotheses to uncover how regeneration processes may vary with differences in fundamental ecosystem properties. We provide (1) the first explicit test of the relative importance of seed and establishment limitations in low-diversity tropical forest, (2) an examination of the frequency (proportion) of species with habitat associations and niche differentiation in such a system, and (3) a first comparison across tropical forests with differing ecosystem properties using available data from studies that have employed standardized methods. Such studies are enormous logistical undertakings, and this first comparison will motivate future research to test emerging patterns and will provide a framework for refining, synthesizing, and assimilating incoming data.

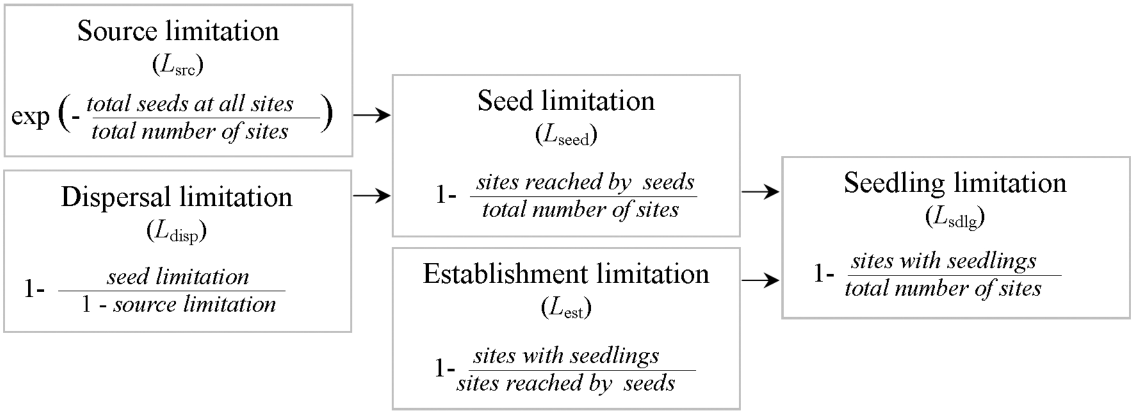

Fig. 1. Components of seedling limitation and their calculations as per Muller-Landau et al. (2002) where seed production determines source limitation (L_{src}), and dispersal limitation (L_{disp}) determines seed availability across sites (seed limitation; L_{seed}). Subsequently, once seeds arrive, habitat characteristics determine establishment limitation (L_{est}). Both seed and establishment limitation contribute to the limitation of seedling distribution across sites (L_{sdlg}).

Table 1. Synthesis of hypotheses from the published literature on how recruitment limitations (seed limitation (L_{seed}) and establishment limitation (L_{est})) and/or the frequency of habitat associations would in theory vary with forest ecosystem properties (P1–3) including explicit predictions for how these would differ based on the known properties of the extremely low-diversity Hawaiian forest relative to high-diversity tropical forests (see *Introduction* for further explanation).

			Prediction for Hawaii v. other high-diversity tropical forests		
Community property	Predicted effect on L_{seed}, L_{est} and/or the frequency of habitat associations	Source	Comparison of properties	L_{seed}	L_{est} and frequency of habitat associations
P1: Stem density and/or basal area	As stem density and/or basal area increases, so does community-wide competition for space and other resources, thereby increasing L_{est} and species habitat associations.	1, 2	Similar structure†	na	Similar
P2: Species diversity	A) As species diversity increases, habitat breadths along resource axes narrow, thereby increasing L_{est} and habitat associations.	3, 4	Lower diversity	na	Lower
	B) As species diversity increases, interspecific interactions among many species become more unpredictable, reducing directional selection for species habitat differentiation, thereby decreasing L_{est} and habitat associations.	4, 5, 6	Lower diversity	na	Higher
P3: Proportion of rare species	A high proportion of rare species leads to high community-wide L_{seed} which decreases direct competition, thereby decreasing L_{est} and habitat associations.	7, 8	Lower proportion of rare species	Lower	Higher

Notes: We found alternative hypotheses with contrasting predictions for the effects of species diversity on recruitment limitations and habitat associations (P2 A and P2 B). Sources are: 1, Pianka (1972); 2, Rusterholz (1981); 3, Ricklefs (2001); 4, Ricklefs (2004); 5, Hubbell (2006); 6, Volkov et al. (2009); 7, Hubbell (2001); 8, Gravel et al. (2006).

† Structural properties such as basal area, stem density, and biomass.

Hawaiian forest, which has extremely low species diversity due to its isolation and small land area (Carlquist 1985), provides a unique opportunity to test hypotheses for how diversity and structure influence regeneration processes because the structure and climate are similar to those of most other tropical wet forests, while the diversity is very different. Though fewer species occur in Hawaiian forest, they are functionally diverse, from the dominant canopy species *Metrosideros polymorpha* which produces many wind-dispersed seeds (Drake 1992) to species with relatively larger seeds contained in bird-dispersed fruits such as *Coprosma rhynchocarpa*. Based on published theories, we made explicit predictions for how seedling ecology in Hawaiian wet forest may differ from high-diversity tropical forests, all else being equal (Table 1). First, niche differentiation and therefore establishment limitations and habitat associations should be similar among forests with similar structural properties (Table 1, P1; Pianka 1972, Rusterholz 1981). Therefore, because aspects of Hawaiian forest structure, including stem density and basal area, are within the range of those of tropical forests with higher diversity (Midgley and Niklas 2004), we expected to find establishment limitations and habitat associations similar to those found in other tropical forests, based on this property alone. Second, the low species diversity in Hawaiian forest may drive lower establishment limitation and fewer habitat associations if fewer species promotes greater niche breadth (Table 1, P2A; Ricklefs 2001, 2004). Alternatively, one may predict the opposite scenario, that the low species diversity in Hawaiian forest would drive higher establishment limitation and more habitat associations if the relatively few species have highly predictable interspecific interactions and if this results in greater niche differentiation (Table 1, P2B; Ricklefs 2004, Hubbell 2006, Volkov et al. 2009). Third, because rare species typically have high seed limitation and Hawaiian wet forest has a lower proportion of rare species than other tropical forests (19% of species with ≤1 individual/ha versus 42% averaged for 13 other tropical forests; $t = 6.63$, $P < 0.001$; Losos and Leigh 2004), we predicted that Hawaiian forest should have lower seed limitation than high-diversity tropical forests (Table 1, P3; Hubbell 2001, Gravel et al. 2006).

We addressed key questions for the first time in low-diversity tropical forest by combining two major approaches to seed and seedling ecology. First, we quantified seed availability and seedling distribution using standard seed traps and seedling plots to determine seed and establishment limitations in low-diversity Hawaiian forest. Second, we quantified seedling densities in substrate and light microhabitats to determine habitat associations and niche overlap. We addressed these questions: (1) How influential is seed limitation relative to establishment limitation for seedling recruitment? (2) What are the frequency and strength of species habitat associations for substrate and light? (3) Is there evidence of interspecific niche differentiation (measured as Pianka's niche overlap)? Further, we utilized previous studies to address for the first time (4) how do the relative importance of seed and establishment limitations and the extent of habitat associations vary across tropical forests with a wide range of diversity?

METHODS

Study site

We conducted this study in the Laupahoehoe Forest Dynamics Plot (FDP) of the Hawaii Permanent Plot Network (HIPPNET; www.hippnet.hawaii.edu), a member of the Smithsonian Tropical Research Institute Center for Tropical Forest Science network (CTFS; www.ctfs.si.edu). The 4 ha FDP is located on Hawaii Island (19°55′ N, 155°17′ W) in the Hawaii Experimental Tropical Forest (HETF; www.hetf.us). The FDP was established in 2008 at 1120 m elevation in native-dominated primary tropical lower montane wet forest (Holdridge 1947). Within the FDP, all native woody species ≥1 cm diameter at breast height (DBH) were tagged, mapped, measured and identified following standard CTFS protocols (Condit 1998). The dominant canopy tree species is *Metrosideros polymorpha* and the subcanopy is dominated by tree ferns in the genus *Cibotium*; these species account for 21% and 27% of the stems, respectively (R. Ostertag, *unpublished data*). Mean annual precipitation is 3440 mm (Giambelluca et al. 2012) and the mean annual temperature is 16°C (Juvik and Juvik 1998). Rainfall is largely aseasonal and monthly temperature averages ranged from 14°C to 16°C during 2011 based on the adjacent above-canopy climate tower. Though the 4 ha FDP size in Hawaii is smaller than that of the majority of CTFS FDPs (25 to 50 ha), due to its extremely low species diversity this FDP provides comparable sample sizes for most species and an adequate representation of species diversity for this forest type, based on species accumulation curves (R. Ostertag, *unpublished data*). Further, the HIPPNET FDPs were selected to be highly representative in their species composition, structure, and dynamics and thus to allow elucidation of the processes occurring across larger areas of Hawaiian forest.

Seed rain and seedling demography censuses

We quantified seed rain and seedling abundances for 2.5 yrs, from September 2009 to January 2012 for seed rain and from December 2008 to June 2011 for seedlings. Within the 160 × 160 m central area of the 4 ha Laupahoehoe FDP, we established a grid of 64 seed and seedling census stations. Following standard CTFS seedling plot protocols (Wright et al. 2005), each census station comprised one 0.5 m^2 seed trap with a fine mesh bag suspended approximately 80 cm above the ground ($N = 64$) and three 1 × 1 m seedling plots within 2 m of each seed trap ($N = 192$; Fig. 2). The arrangement and density of census stations facilitated thorough seed collection from adult trees throughout the 4 ha FDP, with all traps evenly spaced at 20 m intervals. We excluded the outer 20 m of the FDP to reduce seed input from unmapped trees. Given the small FDP size, the density of census stations in this study was high, providing ample sampling intensity and relatively detailed spatial information. For example, the proportion of the total FDP area covered by our seed and seedling plots were

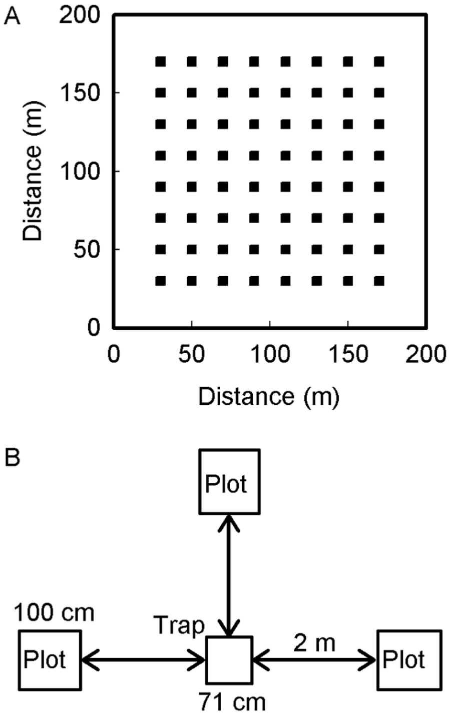

Fig. 2. (A) Schematic of census station locations within the 4 ha forest dynamics FDP in Hawaiian wet forest, and (B) diagram of a census station with three 1 m^2 seedling plots within 2 m of a 0.5 m^2 seed trap.

ten- and four-fold higher, respectively, than for the system in the 50 ha Barro Colorado Island (BCI) FDP (Wright et al. 2005). This design provided sufficient spatial replication to accurately represent the FDP, just as the FDP size allowed it to adequately represent Hawaiian rainforest (see previous section).

In each seedling plot, we censused and measured stem height for all native woody species $<$ 1 cm DBH (hereafter referred to as "seedlings"). For each seedling we recorded species, location, size, and rooting substrate (i.e., soil, root mat, rock, log, or tree fern). We included tree ferns as a rooting substrate because many trees establish epiphytically in Hawaiian forests (Drake and Pratt 2001). Each species was in a different genus, so hereafter we refer to species by their genus names (see Table 2 for complete names). The mean ± SE for seedling height across all censuses was 8.8 ± 0.27 cm, with all individuals <2.6 m.

We measured irradiance and substrate to allow estimation of habitat associations. We determined the percentage cover of each substrate type (categories listed above) in the 160 × 160 m central area of the 4 ha FDP using 20 m long point-intercept line transects ($N = 32$) located in a random stratified design. Substrate data were collected every 10 cm along each transect. To characterize the seedling light environment, we measured understory and above canopy photosynthetically active radiation (PAR, μmol photons$\cdot m^{-2} \cdot s^{-1}$) and determined transmitted PAR (TPAR as understory PAR/above canopy PAR; Anderson 1964, Nicotra and Chazdon 1994). We used mean TPAR values from four measurements (in December 2009, July 2010, December 2010, and June 2011) to represent average light levels for each seedling plot in summer and winter. For each measurement, we recorded two consecutive 15 s average PAR measurements using a 1 m long line quantum sensor (LI-191, LI-COR, Lincoln, NE, USA) positioned 1 m above the center of each seedling plot and above-canopy PAR measurements logged at 1 minute intervals from a point quantum sensor (LI-190; LI-COR) mounted on a climate tower adjacent to the FDP. We determined TPAR on uniformly overcast days to focus on the diffuse irradiance transmitted to the seedlings. Diffuse TPAR measured on overcast days correlates well with mean total daily PAR and long-term mean PAR in the understory (Anderson 1964, Parent and Messier 1996, Tobin and Reich 2009). Further, diffuse irradiance better represents the light available to understory plants and that to which they are acclimated, due to its deeper penetration into the forest canopy versus direct irradiance (Alton et al. 2007, Urban et al. 2007, Tobin and Reich 2009). As confirmation of the validity of sampling on overcast days, we assessed the proportion of diffuse total above-canopy PAR using a BF3 "Sunshine Sensor" (Delta-T Devices Ltd, Cambridge, UK; Wood et al. 2003) mounted on an above-canopy climate tower adjacent to the FDP. Our approach was validated, as the mean ± SE for the proportion of diffuse to total PAR was 91 ± 0.01% during the TPAR measurements.

Analysis

Our analyses focused on seedling recruitment limitations and habitat associations. We quantified recruitment limitation factors across the FDP

Table 2. Species found in seedling plots and/or seed traps in Laupahoehoe FDP; minimum, mean, and maximum heights with number of individuals found (N), and recruitment limitations calculated over 2.5 yrs; limitation formulas in Fig. 1; detailed species data in Appendix: Table A1.

				Limitation component				
Species	Code	Height (cm)	N	Source	Dispersal	Seed	Estab	Seedling
Acacia koa	AK	1.0–**28.0**–188	10	0	0.42	0.42	0.81	0.89
Broussaisia arguta	BA	1.0–**15.0**–82.0	8	1.00		1.00		0.95
Cheirodendron trigynum	CT	0.5–**4.5**–240	1496	0	0	0	0.19	0.20
Clermontia parviflora	CP	12.0–**43.0**–104	3	1.00		1.00		0.95
Coprosma rhynchocarpa	CR	0.5–**8.0**–243	370	0	0.11	0.11	0.14	0.28
Hedyotis hillebrandii	HH	**36.0**	1	1.00		1.00		0.98
Ilex anomala	IA	0.5–**33.0**–186	16	1.00		1.00		0.81
Leptecophylla tameiameiae	LT	2.0–**6.0**–14.0	3	1.00		1.00		0.97
Metrosideros polymorpha	MP	0.5–**3.5**–256	1494	0	0	0	0.14	0.14
Myrsine lessertiana	ML	5.5–**16.0**–28.0	3	0.13	0.95	0.95	0.33	0.97
Perrottetia sandwicensis	PS	2.0–**5.8**–14.0	4	0.48	0.70	0.84	0.70	0.95
Vaccinium calycinum	VC	0.50–**23.0**–175	118	0	0.87	0.88		0.59

Notes: Empty cells indicate that the value could not be calculated from the data. The three most common species appear in bold. Nomenclature follows Wagner et al. (1999) and Stevens (2001 onwards). Sample sizes: seedling plots $N = 192$ and seed traps $N = 64$. Estab, establishment.

after Muller-Landau et al. (2002; see Fig. 1 for logic and formulas). We calculated seed limitation (L_{seed}) and its two subcomponents, source and dispersal limitations (L_{src} and L_{disp}), from seed trap data; and calculated seedling and establishment limitations (L_{sdlg} and L_{est}) from seedling plot census data. We calculated these factors for each species represented in the seedling plots. We excluded *Vaccinium* from seedling and establishment limitation calculations because we could not reliably distinguish true seedlings from vegetative clones. Limitation values range from 0 to 1, with a higher value indicating stronger limitation. The L_{src} formulation used (Fig. 1) assumes that seeds have equal probability of arriving everywhere, and thus are randomly (stochastically) distributed. An alternative equation for L_{src} assumes a uniform or hyper-dispersed distribution of seeds such that seeds are evenly distributed to all sites (Muller-Landau et al. 2002). For our data, both formulas provided similar results and therefore we present results based only on the former. We regressed each variable (L_{seed} and L_{est}) on L_{sdlg} both separately and combined, and regressed seed limitation subcomponents (L_{src}, L_{disp}) on L_{seed} to determine which most closely predicted seed limitation. We conducted analyses using R version 2.15.0 (R Development Core Team 2012).

To test for habitat associations, we conducted randomized χ^2 goodness-of-fit tests on the distribution of each species across habitat categories using Monte-Carlo randomization with 1000 iterations, similar to Webb and Peart (2000). In preliminary tests using Moran's I analysis (Fortin and Dale 2005), we found that spatial autocorrelation existed for irradiance within, but not across, census stations. We accounted for this, and for possible spatial autocorrelation of substrate, by employing a randomization analysis that tests for habitat associations independent of space, similar to that used by previous authors (e.g., Webb and Peart 2000, Harms et al. 2001). Analyses conducted comparing this approach with standard contingency tests and torus-translation randomization methods show that the full randomization method we used was the most conservative of the three (Harms et al. 2001). We used this more conservative test as it could be applied to our habitat data that we collected at the seedling plot scale (for irradiance) or individual seedling scale (for substrate). We tested actual distributions for each species against expected distributions based on relative abundance of substrates within the FDP measured using random transects (as described above). For light habitat, we tested actual distributions against the proportion of seedling plots in each light category. For the analysis of light habitat associations, we transformed TPAR into a categorical variable based on inter-quartile ranges (low TPAR, $<4\%$; low-median TPAR, ≥ 4–6%; median-high TPAR, ≥ 6–8%; high TPAR, $\geq 8\%$; Valencia et al. 2004). As an indication of the degree of habitat association, we used the unsquared χ^2 values as a simple index to examine the degree of deviations from the expected frequencies in each habitat as: (observed frequency − expected frequency)/expected frequency (Agresti 2007). For this metric, zero indicates no difference from random distributions, positive values represent positive associations, and negative values represent negative associations with the value of the number representing the magnitude of the deviation.

Habitat associations for given species suggest the importance of niche processes, but they do not necessarily indicate habitat differentiation *among* species. To test whether substrate and TPAR habitat associations differed among seedling species, we calculated Pianka's niche overlap index (Pianka's *O*) for each pairwise combination of species with adequate sample sizes (total 15 pairs) and compared actual niche overlap values with randomly generated simulations (1000 iterations) to obtain p-values using the bootstrap procedure in the 'pgirmess' package in R (Pianka 1973, Gotelli and Entsminger 2000, Cavender-Bares et al. 2004, Giraudoux 2009). Pianka's *O* measures the relative frequency of shared microhabitat utilization by species pairs; values range from 0 (no overlap) to 1 (total overlap). This approach is commonly used for analysis of habitat use by animals (e.g., Glen and Dickman 2008, Hadi et al. 2012) and may also be effectively applied to vegetation, as the index behaves similarly to other commonly used niche overlap measures (Potts et al. 2004, Rödder and Engler 2011, Wilson and Stubbs 2012). Habitat association and niche overlap analyses were conducted for the six species found in at least four of the seedling plots.

Comparisons of habitat associations and limitation indices among tropical forests

To examine the hypotheses listed in Table 1, we compared limitation indices and the proportion of species with habitat associations across forests varying in diversity. We restricted our comparisons to forest plots that used similar seedling and seed measurement experimental designs (i.e., 1 m^2 seedling plots and 0.5 m^2 seed traps). We compared our mean values for L_{seed}, L_{src}, L_{disp}, and L_{est} with published means from four studies in two other tropical forests: Nouragues, French Guiana (Bongers et al. 2001, Norden et al. 2009) and BCI, Panama (Dalling et al. 2002, Muller-Landau et al. 2002, Losos and Leigh 2004) and we further compared our data for mean L_{src} with that of a temperate plot located in Changbai, China (Li et al. 2012). We compiled results on the proportion of species with habitat associations in four published studies of three forests located in Gunung Palung, Borneo (Webb 1997, Webb and Peart 2000), Yasunì, Ecuador (Queenborough et al. 2007, Metz 2012), and BCI, Panama (Comita et al. 2007). Differences in light availability across microhabitats directly represent the availability of above-ground resources (Denslow 1980) while variations in substrate or topography are likely to affect plants through availability of below-ground resources such as soil nutrients and water (Clark et al. 1999). Thus, we separately examined the proportion of species associated with above-ground habitat factors (e.g., light) and below-ground habitat factors (e.g., substrate, topography, and physiography as proxies for soil water and nutrient resources).

RESULTS

Importance of seed and establishment limitations in low-diversity Hawaiian wet forest

Over 2.5 yrs, nearly 50,000 *Metrosideros* seeds and >36,000 seeds of six other species arrived in seed traps, including seeds for seven of the 12 species for which we found seedlings in seedling plots. All limitations were highly variable among species in Hawaiian forest (Table 2). Of 18 tree species found within the FDP, all but four species had almost complete L_{src} and high L_{disp} (i.e., only dispersing seeds into <5% of traps) and high L_{sdlg} values (i.e., seedlings recruited in <10% of seedling plots). For those species, mean values ± SE for L_{src} and L_{disp} were 0.47 ± 0.14 and 0.44 ± 0.16, respectively. This indicates that, on average, species produced too few seeds to distribute them into half the traps, and dispersed seeds into fewer than half the traps. These limitations resulted in a mean for L_{seed} of 0.68 ± 0.12 (N = 12). By contrast, the three most common species, *Metrosideros*, *Cheirodendron* and *Coprosma* (in order of commonness) had low to zero L_{seed}, L_{src}, and L_{disp}.

Establishment limitation was as important as seed limitation for the most common species in

Hawaiian forest. Indeed, L_{est} was equal to or higher than L_{seed} for four of the six species for which L_{est} could be calculated (Table 2). When averaged across species, L_{est} was statistically similar to L_{seed} (0.39 ± 0.12 and 0.38 ± 0.17, respectively; paired t-test $t = 0.022$, $P = 0.98$). Overall recruitment success differed strongly among species, and the three most common tree species comprised 95% of all seedlings. Species could be divided into two distinct groups: three species with low-to-moderate overall L_{sdlg} (range 0.19–0.23), and 15 species with high L_{sdlg} (range 0.59–1). Across species, L_{sdlg} was more strongly related to L_{seed} than L_{est} ($R^2 = 0.80$ versus 0.64; $F_{1,10} = 40$ and $F_{1,4} = 7.2$; $P < 0.001$ and 0.055, respectively) and L_{seed} was more strongly related to L_{disp} than L_{src} ($R^2 = 0.99$ versus 0.55; $F_{1,5} = 345$ and $F_{1,10} = 12$; $P < 0.001$ and 0.005, respectively), based on linear regression analysis.

Strong habitat associations in Hawaiian wet forest

Species distributions were linked with habitat. Of the six species analyzed, five showed significant associations with substrate type and three with TPAR category. The strength of associations varied across species as indicated by the degree of deviations from the expected frequencies in each habitat, which ranged from −1.0 to 5.6 for substrate (indicating none to >65 times as many seedlings as expected) and −1.0 to 1.1 for TPAR (indicating none to >2 times as many seedling as expected; Fig. 3). All species were positively associated with tree ferns and negatively associated with soil. All species were positively associated with at least two substrates, and in particular, *Metrosideros* was positively associated with all substrates except soil (Fig. 3). All species except *Ilex* were positively associated with high irradiance and negatively associated with low irradiance (Fig. 3). Seedling habitat associations did not reflect commonness of substrates but did reflect commonness of understory irradiance environments. For example, few seedlings were found on soil (7%), though it was the most common substrate, accounting for almost half the substrate cover in the plot (46%). Instead, nearly half of the seedlings occurred on tree ferns (45%), although the tree fern substrate comprised only 9% of estimated cover. For TPAR, species appeared to be relatively evenly distributed

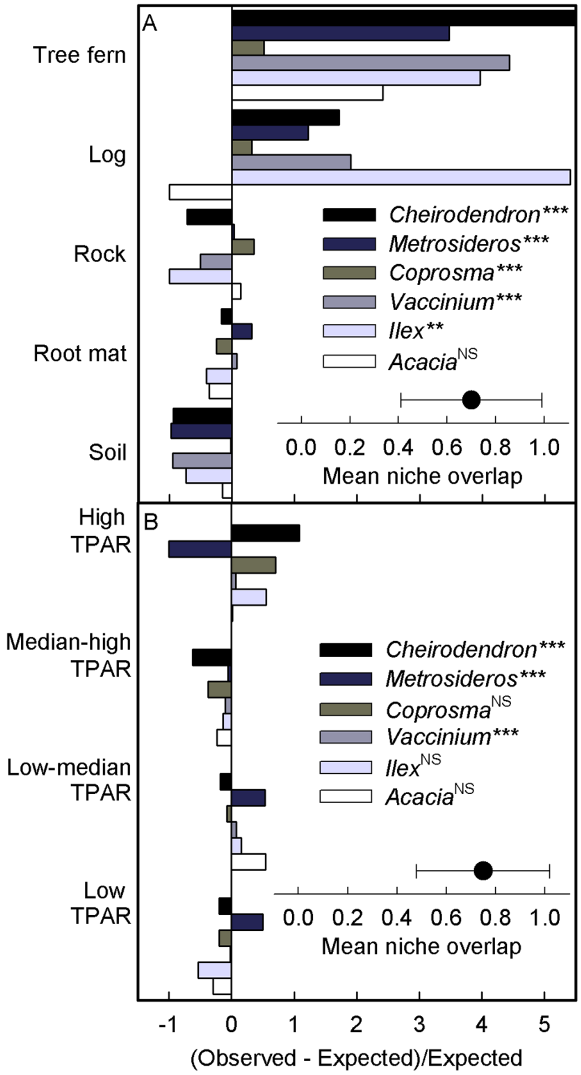

Fig. 3. Degree and direction of habitat associations with (A) substrate and (B) percent transmitted photosynthetically active radiation (TPAR) for Hawaiian wet forest seedlings displayed as the ratio of (observed − expected)/expected such that distributions not different from null expectations equal zero; positive values indicate positive associations and negative values indicate negative associations based on χ^2 randomization tests (** $P < 0.01$, *** $P < 0.001$, $^{\mathrm{NS}}$ not significant) with inset figures indicate Pianka's niche overlap averaged over all 15 pairwise combinations of species (see Appendix: Fig. A1 for means for each species pair). Species sorted in decreasing order of abundance.

across the range of irradiance levels most commonly encountered in seedling plots, with most species showing preferences for low-median TPAR and high TPAR (32% and 30% of seedlings, respectively).

Significant niche overlap in Hawaiian wet forest

Although all species were significantly associated with at least one habitat category, analysis of Pianka's *O* showed that species' habitat distributions across substrate and TPAR categories overlapped more than expected by random chance. Bootstrapped mean Pianka's *O* values among 15 species pairs were similar for substrate and TPAR, indicating that species overlapped similarly in their abundances in substrate and light categories. For substrate, they ranged from 0.45 to 0.94 (mean, 0.70 and 95% CI, 0.29) and for TPAR, they ranged from 0.44 to 0.88 (mean, 0.75 and 95% CI, 0.27; Fig. 3 and Appendix: Fig. A1).

