DISCOVERING THE FOREST AMONG THE TREES: TESTING COMMUNITY ASSEMBLY THEORY IN THE FORGOTTEN LAYERS OF TEMPERATE AND TROPICAL ECOSYSTEMS

by

Michelle Elise Spicer

B.S., Lehigh University, 2012

M.S., Lehigh University, 2014

Submitted to the Graduate Faculty of the

Kenneth P. Dietrich School of Arts and Sciences in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

University of Pittsburgh

2019

UNIVERSITY OF PITTSBURGH

DIETRICH SCHOOL OF ARTS AND SCIENCES

This dissertation was presented

by

Michelle Elise Spicer

It was defended on

November 21, 2019

and approved by

Dr. Mark Rebeiz, Associate Professor,
University of Pittsburgh, Department of Biological Sciences

Dr. Corinne L. Richards-Zawacki, Associate Professor and PLE Director,
University of Pittsburgh, Department of Biological Sciences

Dr. Justin Kitzes, Assistant Professor,
University of Pittsburgh, Department of Biological Sciences

Dr. Stefan A. Schnitzer, Mellon Distinguished Professor,
Marquette University, Department of Biological Sciences

Dissertation Advisor: Dr. Walter P. Carson, Associate Professor,
University of Pittsburgh, Department of Biological Sciences

DISCOVERING THE FOREST AMONG THE TREES: TESTING COMMUNITY ASSEMBLY THEORY IN THE FORGOTTEN LAYERS OF TEMPERATE AND TROPICAL ECOSYSTEMS

Michelle Elise Spicer, Ph.D.

University of Pittsburgh, 2019

Forests are the most diverse and productive terrestrial ecosystems on Earth, so sustainably managing them for the future is a major global challenge. Our understanding of forest plant diversity, however, relies almost exclusively on the study of trees. Here, I show that the other growth-forms (shrubs, lianas, herbs, epiphytes) in fact make up the majority of vascular plant species in both tropical and temperate forests. By comparing the distribution of species among growth-forms for over 3,400 species in 18 forests in the Americas, I construct a high-resolution quantification of growth-form diversity across two important ecological regions. I also quantify the physical distribution of plant species among forest layers, or *where* among the vertical strata plants ultimately live their adult lives. Plant diversity is strongly concentrated on the forest floor in temperate forests, but is evenly distributed among the forest strata in tropical forests. I then use three large-scale field experiments to test drivers of community assembly specifically in these understudied yet species-rich plant communities. First, I simultaneously test the effects of browsing pressure, understory competitors, and the controversial practice of salvage logging on herb regeneration following a large-scale windthrow in Pennsylvania. Although salvaging was thought to be inimical to forest recovery, my results demonstrate that the herbaceous layer is surprisingly resilient to intense salvage logging, interspecific competition, and vertebrate browsing. I also show that salvage logging does not eliminate tip-up mounds, one important structural legacy of windthrow. Importantly, the patterns I show for woody species do not match those of herbaceous plants, which make up 80% of the temperate forest species. Second, I experimentally test hypotheses regarding the assembly of diverse epiphyte communities in a Panamanian cloud forest. In particular, I test the degree to which host tree substrate traits regulate the early germination and survival of epiphytes. All in all, my research provides evidence that the major drivers of *tree* community change do not necessarily drive *forest* community change. Thus, forest management plans that encompass a broader suite of plant growth-forms will be essential to global biodiversity conservation efforts.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

I would like to thank the many members of my own community who facilitated the assembly of this dissertation. First, to my academic community: your criticism, guidance, mentorship, and colorful personalities have certainly shaped my development as a scholar and person. To Walt Carson, my advisor, who offered me a smorgasbord of project ideas my first year, then let me follow my passion to a whole new system for us thereafter; who had faith in my judgement on my ambitious adventure setting up an experiment in the treetops of rural Panama; who called upon his vast network of colleagues to support me; who provided endless critique to improve my writing; and who, over the course of six years and many more laughs and tears, has become a friend and colleague. To John Wenzel, the Powdermill Nature Reserve staff, and associates, especially Alex Royo and Katie Barry, who provided support and mentorship while I tumbled through the spiny plants of the windthrown forest. To my committee members, present (Cori Richards-Zawacki, Mark Rebeiz, Stefan Schnitzer, and Justin Kitzes), and past (Jonathan Pruitt and Nathan Morehouse), who encouraged me to think broadly and think ahead. To the Pruitt lab and Carson lab members, who have continuously supplied support, wisdom, critique, motivation, and hilarity to my PhD career. I appreciate the Pitt E&E community, who offered insight at joint lab meetings, career advice, and academic mentorship. Sara Kuebbing and Corlett Wolfe Wood have been particularly generous with their time, and both inspire me to find balance. I thank the Center for Latin American Studies and the many wonderful scholars and friends I have met there, in particular for supplying numerous fellowships, valuing interdisciplinary education, and encouraging me to be a bridge between social sciences and STEM. I thank the Smithsonian

Tropical Research Institute, Yaguará Panamá, and MiAmbiente for help with the logistics of my research in Panama, and to the Yanoviak lab for starting me climbing trees there.

Second, I feel a deep gratitude to my personal community, who were just as vital to my PhD. To my dear friend Yusan Yang, with whom I have spent incalculable hours writing in a silent room in the library, finding solace from PhD stress through camaraderie, and sharing adventures and delicious food across the world. To Kylia Williams, my beloved PalPittations, and Infraorbital Groove, whose music and friendship are the best therapies I've found at Pitt. I am grateful to Tiffany Betras, for all of our rambunctious times together in and out of the field. I thank Rachel Coombs and our Women In Science and Engineering Graduate Student Organization community for connecting me to other women leaders in STEM and showing me that there are many ways to advocate for what is right. To the rest of my support network, close and far from Pittsburgh: thank you for being my anchors in the storm. Finally, the biggest thanks to my brilliant and beautiful family: my parents Mark and Julie and my sisters Jackie and Kelly. You have shown such strength, patience, and unwavering love for me throughout this whole process. I never could have started or finished this without you. I dedicate this dissertation to my grandmother, Jean Kennedy, who inspires me with her undying optimism, reverence for nature, quiet strength, far-sightedness, and gratitude for the many gifts of life.

1.0 INTRODUCTION

The processes by which plant communities assemble, develop, and maintain diversity are fundamental to ecology (Janzen 1970, Connell 1971, Pickett et al. 1987, Hubbell 2001, Wright 2002, Tilman 2004, Weiher et al. 2011, Pulsford et al. 2014, Pearson et al. 2018). Although we have made great progress in our understanding of these processes, there is still much debate over the generalizability of community assembly rules among different ecosystems (Weiher et al. 2011, HilleRisLambers et al. 2012, Fukami 2015). In part, predictions of which processes will be the major drivers of plant community change are precluded by a hyperfocus on only a subset of the plant community: the trees. To date, the great majority of forest succession and community assembly research has focused solely on trees, ignoring other growth-forms such as lianas, epiphytes, and herbaceous plants (Gilliam 2007, Barry and Schnitzer 2016, Landuyt et al. 2019). This is a major oversight, because different groups of plants have adapted characteristic life history strategies that ultimately result in tradeoffs, and likely, the mechanisms driving community change will reflect those tradeoffs. For example, tree fall gaps are a major driver of liana community change, but do not seem to be a strong determinant of tree species composition (Schnitzer and Carson 2010; Ledo and Schnitzer 2014; Schnitzer 2018). For a more holistic view of how a forest changes, we must take into account all plant groups, rather than just the trees.

My dissertation aims to extend community assembly theory to plant growth-forms that are poorly understood yet vital to ecosystem function. I start by quantifying which growth-forms and layers of the forest strata are most speciose in the Americas (Chapter 2). I compare the distribution of plant species in tropical and temperate forests to identify key differences between these two regions. The results of this research highlight a mismatch between current research effort and contribution to global species pool: non-arborescent plants make up the vast majority of species in both temperate and tropical forests, yet forest ecology and management efforts concentrate almost exclusively on trees. Thus, I focus my subsequent research on two areas that have been vastly understudied: the tropical forest canopy and the temperate forest herbaceous understory layer. To that end, I present three experiments which test the drivers of plant community assembly. In a large-scale, replicated field experiment in western Pennsylvania, I test how the combination of natural and multiple anthropogenic stressors drive subsequent forest regeneration. Specifically, I parse apart the direct effects of salvage logging, deer overabundance, and recalcitrant understory competitors on the diversity and abundance of plant communities recovering from a tornado blowdown (Chapter 3). I also test whether salvage logging can eliminate an important structural legacy of natural disturbance, tree tip-up mounds (Chapter 4). Last, I focus on testing the drivers of community assembly very early during ontogeny in the diverse epiphyte system (Chapter 5). Epiphytes can constitute up to 50% of vascular plant species richness in tropical montane forests and nearly four times as much foliar biomass as their host tree (Nadkarni 1984; Kelly *et al.* 1994). However, our understanding of epiphyte community assembly is limited, especially due to difficulty in accessing arboreal communitites *in situ*. Epiphytes, which use other plants as substrate to gain access to light in the canopy, have a uniquely close relationship with their host tree. Thus, I set up an experiment in the cloud forest of Veraguas, Panama, to test the extent to which host bark texture determines epiphyte germination and establishment.

This suite of field experiments reveals surprising departures from expected results, underscoring the importance of broadening the scope of ecological research to growth-forms other than trees. Moreover, understanding community assembly processes will be an important tool in solving some of the major ecological challenges of today—how systems can handle invasive species, changing climate, and largescale anthropogenic disturbance (Young et al. 2001, Gardner et al. 2009, Wavrek et al. 2017, Pearson et al. 2018, Landuyt et al. 2019). All in all, my dissertation fills several knowledge gaps in the plant community assembly literature, including: 1) quantifying an important physiognomic difference between tropical and temperate forests, 2) demonstrating impressive resiliency of temperate forests to disturbance, and 3) providing critical baseline information and a proof-of-concept for field experiments in epiphyte establishment ecology. My results suggest that the rules that govern community assembly depend on the life-history strategy of the organism of interest, so we must expand our view of the forest to manage and conserve biodiversity sustainably. Below, I provide abstracts for each of my dissertation chapters.

1.1 Chapter 2: Seeing beyond the trees: A comparison of tropical and temperate plant growth-forms and their vertical distribution

Forests are the most diverse and productive terrestrial ecosystems on Earth, so sustainably managing them for the future is a major global challenge. Yet, our understanding of forest diversity relies almost exclusively on the study of trees. Here, we demonstrate unequivocally that other growth-forms (shrubs, lianas, herbs, epiphytes) make up the majority of vascular plant species in both tropical and temperate forests. By comparing the relative distribution of species richness among plant growth-forms for over 3,400 species in 18 forests in the Americas, we construct the first high-resolution quantification of plant growth-form diversity across two ecologically important regions at a near-continental scale. We also quantify the physical distribution of plant species among forest layers—that is, where among the vertical strata plants ultimately live their adult lives—and show that plants are strongly downshifted in temperate forests versus tropical forests. Our data illustrate a previously unquantified fundamental difference between tropical and temperate forests: *what* plant growth-forms are most speciose, and *where* they ultimately live in the forest. Recognizing these differences requires that we re-focus ecological research and forest management plans to encompass a broader suite of plant growth-forms. This more holistic perspective is essential to conserve global biodiversity.

1.2 Chapter 3: Rapid forest understory recovery following combined natural and anthropogenic disturbances

Natural disturbances can maintain forest diversity by creating a heterogeneous resource landscape which can contribute to coexistence of early- and late-successional species. However, much of the eastern deciduous forest is also subject to multiple anthropogenic stressors, which could delay healthy forest regeneration after natural disturbances. Here, we present the first large-scale, replicated field experiment testing the interactions among three drivers of change in the context of post-disturbance forest recovery. Specifically, we test the extent to which: 1. salvage logging, a common forestry practice to generate revenue after natural disturbances, 2. deer browsing, and 3. plant competitors drive subsequent understory plant community development. Our results have two clear, yet surprising, messages. First, all plant communities regenerating from multiple simultaneous perturbations had high species richness, diversity, and cover. This was unexpected given the intensity of the disturbances. Second, we found that analyzing the forest understory as one homogenous community hides ecologically important patterns. Herbs, which constitute 80% of eastern deciduous forest vascular plant species, responded strongly to salvaging: salvaged plots had seven more species and 15% higher diversity than unsalvaged plots.

Conversely, woody species were equally as diverse and abundant in salvaged versus unsalvaged plots, but responded to deer and competitors. Combined, our results show that eastern temperate forests are highly resilient to simultaneous natural and anthropogenic disturbances, including overabundant deer. This resilience is particularly impressive given the known ubiquity and inimical impact of deer on forest understories across the entire eastern deciduous biome.

1.3 Chapter 4: Does salvage logging erase a key physical legacy of a tornado blowdown? A case study of tree tip-up mounds

While large-scale wind disturbances are rare, they are nonetheless powerful drivers of plant community re-assembly in temperate forests worldwide. These disturbances cause the formation of tree tip-up mounds that serve as regeneration niches, but the timescale at which novel plant communities develop on mounds is unknown. Moreover, salvage logging can cause mounds to "tip back down" and could therefore erase these microsites. Here, we test three hypotheses with a replicated field experiment: 1) Novel plant communities rapidly form on tip-up mounds; 2) Salvaging erases these microsites; and 3) "Tipped down" tip-up mounds are novel intermediate microsites. We salvaged a random half of four 3-6 ha blowdowns created by an F1 tornado, measured 249 mounds, and censused the vegetation on 48 mounds and 48 reference plots. Plant communities on mounds had 2-3 fewer species, 50% less cover, and lower diversity than reference communities. However, salvaging caused modest increases in species richness and diversity on mounds and caused 40% of mounds to tip back down. The physical characteristics and vegetation of these tipped-down "inclined mounds" were more similar to vertical mounds than to reference plots. Our results suggest that salvaging may increase microsite heterogeneity across the landscape by creating novel intermediate mounds.

1.4 Chapter 5: Substrate texture mediates vascular epiphyte establishment: Experimental evidence from a Panamanian cloud forest

Epiphytes are a unique plant growth-form that live non-parasitically on other plants and constitute approximately one-third of tropical vascular plant diversity in the Neotropics. Although epiphytes make vital contributions to tropical forest structure and function, the mechanisms governing epiphyte community assembly are poorly understood. The properties of substrates are likely critical to the establishment of diverse epiphyte communities, because of the inherently close connection between an epiphyte and its host tree. However, little experimental evidence exists for *when* during ontogeny that host traits are most important, or *what* host traits drive epiphyte community development. Here, we use an *in situ* experiment in the cloud forest of Santa Fé, Panama to test the extent to which substrate texture serves as a filter to epiphyte establishment. We experimentally varied the rugosity (roughness) of substrates derived from a native tree species, applied a mix of various epiphyte seeds to the substrates, and monitored seed germination and establishment over several months. We present some of the first experimental field evidence that substrate texture mediates epiphyte establishment. Rougher substrates facilitated higher epiphyte establishment, and epiphyte seedling abundances differed between the smoothest and the two substrates with the highest rugosity. After just two months, less than 1% of all seedlings on average were present on the smoothest substrate while 34% of the seedlings remained on the second-roughest substrate. Epiphyte cohort survival rates differed among rugosity treatments, but nearly all germinated seedlings died after approximately one year. Our results suggest that the texture of the substrate can account for some of the variability in epiphyte seedling survival at this early bottleneck stage. This variability may contribute to observed niche differentiation of epiphytes both within- and among-host trees.

1.5 Bibliography

Barry, K. E., and S. A. Schnitzer. 2016. Maintenance of Plant Species Diversity in Forest Ecosystems. Page *in* S. S. Gill and A. Ansari, editors. Plant Biodiversity: Monitoring, Assessment, and Conservation. CAB International.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 Dynamics of numbers in populations. Proceedings of the Advanced Study Institute on dynamics of numbers in populations. Oosterbeck.

Fukami, T. 2015. Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. Annual Review of Ecology, Evolution, and Systematics 46:1–23.

Gardner, T. A., J. Barlow, R. Chazdon, R. M. Ewers, C. A. Harvey, C. A. Peres, and N. S. Sodhi. 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecology Letters 12:561–582.

Gilliam, F. S. 2007. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems 57:845–858.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. Annual Review of Ecology, Evolution, and Systematics 43:227–248.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. 32nd edition. Princeton University Press.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American naturalist 104:501–528.

Kelly, D. L., E. V. J. Tanner, E. M. Nic Lughadha, and V. Kapos. 1994. Floristics and Biogeography of a Rain Forest in the Venezuelan Andes. Journal of Biogeography 21:421–440.

Landuyt, D., E. De Lombaerde, M. P. Perring, L. R. Hertzog, E. Ampoorter, S. L. Maes, P. De Frenne, S. Ma, W. Proesmans, H. Blondeel, B. K. Sercu, B. Wang, S. Wasof, and K. Verheyen. 2019. The functional role of temperate forest understorey vegetation in a changing world. Global Change Biology:gcb.14756.

Ledo, A., and S. A. Schnitzer. 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. Ecology 95:2169–2178.

Nadkarni, N. M. 1984. Biomass and mineral capital of epiphytes in an Acer macrophyllum community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Canadian Journal of Botany 62:2223–2228.

Pearson, D. E., Y. K. Ortega, Ö. Eren, and J. L. Hierro. 2018. Community Assembly Theory as a Framework for Biological Invasions. Trends in Ecology and Evolution 33:313–325.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. Botanical Review 53:335–371.

Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2014. A succession of theories: purging redundancy from disturbance theory. Biological Reviews.

Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849–857.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences 101:10854–10861.

Wavrek, M., J. M. Heberling, S. Fei, and S. Kalisz. 2017. Herbaceous invaders in temperate forests : a systematic review of their ecology and proposed mechanisms of invasion. Biological Invasions 19:3079–3097.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2403–2413.

Wright, S. J. 2002. Plant Diversity in Tropical Forests: A Review of Mechanisms of Species Coexistence. Oecologia 130:1–14.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community Succession and Assembly: Comparing, Contrasting and Combining Paradigms in the Context of Ecological Restoration. Ecological Restoration 19:5–18.

2.0 SEEING BEYOND THE TREES: A COMPARISON OF TROPICAL AND TEMPERATE PLANT GROWTH-FORMS AND THEIR VERTICAL DISTRIBUTION

Spicer, M. E., H. Mellor, and W. P. Carson. 2019. Seeing beyond the trees: a comparison of tropical and temperate plant growth-forms and their vertical distribution. In revision at *Ecology*.

2.1 Introduction

Forest ecology has been strongly biased towards the study of trees, because this growth-form contributes the most to carbon sequestration, plant biomass, and economic value (Braun 1950, Richards 1952, Spurr and Barnes 1973, Condit 1995, Linares-Palomino et al. 2009, Lewis et al. 2009, Muller 2014, Lutz et al. 2018). This selective view of forest ecology is inimical to diversity conservation because it overlooks plant growth-forms that significantly contribute to biodiversity, faunal habitat, and forest function (Johansson 1974, Gentry and Dodson 1987, Schnitzer and Carson 2000, Gilliam 2014, Thrippleton et al. 2016, Landuyt et al. 2019). Epiphytes, for instance, are particularly diverse in montane forests, where they can comprise as much as 50% of the flora, and may be particularly vulnerable to both anthropogenic and natural canopy disturbances (Kelly et al. 1994, Foster 2001, Nadkarni and Solano 2002, Woods and DeWalt 2013). Including non-tree vegetation in ecological studies can also change our understanding of fundamental ecological processes. Research on lianas (woody vines), a once-overlooked growth-form, demonstrates that lianas regulate gap dynamics, water relations, and canopy-to-canopy connectivity in Neotropical forests (Schnitzer and Carson 2010, Adams et al. 2017, Schnitzer 2018). A systemic bias towards trees means we are missing key components of forest function, rendering it difficult to identify the processes that promote and maintain biodiversity of all growth-forms.

Our understanding of forest *structure* is also biased, likely because of the limitation of ground-based censuses. Forest spatial ecology has focused on the two-dimensional distribution of plant diversity, despite the long-standing importance of three-dimensional structure for biodiversity and ecosystem processes (MacArthur and MacArthur 1961, Smith 1973, Terborgh 1985). Overlapping forest layers create strong vertical abiotic and biotic gradients, ranging from the exposed, disturbance-prone canopy, to the deeply shaded, microbially-rich understory (Parker 1995, Schnitzer and Carson 1999, Gilbert and Reynolds 2005, Gora et al. 2019); this complexity maintains high faunal diversity (MacArthur and MacArthur 1961, Smith 1973). Given the long history of studying the vertical niche-partitioning of both plants (Johansson 1974) and animals (MacArthur and MacArthur 1961), it is surprising that studies that map forest habitats rarely explicitly incorporate a three-dimensional component. While the field of forest physiognomy has long recognized the categorical structural differences among biomes (Richards 1939, 1952, Kuchler 1949, Beard 1955, Webb 1959), there have been few studies that rigorously quantify these physiognomic differences, which no doubt underlie major forest structure-function links. Comparisons of vertical structuring of diversity among ecosystems across the world are needed to identify biodiversity priorities and create biome-wide yet region-specific management plans.