Comparisons of habitat associations and limitation indices among tropical forests

Seedling recruitment factors were remarkably similar when averaged across species and comparing forest sites overall. Across forests varying strongly in diversity, mean values for L_{sdlg} and L_{seed} were similar while L_{est} was higher for BCI than for Laupahoehoe, and lowest for Nouragues. Thus, the low-diversity site was intermediate in L_{est} to two high-diversity sites. When we examined the two components of L_{seed}, we found that L_{src} in Laupahoehoe was intermediate and mean L_{disp} was similar across forests varying in diversity (Fig. 4). However, limitation indices varied considerably among species within each of the forests compared.

We found a higher proportion of species with habitat associations in Hawaii than reported in previous studies of other tropical forests (Table 3), except for a recent study in Yasuni, Ecuador (Metz 2012). In the Laupahoehoe FDP, 57% of seedling species were associated with TPAR and 86% were associated with substrate, compared with an overall average of 30% ± 10 (SE) of species with habitat associations in other studies. When habitats associated with above- or below-ground resources were considered separately (e.g., light as an above-ground resource versus substrate and topography as below-ground resources), there was the first indication of a potential inverse relationship between the frequency of seedling light habitat associations and diversity across the three forests compared (Table 3). By contrast, though Laupahoehoe had higher associations than the other FDPs, there was no apparent trend for decreasing habitat associations with increased diversity for below-ground resources (e.g., topography and substrate; Table 3).

DISCUSSION

Strong importance of seed and establishment limitation in low-diversity Hawaiian wet forest

Although both L_{seed} and L_{est} were high for most of the Hawaiian forest species, L_{seed} was most important for defining seedling regeneration patterns. Fourteen of 18 species found in the FDP were highly seed limited while the four most common seedling species had low L_{seed}. Indeed, across species, L_{sdlg} was driven by low seed availability and dispersal rates, and L_{est} influenced seedling distribution to a lesser extent. Although L_{src} was widespread and probably limits the regeneration of most species, L_{disp} better predicted seedling distributions, suggesting that seed dispersal, rather than seed production, was the primary determinant of differences in seedling recruitment for the majority of species. We note that species varied substantially in dispersal mode from *Metrosideros* with abundant wind dispersed seeds versus *Ilex* with larger animal dispersed fruits.

The relative importance of L_{seed} versus L_{est} was associated with species' relative abundances. One striking finding was that two species, *Metrosideros* and *Cheirodendron*, had zero seed limitation, a phenomenon not previously reported for any studies of comparable duration (Dalling and Hubbell 2002, Muller-Landau et al. 2002, Norden et al. 2009). In other forests, such a phenomenon might be observed after masting years (Metz et al. 2008), but the biology of *Metrosideros* is apparently distinctive in showing this kind of output, each year saturating the landscape with a large number of tiny seeds (Drake 1992). The other species, *Cheirodendron*, is a ubiquitous midstory tree that produces abundant bird-dispersed fruits. However, aside from these exceptionally successful species, most of the tree species recorded in the FDP were completely

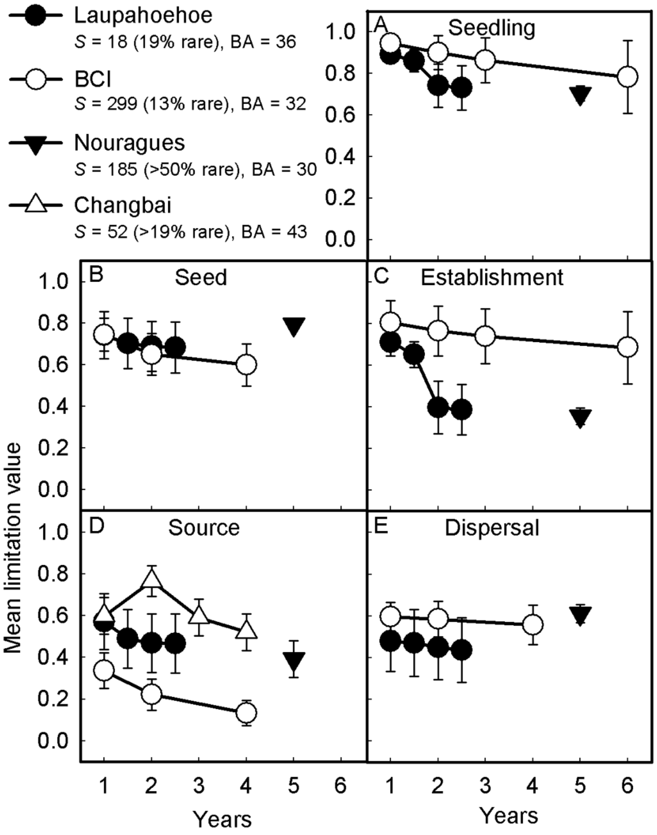

Fig. 4. Seedling recruitment limitation components (as described in Fig. 1) for three forest sites (A) seedling limitation, (B) seed limitation, (C) establishment limitation, (D) source limitation, and (E) dispersal limitation; with the mean ± SE across all species for all time intervals reported; the number of freestanding woody species ≥1 cm DBH within each FDP (S); and the basal area in $m^2 \cdot ha^{-1}$ (BA) from Bongers et al. (2001), Losos and Leigh (2004), and Chave et al. (2008). The number of species included in average ranges for each site (N) are: Laupahoehoe, Hawaii $N = 6–12$ as in Table 2; BCI, Panama $N = 15$ for seed, source, and dispersal limitations (Dalling et al. 2002) including two from Muller-Landau et al. (2002), and $N = 4$ for seedling and establishment limitations (Muller-Landau et al. 2002); Nouragues, French Guiana $N = 14$ (only 5 yr averages were reported; Norden et al. 2009); Changbai, China $N = 25$ (temperate forest; Li et al. 2012).

seed limited ($L_{seed} = 1$), including five of the species with seedlings found in seedling plots. Consequently, L_{seed} may scale up to determine the relative abundances not only of seedlings, but also of canopy trees, which in turn determines L_{seed}, possibly establishing a positive feedback mechanism. Such tantalizing linkages between seed, seedling, and tree abundance require further confirmation because interpretations of the relative importance of recruitment limitations can be affected by study length and type. For example, L_{seed} has been found to be lower for longer field studies (Muller-Landau et al. 2002) and for experimental studies (Clark et al. 2007). Additionally, L_{est} may be underestimated for rare species or those with extremely patchy distributions. Nevertheless, the negative linkage of L_{seed} with species abundance is strong at the scale of our study and confirms expectations from theory and other forests (Muller-Landau et al. 2002, Losos and Leigh 2004, Gravel et al. 2006).

Strong habitat associations and niche overlap for seedlings in low-diversity Hawaiian forest

In Hawaiian wet forest, most species were strongly associated with specific ranges of irradiance and/or substrate types. However, all species were positively associated with more

Table 3. Extent of habitat associations (percentage of species) in tropical forests with the number of species tested in parentheses, plot location and size, and the analysis used to test significance of habitat associations.

Habitat variable	Site	S	Habitat associations (%)	Analysis	Source
Aboveground					
Light	Laupahoehoe, Hawaii	18	57 (7)	χ^2 randomization	1
	Gunung Palung, Borneo	325	17 (45)	Logistic regression	2
	Yasunì, Ecuador	1114	13 (15)	Logistic regression	3
Belowground					
Substrate	Laupahoehoe, Hawaii	18	86 (7)	χ^2 randomization	1
Topography	BCI, Panama	299	24 (80)	Torus translation	4
Physiography	Gunung Palung, Borneo	325	23 (22)	χ^2 randomization	2
Topography	Yasunì, Ecuador	1114	71 (83)†	Torus translation	5

Notes: Differences in light across microhabitats directly represents availability of above-ground resources (Denslow 1980) while variation in substrate or topography are likely to affect plants through availability of below-ground resources such as soil nutrients and water (Clark et al. 1999), thus we grouped studies by whether above- or below-ground habitat variables were assessed and then sorted the studies in ascending order of species richness (S). Basal area of Gunung Palung is 43 $\mathrm{m^2 \cdot ha^{-1}}$ (Webb 1997); and Yasunì is 33 $\mathrm{m^2 \cdot ha^{-1}}$ (Losos and Leigh 2004). The Gunung Palung site is comprised of 28 0.6 ha plots, while BCI and Yasunì sites are each 50 ha FDPs. Sources: 1, this study; 2, Webb and Peart (2000); 3, Queenborough et al. (2007); 4, Comita et al. (2007); 5, Metz (2012).

† Averaged over 8 yrs of data collection.

than one habitat category, and species' habitat associations overlapped substantially. Our results are consistent with studies in high-diversity forests in which new recruits had weak habitat specificity (Kanagaraj et al. 2011) or in which a number of tree species shared preferred habitats (Webb and Peart 2000). The co-occurrence of strong habitat associations and high niche overlap found here for seedling species may be a typical pattern and should be further examined across forests and life-stages. More generally, we note that niche differentiation is often inferred from the existence of habitat associations (Hutchinson 1957, Whittaker 1965, Tilman 1987, Chesson 2000, Wright 2002, Yamada et al. 2006, Chen et al. 2010, Chuyong et al. 2011). However, given the potential commonness of overlapping habitat preferences we suggest caution in treating these as equivalent since they may often be decoupled.

There are several possible explanations for the substantial niche overlap at the scale observed in low-diversity Hawaiian forest. A first explanation may relate to the specifics of the forest community in which we conducted the study. For example, the strong association of Hawaiian forest seedlings with tree ferns resulted in significant overlap in species' substrate preference. This important role of tree ferns for seedling establishment has previously been indicated for other forests in Hawaii and New Zealand (Scowcroft 1992, Coomes et al. 2005, Gaxiola et al. 2008, Cole et al. 2012). Tree ferns are a significant component of Hawaiian wet forests (Kitayama et al. 1997). Their trunks are composed of adventitious roots which trap organic matter; therefore this substrate may increase plant water and nutrient availability (not measured in our study). Further, the Hawaiian forest might have a particularly limited range of acceptable substrates because of invasive feral pig-disturbance to soil (Drake 1992, LePage et al. 2000, Baltzer and Thomas 2010) and tree ferns can provide a refuge from soil disturbance caused by invasive pigs (Cole et al. 2012). High native and non-native swine densities are common in many forests, including other FDPs, and are known to significantly affect native tree regeneration (Barrios-Garcia and Ballari 2012). Though we observed feral pig activity in some seedling plots, we did not directly investigate the linkage between pig presence and substrate. According to the principle of competitive exclusion, specialization on tree ferns could lead to reduced diversity over time. Experimental assessment of growth and survival on tree ferns versus soil would be extremely valuable to determine how different substrates affect recruitment to larger size classes.

Other explanations for the high niche overlap observed in Hawaiian forest may be derived from the unique properties of these forests. Hubbell (2006) predicted that a low-diversity system should have more predictable pairwise interspecific interactions between few species and thus particularly strong niche differentiation. Although the forest we studied has only 18 tree species, diversity might still be too high for the effect predicted by Hubbell (2006) to be apparent. Additional cross-site studies would be necessary to identify a low-diversity threshold that might lead to strong niche differentiation by that mechanism. Another explanation is that species may require more time to evolve niche differences than has been available in the assembly of the Hawaiian forest community. However, given that the majority of native Hawaiian species radiated from ancestral colonists into endemic species (Carlquist 1985, Price and Clague 2002, Givnish et al. 2009), it seems reasonable to expect that there has been adequate time for habitat niche differentiation in response to interspecific competition and habitat heterogeneity to also occur (Lankau 2011).

Another explanation may relate to the particular limitations of our study design. Plants respond to many resources and we might have found niche differentiation had we measured species associations with, for example, soil moisture or nutrients (Baltzer et al. 2005, Baraloto et al. 2006, Baraloto et al. 2007, Comita and Engelbrecht 2009). Indeed, while light adaptation is generally a major axis of variation among species in most forests (Augspurger 1984, Denslow 1987, Poorter 1999, Hubbell 2006), plants tend to show the strongest differentiation in relative performance at very low irradiances (Kobe 1999), and the Laupahoehoe FDP had relatively high understory irradiance (6.4% transmitted irradiance versus 0.01–3.0% in other evergreen rainforests; Coomes and Grubb 2000). Further, although niche differences are expected to be apparent at the seedling stage (Grubb 1977), we might find more evidence of niche differences in larger size classes which reflect cumulative survival responses to environmental conditions (Comita et al. 2007). Future studies can provide valuable insight into regeneration and community assembly processes by disentangling and elucidating these mechanisms.

Finally, there is a strong likelihood that the high niche overlap we observed is related to the high seed limitation of most species, and on average, of the entire community. Theories propose that all limitations on recruitment, especially L_{seed}, should equalize interspecific interactions and enable species coexistence in the absence of niche differences (Tilman 1994, Hurtt and Pacala 1995, Chesson 2000, Hubbell 2005). Thus, our results may be taken as one case in support of strong recruitment limitations permitting coexistence without strong niche differentiation among most species in low-diversity forest.

Comparisons of habitat associations and limitation indices among tropical forests

Our results were partially aligned with theoretical expectations for how recruitment limitations and the frequency of habitat associations may vary across forests varying in diversity and structure (Table 1). Our comparisons provided some evidence in support of the prediction that habitat associations would be higher in forests with low species diversity (Table 1, P2B). This effect may have overwhelmed the tendency for a similar importance of habitat for establishment in forests with similar overall structure (Table 1, P1). However, the low diversity of Hawaiian forest was not a complete explanation for even the greater light habitat associations because the predicted mechanism for increased associations in low-diversity forest was increased niche differentiation due to highly predictable interspecific interactions among relatively few species (Hubbell 2006), whereas instead we found high niche overlap. The strong variation in seedling recruitment limitations among species within each FDP, rather than among FDPs, implies that variation in species' life-history characteristics may influence the relative importance of recruitment limitations more so than variation in ecosystem characteristics. Thus, regeneration limitations appear analogous to species traits such as leaf structure and processes such as litter decomposition, in that they may vary more among species within an ecosystem than across ecosystems (Sack and Holbrook 2006, Cornwell et al. 2008).

A high frequency of habitat associations in low-diversity forest was also predicted by a lower proportion of rare species in low-diversity forest (Table 1, P3). The hypothesized mechanism for that effect was that a lower L_{seed} would increase the potential for species competitive interactions and therefore increase the relative importance of habitat differentiation. Instead, the available data showed that L_{seed} did not co-vary with diversity among forests (Fig. 4). Thus, P3 could not be accepted as the explanation for the strong habitat associations in Hawaiian forest. Indeed, mean L_{seed} in Hawaiian forests was similar to mean values from other tropical forests, while L_{est} was lower, which was contrary to this prediction (Fig. 4). We note that the BCI and Laupahoehoe FDPs had a similar proportion of rare species, and thus based on species rarity we would not have expected dramatic differences to arise between these two forests. Further, Nouragues has an extremely high proportion of rare species (>50%; Bongers et al. 2001) but mean L_{seed} across species was only slightly higher than in Hawaiian forest. We note that the relative abundance of pollinators, dispersers, and seed predators in Hawaii versus other forests is unknown, and that these factors may act in concert with diversity and species rarity to equalize L_{seed} among forests.

Seedling habitat niche overlap might have been similar among forests, but we were unable to evaluate this because seedling niche overlap was not analyzed in the other studies in our comparison group. We note that a greater proportion of species with significant habitat associations does not necessarily indicate greater differentiation among species in their preferred habitats. Indeed, a number of recent studies found that habitat associations overlap among species within high-diversity forests, which may be expected given the large number of species and relatively few habitat categories typically examined. For instance, at BCI all but one of 30 species with significant positive associations were associated with more than one habitat at the seedling stage (Comita et al. 2007). Queenborough (2007) concluded that strict habitat partitioning alone could not account for the coexistence of the 16 Myristicaceae species examined in Yasunì, despite evidence of habitat associations. Potts et al. (2004) examined tree elevational distributions using an index of niche overlap comparable to ours, and found overlaps ranging from 0.62 ± 0.07 to 0.70 ± 0.05 SE; only slightly lower than the average Pianka's *O* among species pairs in the Laupahoehoe FDP (0.73 ± 0.04). This suggests that niche overlap in high-diversity forests could be as extensive as in low-diversity forest. Conversely, experimental studies in tropical forests have indicated substantial species differences in seedling resource responses (Augspurger 1984, Kobe 1999, Givnish et al. 2004, Baraloto et al. 2005). Our findings point to the need for controlled cross-site studies with detailed environmental measurements and the application of consistent methods to evaluate the degree of niche overlap among species.

Comparison of seedling recruitment factors and habitat associations across forests is essential to test the generalizability of hypotheses regarding tropical forest regeneration patterns and coexistence. Thus, we argue that the comparative approach outlined in our study is valuable as a first approximation despite the lack of standardized methods across sites and few available data. We note that differences among forest sites in the number and type of species selected, the size of the plot, study duration, and/or analytical methods (for habitat association analysis) might be expected to influence comparisons. Encouragingly, our analyses found that differences among sites appeared largely robust to most of those factors. While limitation factors showed clear temporal trends, we found that site ranks among forests for limitation indices remained similar over time (Fig. 4). We do not expect that our finding of especially strong habitat associations in Laupahoehoe is due to differences in analyses since the randomization tests we employed are more conservative than torus-translation tests which found fewer associated species (Harms et al. 2001). In addition, Metz (2012) analyzed the habitat distributions of 21–110 species over an eight year period and the proportion of species with habitat associations varied by only 11% (from 66–76%) across years and did not appear to be affected by the number of species sampled. Thus, we doubt that these results are an artifact of the study duration or the number species sampled. Finally, we do not expect that differences in plot sizes drove the seedling recruitment patterns we discovered across forests; we found no obvious trend between plot size and either limitations or habitat associations (Table 3 and Fig. 4). For example, the smallest plot had the highest proportion of habitat associations for below-ground resources, followed by two 50 ha FDPs which differed by 47% (Table 3). In addition, our 4 ha FDP had L_{src} values intermediate to a 25 ha and 50 ha FDP. Thus, we propose that the variation among forests in recruitment limitations and habitat associations involves some uncertainty, but that the overall patterns we found should be robust. Further, these first comparisons made with the available data provide a framework and stimulus to motivate further studies that can incorporate standardization of methods across a wider range of forest sites.

Conclusions and future work

To our knowledge this is the first study in low-diversity tropical forest to examine the extent of habitat associations and niche differentiation and the relative importance of seed and establishment limitations to community assembly processes. We answered three key questions for low-diversity Hawaiian wet forest and determined whether these answers were consistent with expectations from previous theory. Further, using the available published data, we examined how recruitment limitations and habitat associations vary among tropical forests. This study provides a critical first test of hypotheses linking recruitment limitations to ecosystem properties, leading to novel insights into how recruitment limitations and habitat associations vary with diversity within and among across tropical forests.

While many abiotic and biotic factors contribute to forest regeneration dynamics, this study showed that L_{seed} powerfully influenced regeneration patterns for less common species in a low-diversity forest. Further, both high-diversity and low-diversity tropical forests appeared to have similar seed limitation values when averaged across species. This was true despite substantial variation in L_{seed} among species within forests, and the dominance in Hawaiian wet forest of a species with zero seed limitation (*Metrosideros polymorpha*). The strong influence of L_{seed} across tropical forests likely contributes to species coexistence as a factor that leads to reduced competition, consistent with hypotheses of the maintenance of coexistence for species that overlap in habitat distributions, as found in Hawaiian forest. The degree to which the equalizing influence of strong L_{seed} may enable species to overlap in their preferred habitats in high-diversity forests, as indicated here for Hawaiian forest, requires further investigation.

Our results are an important step towards explicitly linking species diversity with recruitment limitations and habitat associations. Comparisons across tropical forests provide insight into how well current hypotheses from coexistence theory predict differences among ecosystems, but suggest that forest-specific mechanisms for recruitment limitations and habitat associations must be further investigated to explain these general patterns. As the first study to attempt to synthesize and extend current theories toward testable predictions for low-diversity forest, our findings open the discussion for further research and point to the necessity of future studies on recruitment limitations to better understand forest composition and dynamics across a wide range of forests.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Life history information for species found in seedling plots and/or seed traps in Hawaiian wet forest: life forms (C: canopy tree, M: midstory tree, S: shrub); adult tree relative abundance (RA) was calculated as number of individuals of species$_i$/number of individuals of all species.

Species	Auth.	Family	Life form	Propagule type	Seed size (mm)	Dispersal syndrome	RA
Acacia koa	A. Gray	Fabaceae	C	Pod	8.7	Gravity	1.58
Broussaisia arguta	Gaudich.	Hydrangaceae	S	Fruit	1	Bird	3.04
Cheirodendron trigynum	(Gaudich.) A. Heller	Araliaceae	M	Fruit	4	Bird	37.2
Clermontia parviflora	Gaudich. ex A. Gray	Campanulaceae	S	Fruit	0.7	Bird	0.21
Coprosma rhynchocarpa	A. Gray	Rubiaceae	M	Fruit	5.3	Bird	10.9
Hedyotis hillebrandii	(Fos.) Wagner & Herbst	Rubiaceae	S	Fruit	1.5	Bird	0.49
Ilex anomala	Hook. & Arn.	Aquifoliaceae	M	Fruit	2	Bird	10.8
Leptecophylla tameiameiae	(Cham. & Schltdl.) C. M. Weiller	Ericaceae	S	Fruit	3.5	Bird	0.02
Metrosideros polymorpha	(H. Lév.) H. St. John	Myrtaceae	C	Capsule	1.65	Wind	29.5
Myrsine lessertiana	A. DC.	Myrsinaceae	M	Fruit	4	Bird	2.65
Perrottetia sandwicensis	A. Gray	Celastraceae	M	Fruit	1.2	Bird	0.39
Vaccinium calycinum	Sm.	Ericaceae	S	Fruit	0.75	Bird	2.86

Notes: Nomenclature follows Wagner et al. (1999) and Stevens (2001–). Seed lengths are from the Bishop Museum Hawaii Ethnobotany Online Database (http://173.201.252.229/ethnobotanydb/ethnobotany.php). The three most common species appear in bold.

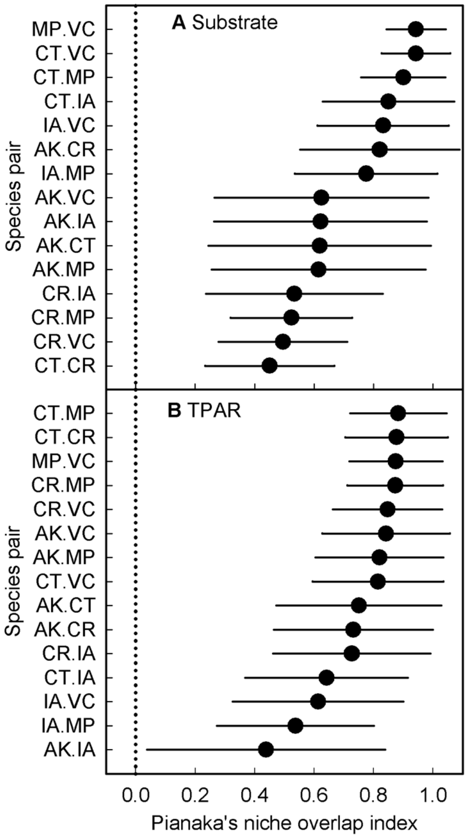

Fig. A1. Light and substrate niche overlap for 15 pairwise combinations of Hawaiian wet forest seedling species with adequate sample sizes; circles represent bootstrapped means (1000 iterations) and error bars represent 95% CIs; all values with CIs not overlapping zero represent significant niche overlap for that species pair; sorted in order of highest to lowest niche overlap; species codes as in Table 2.

CHAPTER 3

Niche differentiation of native tree seedlings in Hawaiian wet forest

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Abstract

For niche differences to maintain coexistence of sympatric species, each species must grow and/or survive better than each of the others in at least one set of conditions. However, the extent of niche differentiation in tropical forests is a subject of continued debate. We present the first test of performance (growth and survival) trade-offs for wild seedlings in a tropical forest. We measured seedling performance of four common native woody species across 22 irradiance, substrate, and topography microhabitats within Hawaiian montane wet forest over 2.5 years. All six species-pairs exhibited significant performance trade-offs across microhabitats and trade-offs for growth versus survival within the same microhabitat. Some species-pairs showed strong competitive differences (*i.e.*, the less competitive species, e.g., *Cheirodendron trigynum*, "won" few microhabitats versus the more competitive species, e.g., *Metrosideros polymorpha*). We also found evidence of competitive equivalence, with one species-pair, *C. trigynum* and *Coprosma rhynchocarpa*, having similar relative growth rates (RGR) in up to 24% of comparisons. Across species, survival under low-irradiance was negatively associated with RGR under high-irradiance. Topography (slope, aspect, and elevation) explained most variation in RGR (58%) followed by irradiance (19-24%) and substrate (18-23%). However, the relative effects of habitat resources differed among species and growth metric; irradiance was most important for height and mass RGR and substrate was most important for leaf RGR. These findings indicate that differential responses to microhabitats among species during regeneration fulfill the theoretical requirements for niche differentiation to contribute to species coexistence in low-diversity tropical forest, though other mechanisms may be required for the coexistence of species with small competitive differences.

Key-words

light, regeneration niche, relative growth rate, substrate, topography, trade-offs, tropical forest, rank changes, tropical forest diversity, seedling, survival

Introduction

Ecologists debate the extent to which partitioning of regeneration niches, defined as differential performance across environmental gradients, contributes to plant species coexistence (Grubb 1977, Chesson 2000, Wright 2002, Metz 2012). For niche differences to drive coexistence, species must change ranks in performance (i.e., growth or survival) such that each species outperforms each of the others in at least one habitat condition (Abrams 1983, Chesson 2000, Wright 2002). However, some authors have argued that trade-offs in given aspects of performance across habitats are infrequent and have only a small contribution to tropical forest community assembly because species and habitat differences are small (Kitajima and Bolker 2003). There has accumulated more evidence that a second type of trade-off – between growth and survival within and across habitats – contributes to coexistence. For example, high growth in high resource environments is associated with lower survival in low resource environments (Kitajima 1994, Walters and Reich 1996, 1999, Davies 2001, Sack and Grubb 2001, Dalling and Hubbell 2002, Dent and Burslem 2009, Wright et al. 2010). Differential species responses to environmental variation are well documented in tropical forests (*e.g.*, Augspurger 1984, Wright et al. 2003, Engelbrecht et al. 2007). However, fewer field-based studies have clearly demonstrated that species differ in their regeneration niche such that seedlings change performance ranks across habitats (Ashton and Gunatilleke 1995, Kobe 1999, Montgomery and Chazdon 2002, Baraloto et al. 2005, de Gouvenain et al. 2007). Most previous trade-off studies examined saplings or adult trees in the field (e.g., Pacala et al. 1994, Davies 2001) or experimentally manipulated seedlings in greenhouses (e.g., Sack). These data may not accurately represent adaptations of young plants in the wild (Bloor 2003, Cornelissen et al. 2003). We aimed to investigate performance trade-offs across microhabitats for seedlings of four common woody species in native-dominated Hawaiian montane wet forest. To our knowledge, this is the first study to examine trade-offs across multiple habitat dimensions for (1) naturally established seedlings or (2) species in low-diversity tropical forest.

We expected to find strong evidence of performance trade-offs for four reasons. First, niche differences should be most apparent during early tree regeneration stages because seedlings are more sensitive to environmental variation than adult trees (Grubb 1977, Poorter 2007). Second, assuming they are well-mixed spatially, common species interact with each other more frequently and are therefore more likely to evolve niche differences in response to interspecific competition than are rare species (Hubbell 2006). Third, niche differences may be the primary coexistence mechanism in low-diversity forests because other coexistence mechanisms, such as negative density-dependence and dispersal limitation, are predicted to be weaker (Janzen 1971, Hurtt and Pacala 1995, Gravel et al. 2006), though we lack evidence to support that classic assumption. Fourth, we measured multiple axes of microhabitat variation (irradiance, substrate, and topography) and multiple growth response variables (relative growth rate for height, biomass, and leaf area), to achieve a high power to resolve species differences (Russo et al. 2012). Because their extreme isolation and small land area, Hawaiian forests harbor a lower species diversity than most tropical forests of comparable climate and structure (Carlquist 1985, Price and Clague 2002, Losos and Leigh 2004), thereby providing a unique model system for testing hypotheses about niche differentiation and co-existence. In a previous study (Inman-Narahari et al. 2012) we showed that seedling distributions of common species are strongly limited by establishment and that species distributions show strong habitat associations, suggesting the possibility of niche differentiation.