Here, we test the idea that the three-dimensional distribution of plant species represents an intuitive, yet thus far unquantified, intrinsic difference between tropical and temperate forests. Specifically, we hypothesize that tropical and temperate forests differ in which plant *growth-forms*, and which *vertical strata*, are most speciose, what we term the Forest Physiognomy Concept (**Figure 1)**. We make two predictions that characterize this difference. First, in Neotropical forests, the majority of plant species will reach reproductive maturity in the overstory due to the structurally dependent growth-forms of epiphytes and lianas. Second, in temperate forests, the majority of plant species will reach reproductive maturity in the understory, due to a spring ephemeral niche and thus species-rich terrestrial herbaceous and shrub growth-forms. These predictions, although not explicitly rooted in classical ecological theory, are drawn from some of the earliest comparisons of tropical and temperate forests, which noted the unique diversity of tropical plants inhabiting the canopy (Hartwig 1863, von Humboldt 1873, Wallace 1878).

To test our hypothesis, we build off of classification schemes that use plant traits (e.g., woodiness) to characterize forest types and profiles among diverse habitats (Raunkiaer 1934, Richards 1952, Beard 1955, 1978, Baker and Wilson 2000, reviewed in Loidi 2018). Specifically, we collected data on the growth-form and ultimate stratum for 3,456 plant species from nine tropical and nine temperate sites. We define *ultimate stratum* as the location in the vertical forest profile where a plant species typically spends its adult life and becomes reproductive. Our 18 sites spanned a wide variety of latitudes, elevations, and ecological habitats throughout the Americas (**Figure 3, Table 1**). Our data illustrate a previously unquantified fundamental difference between tropical and temperate forests: *what* plant growth-forms are most speciose, and *where* they ultimately live in the forest. Recognizing these differences requires that we broaden our focus in conservation biology and plant ecology to non-arborescent plant growth-forms. This more holistic perspective is essential to conserve global plant diversity.

2.2 Methods

2.2.1 Site selection

We selected a total of 18 primarily closed-canopy mature forest research sites that had open-access vascular plant species lists, published species lists in downloadable form, or were data from our collaborators (**Figure 3, Table 1)**. All sites are primarily old-growth or uncut forest, but many have younger or disturbed forest as part of their landscape matrix. Our focal forests varied in size (112 to 400,000 hectares), elevation (35 to 3,450 meters above sea level), land use history, and life zone categorization, spreading across the Americas from Canada to Brazil (see **Table 1** for details). Sites spanned a total latitudinal range of 62° from the northernmost part of the eastern deciduous forest (46.8°N) to the southern end of the tropical forest in the Americas (15.2°S). We selected 9 sites throughout each of these two major temperate and tropical forest regions (Braun 1950, Holdridge 1967). Although these sites are non-randomly distributed, our approach well-characterizes a variety of Neotropical forests because we selected high-resolution, site-level data, amassed over many decades, representing all vascular plant growth-forms at each site.

Because the species lists commonly contained more than 500 species (range: 244 to 2,086), we randomly subsampled 20% of the species to characterize growth-form and strata of species within each forest. This subsampling was necessary for feasibility; we systematically read through dozens of herbarium specimen descriptions per species and per site, which was often necessary to obtain our two key response variables (i.e. growth form and strata). In total, we examined more than 100,000 records (see “Physiognomic data collection” below). Although this approach limited our taxonomic scope (how many total species we studied), it holds one advantage over automated data extraction and collection: specific search terms were not pre-selected. Thus, descriptions with misspellings, synonyms, and multiple languages were included, which would be quite difficult with an automated approach. Nonetheless, to verify that a 20% subsample accurately reflected the true relative proportion of each forest growth-form and ultimate stratum distribution, we evaluated the entire species list from one temperate and one tropical site (Allegheny National Forest Region with 244 species, and La Planada in Colombia with 893). Our analysis confirmed that 20% subsamples accurately represent the population of growth-form and ultimate strata distributions (see **Figure 4;** Methods: Statistical analysis). We only included plants that were identified to species in data collection and removed strictly aquatic (submerged) plant species from both temperate and tropical sites. Had we included these, herbs would have been even more proportionally diverse than we report (see below).

2.2.2 Physiognomic data collection

For each selected species, we used the USDA PLANTS database and TROPICOS herbarium database to identify the growth-form (tree, shrub, liana, herb, or epiphyte) and maximum height in the forest strata where the plant was observed as a reproductive adult. Ultimate stratum categorizations (forest floor, understory, subcanopy, canopy, or emergent) were made via explicit statements in the annotated descriptions of the databases (e.g. “liana reaches canopy”, “understory tree”, “forest floor herb”). We collected data on reproductive specimens by checking their annotated descriptions for key words (e.g., “flowering”, “fruiting”, “fertile”, “adult” etc.). If a categorical maximum height was not explicitly stated for a given species, but the collector specified the height of the species, we identified the appropriate stratum of that species using strata described in Terborgh (1985) and Richards (1952). In this case, we categorized the strata as the forest floor (0-2 m), understory (2-15 m), subcanopy (15-30 m), canopy (30-45 m), and emergent layer (>45 m). Note, we report only the categorical strata heights; we do not compare continuous height data because not all maximum canopy heights are the same (e.g., montane forests are shorter overall than lowland forests). Whenever TROPICOS had more than 100 specimens for any given species, we collected data from at least 50 records and noted the maximum height of all 50 records. We categorized each species into one of five major growth-forms: tree, shrub, liana, herb, or epiphyte. Due to continued debate over hemiepiphyte classifications (Zotz 2013), we classified all of the following aerial or climbing plants into a single broad "epiphyte" category: holoepiphytes, primary hemiepiphytes, secondary hemiepiphytes, nomadic vines (*sensu* Moffett 2000), suffratescent climbers, and herbaceous vines. When species information was not available on either TROPICOS or PLANTS, we used published literature via Google Scholar searches with the scientific name to gather our two response metrics (growth-form and ultimate stratum).

We often found that the ultimate stratum data were limited for epiphytic species relative to data on other growth-forms. Specimens collected opportunistically may lack height data (and therefore are not included in the ultimate stratum), or are more likely to be from individuals that occur low in the forest profile. Because climbing into the canopy to survey arboreal plants is difficult, expensive, and dangerous, epiphyte collections are frequently serendipitous, and only contain those individuals (and species) that can be reached by an outstretched hand (under 2m in height). Although many epiphyte species do have wide ranges of suitable substrate heights (Johansson 1974, Zotz and Schultz 2008, Woods et al. 2015), we suspect the maximum height we report for epiphytes are substantial underestimates because they remain less frequently sampled or seen high in the canopy. Thus, we would expect the up-shift in tropical species to be even more striking (see below) if we had more accurate epiphyte height data.

To explore the spring ephemeral niche as a possible mechanism for differences in plant species allocations between temperate and tropical forests, we collected phenology data for all of the temperate forest floor herbs included in the main analysis (854 species). We used online databases such as the Missouri Botanical Garden, Efloras, and the University of Texas Austin's wildflower.org to categorize each species into "true ephemerals," "spring blooms," or "other." We defined spring blooms as plants that bloomed between March and May, and true ephemerals as spring blooms that senesced before July 1st; most of these species are perennials.

2.2.3 Statistical analysis

To test our hypothesis that plant species richness is concentrated in different forest layers between tropical and temperate forests, we ran five separate generalized linear models for each of the forest strata, with forest type (temperate or tropical) predicting relative species richness in the strata. Our statistical approach was conservative, because we interpreted the resulting p-values with a Bonferroni correction to account for the inherent dependency among the proportions ($\alpha_{\text{Bonferroni}}=0.05/5=0.01$). We similarly used five Bonferroni-corrected generalized linear models to analyze whether forest type predicts relative species richness for each growth-form to test the hypothesis that vascular plant growth-form composition differs between tropical and temperate forests. For both sets of GLMs, the response variable was the proportion of species in each growth-form or strata, weighted by the total number of species studied (specified with the *weights* function in the *stats* package) (Zuur et al. 2009). We modeled the response variable (proportion of plant species richness in each site) with a quasibinomial distribution, which is particularly appropriate for overdispersed proportional data (Bolker 2008). To test whether overall herbaceous plant relative species richness was higher in tropical or temperate forests, we re-grouped the species in each site to be either woody (trees, shrubs, lianas, and woody epiphytes) or herbaceous (graminoids, ferns, forbs, and herbaceous epiphytes). We then use the same type of binomial GLM to test whether the proportion of total species that were herbaceous plants (response variable) differed between the two forest types (predictor variable). All analyses were run with R version 3.6.0 (R Core Development Team 2019) in R Studio version 1.0.153 (RStudio Team 2016).

To confirm that using 20% of the species was a sufficient subsample and characteristic of the whole dataset, we used a bootstrap approach to characterize the random sampling error of two sites where we collected growth-form and ultimate strata data on all species (Allegheny National Forest Region, with 244 species, and La Planada, with 893 species). We iteratively sampled 20% of each full dataset 1000 times for both growth-form and strata distributions. The patterns we observed in the iterative approach match the overall patterns of all subsampled datasets; almost all categories of growth-form and strata from the full samples overlap the overall (among-site) subsamples (**Figure 4**).

2.3 Results

Our results clearly demonstrate that tropical and temperate forests contrast sharply in growth-form composition (**Figure 2A, Table 2**). In temperate forests, herbs are the predominant growth-form (80%) and trees represent a mere 7% of plant species. Although herbs are the majority of temperate forest species, only 4% are true spring ephemeral species (**Figure 5**). In tropical forests, conversely, trees are the most species rich group (30%) and species are relatively evenly allocated among the five growth-forms (**Figure 2A, Table 2**). Lianas and epiphytes are a characteristic and speciose part of tropical forests (27% of plant species), but are depauperate in temperate forests (<2% of species). Woody species (trees, shrubs, lianas, and woody epiphytes) are predominant in tropical forests (63% of species) but in temperate forests, only 19% of species are woody (N=18, t=-9.875, p<0.0001; **Figure 6**).

Tropical forests also differ strongly from temperate forests in how species are distributed throughout the vertical forest profile (**Figure 2B, Table 2**). The vast majority of plant species in temperate forests (83%) are downshifted, reaching reproductive maturity near the forest floor (0-2m). Conversely, while plant species in tropical forests are distributed more evenly among forest layers, they are also up-shifted, reaching peak species richness (50%) in the understory stratum (2-15m).

2.4 Discussion

Several mechanisms likely contributed to the stark differences we demonstrated between tropical and temperate forests (**Figures 1, 2**) in both growth forms and strata. The vertical up-shift in the forest profile for tropical species may be more pronounced than reported here because many plant species inventories are biased in favor of plants rooted in the soil. We also did not consider bryophytes, a highly diverse and abundant nonvascular epiphyte group in many Neotropical and temperate rainforests. Moreover, even extensive vascular plant lists may be missing many species from high in the diverse, yet poorly studied, forest canopy (Nakamura et al. 2017).

The overwhelming preponderance of herbs in temperate forests may be due to a spring ephemeral niche, which does not occur in evergreen or asynchronous deciduous tropical forests (Lapointe 2001). If the vast majority of temperate herb species were spring ephemerals, this would have supported the hypothesis that synchronized deciduousness facilitates a downshift in plant diversity. However, we found that very few species of temperate herbs are limited to periods with high light availability during the early-spring (only 4%; **Figure 5**). To truly test whether there exists a window of ephemerals in tropical forests, we would need data from seasonal light increases during the dry season in semi-deciduous tropical forests. Because these data were limited, we did not gather or statistically analyze any tropical ephemeral information. Instead, we provide the quantitative measure of ephemeralism in temperate forests, and encourage future research to test whether this process could drive differences in species allocations between tropical and temperate forests. Moreover, there are likely other factors that more parsimoniously explain the overrepresentation of forest floor herbs in temperate forests.

Phylogenetic and biogeographic histories undoubtedly contribute to the high relative species richness of some growth-forms, particularly herbs in temperate forests and bromeliads in the Neotropics (Guo and Ricklefs 2000, Givnish et al. 2011, Christenhusz and Chase 2013). Physiological constraints restrict structurally dependent growth-forms (epiphytes, lianas) to primarily lower latitudes, because traits such as succulent leaves and efficient vascular systems would be subject to freeze-thaw embolism in temperate zones (Zotz 2016, Schnitzer 2018). The low relative abundance of herbs in tropical forests may be partly due to two ecological factors: deep shade and abundant enemies. Light availability at the forest floor is much lower in tropical forests versus temperate forests (Leigh 1975, Chazdon and Fetcher 1984, Terborgh 1985, Canham et al. 1990, Schnitzer and Carson 1999), and soil pathogens cause extensive plant mortality (Gilbert 2002, Mangan et al. 2010, Barry and Schnitzer 2016). Enemies may contribute to the high relative abundance of epiphytes in tropical forests, because the evolution of an aerial growth habit would allow escape from terrestrial soil-dwelling pathogens. We term this potential explanation the Epiphyte Enemy Escape Hypothesis, but it remains to be tested. The mechanisms for the *proportional* differences in growth-form distributions in tropical versus temperate forests remain speculative.

Our findings should be broadly applicable across much of the world. European temperate forests are even less speciose than North American ones, and are frequently dominated by only a few tree species (Röhrig and Ulrich. 1991, Gilliam 2014). Thus, European herbaceous plants likely make up an even higher proportion of temperate vascular plant diversity. In tropical forests in China, trees represent 35-58% of all plant species, herbs 7-26%, lianas 9-19% and shrubs 9-10%, and a higher proportion of east Asian forest species are woody than in North American temperate forests (Guo and Ricklefs 2000, Zhu et al. 2005). These proportions resemble our Neotropical forest findings, though epiphytes were not quantified. Notably, epiphytes make up a smaller proportion of the vascular plant diversity in Eurasia and Africa versus the Neotropics, but epiphytes are more speciose in tropical versus temperate forests (Johansson 1974, Zotz 2005, 2016). Australian tropical forests appear to be even more dominated by woody growth-forms (>75% of species) than Neotropical forests (Russell-Smith 2006). Overall, more quantitative comparisons are needed to test the extent to which the Forest Physiognomy Concept applies globally.

Our results have critical implications for biodiversity conservation and management. Because tropical plant species are located higher in the vertical strata (**Figure 1, 2B**), the forest structure is more complex, and the plants are more interdependent. Logging of tropical forests not only removes trees, but also impacts the epiphytes and lianas that are structurally dependent on trees (together, 57% of tropical species). While lianas appear to do well following disturbance or logging, epiphytes often require nearby propagule sources to recolonize and are usually slow to redevelop diverse assemblages (Nadkarni 2000, Schnitzer et al. 2004, Woods and DeWalt 2013, Reid et al. 2016). Consequently, even small-scale harvesting will substantially reduce overall biodiversity. Moreover, the complex architecture of large old trees is known to create vital hotspots of diversity and should be a renewed priority in tropical conservation (Díaz et al. 2010, Woods and DeWalt 2013, Lindenmayer and Laurance 2017, Lutz et al. 2018).

In contrast, temperate forests may be more resilient to small-scale logging. Over 90% of temperate forest species never reach the canopy; logging does not target these diverse herb and shrubs, and sometimes these communities recover quickly (Roberts 2004, Spicer et al. 2018: Chapter 4). In temperate forests the most pernicious threats to the understory may lie elsewhere. Indeed, overbrowsing by large ungulates and fire suppression collapses temperate biodiversity and causes the formation of persistent depauperate understory communities across vast spatial scales (Côté et al. 2004, Nuttle et al. 2013). These depauperate and open forest understories may subsequently become inundated with invasive species (Knight et al. 2009, Wavrek et al. 2017). We suggest that these pressures on temperate forest understories, which have already caused plant diversity collapses, should become conservation priorities by forest managers. Instead, forest management (in both tropical and temperate regions) focuses almost exclusively on trees, because trees generate revenue and sequester the most carbon dioxide. To illustrate this oversight, we reviewed two prominent forest ecology journals (*The Canadian Journal of Forest Research* and *Forest Ecology and Management*) and found that *92%* of temperate plant-related publications focused on trees (**Figure 7;** see Appendix A: Chapter 2 Supplemental Review Methods).

Understudied plant growth-forms and forest strata provide numerous ecosystem services, reinforcing their high conservation value. For instance, while controversial, there is now growing evidence of a worldwide and dramatic decline in insect diversity and abundance (Sánchez-Bayo and Wyckhuys 2019). The retention of species-rich temperate understory layers, particularly in fragmented forests (Carson et al. 2005, Comisky et al. 2005), can provide pollinator refugia that may help mitigate declines in insect communities, especially in pollinator deserts characteristic of agricultural landscapes (Brockerhoff et al. 2017, Landuyt et al. 2019). A diverse temperate understory layer can also aid in nutrient retention and mediate water dynamics during flooding events (Peterson and Rolfe 1982, Muller 2014, Landuyt et al. 2019). These ecosystem services will only become more valuable in the future, as recent changes in climate have increased the frequency and intensity of storm events in temperate areas (Gilliam 2014, Brockerhoff et al. 2017). A complex and diverse tropical canopy structure, replete with epiphytes and lianas, provides floral and fruit resources to herbivores, frugivores, and pollinators alike (Zotz 2016, Schnitzer 2018). Epiphytes modify their host tree microenvironment and mediate ecosystem processes (Díaz et al. 2010, Angelini and Silliman 2014, Zotz 2016). Indeed, epiphytes can contribute more foliar biomass than their host trees and intercept >20% of rainfall (Nadkarni 1984; Hofstede et al. 1993, Van Stan and Pypker 2015). Lianas uptake carbon even during droughts and long dry seasons when trees are relatively stagnant (Schnitzer 2018; Schnitzer and van der Heijden 2019).

2.5 Conclusions

A bias in favor of trees in ecological field studies impedes a comprehensive understanding of forest diversity. Herbs, shrubs, lianas, and epiphytes comprise the vast majority of both tropical and temperate forest plant species, and are vital components of ecosystem processes. Only by expanding our view of the forest, to include these understudied plant growth-forms and forest strata, can we tailor conservation and management plans to sustain a more diverse, productive, and resilient plant community. We make the following recommendations to address some of our conservation concerns described above. 1) Explicitly incorporate non-tree plant groups into long-term forest monitoring research, with standardized protocols for measurement (e.g., CTFS-ForestGEO, Forest Inventory and Analysis). 2) Include non-tree plant groups in forest management plans and urban planning (e.g., creating city parks with native understory plants underneath trees instead of non-native grasses). 3) Test the generality of classic ecological theories in plant growth-forms other than trees (e.g., Dyer et al. 2010; Schnitzer 2018). 4) Routinely quantify the responses of herbs at the species level to both natural and anthropogenic disturbances (*cf*. Royo et al. 2016). 5) Contribute non-tree data to open-source databases to identify global patterns and processes (e.g., Map of Life, GBIF). 5) Study hard-to-access strata such as the canopy. 6) Shift education and science communication to include non-trees in the public understanding of the value of forests and natural spaces.

2.6 Acknowledgements

We thank Alex Royo for providing a species list for the Allegheny National Forest Region and Stephen McCanny for connecting us to the La Mauricie and Bruce Peninsula species lists. Samantha Sutton assisted with the spring ephemeral data collection, Aaron Lauer and Zachary Clemens assisted with the review, and dozens of students at the University of Pittsburgh helped with physiognomic data collection. We thank Jackie Spicer for her artistic talent and patience in providing digital illustrations. Many people improved the development and the writing of the manuscript, especially Yusan Yang, and also Evan Siemann, Alex Royo, Radim Hédl, Tiffany Betras, Jonathan Pruitt, and the Pruitt lab members. Funding was provided by the University of Pittsburgh.

2.7 Figures and tables

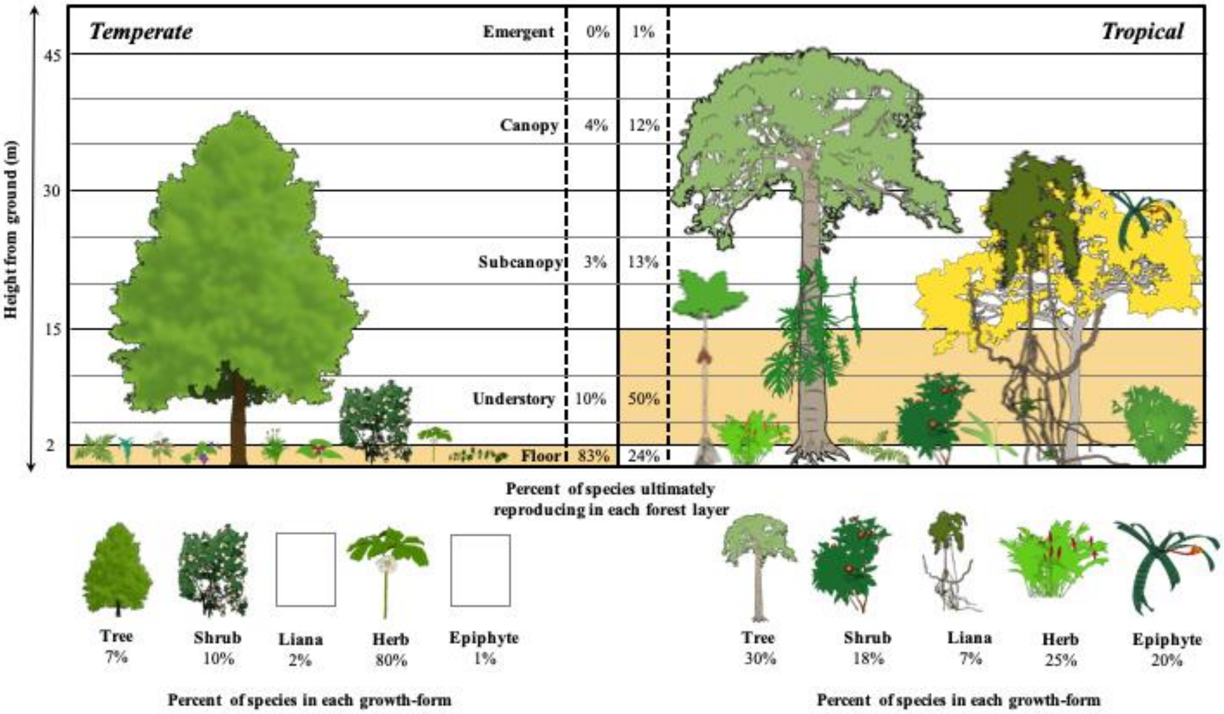


Figure 2-1 The Forest Physiognomy Concept.

A comparison of how species are allocated to growth-forms and strata between temperate versus tropical forests. Temperate forests (left) are dominated by herbs concentrated on the forest floor. In contrast, species in Neotropical forests (right) are more evenly distributed among growth-forms and strata. Growth-forms that make up less than 2% of species are indicated by blank boxes (bottom panel). The relative contribution of each plant growth-form to total species richness is accurately represented by the different number of species depicted for each growth-form. Plants are distributed within their appropriate ultimate strata across the forest profile, although true heights (y axis) may vary among forests. The orange shading depicts the ultimate stratum with maximum relative species richness.

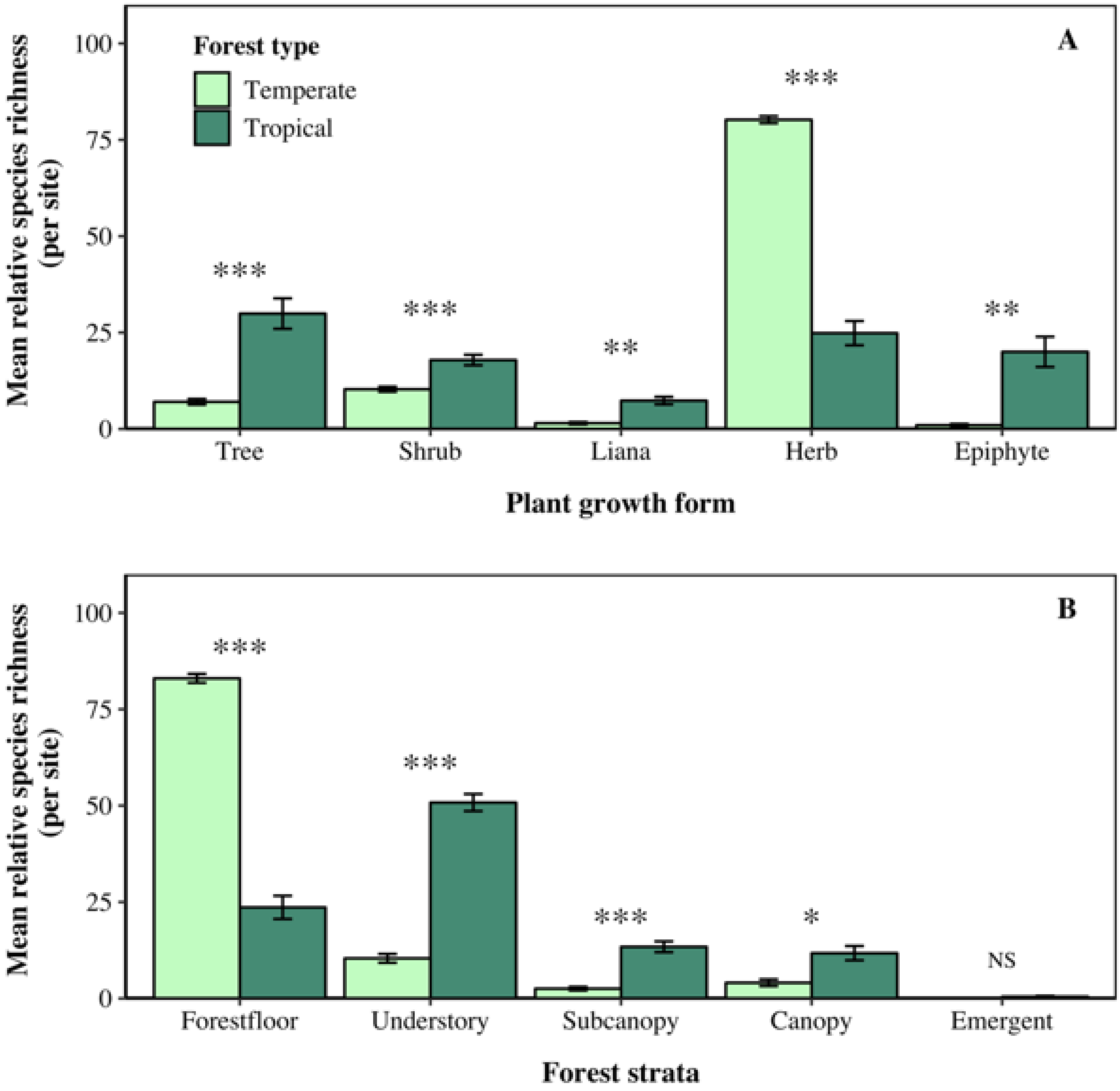


Figure 2-2. Two physiognomic differences between tropical and temperate forests.

Mean (±SE) within-site relative species richness among A) the five major vascular plant growth-forms, and B) the five ultimate strata, comparing temperate (light green bars) and tropical (dark green bars) forests in the Americas. Ultimate strata represent the maximum height in the forest layers where species typically reach reproductive maturity. Asterisks indicate Bonferroni-corrected statistical differences from generalized linear models (N=18, $p<0.01$=*;$p<0.001$=;$p<0.0001$=***).**

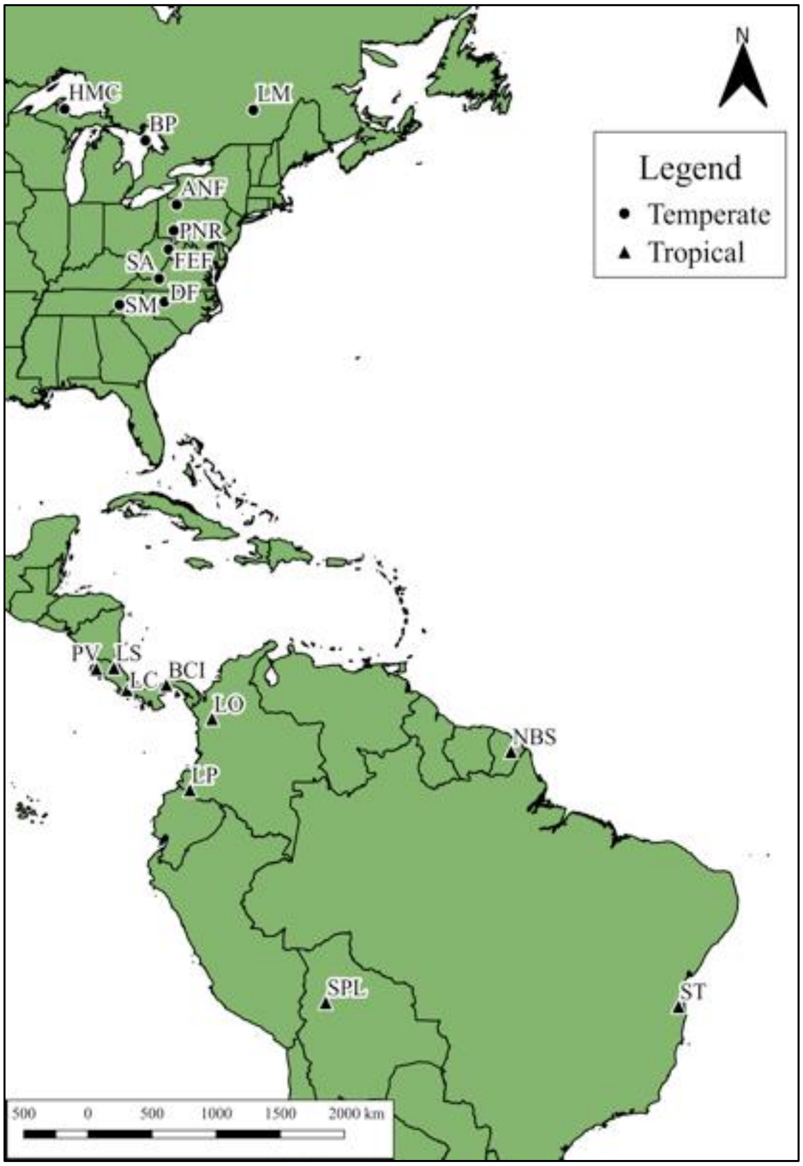


Figure 2-3. Map of tropical and temperate sites used in the study.

Site abbreviations: HMC=Huron Mountain Club, LM=La Mauricie, BP=Bruce Peninsula, ANF=Allegheny National Forest Region, PNR=Powdermill Nature Reserve, FEF=Fernow Experimental Forest, SA=Southern Appalachia, SM=Smoky Mountains, DF=Duke Forest, PV=Palo Verde, LS=La Selva, LC=Las Cruces, BCI=Barro Colorado Island, LO=Las Orchídeas, LP=La Planada, NBS=Nourages Biological Station, SPL=Serranía de Pilón Lajas, ST=Serra do Teimoso. Full site descriptions are included in Table 1. All data are projected in WGS-84 Pseudo-mercator. Base maps are open source from DIVA-GIS (country borders) and from Esri ArcGIS (USA state borders).

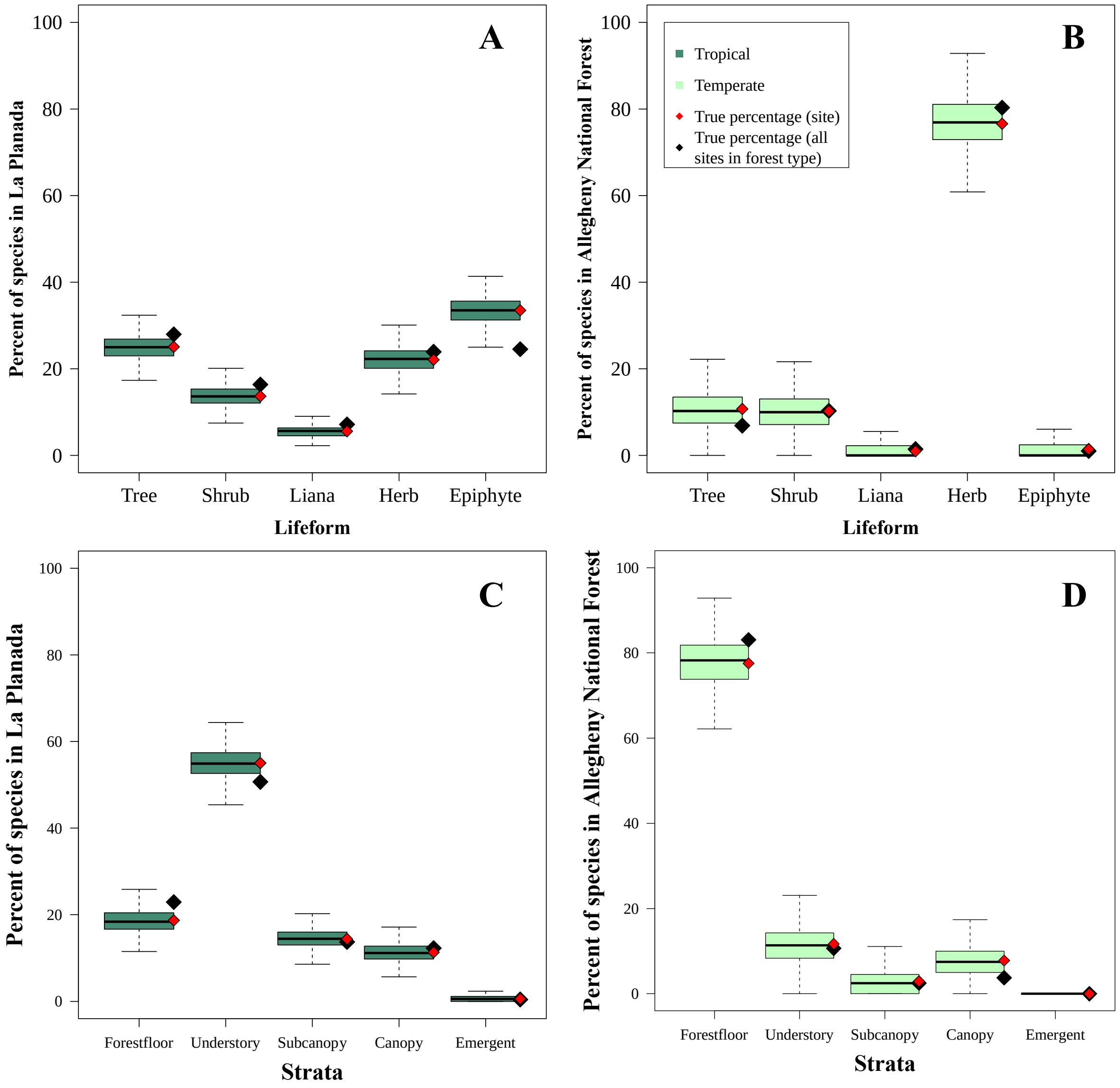


Figure 2-4. Affirmation of 20% subsampling technique.

Box-and-whisker plots showing 1000 bootstrapped runs of 20% subsampled intervals for the distribution of species in each forest strata and growth-form at the two sites where we had a complete dataset. Tropical: La Planada (total N=893 species, A,C); Temperate: Allegheny National Forest Region (total N=244 species, B,D). A. Tropical growth-form distribution. B. Temperate growth-form distribution. C. Tropical ultimate strata distribution. D. Temperate ultimate strata distribution. Red diamonds represent true percentages of each site; black diamonds represent reported percentages of all 9 sites from our 20% subsampling approach used in the main analyses (Figure 2); tropical site percentages are displayed on La Planada for comparison (A,C); temperate sites percentage are displayed on Allegheny National Forest Region (B,D).

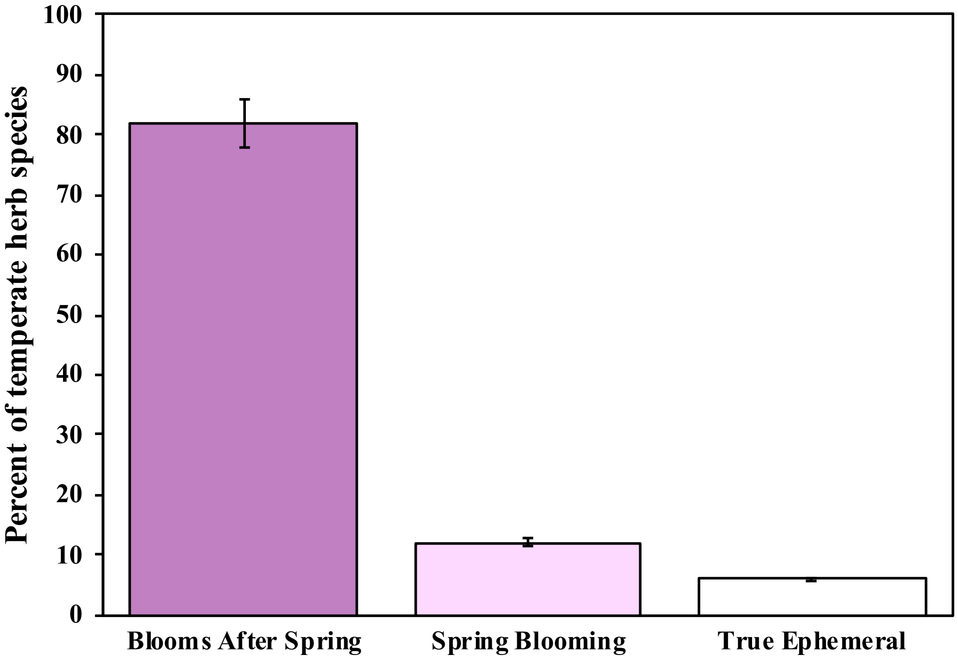


Figure 2-5. Phenology of temperate forest herbs.

Mean (±SE) percent of temperate herb species that bloom after spring (after June 1), bloom during spring (March-May), or are a "true ephemeral", blooming in the spring and senescing before summer. Only 4% of the 854 species were true ephemerals, lending little support for an early spring niche as the main mechanism for why herbs are so speciose in temperate forests when compared to tropical forests.

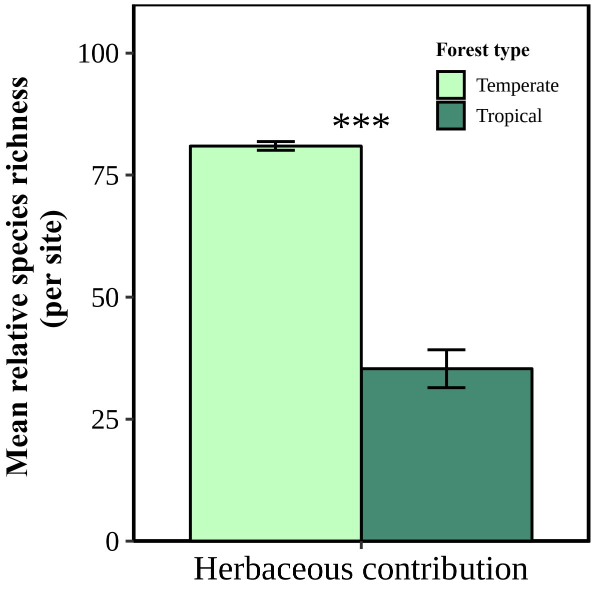


Figure 2-6. The contrasting herbaceousness of temperate versus tropical forests.

Mean (±SE) percent of tropical and temperate forest species that are herbaceous versus woody. Herbaceous growth-forms include herbs (graminoids, ferns, forbs) and herbaceous epiphytes. The remaining species are woody growth-forms, which include trees, shrubs, lianas, and woody epiphytes. Asterisks indicate statistical differences from a generalized linear model (N=18, t=-9.875, p<0.0001).

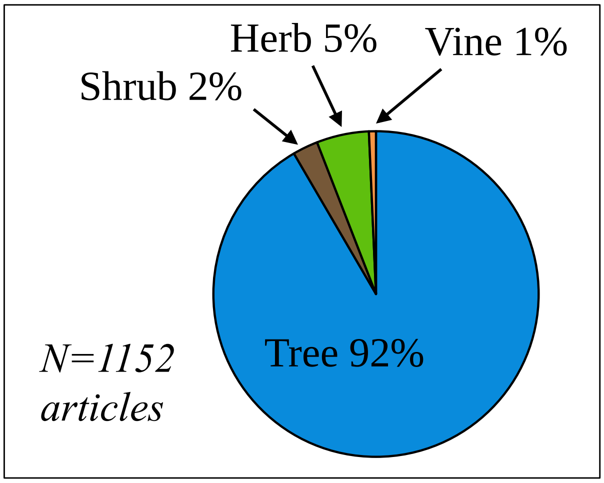


Figure 2-7. Bias towards trees.

Pie chart representing plant growth-form bias in plant-related publications from Forest Ecology and Management and Canadian Journal of Forest Research in the time period 2000-2017.

Table 2-1. Site details for the 18 tropical and temperate forests used in the study.

Coordinates in decimal degrees (Coord), approximate area (Area), elevation range (Elev), mean annual precipitation (Precip), mean annual temperature (Temp), reported total vascular plant species richness (Total SR), year the site was established (Est. year), and references for data sources (full citations below). When unreported in the literature, temperature and precipitation are annual averages over the period of 1970-2000, using nearest neighbor interpolations to extract monthly data from 30-second cells over the course of each year (denoted with an asterisk).

Site (Abbrev)	Coord (DD)	Area (ha)	Elev (masl)	Precip (mm)	Temp (°C)	Total SR	Est. year	References
Huron Mountain Club (HMC)	46.89, -87.87	10000	183-500	783	6	835	1889	(Yanoviak & McCafferty 1996; Flaspohler & Meine 2006; Woods 2015)
La Mauricie National Park (LM)	46.83, -73.00	53670	150-500	1068	4.5	647	1970	(Lothian 1987; Larivière *et al.* 1994; Latourelle & Bouin 2010; Marchand & Filion 2014)
Bruce Peninsula National Park (BP)	45.22, -81.50	15400	190-250	740	5.25	896	1987	(Suffling & Scott 2002; Gruchy *et al.* 2005; Kor *et al.* 2012)
Allegheny National Forest Region (ANF)	41.49, -70.10	30628	319-690	1070	7.6	244	1923	(Anacker & Kirschbaum 2006; Royo *et al.* 2010)
Powdermill Nature Preserve (PNR)	40.16, -79.27	812	392-647	1100	8.3	854	1956	(Utech 1999; Murphy *et al.* 2016; Perry *et al.* 2018)
Fernow Experimental Forest (FEF)	39.05, -79.67	1682	530-1100	1470	8.3	461	1934	(Madarish *et al.* 2002; Adams & Kochenderfer 2015)
Southern Appalachia (SA)	37.29, -80.43	112	600-1050	1150	10.8*	420	1997	(Hammond 1997)
Duke Forest (DF)	35.87, -80.00	2857	122-610	1140	15.5	984	1931	(Nemeth 1968; Stuble *et al.* 2013)
Great Smoky Mountains National Park (SM)	35.69, -83.54	211418	256-2025	1550*	13.6*	1450	1934	(Hoffman 1964; Harmon 1984; Linzey 2008)

Site (Abbrev)	Coord (DD)	Area (ha)	Precip (mm)	Elev (masl)	Temp (°C)	Total SR	Est. year	References
La Selva Biological Station (LS)	10.43, -83.98	1536	4000	35-2906	25	1600	1968	(McDade *et al.* 1994; Matlock & Hartshorn 1999)
Palo Verde Biological Station (PV)	10.36, -85.36	4757	1250	0-200	27	810	1968	(Hartshorn & Poveda 1983; Fauth *et al.* 1989)
Barro Colorado Island (BCI)	09.15, -79.85	1500	2600	120-160	27	1085	1923	(Leigh *et al.* 1996, 2004; Leigh 1999)
Las Cruces Biological Station (LC)	08.78, -82.96	227	4000	1100-1500	24	2000	1973	(Hartshorn & Poveda 1983; Daily *et al.* 2003; Santos Barrera *et al.* 2014)
Las Orquídeas National Park (LO)	06.58, -76.24	29118	3500	300-3450	15	2476	1974	(Meganck 1975; Pedraza-Peñalosa & Betancur. 2015)
Nourages Biological Station (NBS)	04.08, -52.68	114347	2990	40-430	26.3	1541	1995	(Marquis 2004; Bongers *et al.* 2013)
La Planada Nature Reserve (LP)	01.16, -77.99	3200	4800	1500-2100	19	891	1987	(Mendoza-Cifuentes & Ramírez-Padilla 2001; Ramírez-Padilla & Mendoza-Cifuentes 2002)
Serranía de Pilón Lajas Biosphere Reserve (SPL)	14.93, -67.29	400000	2550	300-2000	25.9	736	1977	(Smith & Killeen 1995; Fuentes & Parker 2005)
Serra do Teimoso Biological Station (ST)	15.22, -39.48	200	1375	350-850	23	727	1997	(Amorim *et al.* 2005)

Table 2-2. The extent to which forest physiognomy traits differ between temperate and tropical sites.