We focused on seedling responses to three environmental factors – irradiance, topography, and substrate – because these factors affect plant growth and survival. First, irradiance is often the most limiting resource for plant growth in tropical wet forests and many studies demonstrated that plant species respond differentially to irradiance gradients (e.g., Augspurger 1984, Kobe 1999, Sack and Grubb 2001, Montgomery and Chazdon 2002, Poorter and Arets 2003). Second, many plant species are strongly associated with topographic gradients (John et al. 2007, Comita and Engelbrecht 2009, Metz 2012). Topography typically correlates with essential plant growth resources such as soil moisture and nutrient availability with, for example, higher soil moisture availability on slopes than plateaus (Becker et al. 1988, Daws et al. 2002, Sørensen et al. 2006). Third, we expected substrate to be an important axis of niche differentiation because many native species regenerate on organic substrates such as logs and downed tree ferns given feral ungulate soil disturbance in Hawaiian wet and mesic forests (Cole et al. 2012, Inman-Narahari et al. 2012).

We addressed the following three questions: (1) Do species differ in their performance (growth and survival) across habitats such that each species outperforms each of the others under some set of conditions (microhabitat trade-offs)?; (2) Do species change ranks between growth and survival within and across microhabitats (growth-survival trade-offs)?; (3) What is the relative importance of topography (aspect, slope, elevation), irradiance, and substrate microhabitats for seedling growth?

Materials and methods

Study site. — We conducted this study in the 4 ha Laupāhoehoe Forest Dynamics Plot (FDP), part of the Hawai‘i Permanent Plot Network (www.hippnet.hawaii.edu) and of the Smithsonian Tropical Research Institute Center for Tropical Forest Science (CTFS) network. The Laupāhoehoe FDP is located on Hawai‘i Island (19°55′N, 155°17'W) in the Laupāhoehoe Hawai‘i Experimental Tropical Forest (HETF). The FDP was established in 2008 at 1120 m elevation in native-dominated primary tropical lower montane wet forest (Holdridge 1947). The climate is largely aseasonal with 3440 mm mean annual rainfall (Giambelluca et al. 2011) and 16^{o}C mean annual temperature (Juvik and Juvik 1998). Within the FDP, all native woody species ≥1 cm DBH (diameter at breast height, i.e., at 1.3-m) were tagged, mapped, measured, and identified following standard protocols applied throughout the CTFS plot network (Condit 1998). The Laupāhoehoe FDP comprises 21 native woody species including three tree fern species.

Data collection. — In October-December 2008, we established a grid of 192 subplots of 1 m × 1 m within the 160 m × 160 m central area of the Laupāhoehoe FDP following CTFS seedling plot protocols (Wright et al. 2005; Fig. S1). Within subplots, we tagged all native woody species < 1 cm DBH (seedlings), measured stem height from stem base to apex to the nearest 0.5 cm, and counted the number of leaves, including cotyledons. Following our initial census in November/December 2008, we re-measured previously tagged seedlings and measured new seedlings four times over 2.5 yrs: in December 2009, July 2010, December 2010/January 2011, and July 2011.

We examined the four species that were sufficiently abundant ($N > 30$) within seedling plots to analyze performance differences: *Cheirodendron trigynum*, *Metrosideros polymorpha*, *Coprosma rhynchocarpa*, and *Vaccinium calycinum* (nomenclature follows Wagner et al. 1999;

we hereafter refer to these species by genus). These species vary substantially in growth form: *Metrosideros* is the dominant canopy tree in the Hawaiian Islands, *Cheirodendron* and *Coprosma* are midstory trees, and *Vaccinium* is an understory shrub. These four species comprised 98% of the seedlings found in seedling plots over the course of the study. They also represent 22% of the 18 species and 58% of the relative abundance (RA) of native woody species that reach ≥ 1 cm DBH in the Laupāhoehoe FDP (Table 3-1). Due to the low species diversity in Hawaiian forest, these four species represent a larger proportion of species diversity than in previous studies of performance trade-offs in forests that are more diverse. For example, of the hundreds of tree species in lowland wet forest in Costa Rica and French Guiana, Kobe (1999) and Baraloto et al. (2005) studied four and nine and species, respectively.

To evaluate topography, we used small-footprint, high-power airborne Light Detection and Ranging (LiDAR) developed by the Carnegie Airborne Observatory to create a digital elevation model (DEM) of the ground surface (Asner et al. 2007, Wu et al. 2012). For each seedling plot, we extracted slope, aspect, and elevation data from the DEM using the Spatial Analyst Tools in ArcGIS 10.0 (ESRI, Redlands, CA, USA). To quantify light, we measured diffuse photosynthetically active radiation (PAR, μmol photons$\cdot$m$^{-2}\cdot$s^{-1}) at each seedling plot and paired these measurements with above-canopy PAR measurements to calculate transmitted PAR (TPAR) for each seedling plot (Nicotra and Chazdon 1994, Montgomery and Chazdon 2002). To compare growth and survival among species across microhabitats, we distinguished four discrete microhabitat categories (low, low-intermediate, high-intermediate, and high) for each continuous environmental variable (slope, elevation, aspect, and TPAR). We recorded the rooting substrate of each seedling in six categories: live tree fern, dead tree fern, log, rock, root mat, and soil. Detailed methods for topography and TPAR data collection are in Appendix S3-1, and category values and means and variation in environmental conditions within the 4 ha FDP are in Appendix Table S3-1.

Analysis. — For each seedling, we calculated three growth metrics: stem height RGR (RGR_{ht}, $mm \cdot mm^{-1} \cdot yr^{-1}$), whole plant dry mass RGR (RGR_{mass}, $g \cdot g \cdot^{-1} yr^{-1}$), and total leaf area RGR (RGR_{leaf}, $cm^{2} \cdot cm^{-2} \cdot yr^{-1}$) using the classic formula: RGR = ln(final size) − ln(initial size)/(final date-initial date) (Hoffmann and Poorter 2002). For analysis of performance differences, we included only seedlings with RGR >0 because we were interested in trade-offs for seedlings exhibiting positive RGR, rather than for seedlings overcome by disease or herbivory. Because relative and absolute growth rates typically change with size (Poorter and Garnier 1996), we equalized starting sizes by including only individuals with initial heights below species-specific size thresholds which were approximately the mean size of new recruits (i.e., seedlings tagged after the first census; Table 3-1). We estimated plant biomass and leaf area from species-specific linear regressions of plant dry mass or mean area per leaf versus height of whole plants harvested in the nearby forest outside the FDP (Montgomery and Chazdon 2002; details in Appendix 3-1). We determined median survival (time at which 50% mortality occurs) for each species in each microhabitat from non-parametric Kaplan-Meier survival curves ('survival' R package; Stevenson 2011). To test for performance (RGR and survival) differences among species in each species-pair within each microhabitat category in which a sufficient number of seedlings of both species were present (≥3 for survival and >1 for RGR analyses), we used standard t-tests (for RGR) and rank-sum tests (for survival) with p-values corrected for multiple comparisons using false discovery rate correction (FDR; Benjamini and Yekutieli 2001). For the comparisons of performance in each microhabitat, we averaged values across all the other habitat categories (e.g., two species' values for RGR on logs were compared averaging values for seedlings of all irradiance and topography categories). Additionally, we used these performance differences to test for (a) growth-survival trade-offs for each species-pair within each microhabitat, and (b) trade-offs between low-irradiance survival and high irradiance RGR for each species pair (using low and high TPAR values). We chose to test for these particular trade-offs because they have been tested in the previous literature, though no previous study has tested these so comprehensively in many habitats in the field.

To determine the effects of environmental factors on RGR, we conducted relative importance analysis for the contribution of topography, TPAR, and substrate with initial height included as a covariate ('relaimpo' R package; Lindeman et al. 1980, Grömping 2006). We conducted all statistical analyses using R 2.13.2 (R Development Core Team 2012).

Results

Differences among species across all microhabitats.— Species initial sizes, relative growth rates, and survival differences averaged across all microhabitats indicate inherent competitive differences. *Metrosideros* was the strongest competitor overall, outperforming at least one other species in 81% of all comparisons of RGR or survival across all microhabitats in which species significantly differed (Table 3-1). *Vaccinium* was the second most competitive species, winning 74% of all microhabitats in which species differed in RGR or survival, followed by *Coprosma* and *Cheirodendron* (Table 3-1). All four species differed in median survival time when averaged over all microhabitats, with *Vaccinium* having 36%, 47% and 55% higher survival than *Coprosma*, *Metrosideros*, and *Cheirodendron*, respectively (Fig. 3-1).

Differences in performance across microhabitats.— We found substantial evidence for shifts in species' relative performances across microhabitats for all six species-pairs (Fig. 3-2A).

Among the four focal species, even the least competitive species outperformed the more competitive species in at least one microhabitat (Fig. 3-2A). Further, all species-pairs showed equivalence in at least one microhabitat for at least one RGR metric (Fig. 3-2A and Table S3-3). Indeed, the only species-pair that showed no ties across microhabitats was *Cheirodendron* and *Metrosideros* for $\mathrm{RGR}_{\mathrm{leaf}}$. We typically found a larger proportion of ties for survival than for RGR, possibly because survival is a coarser variable than RGR (*i.e.*, binary versus continuous variable).

Growth-survival trade-offs. — All species-pairs showed growth-survival trade-offs within at least one microhabitat (*e.g.*, RGR on logs versus survival on logs; Fig. 3-2B). Four of six species-pairs exhibited "win-lose" trade-offs such as, for example, species-A had significantly higher RGR but lower survival than species-B within a particular habitat. However, all species-pairs exhibited "win-tie" trade-offs such as, for example, species-A had higher survival than species-B but the species did not differ in RGR within a particular habitat. For example, we found growth-survival trade-offs for three of six species-pairs at low-intermediate elevation, with *Metrosideros* and *Cheirodendron* exchanging ranks for $\mathrm{RGR}_{\mathrm{mass}}$ and survival and both having higher $\mathrm{RGR}_{\mathrm{mass}}$ but not survival than *Coprosma*. Up to six species-pairs had growth-survival trade-offs within any one of the 22 microhabitats, with the most growth-survival trade-offs on dead tree ferns, intermediate-high elevation, low-intermediate slopes, and low TPAR.

We found strong trade-offs between low-irradiance survival and high irradiance RGR (*i.e.*, survival in low TPAR and RGR in high TPAR). For example, *Metrosideros* had the highest $\mathrm{RGR}_{\mathrm{mass}}$ rank at high TPAR but the lowest survival rank at low TPAR, while the rankings for *Vaccinium* were the opposite. The proportion of rank reversals varied among RGR metrics. We found significant reversals for five species-pairs for $\mathrm{RGR}_{\mathrm{leaf}}$, one species-pair for $\mathrm{RGR}_{\mathrm{mass}}$, and none for $\mathrm{RGR}_{\mathrm{ht}}$ (detailed results in Appendix S3-5)

Relative importance of microhabitat factors for seedling growth. — The relative importance of microhabitat factors varied by both species and RGR metric, though topography generally explained the largest proportion of variance in RGR. Over all species and RGR metrics, the microhabitat factors we measured explained 8-48% of the variation in seedling RGR (mean 20% ±4 SE) and initial height explained from 3-45% (mean 22% ±5 SE). When averaged over species, topography explained the majority of variation (51-52% ±5-7 SE) for all growth metrics. However, the second-most important factor varied among growth metrics, with TPAR the second most important for $\mathrm{RGR}_{\mathrm{ht}}$ and $\mathrm{RGR}_{\mathrm{mass}}$ (25% ±2 SE) and substrate the second most important for $\mathrm{RGR}_{\mathrm{leaf}}$ (32% ±5 SE). The relative importance of habitat factors also varied among species. For example, topography was the most important microhabitat factor for *Cheirodendron*, *Coprosma*, and *Metrosideros*, explaining 39 - 80% of variation in RGR when averaged across all growth metrics (Fig. 3-3). However, for *Vaccinium*, substrate type was most important, explaining 46-56% of variation in RGR. The relative importance of topographic attributes (slope, elevation, or aspect) also varied among species. Slope was most important in determining RGR for *Cheirodendron*, *Metrosideros*, and *Vaccinium*, whereas aspect was most important for *Coprosma* (Fig. 3-3).

Discussion

Strong differences in seedling performance across microhabitats. — In support of niche hypotheses, we found substantial shifts in seedling performance across heterogeneous microhabitats. All six species-pairs exchanged ranks for RGR and/or survival in at least one microhabitat, supporting predictions of shifting performance hierarchies across habitats in low-diversity Hawaiian forest. The less competitive species (*Coprosma* and *Cheirodendron*) outcompeted the superior competitors (*Metrosideros* and *Vaccinium*) in relatively few microhabitats categories, indicating strong competitive inequality among some species. Because there were few habitats in which the less-competitive species might beat more-competitive species, neutral mechanisms may be more important for coexistence of less competitive species. Another key finding was the importance of competitive equivalence, represented as ties where neither species in a pair exhibited significant differences in RGR or survival. For example, *Cheirodendron* was equivalent in performance to *Coprosma* in 34% of microhabitats. These results suggest that microhabitat trade-offs at the regeneration stage contribute to tree coexistence in low-diversity Hawaiian wet forest, but the relative importance of niche and neutral mechanisms may vary among species.

We found a larger proportion of species-pairs that differed in performance across habitats in Hawaiʻi than has been reported for other forests using a similar analysis to ours (Baraloto et al. 2005, Dent and Burslem 2009). For example, a study in French Guyana found performance differences across microhabitats for only three of 36 species-pairs of transplanted seedlings across irradiance and soil treatments (Baraloto et al. 2005), and a Borneo study found no reversals for three species in a shade-house experiment comparing seedling growth across irradiance and soil treatments (Dent and Burslem 2009). Other studies employing different analyses have also shown species' performance shifts across irradiance levels, but did not quantify shifts by species-pair (Agyeman et al. 1999, Sack and Grubb 2001). One explanation is that habitat differentiation may be higher in low-diversity forests because species have more predictable inter-specific interactions than in high-diversity forests (Hubbell 2006), and previous studies were conducted in high-diversity forests where hundreds of tree species coexist whereas the FDP where we conducted this study has far fewer species. Further, the species in this study all have low to no seed limitation (Inman-Narahari et al. 2012); low seed limitation is expected to increase the importance of niche relative to neutral mechanisms by increasing the potential for interspecific interactions (Hubbell 2001, Gravel et al. 2006). Another explanation is that we examined seedling responses to a larger number of habitat categories than most previous studies, which may increase the potential for discovering trade-offs (Kitajima and Poorter 2008, Philipson et al. 2011). In particular, the high-resolution topographic data provided by airborne LiDAR adds a unique new three-dimensional context in which to test ecological theories. These results point to the necessity of measuring several habitat characteristics across a range of forest types to further understand the extent of niche differentiation in tropical forests.

Growth-survival trade-offs within microhabitats. — We found substantial evidence of growth-survival trade-offs for given species-pairs within given microhabitats. In a study that used comparable methods, only two of 36 species-pairs showed "win-lose" growth-survival trade-offs within the same microhabitat (Baraloto et al. 2005). In our study, a larger proportion of species pairs, four of six, exhibited "win-lose" growth-survival trade-offs. These growth-survival trade-offs often permitted the slower-growing species, *Cheirodendron* or *Coprosma*, to outcompete faster-growing species, e.g., *Metrosideros*, by having higher survival. Thus, the slower-growing and large-seeded species appeared to be more shade-tolerant than the smaller-seeded faster-growing pioneer species. We propose that growth-survival trade-offs within microhabitats may be an important mechanism promoting coexistence and should be more widely investigated.

Growth-survival trade-offs across irradiance microhabitats. — When examined across microhabitats, we found substantial evidence of trade-offs between RGR in high irradiance versus survival in low irradiance, consistent with the theory of a general trade-off in physiological capabilities between shade-tolerators and light-demanders (Kitajima 1994, Sack and Grubb 2001, Kitajima and Poorter 2008). The proportion of species-pairs with trade-offs in Hawaiian forest was again higher than for other studies. For example, Augsperger (1984), Kobe (1999), and Baraloto (2005) found high-light RGR versus low-light survival trade-offs for 14%, 33%, and 22% of species-pairs, respectively. In our study, all six species-pairs showed a negative correlation between high irradiance mass-based RGR versus low irradiance survival. Similar to our results for within-microhabitat growth-survival comparisons, high-low irradiance growth-survival trade-offs permitted *Cheirodendron* and *Coprosma* to outcompete *Metrosideros* by having higher survival in low irradiance despite lower RGR in high irradiance. This suggests that these performance differences have the potential to facilitate species coexistence.

Relative importance of microhabitat factors.—Topography, specifically slope and aspect, was the most important environmental variable for predicting seedling RGR, pointing to the importance of soil resources for seedling growth. While we did not directly measure soil resources, studies in other forests have found that topographic variation correlates with variation in soil resources (*e.g.*, water and nutrients; Daws et al. 2002, John et al. 2007) and that soil and topographic resources strongly determine species growth differences across habitats (Palmiotto et al. 2004, Engelbrecht et al. 2007, Metz 2012). The relative importance of topography suggests that soil resources are stronger drivers of seedling RGR than either irradiance or substrate for most species in this forest. The observed weaker role of irradiance was consistent with a recent study reporting that light availability explained <12% of variation in tree growth rates within a lowland tropical forest in Panama (Rüger et al. 2011). Nonetheless, the relative importance of microhabitat factors requires much more investigation to understand how plant available resources vary with topography and the physiological mechanisms by which topography and irradiance affect seedling growth in forests.

Growth metrics matter. — Another important finding of this study was that interpretations of habitat trade-offs can depend on growth metrics. For example, if we had restricted our analysis to only height- or mass-based RGR, we would have found shifts in performance across microhabitats in RGR for only one of the six species-pairs. Similarly, a recent study in tropical China found trade-offs for mass but not height growth metrics (Yang et al. 2011). We found the most shifts in performance between species across microhabitats for leaf area-based RGR, which is less often measured than height- or mass-based RGR in comparative seedling studies. To our knowledge, this is the first time leaf area-based RGR has been used to analyze species performance differences across microhabitats. However, an experiment on seedling responses to regional environmental gradients in Panama also found stronger responses for leaf area than height (Brenes-Arguedas et al. 2010). Indeed, the fact that these variables are examined less frequently in studies of performance differences across habitats might partially explain the large proportion found in this study compared with previous research (Kobe 1999, Baraloto et al. 2005, Dent and Burslem 2009). Different growth metrics may provide different insights into plant growth. For example, rapid height growth may lead to increased irradiance interception and eventually contribute to competitive dominance where vertical irradiance gradients are very steep (Givnish 1982). However, leaf area growth can likewise increase irradiance interception and corresponds to photosynthetic area for potential carbon gain (Koyama and Kikuzawa 2009). This may be more important for small seedlings because their growth is more restricted by their ability to acquire limited resources in the understory than by direct competition with one another (Paine et al. 2008). Thus, until the precise measure of growth that best quantifies seedling relative performance is well resolved, the most comprehensive approach is to measure several aspects of plant growth to determine interspecific differences, ensuring as we did that statistical significance is determined after correcting for multiple tests. Leaf area growth may be an especially important measurement to resolve species trade-offs.

Competitive asymmetry and equivalence. — Despite evidence of shifts in species' performances across microhabitats, competitive relationships among species-pairs differed considerably, with some species-pairs showing a clear dominance hierarchy and others indicating relative equivalence. For instance, species ranks tended to follow a similar pattern that a less competitive species infrequently disrupted by outcompeting the typically superior competitor. However, some species-pairs tied for RGR on up to 24% of microhabitats and for survival on up to 90% of microhabitats. When species are ecologically equivalent (*i.e.*, neither species outperforms the other in any situation; Hubbell 2001), 'winners' at a particular site may be determined by neutral or other mechanisms such as density dependence (Janzen 1970, Connell 1971, Tilman 1994, Chesson 2000) or priority effects (*i.e.*, who arrives first; Connell and Slatyer 1977, Urban and De Meester 2009). Thus, niche mechanisms may primarily determine coexistence among the strongest competitors (*e.g.*, *Metrosideros* and *Vaccinium*), whereas neutral or other mechanisms may be more important for coexistence among the least competitive species (e.g., *Cheirodendron* and *Coprosma*).

Caveats regarding coexistence. — Our findings indicate that differential responses to microhabitats during regeneration may contribute to species coexistence in low-diversity tropical forest. However, we do not know if (1) competitive displacement caused the species differences,

(2) lack of niche differences among species will lead to competitive exclusion of all but one of these species, or (3) the observed seedling trade-offs control species relative abundance in the forest. Nevertheless, some trade-off patterns were consistent with the observed species relative abundance in the Laupāhoehoe FDP. For example, *Metrosideros* in the majority of conditions had higher RGR or survival than the three other species examined, consistent with it being the dominant canopy tree in this Hawaiian montane wet forest (Asner et al. 2009, Vitousek et al. 2009). On the other hand, *Cheirodendron*, a less-competitive midstory tree, had higher FDP-wide relative abundance than *Metrosideros* (Table 3-1), suggesting that adult size differences may be an aspect of significant niche differentiation which occur at later life-stages that our analysis did not take into account (Baraloto et al. 2005). Further, a complete examination of seedling trade-offs would consider seedling growth under combinations of given factors (e.g., on logs in high TPAR versus logs in low TPAR). Nevertheless, our data support the concept that niche differentiation, in concert with other mechanisms, are a potential contributor to patterns of forest dominance for endemic tree species in Hawaiian montane wet forest.

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Tables and figures

Table 3-1. Information for the focal species analyzed in Hawaiian wet forest. Means ± SE with sample sizes in parentheses are shown. Species sharing the same letter are not significantly different based on one-way ANOVA with Tukey's HSD."Wins" refers to the proportion of microhabitats in which each species performed significantly better than at least one other species

Variable	*Cheirodendron trigynum*	*Coprosma rhynchocarpa*	*Metrosideros polymorpha*	*Vaccinium calycinum*
Family	Araliaceae	Rubiaceae	Myrtaceae	Ericaceae
Author	(Gaudich.) A. Heller	A.Gray	(H. Lév.) H. St. John	Sm.
Species code	*CT*	*CR*	*MP*	*VC*
Habit	Midstory tree	Midstory tree	Canopy tree	Understory shrub
Tree RA (%)	27	7.9	21	2.1
Tree RD (%)	6.2	0.87	38	0.049
Tree RF (%)	10.2	10.1	10.2	5.23
Initial height threshold (cm)	5.0	5.0	2.0	10
Mean initial height of new recruits (cm)†	2.7^{A} ± 0.49 (1223)	3.5^{B} ± 1.6 (252)	0.65^{C} ± 0.16 (1199)	5.5^{B} ± 13.7 (32)
Seedling LMA ($g\cdot m^{-2}$) ‡	37^{A} ± 2.9 (11)	30^{B} ± 2.2 (14)	45^{C} ± 4.6 (19)	43^{D} ± 4.7 (7)
Seed mass (g)§	5.57×10^{-3} ± 7.97×10^{-5}	1.95×10^{-2} ± 1.10×10^{-3}	3.30×10^{-5} ± 5.70×10^{-6}	1.31×10^{-4} ± 6.12×10^{-6}
N for RGR_{ht} and RGR_{mass} / RGR_{leaf} /survival¶	394/ 321/ 1350	113/ 102/ 279	308/ 307/ 1179	27/ 26/ 43
RGR_{ht} wins	0.06	0.35	1.00	0.78
RGR_{mass} wins	0.36	0.02	1.00	0.68
RGR_{leaf} wins	0.08	0.43	0.81	0.71
Survival wins	0.08	0.43	0.81	0.71
Wins for all metrics	0.17	0.34	0.81	0.74

Notes: Relative abundance (RA = number of individuals of $species_i$ / number of individuals of all species × 100), relative dominance (RD = basal area of individuals of $species_i$ / basal area of all species × 100), and relative frequency (RF = number of 20 × 20 m quadrats in which species was recorded/ total number of quadrats × 100) are for trees ≥1 cm DBH within the 4 ha Laupāhoehoe FDP.

†New recruits defined as seedlings tagged following the first census.

‡ Leaf mass per area (LMA = leaf mass / leaf area) calculated for seedlings harvested outside of FDP boundaries (N = 5 to 21 individuals per species).

§Seed mass based on ≥ 3 samples of 30 – 228 seeds dried for ≥ 48 hours at 70 °C.

¶Sample sizes were higher for survival than RGR because seedlings must have survived at least one census interval to calculate RGR.

Figure captions

Figure 3-1. Relative growth rate (RGR) and median survival among the four focal species averaged over all habitats in Hawaiian wet forest, (A) height RGR; (B) dry mass RGR; (C) leaf area RGR; (D) median survival; error bars represent 95% CIs for RGR and SE for survival; species sharing the same letter are not significantly different (ANOVA Tukey's Post-Hoc analysis); species: *Cheirodendron trigynum* (*CT*), *Coprosma rhynchocarpa* (*CR*), *Metrosideros polymorpha* (*MC*), and *Vaccinium calycinum* (*VC*); sample sizes in Table 3-1.

Figure 3-2. Shifts in species performance across microhabitats and growth-survival trade-offs for all six species pairs representing four common species in Hawaiian wet forest; (A) the proportion of microhabitats in which each species had significantly higher performance (growth or survival) than the other species in the pair (*i.e.*, wins; listed in order of species 1 v. species 2, *e.g.*, *MP* v. *VC*) and the proportion of microhabitats in which neither species outperformed the other (*i.e.*, ties); 14-22 microhabitats had sufficient seedling numbers to be considered (≥ 3 for survival and >1 for RGR analyses); (B) growth-survival trade-offs showing the proportion of microhabitats where relative growth rate (RGR) rank ≠ survival rank for each growth metric (RGR_{ht}, RGR_{mass}, and RGR_{leaf}); 11-19 microhabitats had sufficient seedling numbers to be considered. Species: *Cheirodendron trigynum* (*CT*), *Coprosma rhynchocarpa* (*CR*), *Metrosideros polymorpha* (*MC*), and *Vaccinium calycinum* (*VC*); sample sizes in Table 3-1; detailed results in Appendix Table S3-3.

Figure 3-3. Relative importance of environmental factors for predicting height, mass, and leaf area RGR for each of four common species in Hawaiian wet forest; calculated by partitioning R^2

of generalized linear models after accounting for the effects of age and initial size; topography variables (aspect, elevation, and slope) are stippled; TPAR = transmitted photosynthetically active radiation; species: *Cheirodendron trigynum* (*CT*), *Coprosma rhynchocarpa* (*CR*), *Metrosideros polymorpha* (*MC*), and *Vaccinium calycinum* (*VC*); sample sizes in Table 3-1.