A comparison of the allocation of relative species richness among the five major plant growth-forms (above) and the ultimate strata (below) between tropical and temperate forests. Percentages listed are site-level means (± standard error) and results are Bonferroni-corrected generalized linear models detecting differences between the 9 tropical and 9 temperate forests ($\alpha_{Bonferroni}$=0.01*; 0.001;0.0001***).**

Growth-form	**Temperate**	**Tropical**	**df**	**t**	**p**
Tree	7.0 ± 0.7%	29.9 ± 3.9%	17	4.9	0.00016**
Shrub	10.3 ± 0.7%	17.9 ± 1.4%	17	3.9	0.0012*
Liana	1.5 ± 0.3%	7.3 ± 1.0%	17	4.5	0.0004**
Herb	80.2 ± 0.9%	24.9 ± 3.1%	17	81	<0.0001***
Epiphyte	1.0± 0.3%	20.0± 3.9%	17	3.4	0.0014*
Ultimate strata	**Temperate**	**Tropical**	**df**	**t**	**p**
Emergent	0 ± 0%	0.5 ± 0.6%	17	0.006	0.99 NS
Canopy	4.1 ± 0.9%	11.7 ± 1.9%	17	3.9	0.0013*
Subcanopy	2.5 ± 0.5%	13.4 ± 1.4%	17	7.1	<0.0001***
Understory	10.4 ± 1.1%	50.1 ± 2.2%	17	11.6	<0.0001***
Forest Floor	83.0 ± 1.2%	23.6 ± 3.0%	17	-14.1	<0.0001***

2.8 Bibliography

Adams, M.B. & Kochenderfer, J.N. (2015). The Fernow Experimental Forest and Canaan Valley: A History of Research. Southeast. Nat., 14, 433–440.

Adams, B. J., S. A. Schnitzer, and S. P. Yanoviak. 2017. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. Ecography 40:1067–1075.

Amorim, A.M., Fiaschi, P., Jardim, J.G., Thomas, W.W., Clifton, B.C. & Carvalho, A.M.V. de. (2005). The vascular plants of a forest fragment in southern Bahia, Brazil. Sida, Contrib. to Bot., 1727–1752.

Anacker, B.L. & Kirschbaum, C.D. (2006). Vascular Flora of the Kinzua Quality Deer Cooperative , Northwestern Pennsylvania, U.S.A. Bartonia, 11–28.

Angelini, C., and B. R. Silliman. 2014. Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree-epiphyte system. Ecology 95:185–196.

Baker, P. J., and J. S. Wilson. 2000. A quantitative technique for the identification of canopy stratification in tropical and temperate forests. Forest Ecology and Management 127:77–86.

Barry, K. E., and S. A. Schnitzer. 2016. Maintenance of Plant Species Diversity in Forest Ecosystems. Page *in* S. S. Gill and A. Ansari, editors. Plant Biodiversity: Monitoring, Assessment, and Conservation. CAB International.

Beard, J. S. 1955. The Classification of Tropical American Vegetation-Types. Ecology 36:89–100.

Beard, J. S. 1978. The physiognomic approach. Pages 33–64 Classification of plant communities. Springer, Dordrecht.

Bolker, B. M. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, NJ, USA.

Bongers, F., Charles-Dominique, P., Forget, P.M. & & Théry, M. (Eds.). (2013). Nouragues: dynamics and plant-animal interactions in a neotropical rainforest. 80th edn. Springer Science & Business Media.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Company, Philadelphia, PA, USA.

Brockerhoff, E. G., L. Barbaro, B. Castagneyrol, D. I. Forrester, B. Gardiner, J. R. González-Olabarria, P. O. B. Lyver, N. Meurisse, A. Oxbrough, H. Taki, I. D. Thompson, F. van der Plas, and H. Jactel. 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodiversity and Conservation 26:3005–3035.

Canham, C. D., J. S. Denslow, W. Platt, J. R. Runkle, T. a Spies, and P. S. White. 1990. Light regimes beneath closed canopies temperate tropical. Canadian Journal of Forest Research 20:620–631.

Carson, W. P., J. A. Banta, A. A. Royo, and C. Kirschbaum. 2005. Plant communities growing on boulders in the Allegheny National Forest: Evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Natural Areas Journal 25:10–18.

Chazdon, R. L., and N. Fetcher. 1984. Light environments of tropical forests. Pages 27–36 Physiological ecology of plants of the wet tropics. Springer, Dordrecht.

Christenhusz, M. J. M., and M. W. Chase. 2013. Biogeographical patterns of plants in the Neotropics – dispersal rather than plate tectonics is most explanatory. Botanical Journal of the Linnean Society 171:277–286.

Comisky, L., A. A. Royo, and W. P. Carson. 2005. Deer Browsing Creates Rock Refugia Gardens on Large Boulders in the Allegheny National Forest, Pennsylvania. The American Midland Naturalist 154:201–206.

Condit, R. 1995. Research in large, long-term tropical forest plots. Trends in Ecology & Evolution 10:18–22.

Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology and Systematics 35:113–147.

Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G. & Sánchez-Azofeifa, A. (2003). Countryside Biogeography of Neotropical Mammals: Conservation Opportunities in Agricultural Landscapes of Costa Rica. Conserv. Biol., 17, 1814–1826.Díaz, I. A., K. E. Sieving, M. E. Peña-Foxon, J. Larraín, and J. J. Armesto. 2010. Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: A neglected functional component. Forest Ecology and Management 259:1490–1501.

Dyer, L. A., D. K. Letourneau, G. V. Chavarria, and D. S. Amoretti. 2010. Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. Ecology 91:3707–3718.

Fauth, J.E., Crother, B.I. & Slowinski, J.B. (1989). Elevational Patterns of Species Richness, Evenness, and Abundance of the Costa Rican Leaf-Litter Herpetofauna. Biotropica, 21, 178–185.

Flaspohler, D.J. & Meine, C. (2006). Planning for Wildness : Aldo Leopold’s Report on Huron. J. For., 159–163.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Science Reviews 55:73–106.

Fuentes, A. & Parker, N. (2005). Una introducción a la vegetación de la región de Madidi. Ecol. en Boliv., 40, 1–31.

Gentry, A. H., and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rainforest. Biotropica 19:149–156.

Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. Annual Review of Phytopathology 40:13–43.

Gilbert, G. S., and D. R. Reynolds. 2005. Nocturnal fungi: Airborne spores in the canopy and understory of a tropical rain forest. Biotropica 37:462–464.

Gilliam, F. S. 2014. The herbaceous layer in forests of eastern North America. Page (F. S. Gilliam, Ed.). Second edition. Oxford University Press, New York, NY.

Givnish, T. J., M. H. J. Barfuss, B. van Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, R. S. Jabaily, D. M. Crayn, J. A. C. Smith, K. Winter, G. K. Brown, T. M. Evans, B. K. Holst, H. Luther, W. Till, G. Zizka, P. E. Berry, and K. J. Sytsma. 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: Insights from an eight-locus plastid phylogeny. American Journal of Botany 98:872–895.

Gora, E. M., J. M. Lucas, and S. P. Yanoviak. 2019. Microbial Composition and Wood Decomposition Rates Vary with Microclimate From the Ground to the Canopy in a Tropical Forest. Ecosystems 22:1206–1219.

Gruchy, M.A. De, Reader, R.J. & Biomass, D.W.L. (2005). Ecological Archives E086-070-A1 Appendix A: Plant biomass, 68–71.

Guo, Q., and R. E. Ricklefs. 2000. Species richness in plant genera disjunct between temperate eastern Asia and North America.

Hammond, D.N. (1997). Characterization of vascular plant species composition and relative abundance in Southern Appalachian mixed-oak forests. Virginia Polytechnic Institute and State University.

Harmon, M.E. (1984). Survival of Trees After Low-Intensity in Great Smoky Mountains National Park. Ecology, 65, 796–802.

Hartshorn, G.S. & Poveda, L.J. (1983). Checklist of Trees. In: Costa Rican Natural History (ed. Janzen, D.H.). University of Chicago Press, Chicago and London, pp. 158–183.

Hartwig, G. 1863. The tropical world: a popular scientific account of the natural history of the animal and vegetable kingdoms in the equatorial regions. Page (Longman, Green, and Roberts, Eds.). Spottiswoode and Co., London, UK.

Hoffman, H.L. (1964). Check list of vascular plants of the Great Smoky Mountains. Castanea, 29, 1–45.

Hofstede, R. G., J. H. Wolf, and D. H. Benzing. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forest. Selbyana:37–45.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

von Humboldt, A. 1873. Vegetation in the tropics. Friends' Intelligencer 30:203.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. Page Acta Phytogeographica Suecia.

Kelly, D. L., E. V. J. Tanner, E. M. Nic Lughadha, and V. Kapos. 1994. Floristics and Biogeography of a Rain Forest in the Venezuelan Andes. Journal of Biogeography 21:421–440.

Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29:110–116.

Kor, P.S.G., Cowell, D.W., Karrow, P.F. & Kristjansson, F.J.R. (2012). The Cabot Head Archipelago: evidence of glacial Lake Algonquin on the Northern Bruce Peninsula, Ontario. Can. J. Earth Sci., 49, 576–589.

Kuchler, A. W. 1949. A physiognomic classification of vegetation. Annals of the Association of American Geographers 39:201–210.

Landuyt, D., E. De Lombaerde, M. P. Perring, L. R. Hertzog, E. Ampoorter, S. L. Maes, P. De Frenne, S. Ma, W. Proesmans, H. Blondeel, B. K. Sercu, B. Wang, S. Wasof, and K. Verheyen. 2019. The functional role of temperate forest understorey vegetation in a changing world. Global Change Biology:gcb.14756.

Lapointe, L. 2001. How phenology influences physiology in deciduous forest spring ephemerals. Physiologia Plantarum 113:151–157.

Larivière, S., Huot, J. & Samson, C. (1994). Daily activity patterns of female black bears in a Northern mixed-forest environment. Am. Soc. Mammologists, 75, 613–620.

Latourelle, A. & Bouin, T. (2010). La Mauricie National Park of Canada: Management Plan.

Ledo, A., and S. A. Schnitzer. 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. Ecology 95:2169–2178.

Leigh, E. G. J. 1975. Structure and Climate in Tropical Rain Forest. Annual Review of Ecology and Systematics 6:67–86.

Leigh, E.G., Dick, C.W., Terborgh, J., Ter Steege, H. & Wright, S.J. (2004). Why Do Some Tropical Forests Have So Many Species of Trees? Biotropica, 36, 447–473.

Leigh, E.G., Rand, A.S. & Windsor, D.M. (1996). The ecology of a tropical forest: seasonal rhythms and long-term changes.

Leigh, E.G.J. (1999). Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press on Demand.

Lewis, S. L., J. Lloyd, S. Sitch, E. T. a. Mitchard, and W. F. Laurance. 2009. Changing Ecology of Tropical Forests: Evidence and Drivers. Annual Review of Ecology, Evolution, and Systematics 40:529–549.

Linares-Palomino, R., V. Cardona, E. I. Hennig, I. Hensen, D. Hoffmann, J. Lendzion, D. Soto, S. K. Herzog, and M. Kessler. 2009. Non-woody life-form contribution to vascular plant species richness in a tropical American forest. Forest Ecology: Recent Advances in Plant Ecology:87–99.

Lindenmayer, D. B., and W. F. Laurance. 2017. The ecology, distribution, conservation and management of large old trees. Biological Reviews 92:1434–1458.

Linzey, D.W. (2008). A natural history guide to Great Smoky Mountains national park. Univ. of Tennessee Press.

Loidi, J. 2018. Plant eco-morphological traits as adaptations to environmental conditions: some comparisons between different biomes across the world. Pages 59–71 *in* A. M. Greller, editor. Geographical changes in vegetation and plant functional types, Geobotany Studies. Springer International Publishing, AG.

Lothian, W. (1987). A Brief History of Canada's National Parks. Minist. Environ.

Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker, E. M. Blomdahl, N. A. Bourg, S. Bunyavejchewin, D. F. R. P. Burslem, C. A. Cansler, K. Cao, M. Cao, D. Cárdenas, L. W. Chang, K. J. Chao, W. C. Chao, J. M. Chiang, C. Chu, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, H. S. Dattaraja, A. Duque, C. E. N. Ewango, G. A. Fischer, C. Fletcher, J. A. Freund, C. Giardina, S. J. Germain, G. S. Gilbert, Z. Hao, T. Hart, B. C. H. Hau, F. He, A. Hector, R. W. Howe, C. F. Hsieh, Y. H. Hu, S. P. Hubbell, F. M. Inman-Narahari, A. Itoh, D. Janík, A. R. Kassim, D. Kenfack, L. Korte, K. Král, A. J. Larson, Y. De Li, Y. Lin, S. Liu, S. Lum, K. Ma, J. R. Makana, Y. Malhi, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, M. Morecroft, P. M. Musili, J. A. Myers, V. Novotny, A. de Oliveira, P. Ong, D. A. Orwig, R. Ostertag, G. G. Parker, R. Patankar, R. P. Phillips, G. Reynolds, L. Sack, G. Z. M. Song, S. H. Su, R. Sukumar, I. F. Sun, H. S. Suresh, M. E. Swanson, S. Tan, D. W. Thomas, J. Thompson, M. Uriarte, R. Valencia, A. Vicentini, T. Vrška, X. Wang, G. D. Weiblen, A. Wolf, S. H. Wu, H. Xu, T. Yamakura, S. Yap, and J. K. Zimmerman. 2018. Global importance of large-diameter trees. Global Ecology and Biogeography 27:849–864.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Madarish, D.M., Rodrique, J.L. & Adams, M.B. (2002). Vascular flora and macroscopic fauna on the Fernow Experimental Forest., Gen. Tech., 37.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466:752–755.

Marchand, N. & Filion, L. (2014). A dendroecological analysis of eastern hemlock and white pine in relation to logging in la Mauricie National Park (Québec, Canada). For. Chron., 90, 351–360.

Marquis, R.J. (2004). Biogeography of Neotropical Piper. In: Piper: A model genus for studies of phytochemistry, ecology, and evolution (eds. Dyer, L.A. & Palmer, A.D.N.). Kluwer Academic/Plenum Publishers, New York, NY, pp. 78–96.

Matlock, R.B. & Hartshorn, G.S. (1999). La Selva Biological Station (OTS). Bull. Ecol. Soc. Am., 80, 188–193.

McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (Eds.). (1994). La Selva: Ecology and natural history of a neotropical rain forest. University of Chicago Press.

Meganck, R.A. (1975). Colombia's national parks: An analysis of management problems and perceived values.

Mendoza-Cifuentes, H. & Ramírez-Padilla, B. (2001). Dicotiledóneas de La Planada, Colombia: Lista de Especias. Biota Colomb., 2, 59–73.

Moffett, M. W. 2000. What 's "Up"? A Critical Look at the Basic Terms of Canopy Biology. Biotropica 32:569–596.

Murphy, S.J., Xu, K. & Comita, L.S. (2016). Tree seedling richness, but not neighborhood composition, influences insect herbivory in a temperate deciduous forest community. Ecol. Evol., 6, 6310–6319.

Muller, R. N. 2014. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. Pages 13–34 *in* F. S. Gilliam, editor. The herbaceous layer in forests of eastern North America. Second edition. Oxford University Press, New York, NY.

Nadkarni, N. M. 1984. Biomass and mineral capital of epiphytes in an Acer macrophyllum community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Canadian Journal of Botany 62:2223–2228.

Nadkarni, N. M. 2000. Colonization of Stripped Branch Surfaces by Epiphytes in a Lower Montane Cloud Forest, Monteverde, Costa Rica. Biotropica 2:358.

Nadkarni, N. M., and R. Solano. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia 131:580–586.

Nakamura, A., R. L. Kitching, M. Cao, T. J. Creedy, T. M. Fayle, M. Freiberg, C. N. Hewitt, T. Itioka, L. P. Koh, K. Ma, Y. Malhi, A. Mitchell, V. Novotny, C. M. P. Ozanne, L. Song, H. Wang, and L. A. Ashton. 2017. Forests and Their Canopies: Achievements and Horizons in Canopy Science. Trends in Ecology and Evolution 32:438–451.

Nemeth, J.C. (1968). The hardwood vegetation and soils of Hill Demonstration Forest, Durham County, North Carolina. J. Elisha Mitchell Sci. Soc., 482–491.

Nuttle, T., A. A. Royo, M. B. Adams, and W. P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecological Monographs 83:3–17.

Parker, G. G. 1995. Structure and microclimate of forest canopies. Pages 73–106 *in* G. G. Parker, M. D. Lowman, and N. M. Nadkarni, editors. Forest Canopies.

Pedraza-Peñalosa, P. & Betancur., J. (2015). Flora of Las Orquídeas National Park: vascular plants of the Colombian Andes and Chocó. New York Bot. Gard. Bronx, New York. Available at: http://sweetgum.nybg.org/science/projects/orquideas/.

Perry, K.I., Wallin, K.F., Wenzel, J.W. & Herms, D.A. (2018). Forest disturbance and arthropods: Small-scale canopy gaps drive invertebrate community structure and composition. Ecosphere, 9.

Peterson, D. L., and G. L. Rolfe. 1982. Nutrient Dynamics of Herbaceous Vegetation in Upland and Floodplain Forest Communities. The American Midland Naturalist 107:325–339.

R Core Development Team, 3.6.0. 2019. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RStudio Team, 1.0.153. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Ramírez-Padilla, B. & Mendoza-Cifuentes, H. (2002). Monocotiledóneas y Pteridófitos de La Planada, Colombia. Biota Colomb., 3, 285–295.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer. Clarendon Press, Oxford.

Reid, J. L., J. M. Chaves-Fallas, K. D. Holl, R. A. Zahawi, M. Chaves-fallas, K. D. Holl, R. A. Zahawi, J. L. Reid, C. Rica, and C. Rica. 2016. Tropical forest restoration enriches vascular epiphyte recovery. Applied Vegetation Science 19:1–10.

Richards, P. W. 1939. Ecological studies on the rain forest of Southern Nigeria: I. The structure and floristic composition of the primary forest. Journal of Ecology 27:1–61.

Richards, P. W. 1952. The tropical rain forest: An ecological study. Cambridge University Press, London, UK.

Roberts, M. R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82:1273–1283.

Röhrig, E., and B. Ulrich. 1991. Temperate Deciduous Forests. Seventh edition. Elsevier, Amsterdam, The Netherlands.

Royo, A. A., Stout, S.L., DeCalesta, D.S. & Pierson, T.G. (2010). Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? Biol. Conserv., 143, 2425–2434.

Royo, A. A., C. J. Peterson, J. S. Stanovick, and W. P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology 97:1566–1582.

Russell-Smith, J. 2006. Classification, species richness, and environmental relations of monsoon rain forest in northern Australia. Journal of Vegetation Science 2:259–278.

Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232:8–27.

Santos Barrera, G., R. Eirlich, P., Bolaños, F., Cháves, G., Mendoza Quijano, F., C. Daily, G., et al. (2014). Diversity, natural history and conservation of amphibians and reptiles from the San Vito Region, southwestern Costa Rica. Rev. Biol. Trop., 56, 755–778.

Schnitzer, S. A. 2018. Testing ecological theory with lianas. New Phytologist.

Schnitzer, S. A., and W. P. Carson. 1999. Tropical environments. Pages 605–609 *in* D. E. Alexander and R. W. Fairbridge, editors. Encyclopedia of environmental science. Chapman and Hall, London, UK.

Schnitzer, S. A., and W. P. Carson. 2000. Have we forgotten the forest because of the trees? Trends in ecology & evolution (Correspondence) 15:375.

Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849–857.

Schnitzer, S. A., and G. M. F. van der Heijden. 2019. Lianas have a seasonal growth advantage over co-occurring trees. Ecology 100:1–12.

Schnitzer, S. A., M. P. E. Parren, and F. Bongers. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. Forest Ecology and Management 190:87–98.

Smith, A. P. 1973. Stratification of temperate and tropical forests. The American Naturalist 107:671–683.