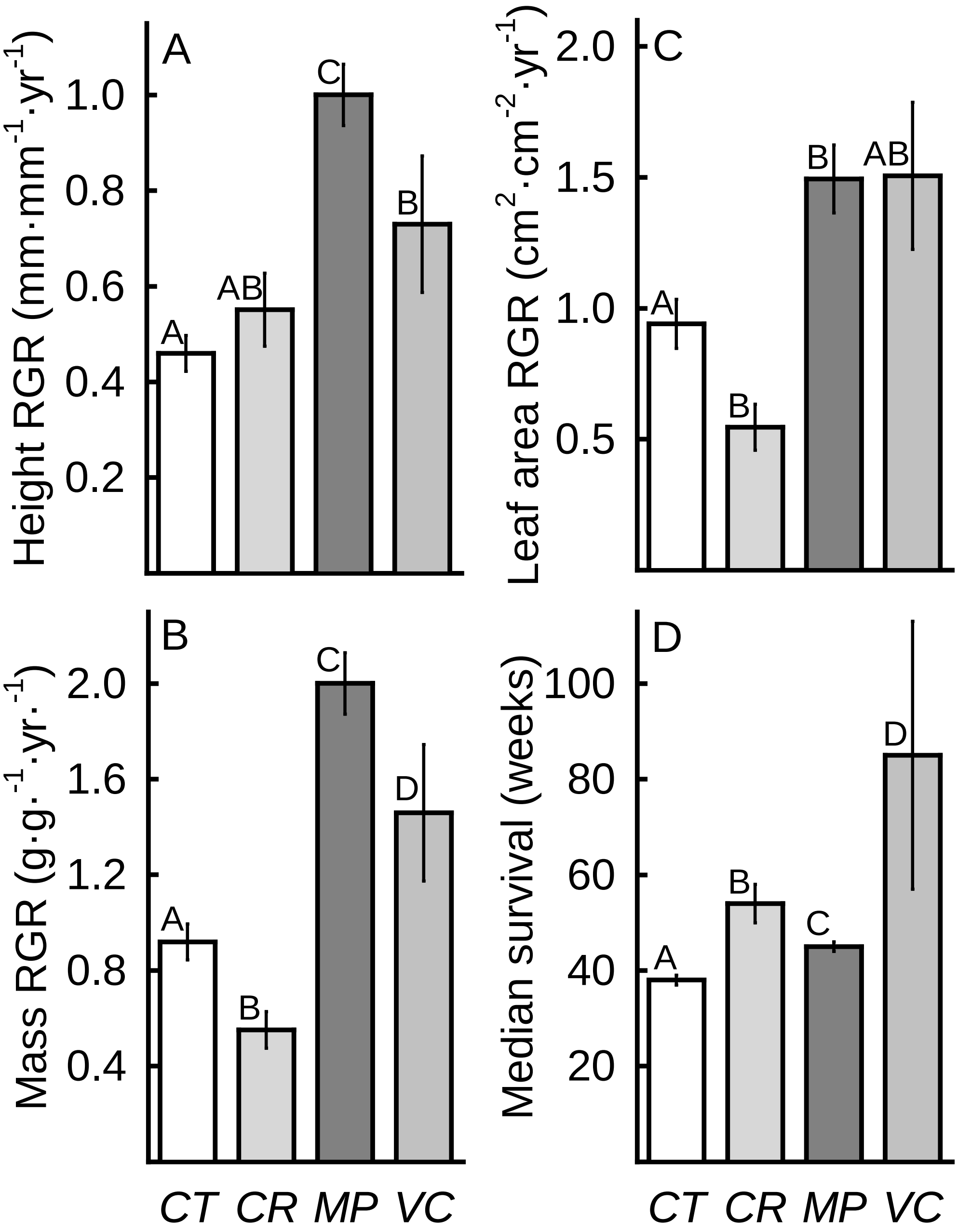
A
B
C
D
Height RGR (mm·mm-1·yr-1)
Mass RGR (g·g-1·yr-1)
Leaf area RGR (cm2·cm-2·yr-1)
Median survival (weeks)
0.2
0.4
0.6
0.8
1.0
1.2
1.6
2.0
0.5
1.5
20
40
60
80
100
A
AB
C
B
A
B
C
D
A
B
B
AB
A
B
C
D
CT CR MP VC
CT CR MP VC

Figure 3-1

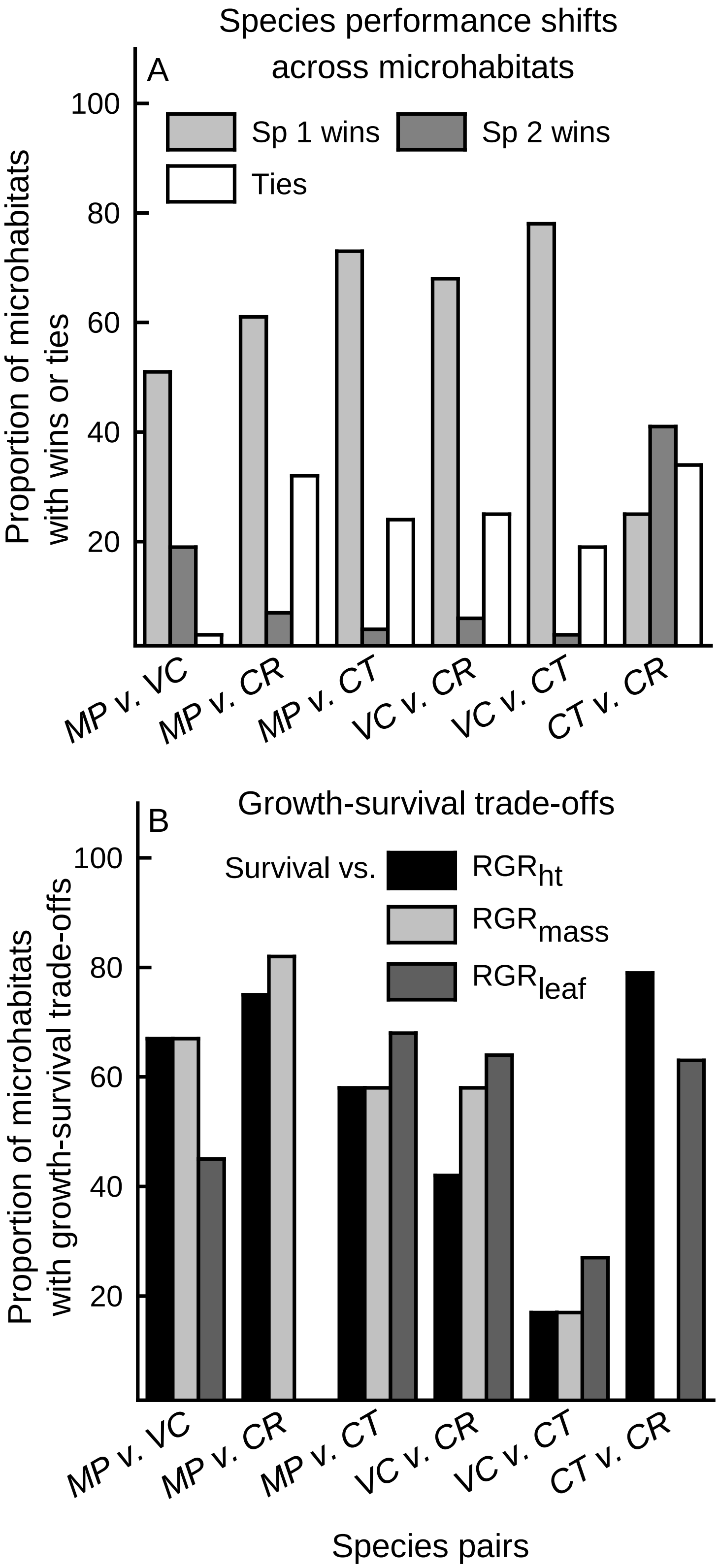
Species performance shifts across microhabitats
A
Sp 1 wins
Sp 2 wins
Ties
Proportion of microhabitats with wins or ties
20
40
60
80
100
MP v. VC
MP v. CR
MP v. CT
VC v. CR
VC v. CT
CT v. CR
Growth-survival trade-offs
B
Survival vs.
RGR$_{ht}$
RGR$_{mass}$
RGR$_{leaf}$
Proportion of microhabitats with growth-survival trade-offs
20
40
60
80
100
MP v. VC
MP v. CR
MP v. CT
VC v. CR
VC v. CT
CT v. CR
Species pairs

Figure 3-2

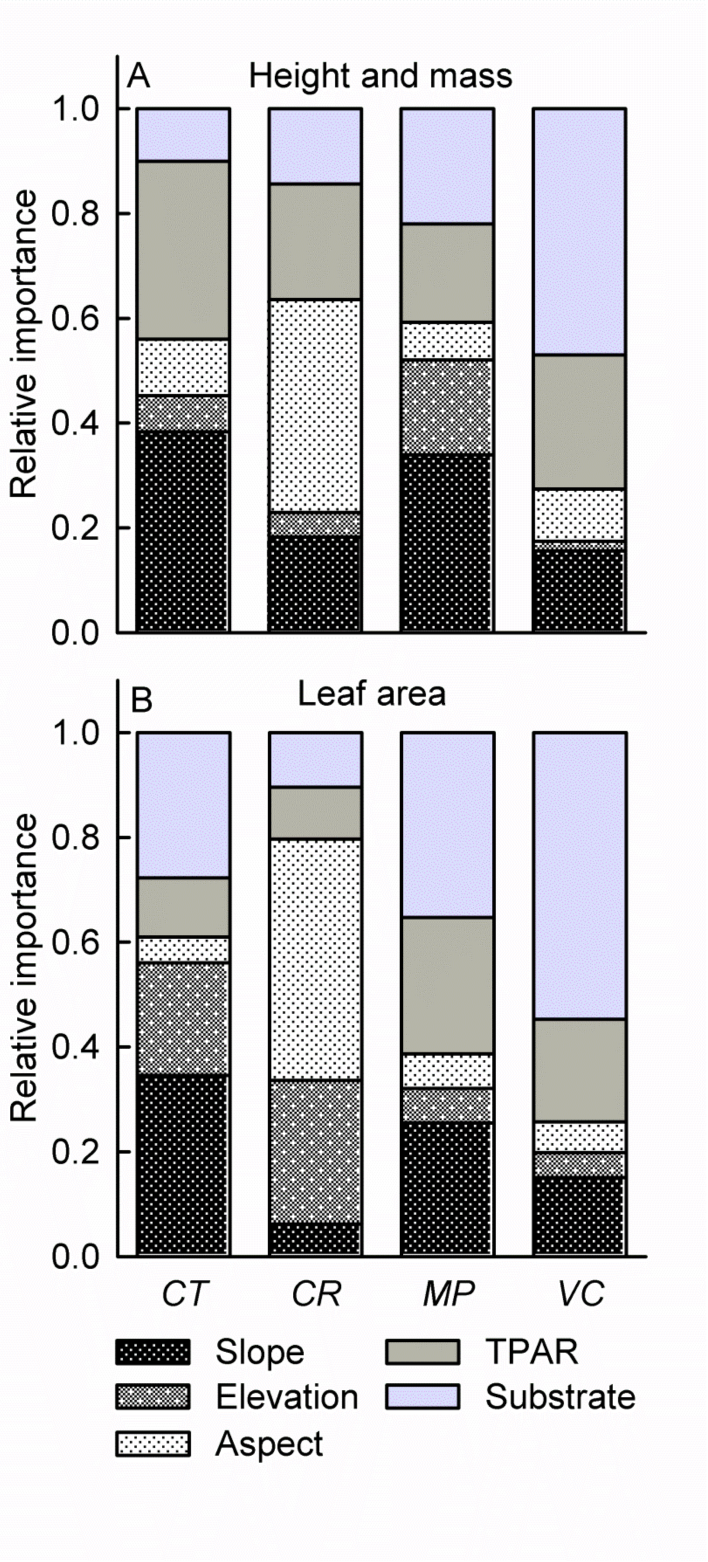
A
Height and mass
B
Leaf area
Relative importance
0.0
0.2
0.4
0.6
0.8
1.0
CT
CR
MP
VC
Slope
Elevation
Aspect
TPAR
Substrate

Figure 3-3

CHAPTER 4

Density-dependent seedling mortality varies with forest type, irradiance and species rarity within and between wet and dry Hawaiian forests

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Summary

1. Negative density dependence (NDD; i.e., higher mortality near conspecifics) is often hypothesized to arise from greater pathogen and/or predator loads and to contribute to the maintenance of biodiversity. We present the first test of this theory for tropical dry forest seedlings, and contrast results with a parallel study conducted in wet forest.

2. We monitored seedling survival for 20 species over 1.5-2.5 years in two 4-ha permanent plots on Hawaii Island. We tested for negative effects of conspecific seedlings on seedling survival (i.e., seedling NDD) and of conspecific adults on seedling survival (i.e., adult NDD).We quantified the percent of diffuse photosynthetically active radiation transmitted to the understory (TPAR; μmol photons$\cdot$m$^{-2}\cdot$s^{-1}) at each seedling plot.

3. Based on hypothesized processes, we expected 1) lower NDD in dry than wet forest, 2) lower NDD with higher TPAR within each forest, and 3) higher NDD for the most abundant versus the less abundant species at both local (1 to 20 m) and community-wide (4 ha) scales. This pattern would result in higher *per capita* mortality of the most abundant species at community-wide scales, a community compensatory trend (CCT) that favors population growth of the less abundant species and contributes to coexistence.

4. Seedling NDD reduced survival for all species in dry forest and for the less abundant species in wet forest. However, adult DD decreased survival only for the less abundant species in wet forest and conspecific adults were associated with greater survival for the most abundant species (= positive density dependence) in the wet forest and for all dry forest species. Seedling survival rates decreased with increased community-wide tree abundance in the wet forest, providing evidence for a CCT.

5. Understory TPAR influenced density dependence differently for dry versus wet forest species. Seedling survival strongly increased with conspecific seedling density in low TPAR in dry forest and in high TPAR in wet forest. Seedling survival increased most with adult conspecific density in high TPAR in both forests.

6. *Synthesis*. The strength and direction of seedling density dependence varied with forest type, TPAR, and species' abundance. These differences suggested a role for climate, abiotic factors and biotic neighborhoods in determining patterns of density dependence, highlighting the need to consider a greater number of factors and interactions in determining mechanisms for species coexistence within and across ecosystems.

Key-words

Community compensatory trend, density dependence, Janzen-Connell hypothesis, light, photosynthetically active radiation, regeneration dynamics, seedling ecology, tropical dry forest, tropical wet forest, island ecology

Introduction

A major goal of ecological research is to understand the maintenance of species diversity in tropical forests (Wright 2002). Of the several hypotheses that have been proposed, one of the best supported is the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). The Janzen-Connell hypothesis posits that species-specific predators and pathogens reduce seed and seedling survival where conspecific adult and/or juvenile densities are high (negative density dependence, NDD; all symbols and abbreviations defined in Table 4-1). Hence NDD facilitates diversity by preventing any one species from dominating the forest (Connell et al. 1984). To distinguish the pattern of NDD from inter-specific competition, conspecific effects must be greater than heterospecific effects (Connell et al. 1984, Freckleton and Lewis 2006). Alternatively, we may find the pattern of positive density dependence (PDD) if conspecific density facilitated seedling survival or if a strong habitat preference leads to clustering of conspecifics (Keddy 1992, Holmgren and Scheffer 2010, Jia et al. 2011). In both temperate and wet tropical forests, numerous studies have shown that NDD influences forest regeneration dynamics (e.g., Harms et al. 2000, Hubbell et al. 2001, Hille Ris Lambers et al. 2002, Metz et al. 2010, Swamy and Terborgh 2010, Johnson et al. 2012, Lin et al. 2012, Paine et al. 2012 but see Hyatt et al. 2003). However, there has been little comparative study and the relative importance of NDD and PDD might vary across habitats and among species. We aimed to test hypotheses for the occurrence of density-dependent seedling survival in low-diversity tropical forest and to quantify for the first time its potential variation between wet and dry forests, with irradiance within forests, and with species abundance.

First, we tested the whether the pattern of NDD proposed by Janzen and Connell was present in low-diversity tropical forest in Hawaii (H1). Janzen (1971) specifically predicted low NDD in Hawaiian forest because the low species diversity would harbour few species-specific predators and pathogens. However, the evidence for NDD across forests varying in species diversity has been contradictory. For example, previous studies in high-diversity tropical forests have found PDD for trees (Condit et al. 1994, Anderson 2009, Zhang et al. 2009) and shrubs (Condit et al. 1992, Hubbell et al. 2001). By contrast, studies in low diversity temperate forests have found NDD (Hille Ris Lambers et al. 2002, Johnson et al. 2012).. To our knowledge, ours is the first study to test the Janzen-Connell hypothesis in low-diversity tropical forest.

Second, we tested the hypothesis that NDD is lower in dry than wet forest (H2). Indeed, the expectation of PDD in dry forest is consistent with the stress gradient hypothesis, which posits that facilitation increases and competition decreases with higher abiotic stress (Bertness and Callaway 1994). Such a pattern would also be promoted if pathogens that contribute to NDD are less abundant in lighter, dryer habitats, as typically found in dry forests, than in the shady, moist environments typical of wet forest understories (Augspurger 1984a, b, Coley and Barone 1996). We found only two published studies on density dependence in tropical dry forest (John et al. 2002, Sullivan 2003). These studies reported weak community-level NDD for trees ≥ 1 cm diameter at breast height (DBH; John et al. 2002) and density-dependent herbivory for *Tabebuia ochracea* saplings (Sullivan 2003). Neither study investigated the seedling stage when NDD is typically highest (Silva Matos et al. 1999, Bagchi et al. 2010, Metz et al. 2010, Fine and Mesones 2011, Luo et al. 2012). Alternately, one might expect a stronger pattern of NDD in dry than in wet forest if drought-stressed seedlings in dry forest are more susceptible to pathogens or if intraspecific resource competition is greater where soil moisture resources are most limited (Bunker & Carson 2005; Chase 2007; Brooker *et al.* 2008; Fajardo & McIntire 2011; Jia *et al.* 2011). Indeed, studies that compared NDD between wet and dry seasons within the same forest suggested that NDD may be stronger when precipitation is lower (Lin et al. 2012). Given that tropical dry forest is the most endangered ecosystem globally (Janzen 1988, Gillespie et al. 2011), is essential to understand regeneration dynamics, particularly the role of density dependence, in this forest type.

Third, we sought a greater resolution of the pattern of density dependence in each forest and its linkage with microclimate. Specifically, we tested the hypothesis that NDD is weaker at high than low transmitted photosynthetically active radiation (TPAR) (H3). Such a pattern would be expected if fungal pathogen-induced seedling mortality decreases with higher canopy openness, as indicated by previous studies (Augspurger 1984a, b). For instance, seedling NDD decreased with higher canopy openness in Borneo (Aiba and Nakashizuka 2007) and Puerto Rico (Comita et al. 2009). These effects may indicate higher pathogen mortality and NDD for shade intolerant species (McCarthy-Neumann and Kobe 2008, Comita and Hubbell 2009, Kobe and Vriesendorp 2011). To our knowledge, no previous study has examined the interaction between density-dependent seedling mortality and TPAR, the irradiance measure most directly related to plant available light.

To further clarify the patterns of density dependence in each forest, we tested the hypothesis that local and community-wide conspecific density decreases seedling survival of the most abundant species more than the less abundant species (H4). Several previous studies have reported that seedling NDD varies with, and contributes to, local species abundance. For example, occasional or rare species (rare species usually defined as < 1 individual/ ha^2) may experience stronger NDD, which may contribute to these species' rarity (Hubbell et al. 2001, Bunker and Carson 2005, Queenborough et al. 2007, Comita et al. 2010, Kobe and Vriesendorp 2011, Lin et al. 2012). Conversely, the most abundant species may experience higher NDD because they are more likely to experience high conspecific density (Lin et al. 2012). At the community scale, NDD may contribute to species coexistence by increasing the population growth of species when they are less abundant and decreasing population growth of species when they are most abundant (i.e., *community-level compensatory trend*, CCT; Connell et al. 1984, Webb and Peart 1999).

We tested the above hypotheses in dry and wet forest on Hawaii Island using data for 3462 seedlings of 20 species in two 4 ha permanent plots. We focused our study on seedling survival, a major population bottleneck that determines future population growth and forest composition (Leck et al. 2008). The importance of this novel investigation is yet higher as many of Hawaii's threatened or endangered plant species occur in dry forests, and this is the first study of patterns of density dependence in Hawaiian forests.

Methods

Data collection.— We conducted this study in the Laupahoehoe (LAU) and Palamanui (PLN) Forest Dynamics Plots (FDPs) which are part of the Hawaii Permanent Plot Network (HIPPNET; www.hippnet.hawaii.edu) and the Smithsonian Tropical Research Institute Center for Tropical Forest Science plot network (CTFS; www.ctfs.si.edu). We established plots in 2008 in native-dominated primary forest on Hawaii Island. We tagged, identified, mapped, and measured all native tree and shrub species ≥ 1 cm DBH within each 4 ha FDP following standard CTFS protocols (Condit 1998). Due to the prevailing wind direction and location of large volcanic mountains, the windward and leeward sides of Hawaii Island have dramatically different mean annual rainfall, making it ideally suited for such a comparison. The LAU plot is in montane wet forest in the Hawaii Experimental Tropical Forest (HETF) on the windward eastern slope of Mauna Kea volcano. The PLN plot is in lowland dry forest on privately owned land on the northwest slope of Hualalai volcano. Mean annual precipitation is more than 4-fold higher in the wet versus the dry forest site based on an analysis of 30 year means (Giambelluca et al. 2013). Mean annual temperature is approximately 4°C lower in wet than dry forest, primarily due to differences in elevation (Juvik and Juvik 1998). We list relevant characteristics of both FDPs in Table 4-2. Further detail on plot establishment, diversity, and structure is available online at www.hippnet.hawaii.edu.

In each FDP we established a grid of 64 seed and seedling census stations each comprised of three 1 m × 1 m seedling subplots within 2 m of one 0.5 m^2 seed trap (N = 192; Fig. S4-1) following standard protocols used in other plots within the CTFS plot network (Wright et al. 2005). We placed the census stations roughly in the centre of 20 m × 20 m quadrats, thus approximately 20 meters apart. We excluded the outer quadrats to minimize seed input from unmapped trees. We recorded the location and condition of all native woody species < 1 cm DBH in each seedling subplot, measuring height to the nearest 0.5 cm from the base to the apical meristem. In the wet forest plot, we conducted the initial census in Nov./Dec. 2008, and re-measured previously tagged seedlings and recorded new seedlings four times: in Dec. 2009, July 2010, Dec. 2010/Jan. 2011, and June 2011. In the dry forest plot, we conducted the first seedling census in Dec. 2010/Jan. 2011 and conducted three recensuses: in June 2011, Jan. 2012, and July 2012. For our analysis, we included only individuals with initial heights ≤ 1 m. Hereafter, we refer to these plants as "seedlings". This included 3159 individuals of 12 species from LAU and 303 individuals of 8 species from PLN (Tables S1a and b). The number of seedlings per species ranged from one to 224 in the dry forest and from one to 1403 in the wet forest. The number of seedlings per species in each seedling subplot ranged from 1 to 4 in the dry forest and 1 to 8.5 in the wet forest, averaged across all census intervals for subplots with seedlings and in census intervals in which a given species was present (Tables S1a and b).

We measured diffuse understory photosynthetically active radiation (PAR, µmol photons·m^{-2}·s^{-1}) in the forest understory on uniformly overcast days by recording two consecutive 15 second average measurements using a 1 m long line quantum sensor (LI-191, LI-COR, Lincoln NE) positioned 1 m above the centre of each seedling subplot. To calculate transmitted TPAR (TPAR), we divided the mean understory value by simultaneous above-canopy PAR measurements logged with a point quantum sensor (LI-190; LI-COR) mounted on an adjacent climate tower (at LAU) or located in an unshaded clearing (at PLN). Thus, we calculated understory transmitted PAR (TPAR) as understory PAR / above-canopy PAR (Anderson 1964, Nicotra and Chazdon 1994). Previous studies showed that understory TPAR determined on overcast days correlates well with mean daily photosynthetic photon flux density and is highly representative of long-term understory irradiance conditions (Anderson 1964, Parent and Messier 1996, Tobin and Reich 2009).

Data analysis.— To test for the presence of density dependence, we modeled individual seedling survial as a function of con-and heterospecific adult and seedling density. As an index of adult tree density, we calculated the sum of the basal area of trees ≥ 1 cm DBH within 10 m of each seedling plot divided by the distance of each tree from seedling plot centres, ($A = \sum$ (basal area /distance), as per Comita and Hubbell (2009). This index integrates both tree size and distance from focal seedlings (Comita and Hubbell 2009). For each seedling, we separately calculated this density index for conspecific and heterospecific adults within 10 m and calculated seedling densities within 1 m^2 subplots.

We used generalized linear mixed-effects models (GLMM; See Appendix) to estimate seedling survival probability. This method is appropriate for analysis of non-normal binary survival data and allows for the inclusion of random effects (Bolker et al. 2009). We used the logit link function to transform seedling fate (e.g., dead = 0 or alive = 1). We included seedling plot as a random effect to control for potential spatial autocorrelation of seedlings due to environmental or other effects. Further, we accounted for the effect of TPAR on seedling survival by including TPAR as a covariate in all analyses as a continuous variable. Because the less abundant and the most abundant species may be expected to have different survival rates, we also included this factor as a covariate. Thus, we modeled the survival (s) of an individual seedling *i* of species *j* in seedling plot *k* as a function of the adult density index (*A*) and of the density of seedlings within the same 1 m^2 seedling plot (*S*) of conspecifics (CON) and heterospecifics (HET), log-transformed initial seedling height (log*H*):

$$\text{logit}\,(s_{ijk}) = \beta_{0j} + \beta_{1j} \bullet S_{\text{CON}jk} + \beta_{2j} \bullet S_{\text{HET}jk} + \beta_{3j} \bullet A_{\text{CON}jk} + \beta_{4j} \bullet A_{\text{HET}jk} + \log H_{ij} + \text{TPAR}_k + \text{commonness}_{ij} + \text{random}\,(k) \qquad \text{(eq. 1)}$$

We report the results of this complete model given that all factors were present and potentially influenced seedling survival, though not all factors were significant. Thus, our results represent the effects of each density variable given the contribution of all other variables present in the model. We calculated seedling survival for each individual seedling in the first year following the first census in which the seedling was tagged. Thus, we based survival analyses on ≤1 yr old seedlings except for seedlings tagged in the initial census for each site.

We created TPAR and species abundance categories to determine the effects of these factors on density-dependent seedling mortality. We divided the range of TPAR measured in seedling plots into three levels (low, medium, and high) for each forest corresponding to tercile ranges across all seedlings (Table 4-2). To obtain species abundance categories, we classified the two most abundant species in dry and wet forest as "most abundant" species and the remaining species as "less abundant". The two most abundant species were those with the highest basal area and the highest stem density. In the wet forest, the most abundant species were *Metrosideros polymorpha*, which comprised 38% of BA, 21.4% of adult stem density, and 41% of seedlings; and *Cheirodendron trigynum*, which comprised 6% of BA, 27% of adult stem density, and 44%

of seedlings. In the dry forest, the most abundant species were *Diospyros sandwicensis*, which comprised 74% of BA, 16% of adult stem density, and 20% of seedlings; and *Psychotria odoratum*, which comprised 15% of BA, 62% of adult stem density, and 74% of seedlings. The less abundant species in wet forest comprised approximately 6% of seedling individuals and 75% of the 11 species found in seedling plots. In dry forest, the less abundant species comprised 15% of seedling individuals and 83% of the 7 species found in seedling plots (Table S4-1a, b).

To test whether density dependent effects differed between 1) wet and dry forests, 2) the most abundant and the less abundant species, and 3) low, medium, and high TPAR categories ($\mathrm{PAR}_{\mathrm{CAT}}$), we included these factors as interaction terms with each of the four density variables (S_{CON}, S_{HET}, A_{CON} and A_{HET}) in separate GLMM analyses. For example, we used the following model to test the interaction between seedling conspecific density and TPAR category ($\mathrm{TPAR}_{\mathrm{CAT}}$):

$$\mathrm{logit}\,(s_{ijk}) = \beta_{0j} + \beta_{1j} \bullet S_{\mathrm{CON}jk} \times \mathrm{TPAR}_{\mathrm{CAT}k} + \beta_{2j} \bullet S_{\mathrm{HET}jk} + \beta_{3j} \bullet A_{\mathrm{CON}jk} + \beta_{4j} \bullet A_{\mathrm{HET}jk} + \log H_{ij} + \mathrm{commonness}_{ij} + \mathrm{random}\,(k) \qquad \text{(eq. 2)}$$

Significant interaction terms indicated that the effects of the density variable differed among forest type, with species abundance, or among TPAR categories. Note that we did not include TPAR as a continuous variable when we included $\mathrm{TPAR}_{\mathrm{CAT}}$ as an interaction term.