Smith, D.N. & Killeen, T.J. (1995). A comparison of the structure and composition of montane and lowland tropical forest in the Serranía Pilón Lajas, Beni, Bolivia. For. Biodivers. North, Cent. South Am. Caribb. Res. Monit., 681–700.

Spicer, M. E., K. F. Suess, J. W. Wenzel, and W. P. Carson. 2018. Does salvage logging erase a key physical legacy of a tornado blowdown? A case study of tree tip-up mounds. Canadian Journal of Forest Research 48:976–982.

Spurr, S. H., and B. V. Barnes. 1973. Forest ecology. Second edition. Wiley.

Stuble, K.L., Pelini, S.L., Diamond, S.E., Fowler, D. a., Dunn, R.R. & Sanders, N.J. (2013). Foraging by forest ants under experimental climatic warming: A test at two sites. Ecol. Evol., 3, 482–491.

Suffling, R. & Scott, D. (2002). Assessment of climate change effects on Canada's national park system. Environ. Monit. Assess., 74, 117–139.

Terborgh, J. W. 1985. The Vertical Component of Plant Species Diversity in Temperate and Tropical Forests. The American Naturalist 126:760–776.

Thrippleton, T., H. Bugmann, K. Kramer-Priewasser, and R. S. Snell. 2016. Herbaceous Understorey: An Overlooked Player in Forest Landscape Dynamics? Ecosystems 19:1240–1254.

Utech. (1999). Checklist of the Vascular Plants of Powdermill Nature Reserve, Westmoreland County, Pennsylvania.

Van Stan, J. T., and T. G. Pypker. 2015. A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. Science of The Total Environment 536:813–824.

Wallace, A. R. 1878. Tropical nature, and other essays. MacMillan and Co., London, UK.

Wavrek, M., J. M. Heberling, S. Fei, and S. Kalisz. 2017. Herbaceous invaders in temperate forests : a systematic review of their ecology and proposed mechanisms of invasion. Biological Invasions 19:3079–3097.

Webb, L. J. 1959. A physiognomic classification of Australian rain forests. Journal of Ecology 47:551–570.

Woods, C. L., C. L. Cardelús, and S. J. DeWalt. 2015. Micarohabitat associations of vascular epiphytes in a tropical wet forest canopy. Journal of Ecology:421–430.

Woods, C. L., and S. J. DeWalt. 2013. The Conservation Value of Secondary Forests for Vascular Epiphytes in Central Panama. Biotropica 45:119–127.

Woods, K.D. (2015). An all-taxa biodiversity inventory of the Huron Mountain Club. Occas. Pap. Huron Mt. Wildl. Found., No. 5.

Yanoviak, S.P. & McCafferty, W.P. (1996). Comparison of macroinvertebrate assemblages inhabiting pristine streams in the Huron Mountains of Michigan, USA. Hydrobiologia, 330, 195–211.

Zhu, H., J. P. Shi, and C. J. Zhao. 2005. Species composition, physiognomy and plant diversity of the tropical montane evergreen broad-leaved forest in southern Yunnan. Biodiversity and Conservation 14:2855–2870.

Zotz, G. 2005. Vascular epiphytes in the temperate zones - A review. Plant Ecology 176:173–183.

Zotz, G. 2013. Hemiepiphyte: A confusing term and its history. Annals of Botany 111:1015–1020.

Zotz, G. 2016. Plants on Plants – The Biology of Vascular Epiphytes. Springer International Publishing, Switzerland.

Zotz, G., and S. Schultz. 2008. The vascular epiphytes of a lowland forest in Panama-species composition and spatial structure. Plant Ecology 195:131–141.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Page (M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, and W. Wong, Eds.). Spring Science and Business Media, New York, NY.

3.0 RAPID FOREST UNDERSTORY RECOVERY FOLLOWING COMBINED NATURAL AND ANTHROPOGENIC DISTURBANCES

Spicer, M. E., A. A. Royo, J. W. Wenzel, and W. P. Carson. Rapid forest understory recovery following combined natural and anthropogenic disturbances. *In preparation, intended for submission to Ecology.*

3.1 Introduction

Natural disturbance is one mechanism of diversity maintenance, and has long been a central focus of ecology (Connell 1978; Pickett and White 1985, Tilman 1990; Platt & Connell 2003; Sheil & Burslem 2003). In forests, a moderate level of disturbance can facilitate long-term coexistence of both light-adapted early successional species and shade-tolerant late successional species (Connell 1978; Molino & Sabatier 2001; Schnitzer & Carson 2001; Fischer *et al.* 2013). However, highly disturbed forest systems, especially when natural disturbance is coupled with anthropogenic disturbance, can be much *lower* in biodiversity, vulnerable to invasion and monodominance by exotic species, and lack resilience to subsequent perturbations (Chazdon 2003; Laurance & Curran 2008; Johnstone *et al.* 2016; Lindenmayer *et al.* 2017). Eastern North American forests are characterized by a century of repeated clearcutting and the near extirpation of apex predators such as wolves and pumas, yet the consequences for forest overall diversity and resilience are still poorly understood. Moreover, climate change models predict that the frequency and intensity of catastrophic disturbances will increase in in the future (Easterling 2000; Dale *et* *al.* 2001; Zscheischler *et al.* 2018), and forests will likely experience higher and perhaps novel levels of disturbance (Barnosky *et al.* 2012; Seidl *et al.* 2017). Thus, understanding forest recovery processes after combined natural and anthropogenic disturbances is a priority (Leverkus *et al.* 2018).

Salvage logging is a common practice throughout North America as a way to recover lost revenue from a variety of natural forest disturbances, including windstorms, fire, and ice storms. However, the ecological consequences of salvage logging remain equivocal and controversial. On one hand, salvage logging can substantially decrease seedling regeneration. For example, in a post-fire salvage logging operation, seedling regeneration was decreased by up to 71% after a year (Donato *et al.* 2006). Salvage logging can also shift the community composition of regenerating plants (Bowd *et al.* 2018; Santoro & D'Amato 2019). Structural heterogeneity, such as coarse woody debris, is usually removed, spatially consolidated, or reduced in salvage logging operations (Russell *et al.* 2006; Bottero *et al.* 2013; Waldron *et al.* 2013; Santoro & D'Amato 2019; but see Donato *et al.* 2006). Forests that were salvage logged, in comparison to unsalvaged forests, have smaller size classes and lower aboveground biomass for several decades (Sass *et al.* 2018). These structural alterations potentially cause declines in animal species associated with coarse woody debris such as cavity-nesting birds or saproxylic beetles (Russell *et al.* 2006; Cahall & Hayes 2009; Thorn *et al.* 2014; but see Werner *et al.* 2015). For plant communities, structural alterations from salvage logging may remove putative browse refugia or create unfavorable regeneration microsites (Krueger & Peterson 2006; Bottero *et al.* 2013; Waldron *et al.* 2013). Thus, salvage logging has been criticized traditionally as detrimental to the regenerating forest flora and fauna.

On the other hand, there is a growing body of literature demonstrating negligible, or even positive, impacts of salvage logging on forest regeneration. These patterns are particularly evident after wind, rather than fire disturbances. In one example, plant diversity (including herbaceous and woody species) was 20% higher in comparison to unsalvaged areas just one year of intense post-windthrow salvage logging (Slyder *et al.* 2019). On similar short time scales (2-5 years), tree seedlings are just as diverse and abundant in areas that were salvage logged versus unsalvaged areas (Kurulok & Macdonald 2007; Peterson & Leach 2008a, b; Royo *et al.* 2016). Post-salvage-logged herbaceous communities, although different in composition from unsalvaged communities, also do not show major declines in diversity (Royo *et al.* 2016). A few studies show that regeneration, measured in abundance or in composition, is comparable in salvaged and unsalvaged areas on decadal scales as well (10-30 years) (Kurulok & Macdonald 2007; Kramer *et al.* 2014). Post-windthrow salvage logging does not seem to completely "destroy" or "erase" structural heterogeneity either (*sensu* Cooper-Ellis *et al.* 1999; Waldron *et al.* 2013, respectively). Spicer *et al.* (2018: Chapter 4) showed that tip-up mounds that "tip back down" post-salvaging actually harbor a plant community indistinguishable from intact tip-up mounds, rather than reflect the off-mound plant community. Likewise, Peterson & Leach (2008b) show a higher heterogeneity of microsites in salvaged areas versus unsalvaged areas two years after combined wind disturbance and salvage logging. Wermelinger *et al.* (2017) showed that arthropod diversity was *highest* in a landscape that contained a mosaic of intact, windthrown, and salvage-logged forest, increasing diversity 2.5 times in comparison to intact forests.

These conflicting results and discrepancies may be due to differences unique to each disturbance (e.g., intensity, type, site; Kramer *et al.* 2014b; Taeroe *et al.* 2019), time, or additional biotic pressures mediating the effects of salvage logging on forest regeneration. When comparing results from a post-fire salvage logging operation in Australia (e.g., Bowd *et al.* 2018) to a post-windthrow salvaging operation in Canada (e.g., Peterson & Leach 2008b), it is difficult to disentangle the effects of fire versus windthrow, intensity of natural disturbance, salvage logging intensity, or environmental context. Because the motivation for salvage logging is often opportunistic and generates the most revenue at large spatial scale, controls (i.e., areas left unsalvaged within the same disturbance) are often lacking. Experimental studies mostly come from single-sites, while multi-site studies often compare wildly differing ages or intensities of disturbances (reviewed in Royo *et al.* 2016; Wermelinger *et al.* 2017). Higher within-site replication or more controlled among-site variation is needed to distinguish site-differences from salvaging-differences.

Moreover, almost all temperate forests are experiencing multiple, simultaneous pressures. White tailed-deer (*Odocoileus virginianus*) have been overabundant in the eastern North America for several decades, causing biodiversity declines of over 80% across large swaths of deciduous and coniferous forests (Rooney 2001; Côté *et al.* 2004; Habeck & Schultz 2015). Because deer have strong feeding preferences for some plant species and not others, they have caused widespread shifts in the plant and animal community (Rooney & Waller 2003; Frerker *et al.* 2014). Particularly concerning for maintaining temperate forest diversity is that browsers target the understory herbaceous plant community (Gilliam 2007), which constitute 80% of the vascular plant species of temperate forests (Gilliam 2007; Spicer *et al.* 2019: Chapter 2). The direct effects of overabundant deer are further compounded by positive feedback cycles of dense, recalcitrant deer-resistant or deer-tolerant plant layers, high seed predation, and the spread of non-native species (Royo & Carson 2006, 2008; Royo *et al.* 2010b; Frerker *et al.* 2014; Wavrek *et al.* 2017). These depauperate understories and monocultures of deer-resistant or deer-tolerant species remain for decades, *even when deer have been removed from the landscape* (Royo *et al*. 2010b; Tanentzap *et al.* 2012; Pendergast IV *et al.* 2015).

Thus, our classical expectations of "healthy" forest recovery after natural disturbance—or even unnatural disturbance such as salvage logging—are unrealistic in the context of decades of deer overabundance. Indeed, Nuttle *et al.* (2013) and Royo *et al.* (2010a) experimentally demonstrated the complexity of interactions among major disturbances and deer in restructuring understory plant communities. Neither fire, nor large canopy gaps, alone, were enough to bring substantial tree diversity back to the understory; when deer were excluded, gaps and fire caused up to fivefold increases in diversity (Nuttle *et al.* 2013). For herbaceous species, canopy gaps and fire increase species diversity more so than either alone, and deer enhance species richness and abundance (Royo *et al.* 2010a) when at low to moderate densities. These unexpected interactions among major drivers of forest change were apparent only with replicated factorial experiments. Separately, salvage logging and overabundant deer have the potential to shift the successional trajectory of regenerating forests; however, to date, there are no studies that explicitly test the independent and combined effects simultaneously. One study which nested deer exclosures within salvage logged areas found that deer counteracted the positive recruitment effect of the natural disturbance (bark beetle outbreak) for the promotion of broadleaved trees (Rozman *et al.* 2015). Without fenced areas outside of the salvaged or damaged areas, however, the positive effects of the natural disturbance and the salvage logging were confounded (Rosman *et al.* 2015). Clearly, it is important to explicitly consider the contribution of deer when assessing post-disturbance forest regeneration, but only more rigorous experimental designs will allow these comparisons.

Here, we present the first large-scale, replicated field experiment explicitly testing the interactions among salvage logging and the direct and indirect effects of deer on a regenerating forest. Specifically, we test the extent to which: 1. salvage logging, 2. deer browsing, or 3. understory plant competitors (the legacy of overabundant deer), are the major driver of plant community change after a large wind disturbance. We predict that the interactions among these factors, rather than any main effect, may explain most of the variation among regenerating forest patches (*sensu* Royo *et al.* 2010a; Nuttle *et al.* 2013). Based on recent work in post-windstorm salvage logging studies (Royo *et al.* 2016; Slyder *et al.* 2019), we further predict that salvage logging may actually *enhance* plant biodiversity not only by creating a more continuous "gap" across the landscape than the windstorm itself, but also by scarifying large patches of soil (Royo *et al.* 2016). Using a unique opportunity, in which one tornado created four separate large blowdowns, we set up the first experiment with both *within-disturbance* and *within-blowdown site* replication. The main aim of this experiment was to draw broad, generalizable conclusions about these interacting processes *across sites*.

3.2 Methods

3.2.1 Study site

Our study took place in the Powdermill Nature Reserve in Westmoreland County, Pennsylvania (40.16°N, –79.27°W). The reserve is a 900 ha property dominated by mature mesophytic forest with temperatures ranging from –20 to 33 °C and mean annual precipitation of approximately 1100 mm (Murphy *et al.* 2015; Spicer *et al.* 2018: Chapter 4). We located our experiment within four large blowdown sites caused by an EF-1 tornado which occurred on June 1st, 2012. More information about the land use history, overstory community, and details of the windstorm can be found in Spicer *et al.* (2018: Chapter 4) and Slyder *et al.* (2019).

3.2.2 Experimental design

We designed a 2x2x2 blocked, split-plot field experiment to examine the independent and interacting effects of 1) salvage logging, 2) deer browsing, and 3) understory plant competition on post-tornado forest regeneration. To test the extent to which salvage logging drives plant regeneration, we intensively salvage logged a random half of each of these four blowdown sites during the winter of 2013-2014, and left the other half unsalvaged. Details and a map of the salvage logged blowdowns are in Slyder *et al.* 2019. We refer to these four blowdowns as *sites*.

To test how deer browsing mediates natural forest regeneration, we set up 32-8x8x2m fences during the summer and fall of 2014 (two years after the tornado). We placed the fences in a blocked random design throughout each of the four blowdown sites (four fences in the salvage logged half, and four in the unlogged half of each blowdown). The fences had a polyurethane mesh of the size 5x5cm and were secured at each corner by zipties attached to metal poles. We also set up 32-8x8m control areas, marking the corners with the same metal poles that support the fences. To account for possible seed dispersal effects from birds perching on fence edges, we ran a metal wire around the border of the control plots at a height of 2m. We refer to these 64 total 64m$_2$ areas (whether fenced or unfenced) as *plots*, and they are the primary unit of replication for this study.

To test whether the layer of understory competition that develops in the first few years after a blowdown and can cause alternative successional trajectories, we physically removed all extant vegetation from a random half of the 64 plots in the summer of 2015. Treatments were blocked within blowdown site such that each half of the blowdown area (salvaged or unsalvaged) contained four plots with understory vegetation removed, and four with vegetation left. Woody stems <5cm in basal diameter were cut with pruning shears and all smaller woody vegetation and herbaceous vegetation was shorn to the ground with a gasoline-powered string trimmer. Thus, we had a blocked, split-plot experimental design with 8 replicate plots of the each of the experimental treatment combinations: salvage logging (Unlogged/Logged), deer access (Deer/Fence), and understory competitors (Left/Removed); two replicates of each combination were at each site.

To establish a baseline of the environmental context of these disturbance plots, we also set up 27 reference plots outside the windthrown area, in the intact forest. Six or seven reference plots were set up around the perimeter of each of the four blowdown sites to capture the community near each site; each plot was at least 30m away from the edge of the blowdown. Thus, these reference plots represent the deciduous forest under “business as usual” model: no large light gaps, high current deer populations, and a legacy of several decades of abundant deer. Reference intact forest plots are used for overall comparisons only and are not included in the main analyses.

3.2.3 Data collection

In the summer of 2017 (five years after the tornado, four years after the logging, three years after the fences, and two years after the removals), we surveyed all 64 plots. To avoid edge effects, we left a 1m buffer around the border of each plot, surveying the center 36m$_2$. In four 1x1m *quadrats* located at the four corners of each 36m$_2$, we identified to species and estimated cover under 1m for all vascular plant species. To get a more thorough survey of the plant community, we augmented the cover estimates with a timed meander survey within the whole 36m$_2$ plot.

3.2.4 Statistical analyses

We calculated average vegetative cover for each plot by taking the mean of all per-species cover estimates. Total vegetative cover (per plot) was calculated as the sum of the average per-species cover estimates. We used the cover estimates to calculate the Shannon Diversity Index (hereafter, diversity) and to perform community analyses, but used the full species list, including the species added in the meander surveys, for species richness.

To test the extent to which salvage logging, deer, and competition regulate understory plant diversity post-windstorm, we modeled the effects of logging treatment (salvage logged or unlogged), deer treatment (deer or fence), competitor treatment (removed or left), and their full two-way and three-way interactions as fixed factors on species richness, diversity, and total cover in three separate linear models. Because environmental context is important for plant communities at the regional and local scale (Kramer *et al.* 2014) we also incorporated forest site effects into our models, but do not focus on these small-scale environmental gradients in this paper. Site was included as a fixed factor in all models, rather than a random blocking factor, because random effects estimated from so few sites would be a poor approximation of site-to-site variability (Bolker *et al.* 2009; Harrison *et al.* 2018). However, because of our low replication within treatments within sites, we did not approximate any site-by-experimental-treatment effects. Instead, we re-ran all analyses at each site separately and detected the same pattern, suggesting that the variation within sites likely reflects among-site and among-treatment variation (data not shown). We emphasize that although we have a low replication within sites, the opportunity to examine multiple blowdown sites in the same area was an unprecedented opportunity to address our hypotheses. In this way, we control for differences among intensities of windthrow, time since storm, season at which the storm occurred, and various other factors that are otherwise confounded with multi-windthrow comparisons.

We explored the main effects of salvage logging, deer, and competitors, their two-and-three-way interactions, and the main effect of site on the overall plant community compositions with a PERMANOVA of a multivariate community matrix using Bray-Curtis distances (Oksanen 2010). We blocked the 64 plots within site for this analysis and visualized these community differences with an NMDS ordination. Because rare species can be overweighted in nonmetric multidimensional analyses, we removed species that occurred in less than five percent of plots (McCune & Grace 2002; Slyder *et al.* 2019). Next, we explored the species-specific responses of plants to salvage logging, deer, and competitors by running three separate indicator species analyses on the community matrix. To encompass the possible important effects of the disturbances on rare species, we included the species which showed up in <5% of the plots in the indicator species analyses (Dufrene & Legendre 1997). Because of the complex and iterative nature of the indicator species analysis, we could only test the main effects of the experimental treatments, and so we interpreted our indicator species analyses results with a Bonferroni-corrected alpha to account for our non-independence of tests (Dufrene & Legendre 1997; De Cáceres *et al.* 2012).

Finally, to test whether different plant growth-forms respond differently to the experimental treatments, we re-ran all of the analyses separately for the herbaceous plants (forbs, ferns, graminoids, and herbaceous vines) and the woody plants (trees, shrubs, and woody vines). We categorized plant species into these growth-forms based on the USDA PLANTS database (USDA 2019).

We compared the overall plant species richness within the disturbance matrix, which we define as the area within the four blowdown sites including all nested experimental treatments, to the intact forest (outside of the blowdown) using species-accumulation curves. We also compared the salvaged and unsalvaged plots within the disturbance matrix to the intact forest. To explore the independent effect on total species richness of each treatment, we compared the species-accumulation curves among the eight plots that had only a single-treatment: 1. salvaged but no fence and no removal; 2. fence but unsalvaged and no removal, and 3. removal but no fence and unsalvaged.

All response variables were modeled with a normal distribution in linear mixed models, and their residual distributions were checked with qq plots. Analyses were run in R version 3.6.0 (R Core Team 2019), within the RStudio platform (RStudio Team 2016). Diversity estimates and species-accumulation curves were calculated with the vegan package (Oksanen *et al.* 2019), linear models testing the main drivers of plant diversity and abundance were constructed with the lme4 package (Bates *et al.* 2014), and indicator species analyses were run with the indicspecies package (De Cáceres 2013).

3.3 Results

We recorded a total of 217 species in the study. 207 of those species were found within the four blowdown sites, five years after the tornado. Species-accumulation curves began to flatten, indicating that we achieved sufficient sampling, especially when including the meander surveys (**Figure 1A**). Surprisingly, mean understory plant species richness, diversity, and total cover were consistent across all disturbances; there were no main effects of salvage logging, deer exclosures, or competitor removals on any diversity response we measured (**Table 1, Figure 2**). Moreover, the only significant interaction we found was between deer and removals, wherein the presence of deer mediated the effects of the competitor removals on subsequent total cover (Deer*Removal p=0.021). Total cover was highest in the plots where competitors had been removed and regenerating plants were protected from deer (136%), but lowest in plots where competitors were left and regenerating plants were protected from deer (107%).

However, when we separated the plants by growth-form, we found that herbaceous plants and woody plants responded to the disturbances differently, perhaps precluding detection of an overall pattern in the pooled analyses (above). For herbaceous plants, salvage logging had a positive impact on both species richness and diversity (**Figure 3, Table 2**). Salvage logged plots had 7 more herbaceous species than unsalvaged plots, and diversity was 13% higher in salvaged than unsalvaged plots. There were no interacting effects of the disturbances on herbaceous regeneration. For woody plants, salvaging had no measurable impact on species richness, diversity, or cover (**Table 3**). We found a significant interaction between deer and competitors for woody plants; woody cover in plots where competitors remained intact was 13% higher than woody cover in plots where competitors had been removed (**Figure 4, Table 3**). This interaction pattern is similar to the pooled analysis above, suggesting that woody plants are driving the pattern in the overall analyses.

Salvage logging, but not deer, competitors, or any interactions, shifted the community composition, even within the context of different site plant communities (Site: p=0.001**; Salvage: 0.001**; all other main effects and interactions p>0.05; **Figure 5**). Our species indicator analyses resulted in three species that were associated with logged sites: *Euthamia graminifolia*

(L.) Nutt., *Prunus pensylvanica* L., and *Solidago canadensis* L. (significant when compared to Bonferroni-adjusted p value of 0.017; **Table 4**).

Compared to the intact forest, the unsalvaged blowdown areas had 42 more species in the plant community. Salvage logging added another 37 species, for a total of 189 species, 79 more than the intact forest (**Figure 1B**). Within the disturbance matrix, just salvage logged plots (no other experimental treatments) had the highest number of total species, with 120. Removing recalcitrant understory competitors, with no other experimental treatment, yielded 112 species. Deer exclosure plots without any other experimental treatments had 97 species, which was actually slightly *fewer* species than plots that only experienced the tornado blowdown, which had 100 total species (**Figure 1C**). Averaged on the plot basis (per 36m$_2$), communities within the blowdown sites had 14 more species on average than the nearby intact forest areas (without the tornado) (**Figure 6**). Blowdown sites also had 30% higher diversity and over twice as much total cover on average per plot (**Figure 6**).

The four sites differed overall in mean species richness, diversity, and cover (**Table 1, Figure 7**). Two sites had approximately 16 more species on average than the first (southernmost) blowdown site. The third blowdown site also had 32% higher diversity and 37% more cover than the first blowdown site. The second and fourth blowdown sites had intermediate levels of all other metrics. We note that the analyses explicitly account for these site differences; therefore a response of zero (below) represents no difference from the site means, and a positive response would represent a higher value even accounting for differences in baseline site diversities. For ease of interpretability, however, we display the mean (across site) differences, rather than the site-adjusted means.

3.4 Discussion

3.4.1 The importance of differentiating plant growth-forms

Our results have two clear, yet surprising, messages. First, our results show that treating the forest understory as one homogenous community can hide ecologically important patterns. The herbaceous and woody plant growth forms responded differently to the disturbances; these patterns were not apparent when we analyzed all plant species together. Herbs, which constitute 80% of the temperate vascular plant species on average, and 72% of our dataset (Gilliam 2007; Spicer *et al.* 2019: Chapter 2), responded positively to salvage logging. Conversely, woody species were equally as diverse and abundant in salvaged versus unsalvaged plots, but their abundance depended on the interaction of deer and competitors. In plots where competitors had been removed, protecting plants from deer *increased* woody cover by 26%, indicating that deer were *suppressing* woody species cover. In plots where competitors were still present, mean woody cover was 16% *higher* when deer had access to the plots, indicating that in this case, deer were *facilitating* growth. We suspect that this interaction may be rooted in competition between herbaceous and woody species, wherein many deer-resistant herbaceous species such as ferns still have a stronghold in the absence of deer. With the exclusion of deer, less deer-resistant woody tree species seem to benefit from the vegetation removal.

The growth-form-specific responses we found provide more concrete experimental evidence of previously-recorded patterns. Royo *et al.* (2016) also found differences in tree- and non-tree responses to post-windthrow salvage logging, although they did not quantify herbaceous diversity responses. In the same time frame as our experiment (five years after salvage logging), they showed that herbaceous communities were more abundant in salvaged plots with scarification, while tree seedlings remained with decreased basal area (Royo *et al.* 2016). Our results highlight the need for more explicit consideration of non-tree growth forms in forest ecology and management, in particular concerning conservation of plant diversity. Our understanding of the mechanisms underlying the diversity and abundance of herbaceous plants lag far behind those of trees (Whigham 2004; Gilliam 2014; Barry & Schnitzer 2016; Murphy *et al.* 2016), even though herbs make up the majority of temperate vascular plant species (Gilliam 2014; Spicer *et al.* 2019: Chapter 2).

3.4.2 The combined effects of salvage logging, deer, and competitors on understory regeneration

First, all plant communities regenerating from multiple simultaneous disturbances had very high species richness, diversity, and total cover. There were almost 100 more species within the disturbance matrix than in the intact forest (**Figure 1A**). This result was unexpected given the intensity of disturbance that the plant communities underwent; each of the four disturbances have been previously shown to dramatically alter plant diversity and abundance independently. Although we did expect higher diversity with a natural disturbance, the additional disturbance, and in particular salvage logging, doubled the number of species present.

Deer browsing and recalcitrant understory plant layers (*sensu* Royo & Carson 2006) are major suppressors of plant diversity in North America (Nuttle *et al.* 2013; Carson *et al.* 2014; Pendergast IV *et al.* 2015), so we predicted a release from these pressures would have a major positive impact on forest regeneration. In particular, we expected that the combination of deer exclosures and a large light gap such as those caused by salvage logging may have interacting effects on plant diversity and abundance, as demonstrated for trees in Nuttle *et al.* 2013 and for herbaceous communities in Royo *et al.* (2010a). Contrarily, our results show that neither deer nor recalcitrant plant layers played a major role in restructuring the new plant community five years after the tornado, even in combination with a complete removal of the overstory.

3.4.3 Plant community differences

Although we did not see major differences among mean species richness or diversity among disturbance types, there were slight compositional changes in the plant community evident after five years. Across all sites, both herbaceous and woody communities differed between salvaged and unsalvaged areas (**Figure 5**). As expected from a large light gap, the three indicator species of the logged plots (*Prunus pensylvanica, Euthamia graminifolia,* and *Solidago canadensis*) are fast-growing, early-successional species that thrive in high light (USDA 2019). Although *Solidago canadensis* is long-lived, it is unlikely that these three species would halt succession and suppress diversity, as suggested as a possible consequence of salvage logging (Lindenmayer *et al.* 2017; Michalová *et al.* 2017; Thorn *et al.* 2017). In fact, the salvage logged areas may be akin to large light gaps typical of old-growth forests (Clebsch & Busing 1989), and the species characteristic of these gaps will be outcompeted by later-successional species over the next few decades, as classic successional theory would predict (Runkle 1982; Taeroe *et al.* 2019). In this way, salvage logging may in fact be maintaining diversity in the forest, by allowing early- and late-successional species to coexist in patches across the landscape (Canham *et al.* 1990). Notably, salvage logging facilitated the presence of species *in addition* to the disturbance-adapted plants that distinguish between the blowdowns and the intact forest areas (**Figure 1B**). One notable species example, although qualitative, further illustrates how salvage logging may in fact be beneficial to herbs. *Hybanthus concolor*, a forb that is not ranked for conservation status in

Pennsylvania but is ranked as vulnerable in New York (NatureServe, NHPA docs 2019), was *only* found in five salvage logged plots.

Although it is not the focus of this paper, we also would like to note how site-differences are likely an important mediator of regenerating plant communities. Our four blowdown sites were within just a few kilometers of each other, but had distinct plant community compositions and mean diversity (**Figure 5, Figure 7**). These large differences among sites is somewhat surprising, because the sites shared storm intensity, time, location, and overall overstory composition. We uniquely have replication within a disturbance event. Seed rain from the nearby intact forest, as well as seed banks, can be strong predictors of regenerating forest communities, as well as long-term successional outcomes in the context of salvage logging (Kramer *et al.* 2014; but see Curtze *et al.* 2018). The mechanisms underlying the site-mediated differences in communities are outside the purview of this study.

3.5 Conclusions

There is a growing body of evidence suggesting that post-windthrow salvage logging in North America is less detrimental for vascular plant diversity than previously expected. Here, we experimentally parse apart the combined effects of salvage logging, deer browsing, and understory competitors on post-windthrow plant regeneration. We found few differences in plant diversity or abundance among all disturbance types. We show that salvage logging may in fact help maintain herbaceous diversity in temperate forests, by promoting light-adapted species within a relatively homogenous forest matrix dominated by shade-tolerant, deer-tolerant woody plants. Thus, we suggest that increasing disturbance on the landscape is one possible remedy to the dramatic collapse in deciduous forest understories due to overabundant deer. In our case, patches of post-windthrow salvage logging in a closed-canopy forest created such a flush of plant growth that deer did not obliterate the regenerating forest. After just five years, many of the woody plants have reached heights out of the browse zone (>2m), and herbs have found refugia under dense thickets of woody saplings. Because herbs constitute the vast majority of vascular plant species in temperate forests, we also suggest that they are more frequently considered, and explicitly quantified, in forest disturbance studies that are concerned with conserving diversity.

3.6 Acknowledgements

We are grateful to Cheyenne Moore, Hannah Mellor, Zoe Merrell, and Margaux Klingensmith for their assistance in the field surveys and with data entry, and Bonnie Isaac for identifying unknown specimens. Mike Czypinski and the Powdermill Nature Reserve Staff aided in experimental setup and logistical support. Kyle Suess, Rosa Brandt, Laissa Leonis do Canto, and Austin Renek assisted with vegetation removals. Funds were provided by the Powdermill Nature Reserve, the University of Pittsburgh Mascaro Center for Sustainable Innovation, and the R. K. Mellon Foundation. Comments by Yusan Yang improved the writing of the manuscript.

3.7 Authorship statement

WPC, AAR, and JWW designed and set up the experiment. MES performed the vegetation removals, collected and analyzed the data, and wrote the first draft. All authors contributed to the writing and editing of the manuscript.

3.8 Figures and tables

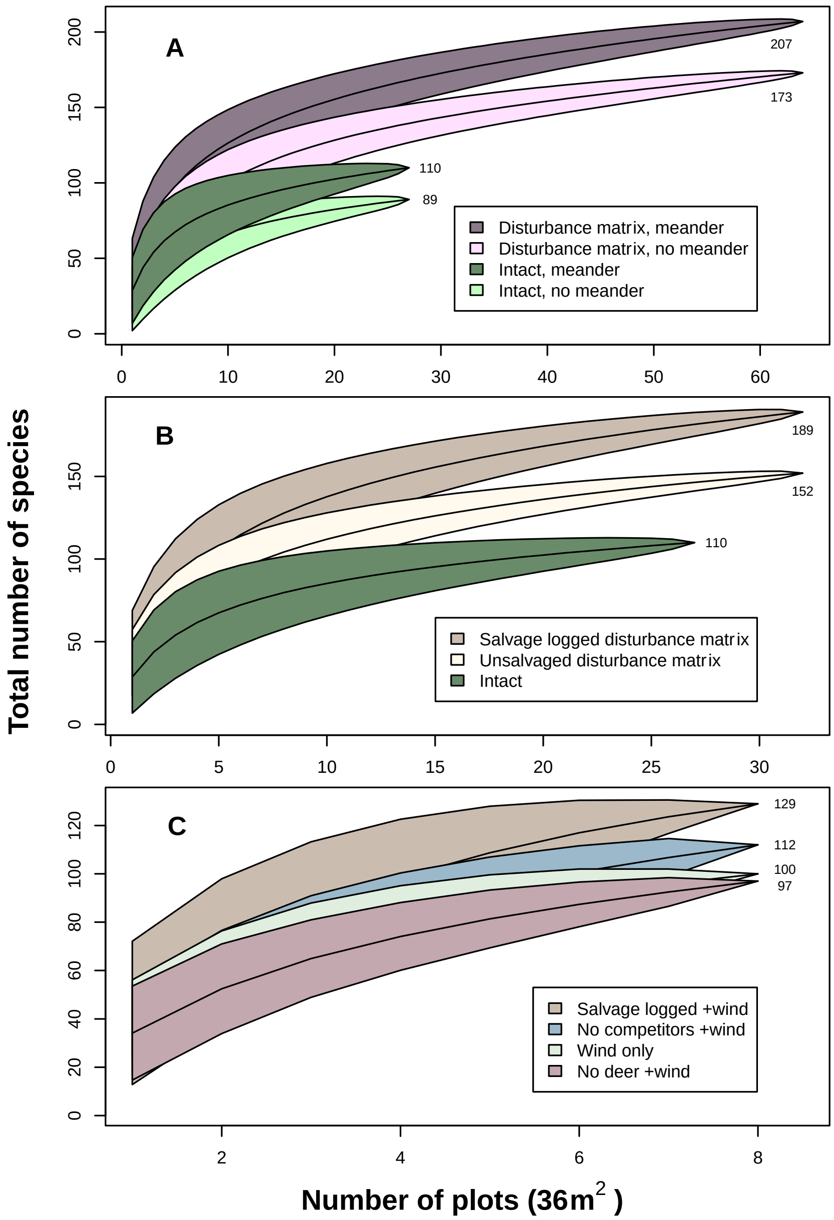


Figure 3-1. Species-accumulation curves.

A. Disturbance matrix plots versus reference intact forest plots (outside of the tornado path). Lighter and darker colors represent surveys within the corner 1x1m$_2$ plots and the meander surveys within the whole 36m$_2$ center areas, respectively. B. Disturbance matrix with and without salvage logging, versus reference plots. C. Within the disturbance matrix, independent species-accumulation curves of salvaged plots, competitor removal plots, and deer exclusion plots, in comparison to "control" plots, with only natural (wind) disturbance (no logging, ambient deer browsing, and understory competitors present).

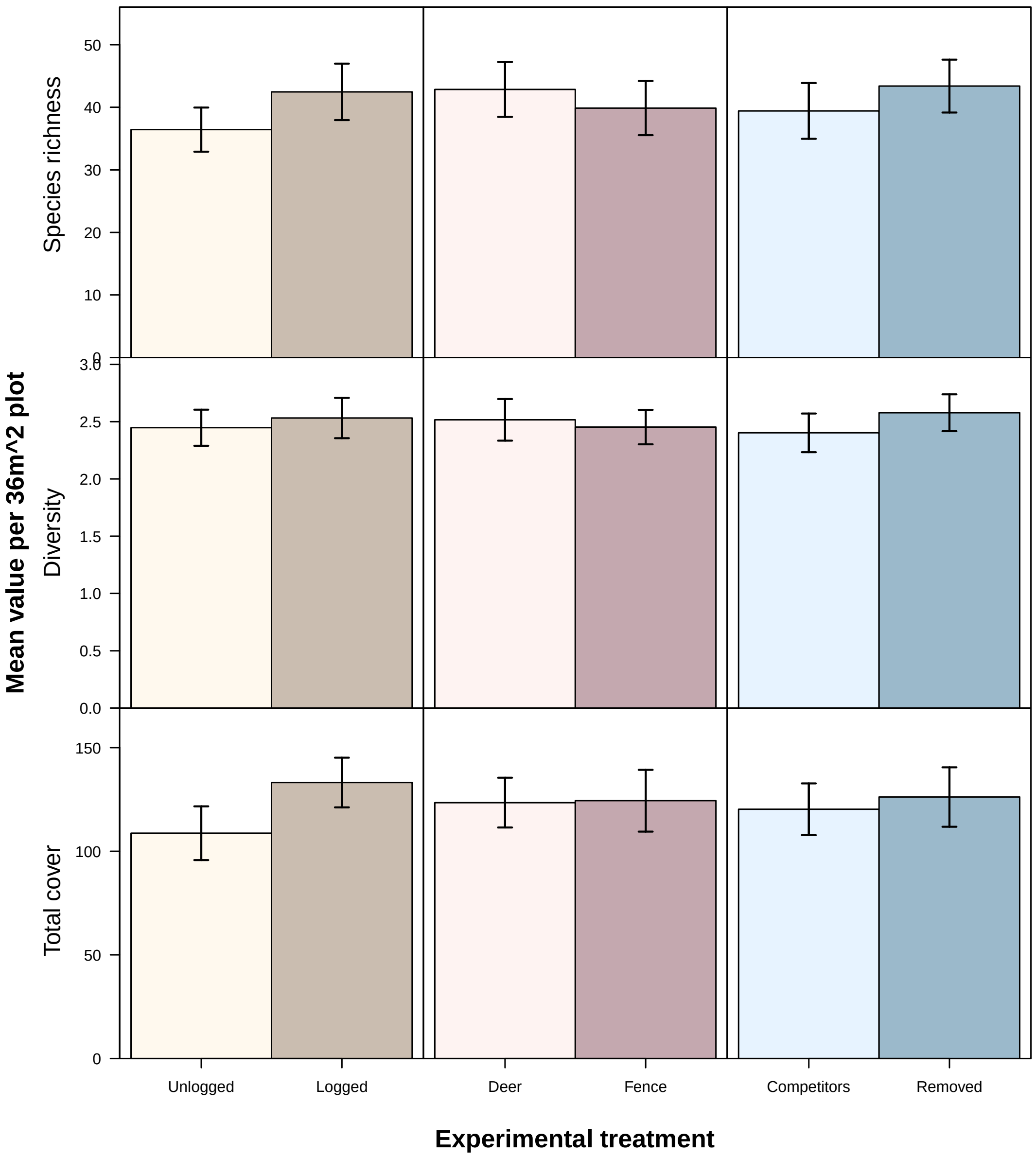


Figure 3-2. Overall plant responses to salvaging, deer, and competitors.

Accounting for site differences (Figure 7), neither salvage logging, deer exclosures, nor competitor removals changed the mean species richness, diversity, or total cover of the plant communities five years post-tornado, when looking at all plant species together.

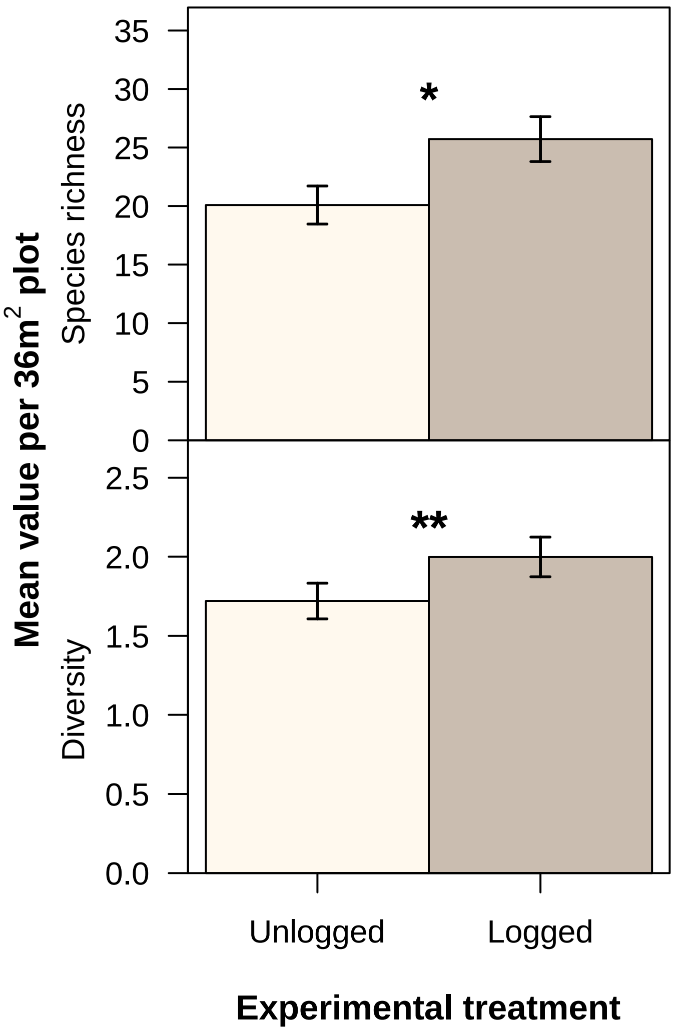


Figure 3-3. Herbaceous plant responses to salvaging.

Salvaged plots had a mean of seven more herbaceous species and 13% higher herbaceous diversity than unsalvaged plots.