To compare the relative magnitude of density dependence between the wet and the dry forests, which varied substantially in tree basal area and seedling density, we developed a novel method to standardise the effect sizes from GLMM analysis. As with traditional logistic regression, the coefficients obtained from GLMM analysis represent the “effect” size and direction of a 1-unit increase in an independent variable on a dependent variable. However, effect sizes from our analyses were not comparable between dry and wet forest sites because these forests differed considerably in adult tree size and seedling density (Table 4-2), which strongly influenced the effects sizes. For instance, a one-unit increase in seedling density at PLN represented a much larger proportionate change in seedling density than at LAU because the overall seedling density was much lower at PLN than LAU (Table 4-2). Therefore, to quantify density-dependent effects in a comparable way, we calculated the mean predicted change in survival for each 10% change in each predictor variable. For example, we divided the range of A_{CON} values at PLN and at LAU into 10 equal intervals, calculated the predicted change in seedling survival across each interval (i.e., predicted change in survival from the start to the finish of the interval) based on the fitted GLMM model, then averaged the predicted changes across all 10 intervals, producing mean values enabling comparison between PLN and LAU. Notably, the predicted changes in survival were non-linear across ranges of most of the predictor variable (as shown in figures), and this method essentially provided a mean of the slopes for each interval of 10% of density, allowing comparison across forests that vary substantially in their ranges of density for trees and/or seedlings.

To examine evidence for a community compensatory trend (CCT), we tested correlations across species in each forest between seedling survival and two measures of community-wide tree abundance, tree density and basal area . We calculated tree density (stems/ha) as the number of individual trees ≥1 cm DBH within each 4 ha FDP and the basal area (BA; $m^2 \cdot ha^{-1}$) of these trees as the estimated area of each stem at DBH. Using GLMM regression analysis, we modeled individual seedling survival for each species as a function of the log-transformed tree density and BA of conspecific adults. We included log-transformed initial height of each seedling as a random effect for analysis of dry forest species and both log-transformed initial height and seedling plot as random effects for analysis of wet forest species because it provided better fits (and results were not substantially different). For these analysis, we excluded all species with fewer than three individual seedlings found in seedling plots (three dry forest species and three wet forest species).

We conduced all analyses using R 2.15.1 (R Development Core Team 2012). We fitted GLMM models using the *glmer* function in the *lme4* package with model parameters estimated using the Laplace approximation (Bolker et al. 2009). We obtained predicted effects from GLMM models using the *effects* package (Fox 2003).

Results

Comparison of characteristics between dry and wet forest types.— The dry and wet forests differed in several striking ways relating to microclimate and canopy tree and understory seedling abundance and composition (Table 4-2). First, TPAR was more than 7-fold higher in dry than in wet forest ($t_{201} = 22$, $P < 0.001$; Table 4-2). Second, the mean plot-wide BA of adults of the species that were also found as seedlings in seedling plots was 5.4-fold greater in wet versus dry forest (Table 4-2). However, BA was highly variable within each forest and thus did not differ significantly among forests ($t_{13.4} = –1.38$, $P = 0.190$). Third, none of the species found as seedlings in the dry forests were also found as seedlings in the wet forest (Tables S1 and S2). Fourth, seedling density (seedlings/m^2) was nearly 10-fold higher in the wet than the dry forest ($t_{202} = –6.03$, $P < 0.001$; Table 4-2). Finally, seedling heights at the initial survey were on average almost 4-fold greater in dry than in wet forest ($t_{310} = 8.81$, $P < 0.001$; Tables S1 and S2).

Despite these differences, overall seedling survival was similar on average and did not differ significantly between dry and wet forests when averaged across species ($t_{13.1}$ = –1.65, P = 0.124) or across individuals (t_{366} = –1.81, P = 0.071; Tables S1 and S2). Survival also varied substantially among species ranging from 0 to 100% within each forest (Tables S1 and S2). However, survival differed significantly among species only in the wet forest (PLN P = 0.701; LAU P = <0.001, GLMM).

Density dependence in low-diversity tropical forest (H1) and comparison between dry and wet forests (H2).— We found substantial evidence of both positive and negative density dependence in Hawaiian forest (Tables 3 and 4). However, the direction and magnitude of density dependence differed between wet and dry forests. First, when analyzed for all species pooled in each forest, adult conspecific density (A_{CON}) was positively correlated with overall seedling survival in both forest types (Fig. 4-1A; Table 4-3; coefficients in Appendix 2). However, predicted seedling survival increased by an average of 9.3% versus 5.5% for every 10% increase in A_{CON} in dry and wet forests, respectively (Table 4-3). Second, the effects of seeding conspecific density (S_{CON}) on seedling survival differed between the wet and the dry forest such that seedling survival was negatively correlated with S_{CON} in dry forest and was uncorrelated in wet forest (Table 4-3; Fig. 4-1B).

In contrast, heterospecific density effects were weak and did not differ between dry and wet forests. All heterospecific density × FDP interactions P-values were > 0.10. Correlations between seedling survival and heterospecific adult density (A_{HET}) showed negative trends in both forests, though the effects were marginally significant only in dry forest (Table 4-3). Heterospecific seedling density (S_{HET}) was uncorrelated with seedling survival of all species pooled in both forests.

Density and TPAR interactions (H3).— Density dependence varied with TPAR differently in each forest type. Dry and wet forest seedling survival increased most strongly with increasing A_{CON} at $\mathrm{TPAR}_{\mathrm{high}}$ (Fig. 4-2A, B) but TPAR × S_{CON} interactions showed opposite trends in dry versus wet forest. Specifically, dry forest seedling survival strongly increased with S_{CON} only in $\mathrm{TPAR}_{\mathrm{low}}$ whereas wet forest seedling survival increased with S_{CON} only in $\mathrm{TPAR}_{\mathrm{high}}$ (Fig. 4-2 C, D). Moreover, dry forest seedling survival tended to decrease with S_{CON} in $\mathrm{TPAR}_{\mathrm{med}}$ and $\mathrm{TPAR}_{\mathrm{high}}$. In wet forest, these trends were reversed such that survival was only weakly affected but tended to decrease with increasing S_{CON} in $\mathrm{TPAR}_{\mathrm{low}}$ and $\mathrm{TPAR}_{\mathrm{med}}$.

Most abundant versus less abundant species and community compensatory trends (H4).— Patterns of density dependence differed between the less abundant and the most abundant species in the wet, but not the dry forest (Table 4-3; Fig. 4-3). In the wet forest, less abundant species showed significant seedling and adult NDD (i.e, negative relationships of survival probability with A_{CON} and S_{CON}) whereas the most abundant species showed adult PDD and no significant seedling NDD (Fig. 4-3; LAU A_{CON} × commonness $P = 0.001$; S_{CON} × commonness $P = 0.010$). In the dry forest, we found no significant density dependence patterns for the less abundant species whereas for the most abundant species we found adult PDD and seedling NDD (Table 4-3). However, patterns of density dependence did not significantly differ between the less abundant and the most abundant seedlings in dry forest (PLN A_{CON} × commonness $P = 0.13$; S_{CON} × commonness $P = 0.92$). Density dependence patterns were similar for the most abundant species and for all species pooled in both forest types (Table 4-3).

We found evidence of a community compensatory trend (CTT) in wet but not dry forest. In the wet forest, seedling survival decreased with increased community-wide tree density for all species pooled, but the relationship with basal area was non-significant (Table 4-5). When we repeated the analysis with only the less abundant wet forest species, we found a much stronger negative relationship between seedling survival and both tree density and basal area. In contrast, seedling survival of dry forest species was positively correlated with basal area, and uncorrelated with tree density. For the less abundant dry forest species, seedling survival was uncorrelated with both tree density and basal area.

Discussion

Density dependence in low-diversity tropical forest.— Strong patterns of density dependence were evident in Hawaiian forest, though a major and novel finding of our study was that the magnitude and direction of these patterns depended critically on forest type, transmitted photosynthetically active radiation (TPAR) and species abundance. Our results overall were consistent with the Janzen-Connell hypothesis that conspecific density decreases seedling survival (H1; Janzen 1970, Connell 1971). Seedling conspecific density decreased seedling survival for all species pooled in the dry forest and for the less abundant species in the wet forest. Additionally, conspecific density generally had stronger effects than heterospecific density in Hawaiian forest, showing that conspecific density effects differed from interspecific competition (Connell et al. 1984, Freckleton and Lewis 2006). However, we found adult PDD in both dry and wet Hawaiian forests, contrary to the Janzen-Connell hypothesis (Janzen 1971).

Comparison between dry and wet forest types.— Our hypothesis that we would find lower NDD in dry than in wet forest (H2) was supported by our data. Indeed, patterns of adult PDD was nearly 2-fold higher in the dry than in the wet forest. These results are consistent with the stress-gradient hypothesis, such that facilitation was more important where abiotic stress was higher, and suggest that facilitation was more important than intraspecific competition for drought-stressed seedlings (Bertness and Callaway 1994, Fajardo and McIntire 2011).

Processes that might account for these patterns include the differences among forests in moisture supply and understory irradiance. Our finding are consistent with those of studies showing that shading is more beneficial to survival of species in dry than wet habitats (Sack 2004, Semchenko et al. 2012) and that lower canopy cover reduces pathogen mortality (Augspurger 1984a, b). However, our results differ from those of studies in tropical dry forest in which adult NDD were reported (John et al. 2002). Overall, both intraspecific facilitation and interspecific competition were stronger drivers of adult–seedling interactions in the dry than in the wet forest.

Facilitation and habitat preferences may best explain the patterns of PDD in the dry and the wet forests, respectively (Keddy 1992, Holmgren and Scheffer 2010, Jia et al. 2011). Facilitation implies habitat modifications that increase seedling survival whereas habitat preferences indicate higher survival in habitats also preferred by conspecific adults (Keddy 1992). In dry forest, adult conspecifics likely facilitate seedling survival though shading, which decreases excess irradiance, high temperatures and evaporative load which can aggravate water stress (Holmgren 2000, Cabin et al. 2002, Thaxton et al. 2011). In addition, many seedlings establish in pockets of organic soil that form around large adult trees (pers. obs.). In wet forest, PDD patterns probably arose due to habitat preference more than from direct facilitation by trees because increased shade would not be beneficial in the wet forest where most species are strongly associated with high TPAR (Inman-Narahari et al. 2012).

In contrast to adult–seedling interactions, seedling–seedling interactions for all species pooled supported the alternate hypothesis that NDD would be stronger in the dry than the wet forest. In the dry forest, we found decreased seedling survival with increasing S_{CON}, consistent with the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), whereas seedling survival and S_{CON} were uncorrelated in the wet forest. These results were consistent with those of recent studies showing that local-scale negative density dependence is stronger in dry than wet seasons (Lin et al. 2012). However, our results differed from a recent study in which high seedling density increased survival for drought-stressed seedlings (Fajardo and McIntire 2011), although that study was conducted in a temperate habitat which is predicted to have lower NDD (Janzen 1970, Schemske et al. 2009). Without more information on the underlying mechanisms, we cannot state with certainty the processes driving the negative S_{CON} patterns we observed in the dry forest. Possible factors include species-specific predators and pathogens (as proposed by the Janzen-Connell hypothesis) or high intra-specific competition in resource-limited habitats. Although species-specific pathogens are hypothesized to be a major contributor to mortality of drought-stressed seedlings (Bunker and Carson 2005, Chase 2007, Brooker et al. 2008, Fajardo and McIntire 2011, Jia et al. 2011), we need new collaborations among researchers if pathogen effects on seedling and tree patterns are to be resolved in tropical forests. Alternately, soil moisture resource-partitioning mechanisms similar to those proposed in Walter’s two layer hypotheses, in which grasses use shallow soil moisture sources and trees rely on deeper sources (Walter 1971, 1979 *in* Cordell and Sandquist 2008), may explain the negative seedling–seedling interactions coupled with the positive seedling–adult interactions we found in the dry forest. Perhaps seedlings compete with each other for soil moisture near the soil surface but do not compete as strongly with adults that can access deeper soil moisture resources (Cordell and Sandquist 2008). The lack of a correlation between seedling survival and density in wet forest is consistent with earlier studies showing that small seedlings scarcely interact in tropical rainforests (Paine et al. 2008). Whatever the mechanism, these results suggest that high conspecific seedling density limits regeneration at local scales in the dry, but not the wet forest.

Our study extended the findings of previous research to a tropical forest that is drier than previously studied sites. Mean annual rainfall at the Palamanui site is 835 mm, compared with 1230 mm at Mudumalai (John et al. 2002) and 2076 mm at Guanacaste (Sullivan 2003). However, we note that our comparison between the dry and wet forest types would have been influenced by factors other than climate, including, e.g., species composition, geological substrate age, soils and elevation. Our study is an important first step towards understanding how mechanisms known to be important in other forest types may operate in tropical dry forest and promises to assist with restoration programs that focus on enhancing plant community diversity. These findings are particularly important given the limited extent of tropical dry forest globally, and mounting threats to remaining fragments. This study indicates that seedling density and its interactions with irradiance and forest type should be considered when planting species for forest restoration. For example, it may improve the success of restoration planting for dry forest species if they are planted near adult conspecifics, but where conspecific seedling density is low.

Interactions between plant density and TPAR in determining seedling survival.— Increasing understory TPAR intensified patterns of NDD and PDD within both forests. Consistent with H3, seedlings survived best where both TPAR and adult conspecific density were highest in both forests; and where TPAR and seedling conspecific density were highest in the wet forest. Weaker patterns of seedling NDD in high TPAR suggest a potential importance of fungal pathogens as a mechanism of density-dependent mortality (Connell et al. 1984) because seedlings have lower pathogen-induced mortality in higher irradiance (Augspurger 1984a, b). Our findings differed from the only other study we found that tested the interaction between adult conspecific density dependence and irradiance (measured as canopy openness), which found no significant interaction between these variables (Comita et al. 2009). However, our results complied with this and another study and which found significant positive seedling–seedling interactions in wet forest (Aiba and Nakashizuka 2007, Comita et al. 2009).

In contrast to interaction between TPAR and A_{CON}, the combined effects of TPAR and S_{CON} differed among forest types. Patterns of seedling PDD were found in low TPAR in the dry forest and in high TPAR in the wet forest. In dry forest, seedling PDD in low TPAR suggest either lower intraspecific competition in shadier – and probably moister – sites and/or lower negative effects of pathogens and herbivores where seedlings suffer less drought stress (Lin et al. 2012). In wet forest, we expect that habitat preference best explains seedling PDD in high TPAR because most seedlings have higher recruitment and survival in high TPAR. This is consistent with previous findings from this forest that most seedling species had higher abundance in high TPAR than expected under a null model (Inman-Narahari et al. 2012). Thus, the patterns of seedling conspecific density dependence appear to vary across local and regional environments. The mechanisms underlying these patterns require further investigation to determine the role of pathogen–TPAR interactions and the importance of species' shade tolerances (McCarthy-Neumann and Kobe 2008, Comita and Hubbell 2009, Kobe and Vriesendorp 2011).

Most abundant versus less abundant species and community compensatory trends.—Contrary to our hypothesis (H4), we found either no difference or that only the most abundant species suffered from NDD. In the wet forest, conspecific adult and seedling density correlated with higher seedling survival for the most abundant species (PDD) and lower seedling survival for the less abundant species (NDD). Other researchers have also found stronger NDD for rare versus common species in tropical (Hubbell et al. 2001, Queenborough et al. 2007, Comita et al.

2010, Kobe and Vriesendorp 2011, Lin et al. 2012) and temperate regions (Johnson et al. 2012). However, we note that the criteria for categorizing species as “rare” differed among these studies. However, this trend is by no means universal and some studies found stronger NDD for the most common species (Condit et al. 1992). It may be that effects depend not on abundance but rather on the life form of trees studied. In our study, smaller-stemmed understory species were more likely to be classified as “less abundant” and these appeared to be more sensitive to NDD than the “most abundant” species than included the dominant canopy tree. Likewise, Connell et al. (1984) found NDD for understory trees and shrubs, but not for canopy trees. Alternately, for the most abundant species, high seedling densities near conspecifics may overwhelm predator and pathogen effects, resulting in an overall positive association with conspecific adult density when density-dependent mortality is not overcompensating (Freckleton and Lewis 2006). The significant positive effect of heterospecific density on less abundant species may also indicate that these seedlings benefit from a more phylogenetically diverse neighborhood (Metz et al. 2010). Whatever the mechanism, the fact that less abundant species comprise the majority of diversity in Hawaii (and most other ecosystems) suggests that density-dependent effects on these species may be important drivers of recruitment dynamics and may contribute to species coexistence (Wright 2002). For the most abundant species, the lack of NDD may explain how the dominant species in these forests can achieve such high abundance, because the constraints of NDD do not limit the area where they can survive as seedlings. We propose that perhaps NDD can contribute to diversity not only by reducing dominance of the most abundant species (Connell et al. 1984), but also by contributing to the rarity of a large number of less abundant species.

Community compensatory trends.— We found evidence for a community compensatory trend (CTT) in Hawaiian wet forest, though we found the opposite pattern in the dry forest. Seedling survival was negatively correlated with community-wide abundance of adult trees for wet forest species and positively correlated for dry forest species. These results are consistent with local-scale analysis (i.e., adult conspecific density within 10 m and seedling conspecific density within 1 m), showing positive correlations between seedling survival and adult density in dry forest.

The opposite effects of seedling and adult conspecific density on seedling survival in wet and dry forests appears to lead to different patterns of overall abundance. Although we did find seedling NDD in dry forest, these effects were apparently overridden by the strong positive effects of adult conspecifics. For wet forest species, the strong negative correlation between seedling survival and tree abundance for less abundant species supports our finding that local-scale conspecific density-dependent mortality was higher for less abundant than the most abundant species. A negative relationships between seedling survival probability and community-wide adult abundance is considered to be evidence that NDD is a coexistence mechanism (Connell et al. 1984, Webb and Peart 1999). However, it is not clear if CCTs are the result of NDD or of other inherent factors controlling either the survival rate or population size of a given species. For example, a species may experience strong NDD, and yet still have an overall higher survival rate than another species that suffers high non-density-dependent mortality. Additionally, the CCT theory assumes that all species have equivalent carrying capacities, ignoring that some species may be less abundant due to limited availability of preferred habitats such as gaps. Taken together, negative density dependence at the seedling stage may contribute to species coexistence in Hawaiian wet forest, despite strong PDD for the most abundant species at local scales (Connell et al. 1984, Webb and Peart 1999). However, for dry forest species we expect that other mechanisms, such as niche differentiation or neutral processes are more important for maintaining diversity.

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Table 4-1. Definitions of symbols and abbreviations used in this study

Category/ Symbol or abbreviation	Meaning
Ecological patterns	
NDD	Negative density dependence
PDD	Positive density dependence
CCT	Community compensatory trend
Species traits and environmental variables	
DBH	Diameter at breast height (1.3 m)
PAR	Photosynthetically active radiation (μmol photons$\cdot$m$^{-2}\cdot$s^{-1})
TPAR	Transmitted diffuse understory PAR (μmol photons$\cdot$m$^{-2}\cdot$s^{-1})
TPAR$_{\mathrm{CAT}}$	TPAR category†
TPAR$_{\mathrm{low}}$	Low TPAR category
TPAR$_{\mathrm{med}}$	Medium TPAR category
TPAR$_{\mathrm{high}}$	High TPAR category
Field sites	
FDP	Forest dynamics plot
LAU	Laupahoehoe FDP (wet forest)
PLN	Palamanui FDP (dry forest)
Organizations	
HIPPNET	Hawaii Permanent Plot Network
CTFS	Center for Tropical Forest Science
Stand metrics	
S_{CON}	Seedling conspecific density
S_{HET}	Seedling heterospecific density
A_{CON}	Adult conspecific density
A_{HET}	Adult heterospecific density
DBH	Diameter at breast height (1.3 m)
BA	Basal area of adult trees (area of stems at DBH, m$^{2}\cdot$ha^{-1})
Statistical tests	
GLMM	Generalized linear mixed-effects model

†TPAR category ranges listed in Table 4-2

Table 4-2. Properties of two 4-ha forest dynamics plots on Hawaii Island; errors represent 1 SE from the mean.

Property	Palamanui dry forest (PLN)	Laupahoehoe wet forest (LAU)
Location	19° 44' N, 155° 59' W	19° 55′ N, 155° 17' W
Elevation	240 m	1120 m
Mean annual precipitation†	835 mm	3440 mm
Mean annual temperature	20 °C‡	16 °C§
Number of tree species	15	21 (incl. 3 tree ferns)
Number of seedling species	8 (N = 303)	12 (N = 3159)
Seedling density (seedlings/m^2)	0.96 ±0.23	9.32 ±1.37
Dominant canopy tree species	*Diospyros sandwicensis* (Ebenaceae)	*Metrosideros polymorpha* (Myrtaceae)
Subcanopy dominant	*Psydrax odorata* (Rubiaceae)	*Cibotium* spp. (Cibotiaceae)
BA ($m^2 \cdot ha^{-1}$)	8.59 ± 0.39	67.3 ±1.88
Mean TPAR	47 ±1.8%	6.4 ±0.29%
TPAR categories		
Low ($TPAR_{low}$)	< 37%	< 4%
Medium ($TPAR_{med}$)	≥37% , < 75%	≥ 4%, < 7%
High ($TPAR_{high}$)	≥ 75%	≥ 7%

†Giambelluca et al. 2011; ‡wrcc.dri.edu; §(Crews et al., 1995)

Table 4-3. Change in seedling survival as a function of adult (*A*) and seedling (*S*) conspecific (CON) and heterospecific (HET) density in lowland dry forest (Palamanui) and montane wet forest (Laupahoehoe) modeled using GLMM analysis with all species pooled and with subsets of most abundant and less abundant species; effects reported as the mean and range of the predicted change in survival across 10% intervals for each independent variable (e.g., a 10% change in A_{CON} in the dry forests would result in a 9.3% increase in seedling survival for all species pooled); *P*-values indicate significance of overall effects; means for effects significant at α 0.05 in bold and effects significant at α 0.10 in italics

	Dry forest change in survival			Wet forest change in survival		
Density variable	Mean	Range	*P*	Mean	Range	*P*
All species						
A_{CON}	**0.093**	0.022, 0.146	<0.001	**0.055**	0.040, 0.062	0.002
S_{CON}	**-0.034**	-0.052, -0.017	0.017	0.008	0.008, 0.008	0.472
A_{HET}	*-0.051*	-0.085, -0.017	0.053	-0.010	-0.010, -0.009	0.358
S_{HET}	0.049	0.040, 0.054	0.364	0.025	0.023, 0.026	0.125
Most abundant species						
A_{CON}	**0.093**	0.023, 0.147	<0.001	**0.057**	0.040, 0.066	0.001
S_{CON}	**-0.038**	-0.066, -0.014	0.007	0.016	0.015, 0.016	0.209
A_{HET}	*-0.050*	-0.078, -0.020	0.066	*-0.024*	-0.028, -0.019	0.064
S_{HET}	0.055	0.039, 0.062	0.134	0.013	0.013, 0.014	0.281
Less abundant species						
A_{CON}	0.025	0.019, 0.031	0.495	*-0.044*	-0.187, 0	0.100
S_{CON}	-0.027	-0.225, 0	0.975	**-0.037**	-0.048, -0.024	<0.001
A_{HET}	-0.034	-0.049, -0.019	0.225	0.038	0.035, 0.040	0.265
S_{HET}	0.025	0.019, 0.029	0.929	**0.048**	0.039, 0.052	0.030

Notes: Sample sizes as in Tables 2, S1 and S2.

Table 4-4. Summary of negative, positive, and no density dependence effects of conspecific seedlings and adults; and interactions with Transmitted diffuse understory PAR (µmol photons$\cdot$m$^{-2}\cdot$s^{-1}; TPAR) in Palamanui dry forest and Laupahoehoe wet forest; analysis conducted on all species pooled in each forest

Forest	Variable	NDD	PDD	No DD
PLN (dry)	A_{CON}		✓	
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{low}}$		✓	
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{med}}$		✓	
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{high}}$			✓
	S_{CON}	✓		
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{low}}$		✓	
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{med}}$	✓		
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{high}}$			✓
LAU (wet)	A_{CON}		✓	
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{low}}$			✓
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{med}}$		✓	
	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{high}}$		✓	
	S_{CON}			✓
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{low}}$			✓
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{med}}$			✓
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{high}}$		✓	

Table 4-5. Relationships between seedling survival and species abundance measured as tree density (stems/ha) and basal area (m^2/ha) in lowland dry forest (Palamanui) and montane wet forest (Laupahoehoe) modeled using GLMM analysis first with all species pooled and then with only less abundant species; effects reported as log odds ratios where negative values represent a negative relationship among variables; dashes indicate non-significant relationships

		Dry forest			Wet forest		
Group	Tree abundance metric	Log odds ratio	SE	*P*	Log odds ratio	SE	*P*
All species	Tree density	–	–	–	−0.88	0.20	<0.001
	Basal area	3.77	1.51	0.013	–	–	–
Less abundant species	Tree density	–	–	–	−2.24	0.49	<0.001
	Basal area	–	–	–	−1.28	0.24	<0.001

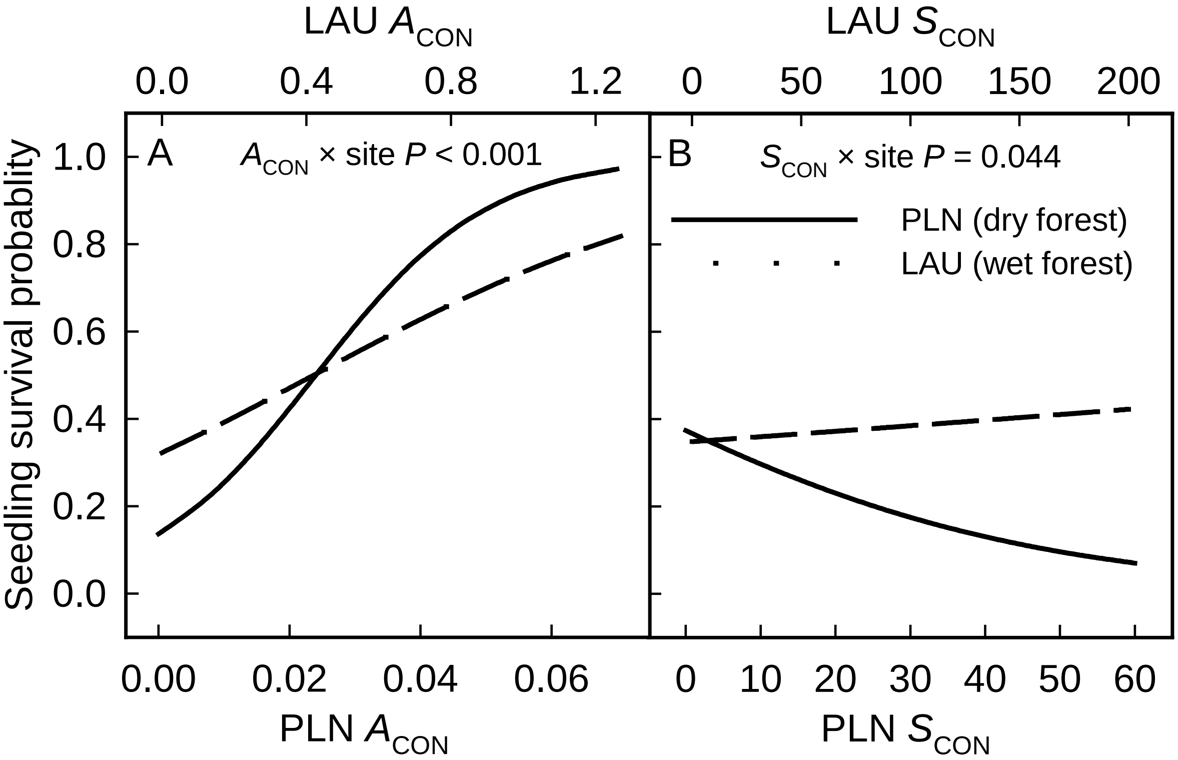

Fig. 4-1. Seedling survival as a function of (A) conspecific adult density within 10 m (A_{CON}), and (B) conspecific seedling density within 1-m^2 seedling subplots (S_{CON}); lines represent predicted values from GLMM analysis analyzed across all species in Palamanui lowland dry forest (PLN; bottom axis) and Laupahoehoe wet forest (LAU; top axis) after accounting for the effects of all other variables held at their means (see Methods); samples sizes are listed in Table 4-1; note different x-axis scales.