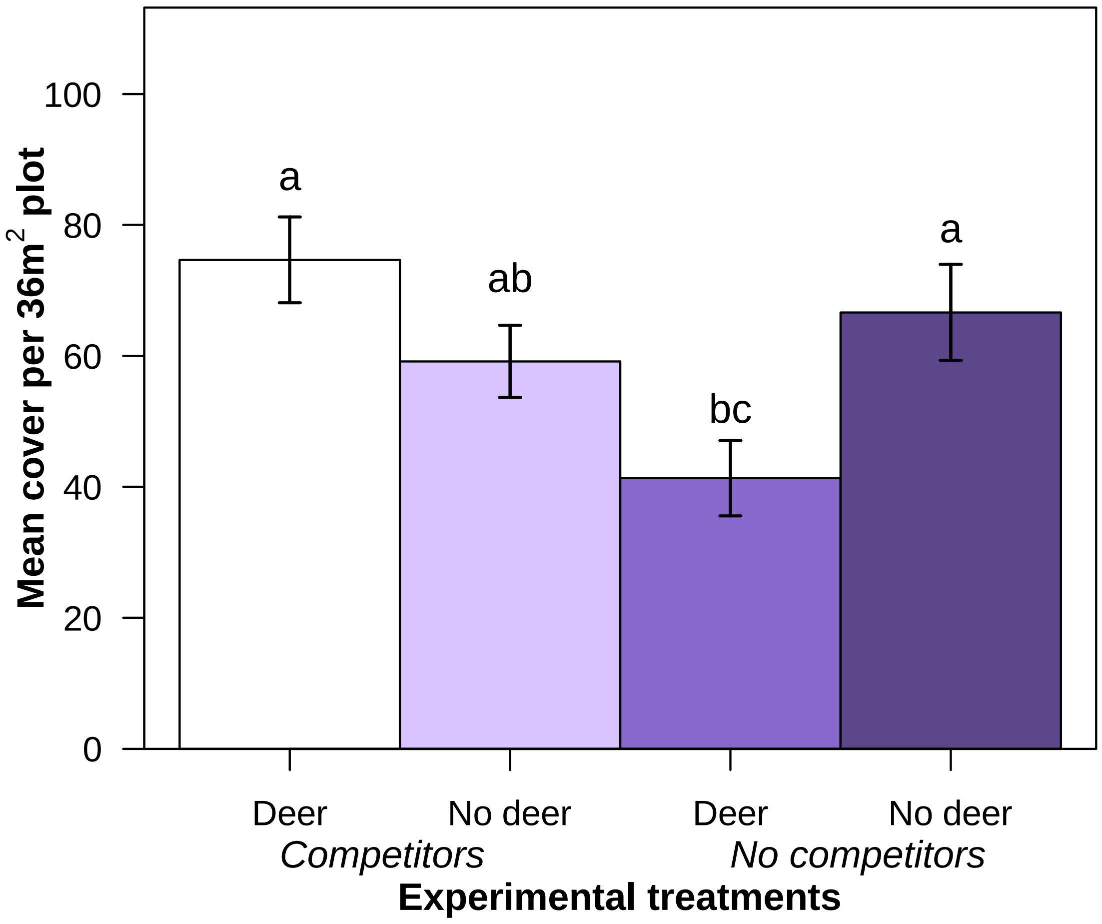


Figure 3-4. Woody plant responses to deer and competitors.

Deer and competitors had interacting effects on woody abundance, as measured in mean total cover.

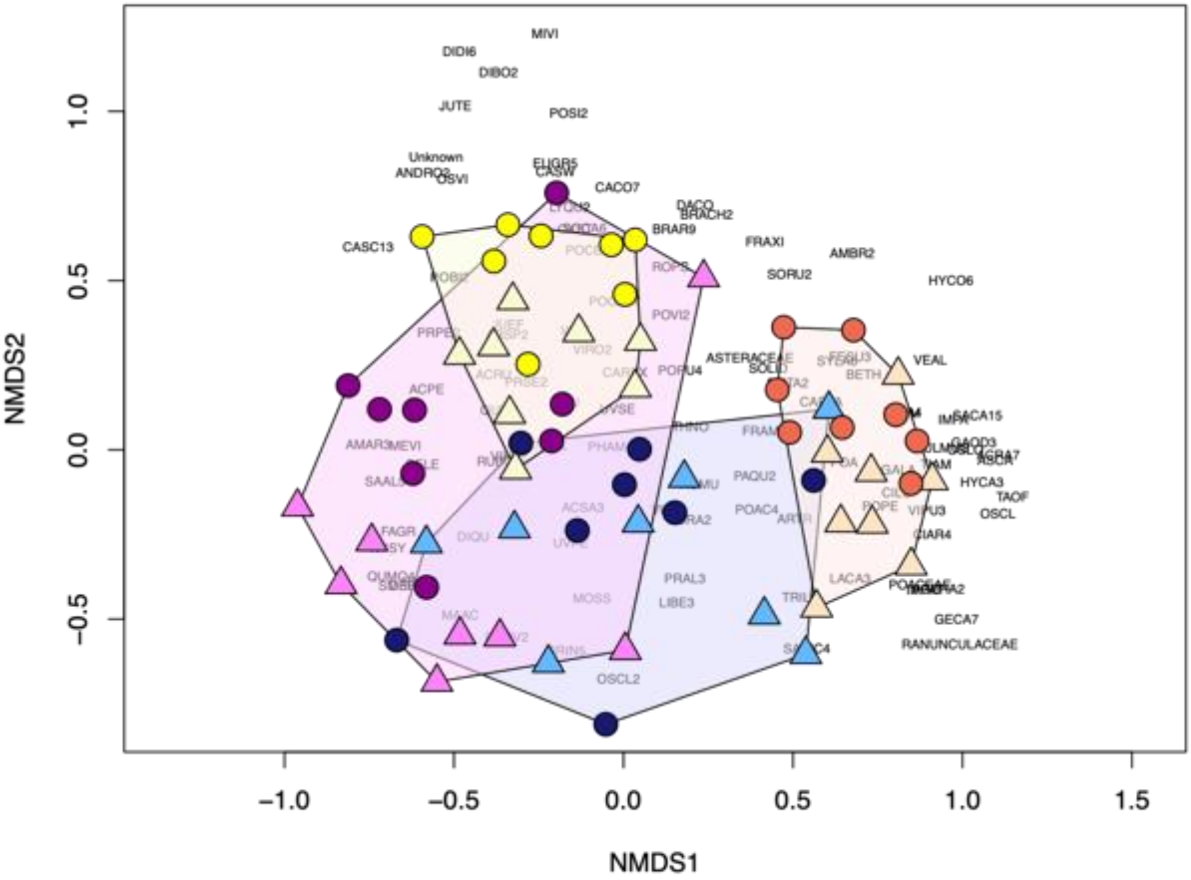


Figure 3-5. Plant community composition.

Plant communities differed among sites (colors and polygons) and between salvage logged and unlogged areas (darker circles versus lighter triangles; p=0.001). Colors for sites correspond to Figure 7.

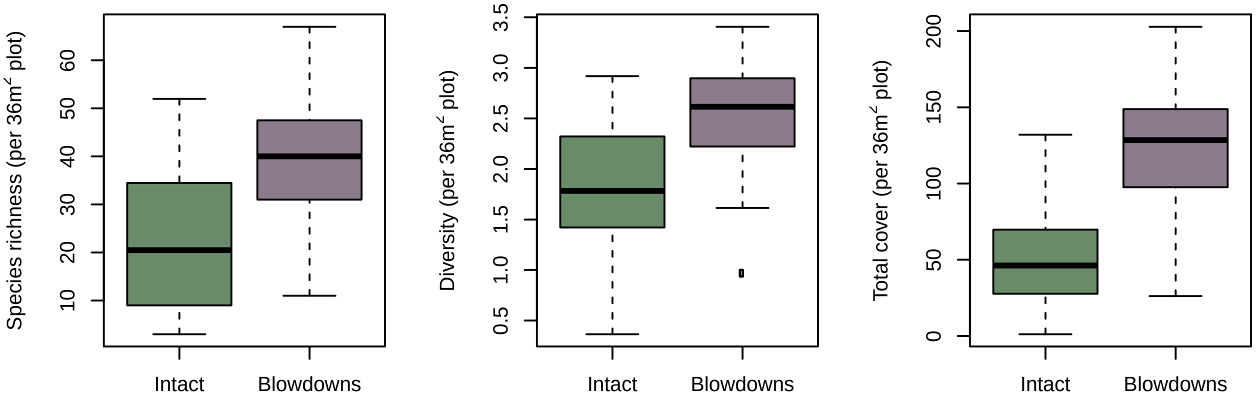


Figure 3-6. Intact forest versus disturbance matrix.

Comparison of species richness, diversity, and total cover in the 36m2 plots within the blowdown areas versus the intact forest plots (outside of the tornado plots). Data include meander surveys.

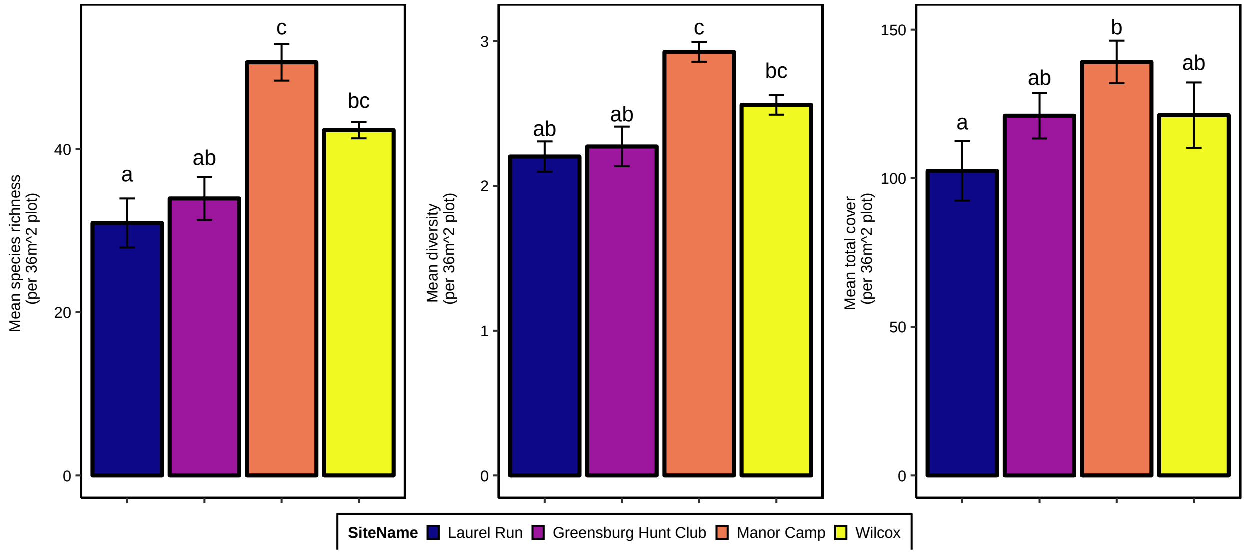


Figure 3-7. Site diversity differences.

Comparison of species richness, diversity, and total cover in the 36m2 plots among the four blowdown sites. From left to right, sites are listed in the order which the tornado moved, as well as in the order which we salvage logged the plots. Letters correspond to post hoc Tukey differences among sites.

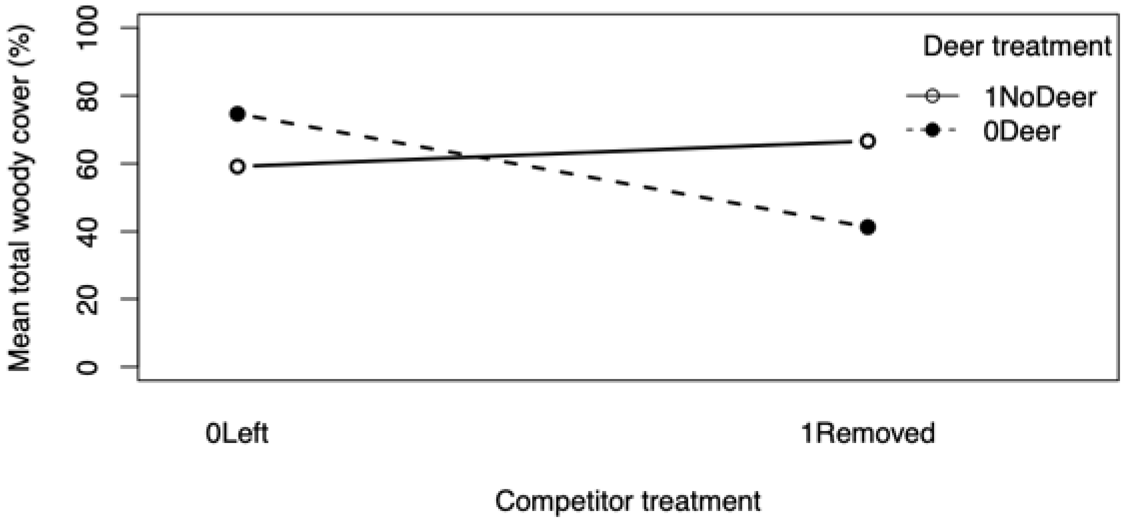


Figure 3-8. Interaction plot for woody plant responses.

Deer and competitors had interacting effects on woody abundance, as measured in mean total cover.

Table 3-1. Results of linear models: All species combined.

Results of linear models analyzing the combined effects of salvage logging, deer, and competitors on post-windthrow plant regeneration, as measured by mean species richness, Shannon diversity, and overall cover (%). Diversity and cover are reported as plot-level means, based on four 1x1m^2 surveys. Species richness values are reported as the cumulative list of species in the four 1x1m^2 quadrats and the meander survey of the whole 36m$_2$ plot.

Response variable	*Effect*		*Estimate*	*Standard error*	*t-value*	*p*
Species richness	Sites	MC-GHC	16.69	3.19	5.23	<0.0001***
		WX-GHC	8.38	3.19	2.63	0.011*
	Logging		5.75	4.51	1.28	0.21
	Deer		-3.13	4.51	-0.69	0.49
	Removal		1.88	4.51	0.42	0.68
	Logging*Deer		-1.00	6.38	-0.16	0.88
	Logging*Removal		2.25	6.38	0.35	0.73
	Deer*Removal		2.25	6.38	0.35	0.73
	Logging*Deer*Removal		-1.38	9.02	-0.15	0.88
Shannon diversity index	Sites	MC-GHC	0.65	0.14	4.58	<0.0001***
		WX-GHC	0.29	0.14	2.02	0.049*
	Logging		0.06	0.20	0.29	0.78
	Deer		-0.03	0.20	-0.14	0.89
	Removal		0.20	0.20	1.01	0.32
	Logging*Deer		0.02	0.28	0.07	0.94
	Logging*Removal		0.04	0.28	0.13	0.90
	Deer*Removal		-0.09	0.28	-0.31	0.76
	Logging*Deer*Removal		-0.01	0.40	-0.02	0.98
Total cover (%)	Sites		-	-	-	NS
	Logging		20.22	16.75	1.21	0.14
	Deer		-24.88	16.75	-1.49	0.14
	Removal		-25.30	16.75	-1.51	0.12
	Logging*Deer		3.54	23.69	0.15	0.89
	Logging*Removal		14.16	23.69	0.60	0.55
	Deer*Removal		57.16	23.69	2.41	0.02*
	Logging*Deer*Removal		-18.31	33.51	-0.55	0.59

Table 3-2. Results of linear models: Herbaceous species.

Results of linear models analyzing the combined effects of salvage logging, deer, and competitors on post-windthrow herbaceous plant regeneration.

Response variable	*Effect*		*Estimate*	*Standard error*	*t-value*	*p*
Species richness	Sites	MC-GHC	15.44	2.54	-1.28	<0.0001***
	Logging		7.25	3.60	2.12	0.049*
	Deer		-1.50	3.60	-0.42	0.68
	Removal		3.63	3.60	1.01	0.32
	Logging*Deer		-2.50	5.08	-0.49	0.63
	Logging*Removal		-0.88	5.08	-0.17	0.86
	Deer*Removal		0.63	5.08	0.12	0.90
	Logging*Deer*Removal		0.25	7.19	0.04	0.97
Shannon diversity index	Sites	MC-GHC	0.85	0.18	4.62	<0.0001***
	Logging		0.71	0.26	2.70	0.009**
	Deer		0.17	0.26	0.65	0.52
	Removal		0.52	0.26	2.00	0.05
	Logging*Deer		-0.67	0.37	-1.81	0.08
	Logging*Removal		-0.67	0.37	-1.81	0.08
	Deer*Removal		-0.50	0.37	-1.36	0.18
	Logging*Deer*Removal		0.97	0.52	1.86	0.07
Total cover (%)	Sites		-	-	-	NS
	Logging		3.82	15.47	0.25	0.81
	Deer		-3.53	15.47	-0.23	0.82
	Removal		9.04	15.47	0.58	0.56
	Logging*Deer		-14.20	21.88	-0.65	0.52
	Logging*Removal		12.49	21.88	0.57	0.57
	Deer*Removal		16.54	21.88	0.76	0.45
	Logging*Deer*Removal		-12.64	30.95	-0.41	0.68

Table 3-3. Results of linear models: Woody species.

Results of linear models analyzing the combined effects of salvage logging, deer, and competitors on post-windthrow woody plant regeneration.

Response variable	*Effect*		*Estimate*	*Standard error*	*t-value*	*p*
Species richness	Sites	WX-GHC	4.88	1.25	3.89	0.0003***
	Logging		-1.88	1.78	-1.06	0.29
	Deer		-1.88	1.78	-1.06	0.29
	Removal		-2.13	1.78	-1.20	0.24
	Logging*Deer		2.00	2.50	0.80	0.43
	Logging*Removal		3.63	2.50	1.45	0.15
	Deer*Removal		2.13	2.50	0.85	0.40
	Logging*Deer*Removal		-2.13	3.54	-0.60	0.55
Shannon diversity index	Sites		-	-	-	NS
	Logging		-0.24	0.19	-1.27	0.21
	Deer		-0.15	0.19	-0.82	0.41
	Removal		-0.03	0.19	-0.15	0.88
	Logging*Deer		0.38	0.26	1.43	0.16
	Logging*Removal		0.31	0.26	1.17	0.25
	Deer*Removal		0.23	0.26	0.87	0.39
	Logging*Deer*Removal		-0.57	0.37	-1.53	0.13
Total cover (%)	Sites		-	-	-	NS
	Logging		16.05	11.23	1.43	0.16
	Deer		-21.51	11.23	-1.92	0.06
	Removal		-34.37	11.23	-3.06	0.35
	Logging*Deer		12.00	15.88	0.76	0.45
	Logging*Removal		2.05	15.88	0.13	0.90
	Deer*Removal		40.81	15.88	2.57	0.013*
	Logging*Deer*Removal		0.04	22.46	0.00	1.00

Table 3-4. Results of indicator species analyses.

Results of the indicator species analyses run for all species that appeared in the 1x1m^2 cover surveys (162), not including the meander surveys. Species are bolded which are significantly associated with certain experimental treatments, as interpreted by a Bonferroni-adjusted α=0.017 for three non-independent tests (effects of logging, deer presence, and competitor presence).

Experimental grouping	*Indicator species*	*p*
Unlogged	None	NA
Logged	*Carex swanii*	0.029
	Euthamia graminifolia	**0.006**
	Solidago spp.	0.049
	Prunus pensylvanica	**0.016**
	Lysimachia quadrifolia	0.021
	Solidago canadensis	**0.016**
Deer (ambient)	*Polystichum acrostichoides*	0.038
Fenced	None	NA
Left (competitors present)	*Carya sp.*	0.041
Competitors removed	*Viola rotundifolia*	0.024

3.9 Bibliography

Barnosky, A.D., Hadly, E. a, Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., *et al.* (2012). Approaching a state shift in Earth ' s biosphere. *Nature*, 486, 52–58.

Barry, K.E. & Schnitzer, S.A. (2016). Maintenance of Plant Species Diversity in Forest Ecosystems. In: *Plant Biodiversity: Monitoring, Assessment, and Conservation* (eds. Gill, S.S. & Ansari, A.). CAB International.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R Packag. version*, 1, 1–23.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., *et al.* (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127–135.

Bottero, A., Garbarino, M., Long, J.N. & Motta, R. (2013). The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps. *For. Ecol. Manage.*, 292, 19–28.

Bowd, E.J., Lindenmayer, D.B., Banks, S.C. & Blair, D.P. (2018). Logging and fire regimes alter plant communities. *Ecol. Appl.*, 28, 826–841.

De Cáceres, M. (2013). How to use the indicspecies package (ver. 1.7. 1). *Cent. Tecnològic For. Catalunya, Catalonia*.

De Cáceres, M., Legendre, P., Wiser, S.K. & Brotons, L. (2012). Using species combinations in indicator value analyses. *Methods Ecol. Evol.*, 3, 973–982.

Cahall, R.E. & Hayes, J.P. (2009). Influences of postfire salvage logging on forest birds in the Eastern Cascades, Oregon, USA. *For. Ecol. Manage.*, 257, 1119–1128.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.*, 20, 620–631.

Carson, W.P., Royo, A.A. & Peterson, C.J. (2014). A Pox on our Land: A Case Study of Chronic Deer Overbrowsing throughout the Allegheny National Forest Region of Pennsylvania. In: *The Herbaceous Layer in Forests of Eastern North America* (ed. Gilliam, F.S.). Oxford University Press, New York, NY, pp. 400–411.

Chazdon, R.L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.*, 6, 51–71.

Clebsch, E.E.C. & Busing, R.T. (1989). Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology*, 70, 728–735.

Connell, J.H. (1978). Diversity in Tropical Rain Forests and Coral Reefs. *Science (80-.).*, 199, 1302–1310.

Cooper-Ellis, S., Foster, D.R., Carlton, G. & Lezberg, A. (1999). Forest Response to Catastrophic Wind : Results from an Experimental Hurricane. *Ecology*, 80, 2683–2696.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C. & Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Syst.*, 35, 113–147.

Curtze, A.C., Carlo, T.A. & Wenzel, J.W. (2018). The Effects of a Tornado Disturbance and a Salvaged Timber Extraction on the Seed-Rain and Recruitment Community of an Eastern Temperate Deciduous Forest. *Northeast Nat.*, 25, 627–645.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., *et al.* (2001). Climate Change and Forest Disturbances. *Bioscience*, 51, 723–734.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.E. (2006). Post-wildfire logging hinders regeneration and increases fire risk. *Science (80-.).*, 311, 352.

Dufrene, M. & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.*, 67, 345–366.

Easterling, D.R. (2000). Climate Extremes: Observations, Modeling, and Impacts. *Science (80-.).*, 289, 2068–2074.

Fischer, A., Marshall, P. & Camp, A. (2013). Disturbances in deciduous temperate forest ecosystems of the northern hemisphere : their effects on both recent and future forest development. *Biodivers. Conserv.*, 22, 1863–1893.

Frerker, K., Sabo, A. & Waller, D. (2014). Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLoS One*, 9, 1–17.