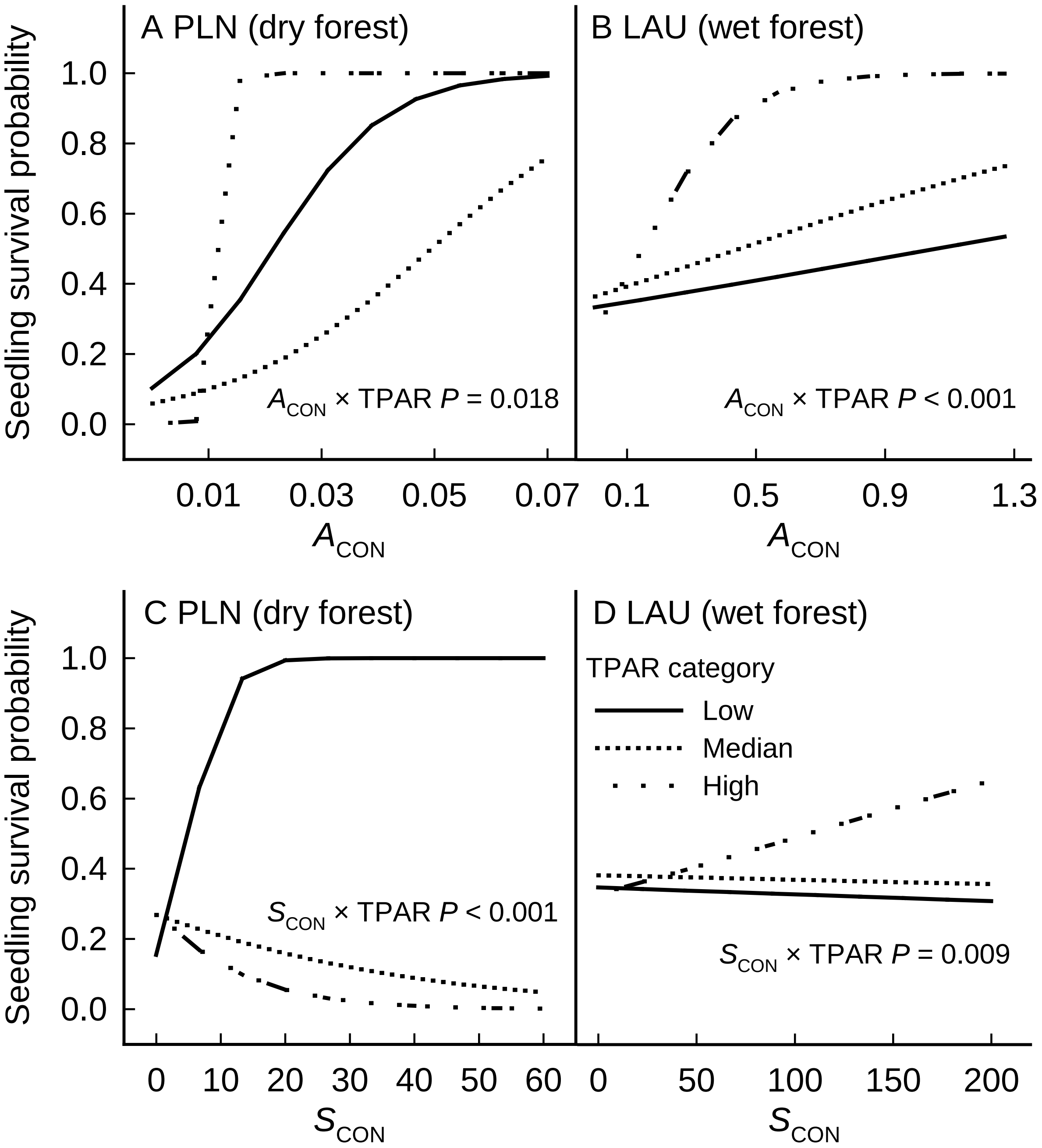

Fig. 4-2. Seedling survival as a function of adult and seedling conspecific density (A_{CON} and S_{CON}, respectively) at high, medium and low transmitted photosynthetically active radiation (TPAR; category ranges in Table 4-1) in Palamanui lowland dry forest (PLN) and Laupahoehoe wet forest (LAU); (A) A_{CON} in PLN, (B) A_{CON} in LAU, (C) S_{CON} in PLN, (D) S_{CON} in PLN; lines represent predicted values from GLMM analysis as in Fig. 4-1; note different x-axis scales.

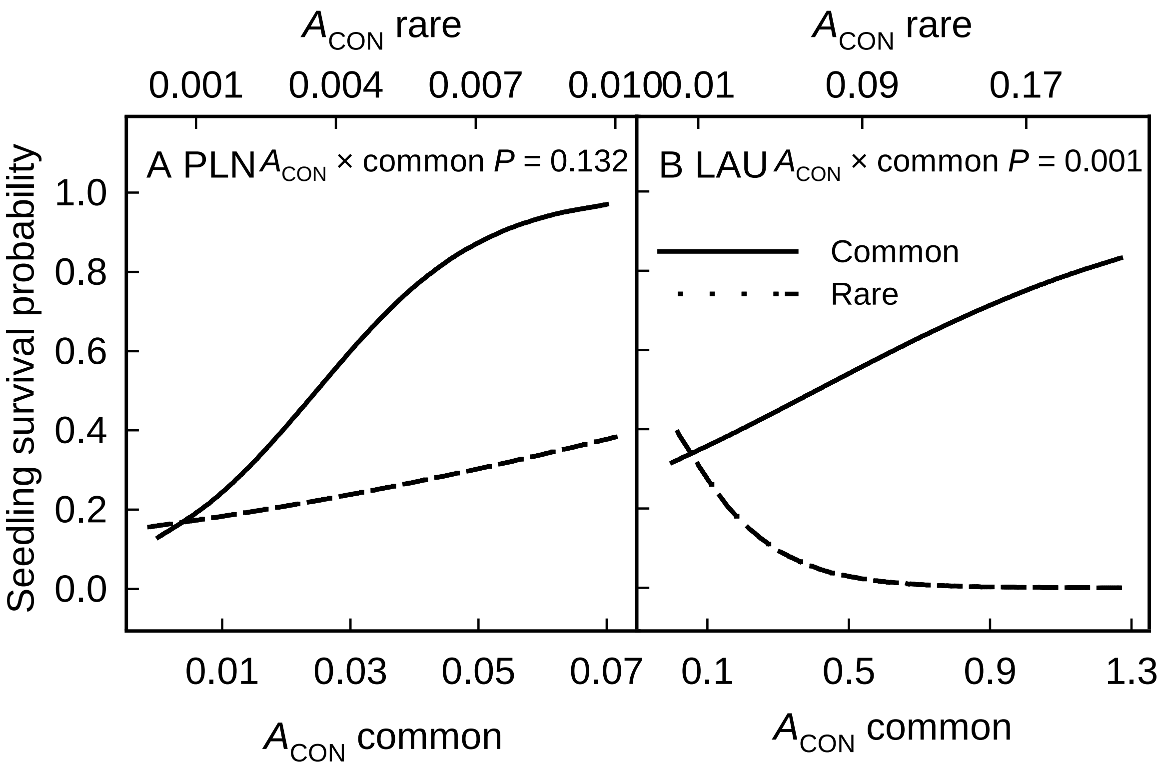

Fig. 4-3. Survival of most abundant (bottom axes) and less abundant (top axes) seedlings as a function of adult conspecific density within 10m (A_{CON}) in Palamanui lowland dry forest (PLN; A) and Laupahoehoe wet forest (LAU; B); lines represent predicted values from GLMM analysis as in Fig. 4-1; note different x-axis scales.

Chapter 4 Appendix

Table S4-1a. Seedling species attributes in Palamanui lowland dry forest with growth form, *G*: *S*, shrub or *T*, tree; in column *SA* we classified the two most abundant seedling species in dry and wet forest as "most abundant" species (*MA*) and the remaining species as "less abundant" (*LA*); mean initial height ranges (minimum - mean - maximum; rounded to the nearest 0.5 cm) and seedling density averaged over censuses (mean ±SE), and number of seedlings per seedling subplot (S/S); adult abundance (*A*; stems/ha), and basal area (*BA*; m^2/ha) for the species found as seedlings; includes only seedlings with initial height ≤100 cm

Species	Family	*G*	*SA*	*N*	Percent survival	Initial height (cm)	Seedling density (m^2)	S/S	*A*	*BA*
Chamaesyce multiformis[1]	Euphorbiaceae	*S*	*LA*	3	0	3.0 - 5.5 - 9.0	0.009 ±0.005	1.0	17.5	0.013
Diospyros sandwicensis[2]	Ebenaceae	*T*	*MA*	60	0.97	5.0 - 43.0 - 99.0	0.302 ±0.115	3.6	552.0	6.410
Dodonaea viscosa[3]	Sapindaceae	*S*	*LA*	10	0.10	1.0 - 10.0 - 69.0	0.024 ±0.011	1.3	575.0	0.359
Osteomeles anthyllidifolia[4]	Rosaceae	*S*	*LA*	1	1.00	18.5	0.005 ±0.005	1.0	36.8	0.090
Psydrax odorata[5]	Rubiaceae	*T*	*MA*	224	0.18	1.0 - 10.0 - 98.0	0.602 ±0.194	3.9	2160.0	1.270
Senna gaudichaudii[6]	Fabaceae	*T*	*LA*	1	0.00	9.5	0.002 ±0.002	1.0	17.5	0.013
Sida fallax[7]	Malvaceae	*S*	*LA*	3	0.33	1.0 - 3.0 - 6.0	0.009 ±0.006	1.0	2.0	<0.001
Sophora chrysophylla[8]	Fabaceae	*T*	*LA*	1	0	12.5	0.002 ±0.002	1.0	33.5	0.024
All species	7			303	0.34 ± 0.15*	1 - 16.5 - 99.5	0.958 ±0.231	3.9	3394.5	8.179

Notes: Authors: [1](Hook. & Arn.) Croizat & O. Deg., (Boiss.) O. Deg. & I. Deg.; [2] (A. DC.) Fosberg; [3] Jacq.; [4] (Sm.) Lindl.; [5](G. Forst.) A. C. Sm. & S. P. Darwin; [6](Hook. & Arn.) H. S. Irwin & Barneby; [7]Walp.; [8](Salisb.) Seem.

† Mean ±SE across species

Table S4-1b. Seedling species attributes in Laupahoehoe montane wet forest with growth form, *G*: *S*, shrub or *T*, tree; in column *SA* we classified the two most abundant species in dry and wet forest as "most abundant" species (*MA*) and the remaining species as "less abundant" (*LA*); mean initial height ranges (minimum - mean - maximum), seedling density averaged over censuses (mean ±SE), and number of seedlings per seedling subplot (S/S); adult abundance (*A*; stems/ha), and basal area (*BA*; m^2/ha) for the species found as seedlings (mean ±SE) ; includes only seedlings with initial height ≤100-cm

FDP/ Species	Family	*G*	*SA*	*N*	Percent survival	Initial height (cm)	Seedling density (m^2)	S/S	*A*	*BA*
Acacia koa[1]	Fabaceae	*T*	*LA*	6	0.17	3.5 - 45.0 - 188	0.052 ±0.018	1.0	35.2	5.492
Broussaisia arguta[2]	Hydrangeaceae	*S*	*LA*	8	0.75	1.0 - 13.0 - 79.0	0.042 ±0.032	2.3	67.8	0.045
Cheirodendron trigynum[3]	Araliaceae	*T*	*MA*	1403	0.31	0.5 - 4.0 - 211.0	7.792 ±1.531	7.7	830.0	4.171
Clermontia parviflora[4]	Campanulaceae	*S*	*LA*	3	0.00	12.0 - 43.0 - 104.0	0.016 ±0.009	1.0	4.8	0.002
Coprosma rhynchocarpa[5]	Rubiaceae	*T*	*LA*	327	0.40	0.5 - 8.0 - 202.0	1.927 ±0.361	2.5	243.0	0.585
Hedyotis hillebrandii[6]	Rubiaceae	*S*	*LA*	1	1.00	34.0	0.005 ±0.005	1.0	10.8	0.020
Ilex anomala[7]	Aquifoliaceae	*T*	*LA*	13	0.69	0.5 - 41.5 - 172.0	0.083 ±0.025	1.0	241.3	0.466
Leptecophylla tameiameiae[8]	Epacridaceae	*S*	*LA*	2	1.00	2.5 - 5.0 - 8.0	0.016 ±0.009	1.0	0.5	0.000
Metrosideros polymorpha[9]	Myrtaceae	*T*	*MA*	1304	0.44	0.3 - 3.5 - 255.5	7.781 ±1.192	4.1	657.8	25.220
Myrsine lessertiana[10]	Myrsinaceae	*T*	*LA*	3	1.00	5.5 - 13.0 - 26.5	0.016 ±0.009	1.0	59.3	0.057
Perrottetia sandwicensis[11]	Celastraceae	*T*	*LA*	2	1.00	5.5	0.021 ±0.013	1.1	8.8	0.008
Vaccinium calycinum[12]	Ericaceae	*S*	*LA*	113	0.76	0.5 - 23.0 - 158.0	0.615 ±0.116	2.4	63.8	0.033
All species	11			3185	0.39 ± 0.10†	1.0 - 5.0 - 255.5	18.44 ±2.40	8.6	2222.0	36.101

Notes: Authors: [1]A. Gray; [2]Gaudich.; [3](Gaudich.) A. Heller; [4]Gaudich. ex A. Gray; [5]A. Gray; [7]Hook. & Arn.; [6](Fosberg) W. L. Wagner & D. R. Herbst; [8](Cham. & Schltdl.) C. M. Weiller; [9](H. Lév.) H. St. John, [10]A. DC., [11]A. Gray, [12]Sm.

†Mean ±SE across species

Table S4-3a. Parameter estimates from GLMM models of seedling survival in the Palamanui dry forest (PLN) and the Laupahoehoe wet forest (LAU); values in bold significant at $\alpha < 0.05$, values in italics significant at $\alpha < 0.01$

Forest	Parameter	Estimate	Std. Error	z value	P
LAU	**A_{CON}**	**2.07**	**0.66**	**3.14**	**0.002**
	A_{HET}	-0.36	0.39	-0.92	0.358
	S_{CON}	0.00	0.00	0.72	0.472
	S_{HET}	0.00	0.00	1.53	0.125
	Initial height	**0.47**	**0.05**	**10.32**	**<0.001**
	TPAR†	1.34	2.45	0.55	0.583
PLN	**A_{CON}**	**62.35**	**14.78**	**4.22**	**<0.001**
	A_{HET}	*-11.11*	*5.74*	*-1.94*	*0.053*
	S_{CON}	**-0.03**	**0.01**	**-2.39**	**0.017**
	S_{HET}	0.03	0.04	0.91	0.364
	Initial height	**1.84**	**0.22**	**8.42**	**<0.001**
	TPAR†	**-1.18**	**0.50**	**-2.36**	**0.018**

† As continuous variable.

Table S4-3b. Parameter estimates from GLMM models of seedling survival in the Palamanui dry forest (PLN) and the Laupahoehoe wet forest (LAU) for most abundant and less abundant species; values in bold significant at α < 0.05, values in italics significant at α < 0.01

Forest	Category	Parameter	Estimate	Std. Error	z value	P
LAU	Most abundant	**A_{CON}**	**2.18**	**0.67**	**3.26**	**0.001**
		A_{HET}	*-0.82*	*0.44*	*-1.85*	*0.064*
		S_{CON}	0.00	0.00	1.26	0.209
		S_{HET}	0.00	0.00	1.08	0.281
	Less abundant	*A_{CON}*	*-34.69*	*21.09*	*-1.65*	*0.100*
		A_{HET}	0.67	0.60	1.12	0.265
		S_{CON}	**-0.04**	**0.01**	**-3.51**	**<0.001**
		S_{HET}	**0.01**	**0.00**	**2.18**	**0.030**
PN	Most abundant	**A_{CON}**	**62.46**	**14.84**	**4.21**	**<0.001**
		A_{HET}	*-10.89*	*5.93*	*-1.84*	*0.066*
		S_{CON}	**-0.04**	**0.01**	**-2.71**	**0.007**
		S_{HET}	0.13	0.09	1.50	0.134
	Less abundant	A_{CON}	100.28	147.10	0.68	0.495
		A_{HET}	-18.12	14.94	-1.21	0.225
		S_{CON}	-13.80	447.87	-0.03	0.975
		S_{HET}	-0.01	0.10	-0.09	0.929

Table S4-3c. Parameter estimates from GLMM models of seedling survival in the Palamanui dry forest (PLN) and the Laupahoehoe wet forest (LAU) for each TPAR category; values in bold significant at α < 0.05, values in italics significant at α < 0.01

Forest	Parameter	TPAR Category†	Estimate	Std. Error	z value	P
LAU	A_{CON}	Low	1.76	1.19	1.48	0.139
		Medium	**2.35**	**0.71**	**3.32**	**0.001**
		High	**7.42**	**1.40**	**5.30**	**<0.001**
	A_{HET}	Low	-0.63	0.53	-1.19	0.234
		Medium	-0.02	0.40	-0.04	0.965
		High	-0.99	0.63	-1.57	0.117
	S_{CON}	Low	0	0	-0.01	0.991
		Medium	0	0	0.44	0.661
		High	**0.01**	**0.00**	**2.38**	**0.017**
	S_{HET}	**Low**	**0.01**	**0.00**	**2.62**	**0.009**
		Medium	0.01	0.00	1.58	0.114
		High	0.00	0.00	-0.07	0.941
PLN	A_{CON}	**Low**	**60.30**	**20.21**	**2.98**	**0.003**
		Medium	**20.95**	**11.38**	**1.84**	**0.066**
		High	30.03	27.05	1.11	0.267
	A_{HET}	*Low*	*-13.12*	*6.90*	*-1.90*	*0.057*
		Medium	**-22.33**	**8.35**	**-2.67**	**0.007**
		High	*-16.78*	*9.16*	*-1.83*	*0.067*
	S_{CON}	**Low**	**0.18**	**0.08**	**2.27**	**0.023**
		Medium	**-0.04**	**0.02**	**-2.42**	**0.016**
		High	-0.10	0.07	-1.37	0.172
	S_{HET}	Low	0.45	0.35	1.29	0.196
		Medium	0.03	0.08	0.39	0.697
		High	**-1.38**	**0.67**	**-2.05**	**0.041**

†Low, medium, and high TPAR category ranges defined in Table 4-2.

Table S4-4a. Interaction terms between density variables and categorical variables (forest type, commonness, and TPAR category) for model parameters in Table S4-3a

Parameter	Chisq	Df	P
A_{CON} × forest	25.27	2	<0.001
A_{HET} × forest	4.07	2	0.131
S_{CON} × forest	6.24	2	0.044
S_{HET} × forest	3.01	2	0.222
Initial height	171.39	2.00	<0.001
TPAR†	9.12	2.00	0.010

† As continuous variable.

Table S4-4b. Interaction terms between density variables and categorical variables (forest type, commonness, and TPAR category) for model parameters in Table S4-3b

Forest	Parameter	Chisq	Df	P
LAU	A_{CON} × commonness	13.12	2	0.001
	A_{HET} × commonness	15.53	2	<0.001
	S_{CON} × commonness	9.21	2	0.010
	S_{HET} × commonness	11.32	2	0.003
PLN	A_{CON} × commonness	4.05	2	0.132
	A_{HET} × commonness	1.52	2	0.469
	S_{CON} × commonness	0.16	2	0.923
	S_{HET} × commonness	0.32	2	0.851

Table S4-4c. Interaction terms between density variables and categorical variables (forest type, commonness, and TPAR category) for model parameters in Table S4-3c

Forest	Parameter	Chisq	Df	P
LAU	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	6.88	2	0.032
	$A_{\mathrm{HET}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	7.13	2	0.028
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	5.93	2	0.052
	$S_{\mathrm{HET}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	4.98	2	0.083
PLN	$A_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	4.07	3	0.254
	$A_{\mathrm{HET}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	1.36	3	0.715
	$S_{\mathrm{CON}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	0.64	3	0.888
	$S_{\mathrm{HET}} \times \mathrm{TPAR}_{\mathrm{CAT}}$	3.44	3	0.329

CHAPTER 5

Convergence and divergence in woody seedling allometries: analysis of Hawaiian and global trends

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Summary

1. Ontogenetic allometry (i.e., changes in plant form and structure during growth, associated with differential resource allocation to plant organs) has profound implications for plant growth, adaptation to environmental conditions, and interspecific competition. Convergence in allometries among species within and across biogeographic regions may relate to common functional or developmental optima, whereas divergences point to different evolutionary trajectories that may relate to niche differentiation, e.g., between canopy and understory species.
2. We analyzed whole-plant data from seedlings of five woody species in Hawaiian forest and global data from 90 published studies including 164 species to test departure from geometric allometry, and for differences among Hawaiian species and between Hawaiian species and trends found in the global dataset.
3. We found striking convergence in allometric trends for Hawaiian juvenile plants; slopes differed among species in only 4/21 of these trends. Most differences related to leaf allocation, though we found weak support for hypothesized differences between canopy and understory species.
4. Allocation to above-ground structures relating to light capture (e.g., leaf area and stem length) strongly increased, with slopes greater than expectations from geometric scaling, whereas stem mass and diameter increased less than expected from geometric predictions.
5. Slopes for Hawaiian species differed on average from global means for slopes of 12 of the 19 allometric relationships tested, particularly for traits related to leaf allocation, supporting hypotheses of the importance of biogeographic shifts in allometries. In particular, leaf mass-plant mass allometries differed between Hawaiian and the global dataset, which contradicts

the assertion that these are “canonical” trait relationships across seedlings, juvenile and adults. Allometric slopes for leaf mass per area and leaf area scaled to total plant mass were 47% shallower for Hawaiian species than for the global dataset, suggesting that differences in allocation related to light capture.

6. Overall, Hawaiian species were more similar to each other in allometric slopes than to seedlings elsewhere, suggesting that, for woody seedlings, biomass allocation allometries converge within, and diverge among, biogeographic regions, supporting the importance of historical contingencies in trait evolution.

Key-words

allocation, biomass partitioning, mass fraction, plant ontogenetic allometry, tropical forest trees, seedling functional morphology, leaf area, light, standard major axis (SMA)

Introduction

Plants adapt to habitat conditions in part by shifting in morphology and proportional allocation of resources to leaves, stems, and roots during growth (Niklas 1994). Form and function are often interrelated, and thus plant morphology affects light, water, and nutrient acquisition, and thereby growth and survival (Niklas 1994, Kingsolver and Huey 2008). Ontogenetic allometry indicates changes in the relative size or shape of a given body part as an organism increases in size (Niklas 1994). In general, plant mass fractions allometries (e.g., leaf mass divided by total plant mass) indicate which resources most limit growth in a particular habitat (Poorter et al. 2012, Poorter and Sack 2012a). For instance, plants tend to allocate relatively more biomass to roots when belowground resources, such as water and nutrients are limiting and more biomass to shoots when aboveground resources, such as light, are the primary limitation (Poorter et al. 2012). However, these relationships are not universal, showing considerable variation among species and across ontogenetic stages (Sack and Grubb 2002, Milla and Reich 2007, Niklas et al. 2007). Large interspecific differences in allometries point to traits that may be more “evolvable” (i.e., capable of adaptive evolution) and that may contribute to niche differentiation among species (Egset et al. 2012). Similar allometric slopes among species support hypotheses of convergence across phylogeny, habitats, and biogeographic regions (Reich et al. 1999, Wright et al. 2004, Egset et al. 2012). Convergence in allometric patterns may be evidence of natural selection for particular trait combinations shifting in benefit during ontogeny, or of a conserved developmental program (Givnish 1988, Poorter 2007, Sack et al. 2012). Allometries are expected to differ between young plants (seedlings < 100 g; Poorter and Sack 2012b) and adult plants (Sack et al. 2002, Cornelissen et al. 2003, Ishida et al. 2005, Enquist et al. 2007, Reich et al. 2007). Our aims were to investigate ontogenetic trajectories of resource allocation for woody seedlings of endemic Hawaiian species and species represented in a global dataset gathered from the published literature to determine (1) if endemic Hawaiian species show interspecific differences that may relate to environmental adaptations; (2) whether Hawaiian species comply with global allometric trends; and (3) how Hawaiian species and species in the global dataset differ from predicted geometric slopes.

If trait relationships are inherent biological properties, then species that evolved in isolation should exhibit the same allometric relationships as species from the global flora (Heberling and Fridley 2012). A good test of this hypothesis is to examine how allometric relationships for endemic Hawaiian species, the world’s most isolated flora, differ from those of species from other regions (Heberling and Fridley 2012). Previous tests have shown that leaf traits of Hawaiian adult plants complied with global trends (Arcand et al. 2008, Heberling and Fridley 2012), supporting the hypothesis that plants follow similar trait patterns globally. However, allometric traits for plants at the seedling stage may reveal greater differences because adaptations to regeneration niches may lead to traits differences among species and regions (Grubb 1977).

In this study, we studied seedling allometries for five native Hawaiian species and compiled a novel global database, to address the following three questions:

1. *How do ontogenetic allometries vary among woody seedlings found in Hawaiian montane wet forest?* — We expected allometric relationships to differ among the Hawaiian species, due to their variation in life-history characteristics and their phylogenetic diversity (the species belong to different families) (Givnish 1988, Heberling and Fridley 2012). In particular, we tested the hypothesis that canopy trees show allometries consistent with their adaptation for vertical growth to reach higher light environments while understory plants are adapted to survive and assimilate light in the shaded understory (Givnish 1988, King 1990, Kohyama and Grubb 1994). If this hypothesis is correct, then we should find greater allocation of resources to stem length and roots to support height growth for canopy trees and greater allocation of resources to leaf area and stem diameter for understory plants relative to total biomass accumulation.

2. *Do Hawaiian seedlings comply with global trends?*— If allometric relationships are intrinsic properties that result from universal responses to environmental conditions, as suggested for leaf traits of mature plants (Reich et al. 1999, Wright et al. 2004 Niklas et al. 2007), then allometric slopes for Hawaiian species should not differ from global trends reported in the literature. Alternately, if scaling relationships differ among plants from separate biogeographic regions, then Hawaiian species, as an extreme example of isolated evolution, in theory should

differ from global trends (Heberling and Fridley 2012). Specifically, species from isolated floras have been hypothesized to face lower selection pressures, leading to lower carbon gain versus cost ratios (e.g., a smaller increase in leaf area per increase in stem mass; Heberling and Fridley 2012). However, a recent study by Heberling et al. (2012) found that the relationship between photosynthetic capacity and nitrogen content was similar for Hawaiian and mainland tropical species. In our study we examined a larger number of trait allometries than these previous studies for seedlings of Hawaiian woody species with a large dataset compiled from the literature including only woody angiosperm dicot seedlings and small saplings.

3. Do Hawaiian species and the global dataset comply with geometric scaling?— Geometric scaling arises when an organism maintains a constant shape and geometry as size increases (Niklas 1994). Thus, allometric slopes reflect dimensions increasing proportionally to their geometry (e.g., slope equal to 1 for allometries of linear measurements such as stem length versus stem diameter; slope equal to 2 for allometries of areal measurements versus linear measurements). The geometric prediction is a useful null hypothesis because slopes diverging from these expectations indicate changes in resource allocation with growth, which may indicate evolutionary adaptations to resource availability and/or interspecific competition (Niklas 1994, Sack et al. 2003, Price and Enquist 2006). Based on previous studies, we expected to find that stem mass increases isometrically while proportional allocation to leaf mass decreases with plant growth (Givnish 1988).

Materials and methods

Hawaiian seedling data collection.— We focused on seedlings in and near the Laupāhoehoe Forest Dynamics Plot (FDP) in the Laupāhoehoe Hawaiʻi Experimental Tropical Forest (HETF), located on Hawaiʻi Island at 19°55′N-155°17'W at 1200 m elevation in primary tropical lower montane wet forest (Holdridge 1947). Mean annual rainfall and temperature are respectively 3500 mm and 16^{o}C (Crews et al. 1995, Giambelluca et al. 2013). The forest canopy is dominated by endemic Hawaiian trees, especially *Metrosideros polymorpha*, with *Cibotium* spp. tree ferns dominating in the midstory (Inman-Narahari et al. 2013). For this study, we selected five native woody species that are common to Hawaiian montane wet forest: *Cheirodendron trigynum* (Gaudich.) A. Heller, *Coprosma rhynchocarpa* A.Gray, *Ilex anomala* Hook. & Arn., *Metrosideros polymorpha* (H. Lév.) H. St. John, and *Vaccinium calycinum* Sm. (Table 5-1). Nomenclature follows (Wagner et al. 1999, Wagner et al. 2012). We hereafter refer to these species by genus or collectively as Hawaiian species. These species represent 28% of the 18 native tree species that reach ≥ 1-cm DBH and account for 98% of the seedlings in census plots in the Laupāhoehoe FDP. These species vary substantially in life-form, ranging from the dominant canopy tree of the Hawaiian Islands (*Metrosideros*), to midstory trees (*Cheirodendron, Coprosma*, and *Ilex*), to an understory shrub (*Vaccinium*). All are endemic to Hawaii except for *Ilex* which is also indigenous to nearby oceanic Pacific islands (Wagner et al. 1999, Wagner et al. 2012). We defined seedlings as individuals ≤ 1 m in height. We chose this size cut-offs because trees and shrubs in this size range are typically in the vegetative growth phase and experience understory habitat conditions typical of the early growth phase and different from the conditions experienced by adults that have reached higher canopy positions. The 1 m size cut-off is also similar to that used by other studies that have examined seedlings (Nicotra et al. 1999), although smaller than some (≥10-20 cm tall and < 1 cm DBH; Comita et al. 2007, Comita and Engelbrecht 2009) and larger than others (≤50 cm tall; Metz 2012) that were conducted in large-scale permanent plots.

For Hawaiian species, we measured several plant morphological variables of seedlings harvested from the forest understory (Table 5-2). We harvested 5 to 21 wild seedlings <1-m in stem height for each of the five species, taking care to collect all fine roots. Variation in habitat conditions, especially irradiance (Coomes and Grubb 1998), may confound comparisons among species, so we collected seedlings across the range of understory irradiance levels most commonly found in this forest. Detailed measurement methods for seedling allocation and understory irradiance are described in Appendix 1.

Global dataset assembly.— To determine whether Hawaiian species comply with global trends, we extracted and analyzed data from previously published studies that reported measurements over time or size for woody angiosperm dicots that we classified as seedlings (≤100 cm tall, ≤50 g total plant mass, and ≤45 g shoot or stem mass). Our reasons for selecting the 1 m height size cut-off is as explained above. The 50 g size cut-off is also in the range of, though somewhat smaller than, that used by a recent meta-analysis of ontogenetic allometries which considered plants ≤100 g as seedlings (Poorter et al. 2012). Our resulting database includes 90 studies covering 164 species across a range of tropical and temperate habitats (details in Appendix 1 and Supplemental Materials). We acknowledge that many more data exist in the literature and proceed with the assumption that the data we assembled are a representative sample. For convenience, we hereafter refer this dataset and the species contained therein as the "global dataset".

Allometric analysis. — To quantify ontogenetic allometric relationships among measured variables for Hawaiian species and global dataset, we conducted standard major axis (SMA) analysis on $\log_{10}$-transformed variables using *SMATR* in R version 2.15.0 (Warton et al. 2006, R Development Core Team 2012). For hypothesis testing among Hawaiian species, and between

Hawaiian species and global dataset, we compared differences in SMA slopes with 1000 randomized datasets and used Wald's tests to examine differences among intercepts. Biomass allocation can vary across irradiance environments (Coomes and Grubb 1998, Poorter et al. 2012), and our sampling of seedlings of a range of sizes across a typical range of natural irradiance levels leads to a level of uncertainty in the influence of irradiance on the allometries. Thus, prior to SMA analysis we determined that irradiance was not a significant covariate using multiple regression analysis of stem length (StL) versus plant mass (PM). We tested whether pooled SMA slopes differed from the predictions of geometric scaling by determining if that slope fell within the determined 95% confidence intervals. We also conducted ordinary least squares (OLS) analysis for the four variables calculated with total plant mass as the denominator, i.e., leaf mass fraction, stem mass fraction, root mass fraction, and leaf area ratio (LMF, StMF, RMF, and LAR; all abbreviations are defined in Table 5-2). Because the results from both analyses were either not different or the SMA slopes were steeper and all other parameters were similar, we provide the SMA results in the Results section and the OLS results in Table S5-1. Note that when naming relationships we always refer to the y-variable first (i.e., Y-X).

Results

Allometric differences among Hawaiian forest seedlings. —Despite considerable variation in plant traits for Hawaiian seedlings (illustrated in Fig. 5-1), we found few differences in ontogenetic allometries. For example, the mean area per leaf ranged from 0.04 to 25 cm^2 among the five Hawaiian species included in this study and from 0.04 to 6.1 cm^2 for *Metrosideros* alone (Table S5-2).

Relations among traits through ontogeny were generally strongly correlated and highly significant for all species pooled (Table 5-4). The mean R^2 over all allometric relations examined for Hawaiian species was 0.72 and all correlations were significant at $P < 0.05$ except RMF-PM; with 19 of 22 relationships having P-values <0.001 (Table 5-4).

Hawaiian species showed similar slopes for the majority of allometries tested, but striking differences in allometric slopes for several traits when examined in relation to total plant mass. The allometric slopes differed across species for only four of the 21 allometries tested (19%) that also had significant slopes (Table 5-3). We found interspecific differences for four slopes and three intercepts of relationships with total plant mass (PM) as the x-variable (Table 5-3). One of the largest differences among Hawaiian species was the LMF-PM slope, which was 63% more negative for *Vaccinium* than for *Metrosideros* (Table 5-3). We also found large differences in LMA-PM slopes; with 32% steeper slopes for *Metrosideros* than for *Coprosma*, reflecting differences in leaf structure between these two species. Additionally, the RL-PM slope was 39-48% steeper for *Vaccinium* than for the other species (Table 5-3).

Compliance of Hawaiian seedlings with global trends. — In general, Hawaiian species differed from global trends, especially for traits related to leaf allocation. Pooled allometric slopes differed for 12 of the 19 significant relationships that we tested for both Hawaiian species and global dataset (63%; greater than the 5% expected from chance; $P < 0.001$; ratio test; Fig. 5-2, Table 5-4. Of the relationships for which Hawaiian species and the global dataset differed, Hawaiian species slopes were shallower than those of the global dataset for nine (75%) and steeper than the global dataset for three (25%; Fig. 5-2, Table 5-4), implying a relatively lower allocation to several plant organs as size increases than for the global dataset. We found especially large differences in allometric slopes between Hawaiian species and the global dataset for LMA-PM and LAR-PM which were 47% shallower for Hawaiian species than for the global dataset and 47% less negative for Hawaiian species than for the global dataset, respectively (Fig. 5-3). Further, Hawaiian species slopes were 42% shallower than the global dataset slopes for StMF-PM, though correlation for these allometries were relatively low (both $R^2 \leq 0.10$; Fig. 5-3). Additionally, Hawaiian species differed from the global dataset for three of the four relationships compared where Hawaiian species also showed interspecific differences (Tables 3 and 4).

Differences from geometric scaling for Hawaiian species and the global dataset. — Pooled slopes of Hawaiian species and the global dataset generally differed from predicted geometric slopes. Pooled Hawaiian species slopes differed from expectations from geometric scaling or 16 of the 21 slopes examined (76%) and the global dataset slopes differed from geometric scaling for all of the 20 slopes examined (Fig. 5-3; note that we excluded comparisons for which SMA slopes were not significant (RMF-PM for Hawaiian species and LMF-PM for the global dataset). Average differences from geometric scaling were similar for both Hawaiian species and the global dataset. For slopes that differed from geometric scaling and could be compared for both Hawaiian species and the global dataset, the mean percent difference from geometric scaling for Hawaiian species was 30% (range 4.8 to 83%) while for the global dataset it was 26% (range 2.4 to 92%). Although we found some large divergences from geometric scaling for mass fraction allometries (PM-LMF, StMF, or RMF) for both Hawaiian species and the global dataset (Fig. 5-3), all the R^2 values for these relationships were low ($\leq$0.12; Table 5-4). The largest differences from geometric scaling for a relationship with a high R^2 value (>0.12) were the slopes for LAR-PM for Hawaiian species (75% steeper than geometric scaling, R^2 = 0.48;) and for the StL-PM slope for the global dataset (92% steeper than geometric scaling; R^2 = 0.57). Hawaiian species and the global dataset showed opposite patterns in allocation for three allometries: StD-PM, LM-PM, and LMA-PM. For these allometries, Hawaiian species' slopes were shallower than expectation from geometric scaling whereas the global dataset slopes were steeper (Fig. 5-3). For example, LMA-PM slopes for Hawaiian species were 35% shallower than expected from geometric scaling whereas the global dataset slopes were 23% steeper.

Discussion

The present study extends earlier investigations of interspecific and regional patterns in ontogenetic allometries for woody angiosperms during the early life stages to a larger number of species. Our results have broad applications for understanding the diversity of plant resource allocation strategies among seedlings of woody species on isolated islands and globally. Overall, we found that ontogenetic allometries for juvenile plants of Hawaiian species were more similar to each other than to the global dataset, suggesting that local adaptations to environmental conditions result in divergent trait strategies across biogeographic regions. These results are contrary to the hypothesis of convergent global relationships, which have been found to be typical for leaves of adult plants (Reich et al. 1999, Wright et al. 2004, Niklas et al. 2007), and supports the hypothesis that species from geographically isolated areas have different trait relationships (Heberling and Fridley 2012). The similarities and differences we found within and among Hawaiian species and the global dataset suggest the existence of convergent global trait strategies for some relationships and interspecific and regional differences in plant resource acquisition strategies for others (Reich et al. 1999, Wright et al. 2004, Heberling and Fridley 2012). One explanation for Hawaiian species being more similar to each other is because they evolved together under similar environmental conditions, and coexist in a single community, and their pronounced difference from the global dataset may arise because Hawaiian species evolved in isolation from other floras.

Allometric differences among Hawaiian forest seedlings. — Contrary to our expectations, we found relatively few differences in allometric slopes among Hawaiian species despite large differences in life-history traits. The interspecific differences we found did not support the hypothesis that canopy species have greater allocation to stem height or roots than understory species and mixed evidence that understory species allocate relatively more to leaf area and stem diameter than canopy species (Givnish 1988, King 1990, Kohyama and Grubb 1994). Allometric slopes for RL-PM differed among Hawaiian species, but in the opposite of the predicted direction (Givnish 1988, King 1990, Kohyama and Grubb 1994), with relatively greater allocation to root length for the understory shrub, *Vaccinium*, than for the canopy or midstory species. None of the allometries relating to stems differed among Hawaiian species, except for StMF-PM slopes, which were significant only for the canopy species, *Metrosideros*, but showed that proportional allocation to stems decreased with growth relative to geometric scaling. In support of the hypothesis that understory species allocate relatively more to leaf area to capture light in the shaded understory than do canopy species (King 1990, Kohyama and Grubb 1994), the midstory species, *Coprosma*, produced relatively more leaf area and thinner and/or less dense leaves with increased growth than did the canopy species, *Metrosideros*. High leaf area allocation is an adaptation for light capture that may help *Coprosma* to grow in the shady forest understory (King 1990, Kohyama and Grubb 1994). On the other hand, *Metrosideros* maintained relatively greater carbon allocation to leaves in proportion to its total size with ontogeny than understory species. This finding is consistent with previous studies showing that *Metrosideros* has shade-tolerant photosynthetic traits (Funk and McDaniel 2010). Similarly, our findings are consistent with previous studies of tropical forest saplings that found either similar above-ground allocation patterns among species (Kohyama and Hotta 1990) or that interspecific variation did not correlate with canopy position (Kohyama and Grubb 1994). However, our results disagree with studies that found substantial differences in above-ground allocation among canopy and understory saplings in tropical (King 1990) and temperate (Cho et al. 2005) forests. These differences in leaf and stem allocation are hypothesized to occur as an adaptation to steep light gradients in dense tropical forest (King 1990), which may not be present in Hawaiian wet forest because it has relatively higher understory irradiance than found in other tropical forests (Coomes and Grubb 2000, Inman-Narahari et al. 2013). Rather, interspecific similarities in allometric slopes suggest selection for optimum resource allocation that is common to all the species examined (Givnish 1988), possibly due to similar environmental constraints within Hawaiian wet forest. Further, interspecific differences in root length and leaf allocation may be important for niche differentiation among Hawaiian species,

Compliance of Hawaiian seedlings with global trends. — Endemic Hawaiian species largely differed from global trends, supporting the hypothesis that biogeographic history is important for determining species traits (Heberling and Fridley 2012). However, the trait differences we found did not support the hypothesis that species from isolated floras, with presumably lower selection pressures, would have a lower carbon gain versus cost ratio (Heberling and Fridley 2012). For example, Hawaiian species allocated more to leaf area relative to total mass (i.e., leaf area ratio; LAR) and developed thinner leaves (i.e., leaf mass per area; LMA and leaf thickness; LT) with growth than did the global dataset through ontogeny; traits that are expected to provide greater carbon gain per carbon investment (Givnish 1988). However, the global dataset did allocate relatively more to height growth than did Hawaiian species, a characteristic indicative of high interspecific competition for light (King 1990, Kohyama and Grubb 1994). On the other hand, stems appeared to become more slender with growth for Hawaiian species (i.e., less increase in stem mass with stem height), indicating more efficient resource investment (Reich et al. 1999; Wright et al. 2004). Although differences were more subtle, species in the global dataset allocated relatively more to roots (both length and mass) than did Hawaiian species. Optimal foraging theory predicts that plants allocate most to the organ that captures the most limiting resource in a given habitat (Chapin et al. 1993). Thus, high allocation to leaf area and stem elongation implies strong competition for light and, perhaps that light may limit growth more strongly for seedlings of Hawaiian species than of species in the global dataset (Givnish 1988). This finding may be in part because many of the plants included in the global dataset were grown in open habitats (e.g., Bruhn et al. 2000, Dickson et al. 2000, Austin et al. 2009). Likewise, greater allocation to roots for species in the global dataset suggests that soil resources were less limiting for Hawaiian species; an expected result given the high precipitation and soil fertility of our study site (Poorter et al. 2012).

Altogether, the trait differences we found suggest that separate evolutionary trajectories (e.g., due to habitat differences or limited genetic diversity of founders) leads to different resource acquisition strategies among biogeographic regions. Although the majority of allometries we tested differed between Hawaiian species and the global dataset, the few allometric slopes that were similar suggest convergence in plant strategies for these traits, possibly indicating that these traits are adaptive across a wide range of habitats (Reich et al. 1999, Wright et al. 2004). However, we examined a larger number of trait allometries than these previous studies. Our results differ from previous studies showing that Hawaiian tree species, while functionally diverse, tend to follow global patterns for correlation among leaf traits

(Sandquist and Cordell 2007, Arcand et al. 2008, Heberling and Fridley 2012Additionally, we examined how plant resource allocation changes with plant growth for seedlings, rather than static allometries of adult plants.

Geometric scaling of Hawaiian species and species in the global dataset. — The largest divergences from isometric slopes point to the importance of resource allocation to height growth and leaf area, perhaps in response to interspecific competition for light (Niklas 1994, Price and Enquist 2006). Importantly, allometries are expected to be different for young plants (seedlings and juveniles) than for adult plants (Sack et al. 2002, Cornelissen et al. 2003, Ishida et al. 2005, Enquist et al. 2007, Reich et al. 2007). Contrary to our hypothesis that proportional allocation to leaf mass would decrease with growth (Givnish 1988), leaf mass increased isometrically with plant mass for Hawaiian species and increased slightly relative to geometric scaling for the global dataset. Additionally, stem mass was not constant with growth but instead increased slightly relative to geometric scaling for both Hawaiian species and the global dataset. However, stem mass fraction and leaf mass fraction both decreased strongly with growth relative to geometric predictions for Hawaiian species and stem mass fraction also decreased strongly with growth relative to geometric predictions for the global dataset. Nevertheless, we found some support for the general idea that plants must maximize carbon gain versus carbon investment, such as by increasing allocation to photosynthetic area (e.g., leaves) versus support structures (e.g., stems). For example, the largest increases in plant allocation relative to geometric scaling for both Hawaiian species and the global dataset were to stem length and leaf area ratio (LAR = leaf area/ total plant mass). This presumably enables the plant to reach higher light levels and increase photosynthetic area (Givnish 1988). These results appear contrary to expectations that plants must trade-off allocation to vertical growth versus leaf area, and that these represent different strategies of separate functional groups (Reich et al. 1999, Wright et al. 2004). Rather, on average, woody seedlings appeared to maximize carbon gain by increasing both height and leaf area. This was apparently done by producing thinner stems and less massive leaves (e.g., decreased stem diameter versus stem length and small or no increases in leaf mass with growth). For Hawaiian species, strong decreases in both LMA and leaf thickness relative to geometric predictions suggest that leaves became thinner with ontogeny. Though LMA increased for the global dataset relative to geometric predictions, we found no leaf thickness or leaf density data to distinguish which aspect of LMA changed with ontogeny. However, previous studies show that leaf thickness generally increases as plants transition from seedlings to adults (Cornelissen et al. 2003). Similarly to stems, plants allocated proportionately more to root length at the expense of root mass. On the whole, these results support previous studies showing strong inter-relationships between leaf area and plant growth for plants of disparate biogeographic lineages (e.g., Poorter 2001, Poorter and Bongers 2006) and point to evolutionary adaptations to resource limitation and interspecific competition (Givnish 1988, Niklas 1994, Egset et al. 2012).

Conclusions. — In summary, our analysis of whole-plant allometries from Hawaii and studies from around the globe reveal striking convergences and divergences in trait relations. Hawaiian species tended to be similar to each other, but differed in many respects from the global dataset, in ways that suggested different adaptation to local environments. In combination with seedling height and density data, leaf area versus height and plant mass versus height allometries can be used to estimate the biomass and leaf area index (LAI) of seedlings in the understory, values that are frequently calculated for canopy trees but not for seedlings. This information would provide insight into how “leafiness” and understory biomass vary among forest types.

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Table 5-1. Biological information and the range of values sampled for each of the five Hawaiian species studied; relative abundance of seedling species calculated as (number of individuals of species x/ number of individuals of all species) × 100

Species	*Cheirodendron trigynum*	*Coprosma rhynchocarpa*	*Ilex anomala*	*Metrosideros polymorpha*	*Vaccinium calycinum*
Family	Araliaceae	Rubiaceae	Aquifoliaceae	Myrtaceae	Ericaceae
Hawaiian name	ōlapa	pilo	kāwau	‘ō‘hia	ōhelo
Life-form	Midstory tree	Midstory tree	Midstory tree	Canopy tree	Understory Shrub
Native status	Endemic	Endemic	Indigenous†	Endemic	Endemic
N	11	16	5	21	8
Seedling mass range (g)	1.8×10^{-2} – 8.4	2.6×10^{-3} – 7.2	1.5×10^{-2} – 7.6	8.4×10^{-4} – 42.9	2.4×10^{-1} – 4.2
Seedling height range (cm)	4.7 – 58.5	1.2 – 62.9	2.2 – 34.6	0.8 – 81.5	12.5 – 44.7
Seed size (mm) ‡	4.0	5.3	2.0	1.7	0.8
Seedling density (individuals/m^2)	3.07	0.75	0.05	3.33	0.45
Relative abundance of seedling species	40%	10%	1%	43%	6%

Notes: †Found outside of Hawaii in Tahiti and Marquesas. ‡Seed sizes from the Bishop Museum Hawaii Ethnobotany Online Database (http://173.201.252.229/ethnobotanydb/ethnobotany.php).

Table 5-2. Abbreviations, calculations, and units for variables included in this study

Variable type	Abbrev.	Variable	Units
Length	StL	Stem length	cm
	RL	Root length	cm
Diameter/ thickness	StD	Stem diameter	mm
	LT	Leaf thickness	mm
Area	LA	Total leaf area	m^2
Mass	StM	Stem dry mass (includes branches and petioles)	g
	ShM	Shoot dry mass (includes leaves and stems)	g
	LM	Leaf dry mass (sum of all leaves on plant; excludes petioles)	g
	RM	Root dry mass	g
	PM	Total plant dry mass	g
Derived	LAR	Leaf area ratio (total leaf area/plant mass)	m^2/g
	StMF	Stem mass fraction (stem mass/ plant mass)	g/g
	LMF	Leaf mass fraction (leaf mass/plant mass)	g/g
	RMF	Root mass fraction (root mass/ plant mass)	g/g
	LMA†	Leaf mass per area (leaf mass/ leaf area)	g/m^2

†LMA is the inverse of specific leaf area (SLA, leaf area/leaf mass), thus allometric slopes with SLA are the inverse of slopes with LMA, though units, and therefore, intercepts differ.

Table 5-3. Relationships between dry mass and other variables for Hawaiian forest seedlings that showed interspecific differences in allometric slopes; for the other 17 relationships, slopes did not differ across species at $P < 0.05$. The parameters are for log (y) = $a + b \times$ log (plant dry mass) fitted by standard major axis (SMA), with ±95% CIs, R^2, and significance level of relationship (*$P < 0.05$, **$P < 0.01$,***$P < 0.001$); superscript letters indicate significant differences among species in the fitted slope; † indicates that slopes differed from geometric scaling.

Y	*C. trigynum*	*C. rhynchocarpa*	*I. anomala*	*M. polymorpha*	*V. calycinum*
RL	b = 0.38 ±0.12^{b} a = 1.23 ±0.24 R^2 = 0.77***	b = 0.39 ±0.09^{b} a = 1.20 ±0.23 R^2 = 0.77***	b = 0.33 ±0.15^{ab} a = 1.11 ±0.56 R^2 = 0.87*	b = 0.36 ±0.05^{b} a = 1.28 ±0.16 R^2 = 0.88***	b = 0.64 ±0.15^{a}† a = 1.25 ±0.16 R^2 = 0.92***
LMF	b = −0.10 ±0.10^{a}† a = 1.56 ±0.17 R^2 = 0^{ns}	b = 0.16 ±0.06^{a}† a = 1.64 ±0.24 R^2 = 0.02^{ns}	b = 0.10 ±0.07^{a}† a = 1.85 ±0.44 R^2 = 0.18^{ns}	b = −0.15 ±0.08^{a}† a = 1.57 ±0.19 R^2 = 0.20*	b = −0.41 ±0.27^{b}† a = 1.50 ±0.20 R^2 = 0.72**
LA	b = 0.88 ±0.09^{ab}† a = −2.00 ±0.15^{ab} R^2 = 0.98***	b = 0.92 ±0.08^{b}† a = −1.91 ±0.19^{b} R^2 = 0.97***	b = 0.89 ±0.12^{ab}† a = −1.89 ±0.32^{ab} R^2 = 0.99***	b = 0.78 ±0.05^{a}† a = −2.08 ±0.14^{ac} R^2 = 0.98***	b = 1.13 ±0.45^{ab}† a = −2.25 ±0.54^{c} R^2 = 0.72**
LMA	b = 0.14 ±0.03^{ab}† a = 1.58 ±0.06^{b} R^2 = 0.87***	b = 0.13 ±0.03^{b}† a = 1.51 ±0.08^{c} R^2 = 0.81***	b = 0.17 ±0.09^{ab} † a = 1.71 ±0.33a R^2 = 0.82*	b = 0.19 ±0.04^{a}† a = 1.72 ±0.15^{a} R^2 = 0.71***	b = −0.75 ±0.95^{c}† a = 1.76 ±0.71^{abc} R^2 = 0.17^{ns}
StMF	b = 0.11 ±0.05^{a}† a = 1.63 ±0.18^{b} R^2 = 0^{ns}	b = −0.13 ±0.09^{a}† a = 1.55 ±0.21^{b} R^2 = 0^{ns}	b = 0.10 ±0.06^{a}† a = 1.35 ±0.26^{a} R^2 = 0.68^{ns}	b = 0.12 ±0.04^{a}† a = 1.53 ±0.16^{b} R^2 = 0.20*	b = 0.57 ±0.31^{b}† a = 1.48 ±0.49^{ab} R^2 = 0.27^{ns}

Notes: Intercepts did not differ among species for RL-PM and LMF-PM

Table 5-4. Parameters from SMA analysis of Hawaiian forest seedlings and the global dataset with ±95% CIs, R^2, and significance level (*$P < 0.05$, ***$P < 0.001$); we list predicted slopes from geometric scaling (GS) and P-values for analysis of difference between slopes of Hawaiian and the global dataset (comparisons only made for relationships that were significant for both groups); abbreviations and units as in Table 5-2

			Parameters for Hawaiian species			Parameters for Global dataset			Hawaiian *v.* Global	
X	Y	GS	Intercept	Slope	R^2	Intercept	Slope	R^2	Int. *P*	Slope *P*
PM	LA	0.66	-2.02 ±0.05	0.84 ±0.05	0.95***	-2.10 ±0.05	0.94 ±0.06	0.77***	0.131	0.012
	LT	0.33	-0.61 ±0.03	0.13 ±0.02	0.47***	no data found for the global dataset				
	LM	1	-0.40 ±0.04	0.96 ±0.04	0.97***	-0.43 ±0.02	1.02 ±0.02	0.94***	0.057	0.009
	LMA	0.33	1.66 ±0.06	0.22 ±0.04	0.36***	1.54 ±0.05	0.41 ±0.06	0.19***	0.006	<0.001
	RL	0.33	1.24 ±0.04	0.38 ±0.04	0.82***	1.09 ±0.05	0.42 ±0.07	0.17***	<0.001	0.414
	RM	1	-0.70 ±0.05	1.05 ±0.05	0.97***	-0.61 ±0.01	1.11 ±0.01	0.96***	0.012	0.026
	ShM	1	-0.11 ±0.02	0.99 ±0.02	0.99***	-0.16 ±0.01	0.97 ±0.01	0.99***	<0.001	0.022
	StD	0.33	0.45 ±0.03	0.32 ±0.03	0.86***	0.43 ±0.07	0.42 ±0.07	0.70***	0.089	0.002
	StL	0.33	1.32 ±0.05	0.48 ±0.05	0.85***	1.12 ±0.06	0.63 ±0.06	0.57***	<0.001	<0.001
	StM	1	-0.46 ±0.05	1.07 ±0.04	0.98***	-0.63 ±0.03	1.10 ±0.03	0.93***	<0.001	0.180
	LAR	-1	-2.06 ±0.06	-0.26 ±0.05	0.48***	-1.84 ±0.06	-0.49 ±0.06	0.13***	<0.001	<0.001
	LMF	1	1.55 ±0.05	-0.16 ±0.05	0.09*	1.46 ±0.03	0.33 ±0.02	0^{ns}		
	RMF	1	1.36 ±0.07	0.19 ±0.04	0.03^{ns}	1.38 ±0.02	0.24 ±0.01	0.12***		
	StMF	1	1.58 ±0.06	0.17 ±0.04	0.10*	1.26 ±0.03	0.30 ±0.03	0.04***	<0.001	<0.001
LM	RM	1	-0.26 ±0.10	1.09 ±0.07	0.93***	-0.08 ±0.04	1.12 ±0.05	0.73***	<0.001	0.495
LM	StM	1	-0.02 ±0.10	1.11 ±0.08	0.92***	-0.10 ±0.04	1.14 ±0.05	0.77***	0.040	0.474
ShM	RM	1	-0.58 ±0.07	1.06 ±0.06	0.95***	-0.43 ±0.02	1.15 ±0.02	0.91***	0.005	0.014
StL	LA	2	-4.41 ±0.26	1.8 ±0.20	0.81***	-3.93 ±0.21	1.52 ±0.14	0.56***	0.047	0.022
StL	ShM	3	-2.84 ±0.26	2.06 ±0.20	0.85***	-2.46 ±0.28	2.02 ±0.22	0.60***	<0.001	0.779
StL	StD	1	-0.42 ±0.12	0.66 ±0.09	0.69***	-0.62 ±0.08	0.89 ±0.06	0.60***	0.019	<0.001
StM	RM	1	-0.24 ±0.10	0.98 ±0.07	0.93***	0.07 ±0.03	0.92 ±0.04	0.72***	<0.001	0.153
StM	StL	0.33	1.53 ±0.06	0.45 ±0.04	0.86***	1.42 ±0.02	0.41 ±0.02	0.90***	0.003	0.086

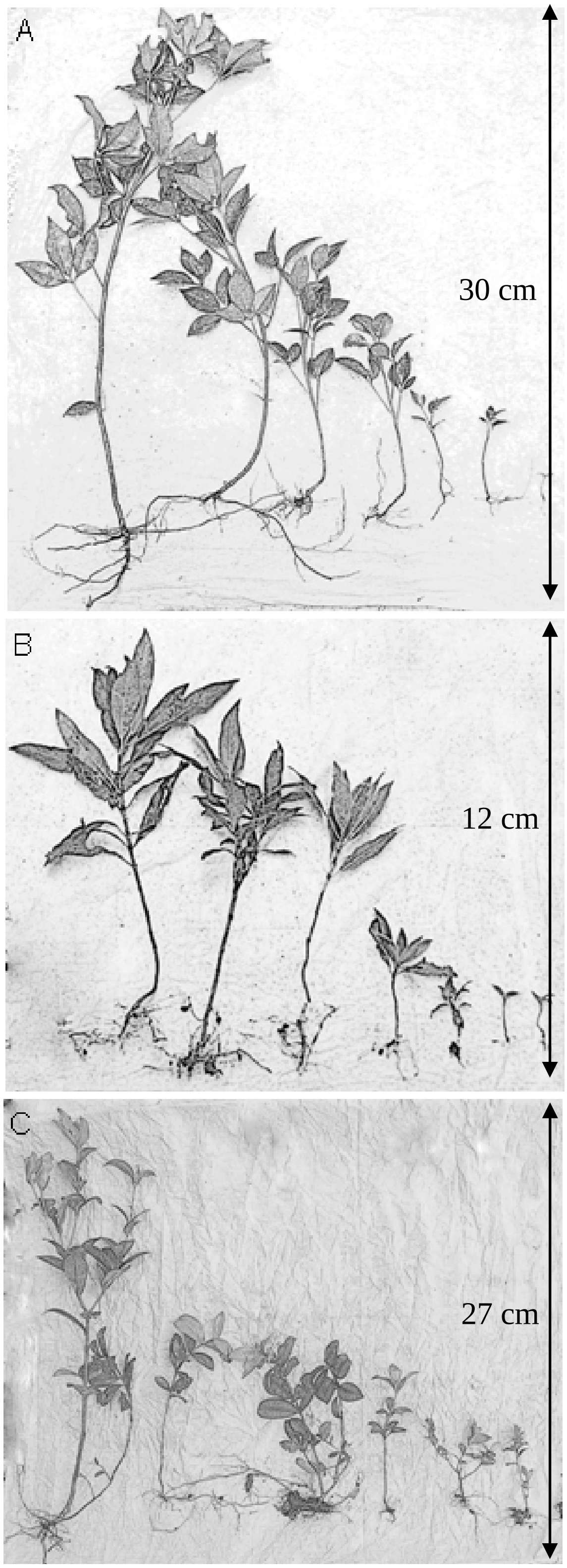

Fig. 5-1. Examples of the ontogenetic trajectories of seedlings for three of the five native Hawaiian species studied: (A) *Cheirodendron trigynum*, (B) *Coprosma rhynchocarpa*, and (C) *Metrosideros polymorpha*.

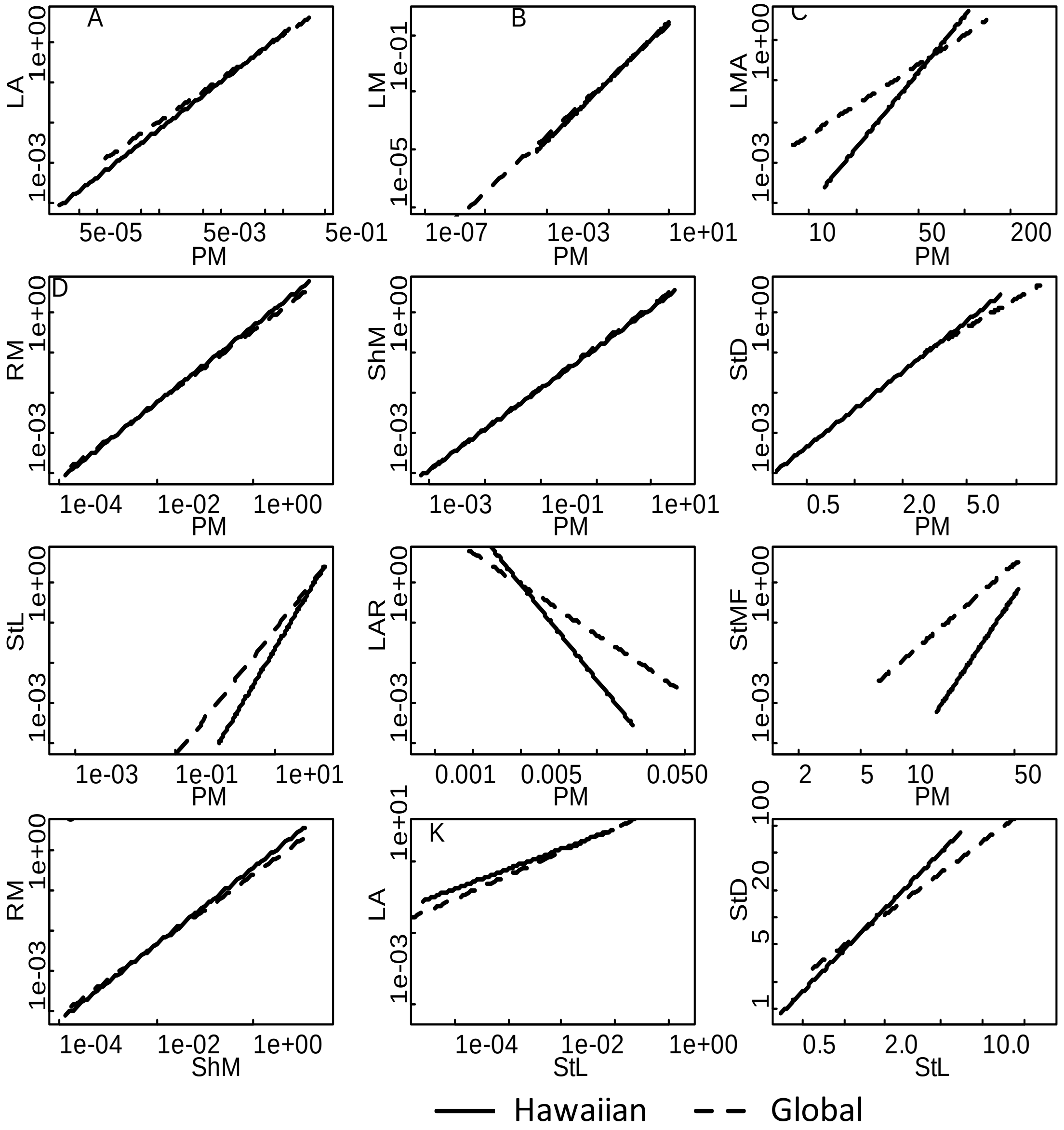

Fig. 5-2. Allometries where Hawaiian and the global dataset differed; values are shown on $\log_{10}$ axes and fitted with standard major axis (SMA) regression lines; parameters in Table 5-4 and sources in Supplementary Material.

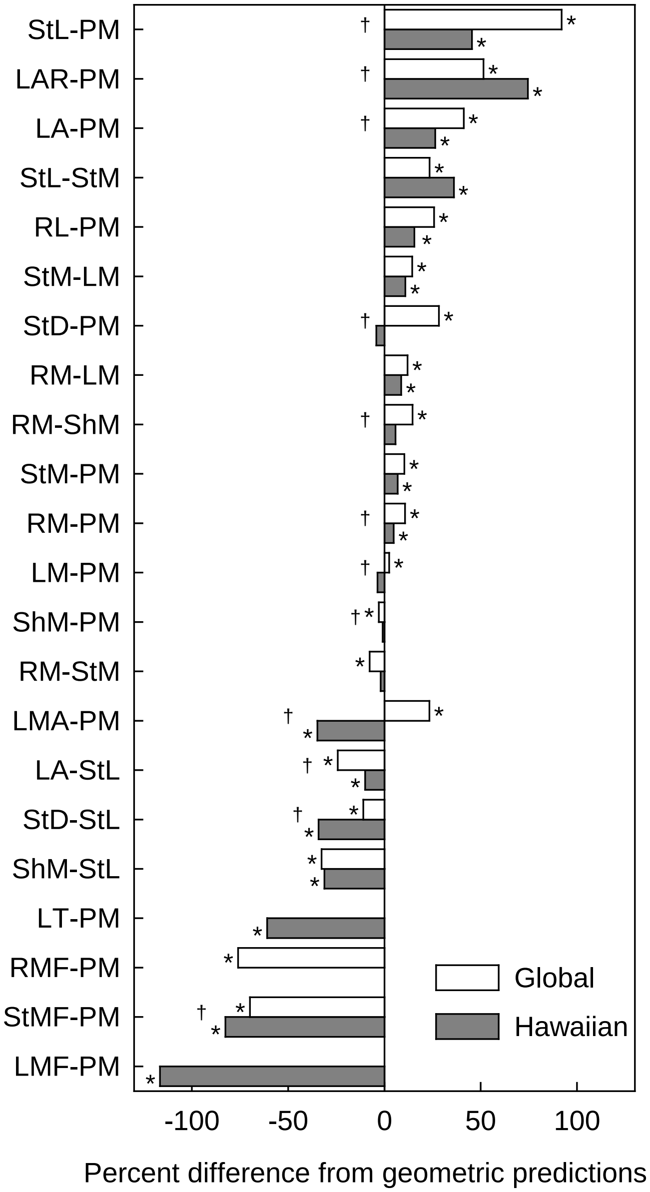

Fig. 5-3. Percent differences from geometric scaling of pooled slopes for Hawaiian and the global dataset sorted by difference from geometric predictions averaged over Hawaiian and the global dataset; values > 0 indicate increasing allocation to the y-variable with increasing values of the x-variable and values < 0 indicate decreasing allocation to the y-variable with increasing values of the x-variable (variables listed as Y-X); asterisks indicate significant difference from geometric predictions and crosses (†) indicate significant differences between Hawaiian and global; abbreviations and units in Table 5-2.

Notes: Where pooled slopes of Hawaiian species differed from geometric predictions and interspecifically, individual species slopes also differed from geometric predictions for all species. Bars are not shown for LMF-PM for the global dataset and for RMF-PM for Hawaiian species because the slopes of the relationships were non-significant, and bars are not shown for LT-PM for the global dataset because no data were available.

Chapter 5 Appendix 1.

Data collection and analysis details

Seedling allocation measurements and analysis.— Following harvest, we clipped seedlings under water at the root collar and rehydrated them in cool conditions (4° C) for at least 24 hours to ensure complete hydration prior to taking a variety of measurements (Garnier et al. 2001; Table 5-2). We ensured that we made measurements on fully hydrated plants by keeping plant parts covered by moist paper towels inside plastic bins (Garnier et al. 2001). We dried plants at 70° C for ≥48 hours prior to taking dry weights and we weighed plants immediately after removal from the plant drying oven. We measured leaf area from high resolution leaf scans analyzed using ImageJ software (Rasband 1997-2011). We included petioles with the stem fraction, as they both functionally serve as support structures and to transport water, nutrients, and sugars (Poorter et al. 2012).

Also called Type II regression and similar to reduced major axes analysis (RMA), SMA is used to assess functional allometric relationships because it allows x and y errors to vary independently rather than assuming that x predicts y as in ordinary least-squares regression (OLS; Smith 1980; Seim & Sæther 1983; Sack et al. 2003; Warton et al. 2006). SMA parameters are a and b for $\log(y) = a + b \times \log(x)$ where a and b are analogous to the intercept and slope in OLS, respectively.

Irradiance measurements.— At each seedling location, we measured light as photosynthetically active radiation (PAR, μmol photons$\cdot$m$^{-2}\cdot$s^{-1}) on uniformly overcast days above and below the canopy using LiCOR quantum sensors (LI-190, LI-COR, Lincoln, NE, USA) to calculate instantaneous transmitted diffuse PAR (TPAR = understory PAR / above canopy PAR; Anderson 1964; Nicotra, Chazdon & Iriarte 1999). At the height of each seedling, we recorded two 15 second averages per seedling location and paired these measurements with simultaneous above canopy measurements taken on an adjacent above-canopy climate tower.

We collected plants across a range of irradiance environments from 1.2% to 15% transmitted PAR (mean ±SE of 4.9% ±0.41%, $N = 60$) to represent mean species values. This range and average was similar to, although slightly lower than, separate measurements taken in the understory of the adjacent 4-ha permanent plot which ranged from 1.4% to 21% transmitted PAR (mean ±SE of 5.9% ±0.23%, $N = 192$; {Inman-Narahari, 2013 #3576}). Light was not a significant covariate in analysis of plant dry mass versus height for any species (all $P > 0.05$).

Global dataset collection and analysis.— We gathered literature sources through ISI Web of Knowledge searches, using allometry OR allometric OR allocation AND seedling OR sapling as keywords. We further filtered by studies conducted on vegetation. We located additional sources by searching the literature referenced by relevant articles. Finally, we searched ISI Web of Knowledge for studies that cited the most relevant articles and studies that cited the SMATR program. This search resulted in 1465 references. We included only studies for which the full text was available online through Google Scholar or the University of California, Los Angeles digital library (53 studies excluded).

We included all studies that examined ontogenetic trends for woody angiosperm dicots that could be classified as seedlings or saplings (≤200 cm tall). Thus, we excluded studies on herbs, grasses, conifers, or mature trees. To examine ontogenetic trends, studies must have presented data or allometric parameters for changes in one size variable versus a second size variable (e.g., height versus mass). Thus, we excluded studies that only presented parameters for trends analyzed across species (i.e., using species values averaged across all sizes as a data point).

For studies which measured plants grown under experimental conditions (e.g., gap versus open, high, ambient versus elevated CO_2), we included measurements from conditions comparable to those of the seedlings we collected in the Hawaiian forest. For example, we included data only from seedlings grown in low irradiance/understory plots and/or in ambient CO_2. Where data for each treatment were not reported by the study but treatments values did not significantly differ from one another, we used average values for all treatments. We also used average values across treatments for studies that manipulated factors for which we have no comparable measure for Hawaiian seedlings (e.g., N fertilizer treatments; Arnone & Gordon 1990). Where studies presented data for a range of sizes, including individuals >100 cm tall, we extracted data only for individuals ≤100 cm tall.

Overall, we included 90 studies covering 164 species across a range of habitats. The majority of studies were conducted in the greenhouse (45%), with 35% conducted under field conditions, 4% conducted in both field and greenhouse, and 16% were not specified. The mean number of species examined per study was 2.09 (range: 1-9) and the mean sample size per species was 12.2 (range: 3-144).

For studies which reported data but not allometric parameters, we calculated allometric parameters using SMA or OLS analysis, as appropriate, using SMATR for R (Warton et al. 2012). Where data were only presented in figures, we extracted data points using the Plot Digitizer program (Huwaldt 2011). Where necessary, we converted reported units to the standard units listed in Table 5-2. We pooled data from all species reported in each study, so the parameters we report in Table 5-4 are pooled slopes and intercepts for all species in each study.

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Chapter 5 Appendix 2.

Additional Tables and Figures

Table S5-1. Allometric relationships analyzed using OLS for Hawaiian species and global dataset; comparisons were only made for relationships that were significant for both groups

	Parameters for Hawaiian species			Parameters for the global dataset			Hawaiian *v.* Global	
Y-X	Intercept	Slope	R^2	Intercept	Slope (*n*)	R^2	Int. *P*	Slope *P*
LAR-PM	-2.03 ±0.05	-0.18 ±0.05	0.10*	-2.03 ±0.05	-0.17 ±0.06	0.13***	0.94	0.95
LMF- PM	1.60 ±0.04	-0.05 ±0.04	0.48***	1.55 ±0.02	0 ±0.02	0^{ns}	0.22	0.16
StMF-PM	1.53 ±0.05	0.06 ±0.04	0.09*	1.39 ±0.03	0.06 ±0.03	0.04***	0.78	0.00
RMF-PM	1.30 ±0.05	0.03 ±0.05	0.03^{ns}	1.4 ±0.01	0.08 ±0.01	0.12***	0.09	0.01

Table S5-2. Means and ranges for seedling measurements of five Hawaiian species harvested from Laupāhoehoe forest listed as: minimum – **mean** – maximum

Species	*Cheirodendron trigynum*	*Coprosma rhynchocarpa*	*Ilex anomala*	*Metrosideros polymorpha*	*Vaccinium calycinum*
<u>Size measurements</u>					
Height (cm)	4.7-**25**-59	1.2-**18**-63	2.2-**11**-35	0.82-**20**-82	13-**33**-45
Root length (cm)	2.4-**15**-34	1.7-**17**-69	3.1-**9.0**-19	1.7-**18**-72	6.0-**23**-46
Stem diameter (mm)	1.0-**3.4**-7.6	0.72-**3.0**-6.1	0.83-**2.4**-6.9	0.36-**2.4**-7.0	0.98-**1.9**-2.7
Leaf thickness (mm)	0.15-**0.21**-0.27	0.14-**0.26**-0.41	0.18-**0.28**-0.42	0.089-**0.21**-0.32	0.14-**0.19**-0.22
Area per leaf (cm^2)	0.68-**7.4**-18	1.8-**8.1**-18	0.38-**6.6**-25	0.04-**2.3**-6.1	0.22-**1.1**-2.8
Total plant leaf area (cm^2)	3.1-**174**-699	14-**227**-608	2.5-**153**-687	0.24-**114**-748	4.8-**94**-203
<u>Biomass measurements (dry mass)</u>					
Stem (g)	0.007-**0.86**-3.4	0.001-**0.74**-3.8	0.002-**0.38**-1.81	0.001-**1.1**-16	0.020-**0.64**-1.6
Leaf (g)	0.0075-**0.8**-3.9	0.0004-**0.67**-2.3	0.006-**1.0**-4.8	0.0005-**0.75**-5.9	0.14-**0.42**-0.98
Shoot (g)	0.015-**1.7**-7.3	0.0025-**1.4**-6.0	0.0081-**1.4**-6.6	0.00071-**1.9**-22	0.18-**1.1**-2.6
Root (g)	0.003-**0.34**-1.1	0.0001-**0.33**-1.4	0.005-**0.21**-0.98	0.0001-**1.2**-21	0.057-**0.63**-2.1
Total (g)	0.018-**2.0**-8.4	0.0026-**1.7**-7.2	0.015-**1.6**-7.6	0.00084-**3.1**-43	0.24-**1.7**-4.2

Chapter 5 Appendix 3

Table S5-3. References for each allometric relationship tested with global dataset

X	Y	N	Refs
PM_g	LA_m2	214	*1-20*
PM_g	LM_g	866	*2-4*, *6*, *7*, *9*, *11-14*, *16-19*, *21-44*
PM_g	LMA_g_m2	148	*2-4*, *6*, *7*, *9*, *11-14*, *16-19*
PM_g	RL_cm	111	*45*, *46*
PM_g	RM_g	1133	*1-4*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-41*, *44-59*
PM_g	ShM_g	1040	*1-4*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-33*, *35*, *36*, *38-41*, *44-46*, *48-54*, *56-59*
PM_g	StD_mm	50	*1*, *9*, *11*, *33*, *44*
PM_g	StL_cm	183	*1*, *4*, *6*, *9*, *12*, *15*, *19*, *20*, *24*, *27*, *33*, *44*, *45*
PM_g	StM_g	436	*2*, *3*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-36*, *38-41*, *44*
PM_g	LAR_m2_g	214	*1-20*
PM_g	LMF	878	*2-7*, *9*, *11-14*, *16-19*, *21-44*
PM_g	RMF	1133	*1-4*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-41*, *44-59*
PM_g	StMF	436	*2*, *3*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-36*, *38-41*, *44*
LM_g	RM_g	458	*2-4*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-33*, *35-41*, *44*
LM_g	StM_g	431	*2*, *3*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-33*, *35*, *36*, *38-41*, *44*
ShM_g	RM_g	1040	*1-4*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-33*, *35*, *36*, *38-41*, *44-46*, *48-54*, *56-59*
StL_cm	LA_m2	205	*1*, *4*, *6*, *9*, *12*, *15*, *19*, *20*, *60-69*
StL_cm	ShM_g	136	*1*, *4*, *9*, *24*, *27*, *33*, *44*, *45*
StL_cm	StD_mm	360	*1*, *9*, *17*, *33*, *44*, *60*, *64*, *65*, *70-79*
StM_g	RM_g	516	*2*, *3*, *7*, *9*, *11*, *13*, *14*, *16-18*, *22-28*, *31-36*, *38-41*, *44*, *77*, *80*
StM_g	StL_cm	125	*9*, *27*, *33*, *44*, *81*

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CONCLUSION

In my study I achieved major, novel findings on several interfacing topics, from methodology, to seedling distributions patterns, to growth dynamics, to scaling “rules” for seedling growth.

In Chapter 1, I found that collecting tree demography data using digital methods increased project efficiency. By comparing the total effort required for data collection (including data entry), I found that using digital methods can substantially reduce data collection effort over using paper data sheets. Large projects with repetitive data collection tasks, such as large scale forest plots, realize especially large benefits because they have lower setup-time to time-savings ratios. By adopting this new technology, projects can collect data more efficiently, thereby saving scarce research funds and enabling more rapid progress of scientific knowledge.

In Chapter 2, I found that recruitment limitations in Hawaiian forest were more similar than expected to mainland forests and appear to be a stronger driver of community assembly than niche processes (Muller-Landau et al. 2002). Recruitment limitations varied strongly among species within Hawaiian forest, whereas average limitations were similar to those found in other forests. Although habitat associations in Hawaiian forest were stronger than those found in high-diversity tropical forests, we also found significant niche overlap in Hawaiian forest. More generally, these findings showed that habitat associations do not necessarily indicate habitat specialization or niche differentiation among species. Rather, seed and dispersal limitations determined abundance and distribution of Hawaiian forest seedlings.

In Chapter 3, new evidence of performance trade-offs suggested that niche differences exist among Hawaiian species, but that the strength of niche differences varied among species. Overall, niche differentiation appeared to be a weak driver of seedling dynamics in low-diversity

Hawaiian wet forest. Although some species-pairs showed evidence of performance trade-offs, others were largely functionally equivalent, showing few performance differences across microhabitats. Species largely responded to differences in micro-topography. Topography (slope, aspect, and elevation) explained most variation in relative growth rate (58%) followed by irradiance (19-24%) and substrate (18-23%). However, the relative importance of microhabitat variables differed among species and for different growth metrics (stem height, biomass, or leaf growth). These findings provide support for theories that both niche and neutral processes drive forest community assembly (Gravel et al. 2006).

In Chapter 4, I found that biotic neighborhoods, climate, and abiotic factors were strongly correlated with seedling survival in Hawaiian forest. However, the strength and direction of density dependence varied with forest type, irradiance, and species' abundance. In dry forest, seedling survival decreased with seedling conspecific density whereas adult conspecific density facilitated seedling survival. Likewise, in wet forest, seedling survival increased with adult conspecific density, but only for the most common species. For rarer species in wet forest, both seedling and adult conspecific density was associated with reduced seedling survival. Understory irradiance influenced density dependence differently for dry versus wet forest species. Seedling survival strongly increased with conspecific seedling density in low irradiance in dry forest and in high irradiance in wet forest. Seedling survival increased most with adult conspecific density in high irradiance in both forests. Finally, seedling survival rates decreased with increased community-wide tree abundance in the wet forest, providing evidence for a community compensatory trend (Connell et al. 1984, Webb and Peart 1999). Thus, density dependence drives seedling dynamics in Hawaiian forests, though further work is needed to determine whether density dependence contributes to the maintenance of biodiversity in these forests.

In Chapter 5, I found that altogether, in their ontogeny of form, Hawaiian species differed less from each other than from global species. These results suggested that biogeography and local habitat conditions jointly influence allometric relationships. This conclusion differs from previous studies emphasized overall universal scaling relationships for leaves of adult trees (Reich et al. 1997), possibly because allometric relationships might be more dynamic and adaptive for seedlings than for adult plants.

Implications

Altogether, the results of these studies indicate that Hawaiian forest regeneration dynamics are influenced by niche, density dependence, and neutral processes. Further, these results suggest that Hawaiian forests differ less in their fundamental ecological patterns from mainland tropical forests than previously thought. Recruitment limitations, habitat associations, and density-dependent seedling mortality were all more similar to mainland forests than expected. However, we did find striking differences in species' life histories and novel differences in seedlings' allometric relationships. Additionally, these results showed how biotic and abiotic processes interacted to influence seedling recruitment dynamics. For example, the effects of conspecific density differed across irradiance levels. This deeper understanding of regeneration dynamics in wet and dry Hawaiian forest should be considered for management and restoration of biodiversity in these threatened ecosystems.

Future research

Further work remains to discover how the patterns we found at the seed and seedling life stages will affect future forest diversity and structure. I conducted these studies in or near permanent plots that are part of the Hawaiʻi Permanent Plot Network (HIPPNET), in which all native woody plants that recruit into the ≥1 cm DBH size class will be measured every five years. These long-term results will improve scientific understanding of establishment trends of native Hawaiian forest species. More data on the conditions under which seedlings recruit to larger size classes will provide direct information on how native Hawaiian forests naturally regenerate. This information will show whether patterns that were apparent at the seed or seedling stage translate to patterns of adult forest trees. By continuing this work over time, it will also be possible to link seed and seedling data to climate data, thereby providing insights into how regeneration patterns may be affected by climate change. This information will be invaluable to conservation planning and management of biodiversity.

Future work should also focus is on the regeneration dynamics of the less common species. These studies should incorporate modified sampling designs to obtain larger sample sizes of species that were rarely found in seedling plots and seed traps. This would permit species-specific analyses that would encompass a larger part of the forest community. By analyzing a larger number of species, we can determine how biotic and abiotic habitats may differently affect rare and common species. In particular, additional study is needed to elucidate the apparent pattern of higher density-dependent seedling mortality for the less common species. This research is urgently needed given the threatened status of a large number of Hawaiian plant species.

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