Gilliam, F.S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems, 57, 845–858.

Gilliam, F.S. (2014). The Herbaceous Layer — The Forest between the Trees. In: *The herbaceous layer in forests of eastern North America* (ed. Gilliam, F.S.). Oxford University Press, New York, NY, pp. 1–10.

Habeck, C.W. & Schultz, A.K. (2015). Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. *AoB Plants*, 7, plv119.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., *et al.* (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 2018, 1–32.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., *et al.* (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.*, 14, 369–378.

Kramer, K., Brang, P., Bachofen, H., Bugmann, H. & Wohlgemuth, T. (2014). Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. *For. Ecol. Manage.*, 331, 116–128.

Krueger, L.M. & Peterson, C.J. (2006). Effects of White-tailed Deer on Tsuga canadensis Regeneration : Evidence of Microsites as Refugia from Browsing. *Am. Midl. Nat.*, 156, 353–362.

Kurulok, S.E. & Macdonald, S.E. (2007). Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. *Can. J. For. Res.*, 37, 2637–2651.

Laurance, W.F. & Curran, T.J. (2008). Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecol.*, 33, 399–408.

Leverkus, A.B., Lindenmayer, D.B., Thorn, S. & Gustafsson, L. (2018). Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. *Glob. Ecol. Biogeogr.*, 1–15.

Lindenmayer, D., Thorn, S. & Banks, S. (2017). Please do not disturb ecosystems further. *Nat. Ecol. Evol.*, 1.

McCune, B. & Grace, J.B. (2002). *Analysis of ecological communities*. 2nd edn. MjM Software Design, Gleneden Beach, Oregon.

Michalová, Z., Morrissey, R.C., Wohlgemuth, T., Bače, R., Fleischer, P. & Svoboda, M. (2017). Salvage-logging afterwindstorm leads to structural and functional homogenization of understory layer and delayed spruce tree recovery in Tatra Mts., Slovakia. *Forests*, 8.

Molino, J. & Sabatier, D. (2001). Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. *Science (80-.).*, 294, 1702–1704.

Murphy, S.J., Audino, L.D., Whitacre, J., Eck, J.L., Wenzel, J.W., Queensborough, S.A., *et al.* (2015). Species associations structured by environment and land-use history promote beta-diversity in a temperate forest. *Ecology*, 96, 705–715.

Murphy, S.J., Salpeter, K. & Comita, L.S. (2016). Higher β-diversity observed for herbs ovaer woody plants is driven by stronger habitat filtering in a tropical understory. *Ecology*, 97, 2074–2084.

Nuttle, T., Royo, A.A., Adams, M.B. & Carson, W.P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecol. Monogr.*, 83, 3–17.

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., *et al.* (2019). Package ‘ vegan .’

Oksanen, J. (2010). Vegan: ecological diversity, 1, 1–14.

Pendergast IV, T.H., Hanlon, S.M., Long, Z.T., Royo, A.A. & Carson, W.P. (2015). The legacy of deer overabundance: long-term delays in herbaceous understory recover. *Can. J. For. Res.*, 1–9.

Peterson, C.J. & Leach, A.D. (2008a). Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecol. Appl.*, 18, 407–420.

Peterson, C.J. & Leach, A.D. (2008b). Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry*, 81, 361–376.

Platt, W. & Connell, J. (2003). Natural disturbances and directional replacement of species. *Ecol. Monogr.*, 73, 507–522.

R Core Development Team, 3.6.0. 2019. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RStudio Team, 1.0.153. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rooney, T.P. (2001). Deer impacts on forest ecosystems: a North American perspective. *Forestry*, 74, 201–208.

Rooney, T.P. & Waller, D.M. (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.*, 181, 165–176.

Royo, A. A. & Carson, W.P. (2006). On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.*

Royo, A. a, Collins, R., Adams, M.B., Kirschbaum, C. & Carson, W.P. (2010a). Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology*, 91, 93–105.

Royo, A.A. & Carson, W.P. (2008). Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests : habitat-mediated predation versus competition. *Can. J. For. Res.*, 38, 1634–1645.

Royo, A.A., Peterson, C.J., Stanovick, J.S. & Carson, W.P. (2016). Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology*, 97, 1566–1582.

Royo, A.A., Stout, S.L., DeCalesta, D.S. & Pierson, T.G. (2010b). Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? *Biol. Conserv.*, 143, 2425–2434.

Rozman, A., Diaci, J., Krese, A., Fidej, G. & Rozenbergar, D. (2015). Forest regeneration dynamics following bark beetle outbreak in Norway spruce stands: Influence of meso-relief, forest edge distance and deer browsing. *For. Ecol. Manage.*, 353, 196–207.

Runkle, J.R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, 63, 1533–1546.

Russell, R.E., Saab, V.A., Dudley, J.G. & Rotella, J.J. (2006). Snag longevity in relation to wildfire and postfire salvage logging. *For. Ecol. Manage.*, 232, 179–187.

Santoro, J.A. & D'Amato, A.W. (2019). Structural, compositional, and functional responses to tornado and salvage logging disturbance in southern New England hemlock-hardwood forests. *For. Ecol. Manage.*, 444, 138–150.

Sass, E.M., D'Amato, A.W. & Foster, D.R. (2018). Lasting legacies of historical clearcutting, wind, and salvage logging on old-growth Tsuga canadensis-Pinus strobus forests. *For. Ecol. Manage.*, 419–420, 31–41.

Schnitzer, S.A. & Carson, W.P. (2001). Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest. *Ecology*, 82, 913–919.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., *et al.* (2017). Forest disturbances under climate change Europe PMC Funders Group. *Nat Clim Chang.*, 7, 395–402.

Sheil, D. & Burslem, D.F.R.P. (2003). Disturbing hypotheses in tropical forests. *Trends Ecol. Evol.*, 18, 18–26.

Slyder, J.B., Wenzel, J.W., Royo, A.A., Spicer, M.E. & Carson, W.P. (2019). Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. *New For.*

Spicer, M.E., Mellor, H. & Carson, W.P. (2019). Seeing beyond the trees: a comparison of tropical and temperate plant growth-forms and their vertical distribution. *Ecology*, in press.

Spicer, M.E., Suess, K.F., Wenzel, J.W. & Carson, W.P. (2018). Does salvage logging erase a key physical legacy of a tornado blowdown? A case study of tree tip-up mounds. *Can. J. For. Res.*, 48, 976–982.

Taeroe, A., de Koning, J.H.C., Löf, M., Tolvanen, A., Heiðarsson, L. & Raulund-Rasmussen, K. (2019). Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative review. *For. Ecol. Manage.*, 446, 304–316.

Tanentzap, A.J., Kirby, K.J. & Goldberg, E. (2012). Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. *For. Ecol. Manage.*, 264, 159–166.

Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., *et al.* (2017). Impacts of salvage logging on biodiversity: A meta-analysis. *J. Appl. Ecol.*, 1–11.

Thorn, S., Bassler, C., Gottschalk, T., Hothorn, T., Bussler, H. & Raffa, K. (2014). New Insights into the Consequences of Post-Windthrow Salvage Logging Revealed by Functional Structure of Saproxylic Beetles Assemblages. *PLoS One*, 9.

Tilman, D. (1990). Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession. *Oikos*, 58, 3–15.

USDA, N. (2019). *The PLANTS Database*. *Natl. Plant Data Team*. Available at: http://plants.usda.gov. Last accessed 18 September 2019.

Utech. (1999). *Checklist of the Vascular Plants of Powdermill Nature Reserve, Westmoreland County, Pennsylvania*.

Waldron, K., Ruel, J.-C. & Gauthier, S. (2013). Forest structural attributes after windthrow and consequences of salvage logging. *For. Ecol. Manage.*, 289, 28–37.

Waldron, K., Ruel, J.-C., Gauthier, S., DeGrandpre, L. & Peterson, C.J. (2014). Effects of post-windthrow salvage logging on microsites, plant composition and regeneration. *Appl. Veg. Sci.*, 17, 323–337.

Wavrek, M., Heberling, J.M., Fei, S. & Kalisz, S. (2017). Herbaceous invaders in temperate forests : a systematic review of their ecology and proposed mechanisms of invasion. *Biol. Invasions*, 19, 3079–3097.

Wermelinger, B., Moretti, M., Duelli, P., Lachat, T., Pezzatti, G.B. & Obrist, M.K. (2017). Impact of windthrow and salvage-logging on taxonomic and functional diversity of forest arthropods. *For. Ecol. Manage.*, 391, 9–18.

Werner, S.A.B., Müller, J., Heurich, M. & Thorn, S. (2015). Natural regeneration determines wintering bird presence in wind-damaged coniferous forest stands independent of postdisturbance logging. *Can. J. For. Res.*, 45, 1232–1237.

Whigham, D.E. (2004). Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol. Evol. Syst.*, 35, 583–621.

Zscheischler, J., Westra, S., Van Den Hurk, B.J.J.M., Seneviratne, S.I., Ward, P.J., Pitman, A., *et al.* (2018). Future climate risk from compound events. *Nat. Clim. Chang.*, 8, 469–477.

4.0 DOES SALVAGE LOGGING ERASE A KEY PHYSICAL LEGACY OF A TORNADO BLOWDOWN: A CASE STUDY OF TREE TIP-UP MOUNDS

Spicer, M. E., K. F. Suess, J. W. Wenzel, and W. P. Carson. 2018. Does salvage logging erase a key physical legacy of a tornado blowdown? A case study of tree tip-up mounds. *Canadian Journal of Forest Research* 48:976–982.

4.1 Introduction

Stand-replacing wind disturbances are powerful drivers of forest dynamics because they create large and highly heterogeneous patches of early successional habitat embedded within a matrix of older forest (Mitchell 2013). These blowdowns are characterized by tree tip-up mounds, which are one of the signature physical legacies left by wind disturbances (Lyford and MacLean 1966, Beatty 1984, Peterson et al. 1990, Schaetzl and Follmer 1990, Vodde et al. 2011). The mounds and corresponding pits often increase plant diversity because they create bare soil patches and unique microsites (Schaetzl et al. 1989, 1990, Simon et al. 2011). The pits and mounds also create steep gradients for an array of abiotic factors including temperature, humidity, snowfall, and soil resources (Beatty 1984, Peterson et al. 1990, Simon et al. 2011). In addition, tall elevated mounds can provide refugia from browsers, and avian frugivores often perch on these mounds thereby dispersing seeds (Thompson 1980, Long et al. 1998). Consequently, the vegetation on mounds often differs from adjacent off-mound reference sites even decades after the disturbance, and the soil characteristics may not return to a pre-disturbance state for centuries (Peterson et al. 1990, Carlton and Bazzaz 1998, Ulanova 2000, Lang et al. 2009, Darabi et al. 2014). What remains unclear is whether novel plant communities will develop rapidly on mounds a few years after a blowdown.

Salvage logging commonly occurs after windthrows and has the potential to eliminate post-disturbance ecological legacies (McIver and Starr 2000, Peterson and Leach 2008, Vodde et al. 2011, Royo et al. 2016, Lindenmayer et al. 2017). Harvesting fallen trees decreases dead trees available for habitat use, scarifies the soil, and homogenizes the landscape (Lindenmayer et al. 2004, Peterson and Leach 2008, Brewer et al. 2012, Waldron et al. 2014, Thorn et al. 2017). In particular, salvage logging can reduce the abundance of intact or vertical tip-up mounds because cutting the bole often causes the root mass and stump to fall back down into the pit (Waldron et al. 2013). Thus, salvaging has the potential to partially erase an important physical legacy left by a stand-replacement disturbance. This process may in turn reduce diversity, particularly if unique plant communities form on tip-up mounds shortly after a blowdown.

Here we test three hypotheses. 1. Novel plant communities with contrasting species composition, richness, and diversity will form on tip-up mounds rapidly after a large stand replacement disturbance. 2. Salvaging will substantially reduce the number of vertical tip-up mounds by causing the root mass to tip back down into the pit after logging and alter the physical characteristics of mounds. 3. Salvaging will create a novel habitat because “tipped-down” tip-up mounds remain elevated relative to reference areas but occur at a shallower angle (relative to the ground) versus near-vertical mounds that did not tip back down (**Figure 1**). To address these hypotheses, we salvaged one half of each of four large windthrows and quantified plant community composition and diversity on 48 tip-up mounds in both salvaged and unsalvaged areas. We also quantified how many once vertical tip-up mounds tipped back down into the pit (hereafter referred to as “inclined mounds”) after the bole was cut and compared the vegetation on these inclined mounds to vertical mounds, and to adjacent randomly selected reference sites off the mound (**Figure 1**).

4.2 Materials and methods

4.2.1 Study site

We conducted this study at four different blowdowns at the Powdermill Nature Reserve in Westmoreland County, PA (40.16◦ N, -79.27 ◦ W). Annual precipitation at Powdermill is approximately 1100 mm and temperatures range from -20 to 33° C (Murphy et al. 2015). Powdermill is 900 hectares of mostly mature mixed mesophytic forest and lies on the Allegheny Plateau with slopes ranging from 8-35% (Murphy et al. 2015, NRCS 2017). The whole forest was likely cut during the 1800s and some sections of the current reserve were actively used for agriculture and mining (Murphy et al. 2015). However, portions of the study area forest have been growing back for more than 100 years and have not experienced anthropogenic disturbance since the establishment of the reserve in 1956. The canopy is dominated by red and sugar maple (*Acer rubrum, Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), and red and white oak (*Quercus rubra, Quercus alba*; Spicer unpublished data). The soils are very stony Rayne channery loams and extremely stony Laidig gravelly loams (NRCS 2017). In June of 2012, an F1 tornado with winds reaching 105 mph created four fairly large blowdowns (5.82, 4.51, 3.84, and 3.47 ha each) (NOAA 2012). We randomly selected one half of each to be salvaged while the other half served as an unsalvaged control. Salvaging occurred during the winter of 2013-2014 and used standard techniques widely applied throughout the region; this approach removed nearly all downed and standing trees at each site (~100% standing stems).

4.2.2 Quantifying mound density, dimensions, orientation, and vegetation

We surveyed the entire area of all four blowdowns via a systematic meander and marked the location of each tip-up mound with a handheld GPS (Garmin Montana 680t). To quantify mound dimensions, we first measured the height from the ground to the top of the mound and second from the bottom of the pit to the top of the mound (Ht1 and Ht2, respectively, **Figure 1A**). We also measured the mound width and the thickness of the uprooted soil mass with a tape measure and meterstick (**Figure 1A**, after Peterson et al. 1990). We determined whether each tip-up mound had "tipped down" back into the pit it originated from, forming an inclined mound, or whether the mound was near-vertical by observing the angle of the tree stump with respect to the ground (**Figure 1B**). Tip-up mounds were considered vertical if: 1) the root plate was near perpendicular (vertical) with respect to the ground, and therefore the angle of the tree trunk or stump was near parallel (horizontal) to the ground, and 2) there was a clear separation between the base of the tip-up mound root plate and the pit.

We quantified the vegetation on 48 (out of 249) randomly selected tip-up mounds, twelve in each of the four sites, six of which were in the salvaged area and six of which were in the unsalvaged area. From June to July of 2015, three years after the tornado, we visually estimated plant cover on each tip-up mound for all species in 1m^2 plots located on the top center of each selected tip-up mound (Royo et al. 2010, Nuttle et al. 2014). For comparison, we also censused a randomly selected 1m^2 reference plot (off-mound) within 2m of each tip-up mound.

4.2.3 Data analysis: Physical tip-up mound characteristics and "tipping down"

We used paired t-tests to determine whether the average density of tip-up mounds per hectare was different in salvaged versus unsalvaged sites. We ran the analyses with all tip-up mounds combined (vertical and inclined) as well as with the inclined mounds removed (to compare to studies in which inclined mounds are excluded; e.g., Waldron et al. 2013). To quantify the extent to which salvage logging created inclined mounds, we ran a GLMM with a binomial distribution testing the effects of salvaging on the position of the tip-up mounds (binary: vertical where the root plate is at or close to vertical relative to the soil surface, or inclined where the stump is at a shallow angle with respect to soil surface; **Figure 1**). Site differences were accounted for with random nested effects in the model.

To test whether salvage logging creates differences in tip-up mound dimensions and therefore potentially drive plant community differences (Lang et al. 2009, Waldron et al. 2014), we compared the measurements of 191 intact vertical tip-up mounds in salvaged and unsalvaged areas with a linear mixed model. We excluded inclined mounds from this analysis to avoid confounding salvaging effects and mound orientation effects. Site and salvage treatment half were included as nested random effects in the model. Heights, width, and thickness measurements were square-root transformed to fit Gaussian model assumptions of the linear model. We adjusted the p-values for multiple tests (Bonferroni $\alpha=0.05/4=0.0125$). Finally, we quantified the physical differences between inclined and vertical mounds by comparing the height measurements of all mounds in the salvaged areas. We excluded unsalvaged mounds in this analysis to avoid confounding salvaging and orientation effects.

4.2.4 Data analysis: Plant community metrics

We compared total plant cover, species richness, and Shannon Diversity Index using percent cover (Magurran 1988, Oksanen et al. 2013) between tip-up mounds and nearby reference plots using generalized linear mixed models constructed with the lme4 package in R version 3.4.1 (Bates et al. 2014, R Core Development Team 2017). Our model included the main (fixed) effects of salvaging (salvaged or unsalvaged), microsite (tip-up mound vs. nearby reference plot), and microsite-by-salvaging interaction. We explicitly accounted for the nested split-plot experimental design using nested random effects of site, salvaging treatment (salvage logged or unsalvaged half) and pair ID (paired tip-up and off-mound reference plots) in the model (Royo et al. 2016). We performed pairwise post-hoc comparisons among the four treatment combinations with the emmeans package (Lenth 2016). Species richness was modeled with a Poisson distribution and log link function and percent cover data were square-root transformed to fit model assumptions with a Gaussian data distribution.

To evaluate whether communities were different among microsites, we used nonmetric multidimensional scaling (NMDS) with a Jaccard distance matrix, centering and PC rotation in the vegan package (Oksanen et al. 2013). We evaluated the similarity of community composition using the cover of each plant species among salvaged and unsalvaged areas and on versus off tip-up mounds with the adonis permutated analysis of variance (PERMANOVA) in the vegan package. We excluded species that occurred in fewer than 5% of the plots because rare species can bias the analyses (McCune and Grace 2002, Nuttle et al. 2013, Royo et al. 2016). Data were blocked by site and the main effects and interaction between microsite and salvaging treatment were evaluated for total cover of all species, for just tree species, and for non-tree species together (herbs, shrubs, and vines).

We followed up the overall community composition analyses with three complimentary approaches. First, we ran an indicator species analysis with the indicspecies package in R to evaluate whether some species were associated with one of the treatments based on specificity and fidelity (Dufrene and Legendre 1997, De Cáceres 2013). Second, we ran simultaneous LMMs on the square-root transformed percent cover estimates of the indicator species to test whether the mean cover was different among the four treatment combinations. We interpreted the results of the LMMs with a Bonferroni-adjusted alpha for multiple tests ($\alpha=0.05/3=0.017$). Finally, we tested whether tip-up mounds hosted any *unique* species by identifying any of the 26 species that were present on tip-up mounds but completely absent in reference plots.

We then analyzed a subset of the data from the 48 tip-up mounds used for community analyses—just from the salvaged areas—to test whether the orientation of the tip-up mound drives differences in plant community metrics. We compared the plant species richness, Shannon Diversity Index, and total cover among the reference plots, the inclined mounds, and the vertical tip-up mounds with GLMMs (distributions and random effects as before). We used a NMDS and a PERMANOVA on the community composition to compare inclined mound communities to reference plots and to vertical mound communities.

4.3 Results

We found a total of 249 tip-up mounds across the four blowdowns. The density of tip-up mounds did not differ significantly between salvaged and unsalvaged sites, regardless of whether or not we included inclined mounds (Mean salvaged, including inclined mounds= 14 mounds per hectare ± 4 SE; mean unsalvaged, including inclined mounds = 13 mounds per hectare ± 3 SE;

p>0.05; Mean salvaged, excluding inclined mounds= 8 mounds per hectare ± 4 SE; mean unsalvaged, excluding inclined mounds = 13 mounds per hectare ± 3 SE; p>0.05). Fifty-two of 124 tip-up mounds "tipped back down" in salvaged areas (37%) forming inclined mounds and only 5 of 125 did so in unsalvaged areas (4%, **Figure 2A**; p<0.0001***).

4.3.1 Physical characteristics of tip-up mounds

Vertical tip-up mounds in salvage-logged areas were half a meter shorter than vertical tip-up mounds in unsalvaged areas, both when measured from the pit (Ht1, p=0.0007**) (**Figure 3A**) and from the ground (Ht2, p<0.0001***) (**Figure 3B**). Tip-up mounds did not differ in width or in root plate soil thickness between salvaged and unsalvaged areas (Width, p=0.08 NS; Thickness, p>0.05 NS) (**Figure 3C,D**). Inclined tip-up mounds were on average 0.6m shorter than vertical tip-up mounds (when measured from the ground, p<0.0001***) but remained elevated as a hillock 0.8m taller than ground level (standard error bars do not intersect height=0m) (**Figure 2B**).

4.3.2 Effects of microsite and salvage logging on plant diversity and community composition

Species richness was lower on tip-up mounds (both inclined and vertical together) compared to adjacent reference plots off the mounds but the magnitude of this difference was reduced in salvaged treatments (significant microsite by salvaging interaction; **Figure 4A**, supplemental **Table 1**). Shannon diversity was significantly lower on tip-up mounds than in reference plots, but only in unsalvaged areas (significant microsite by salvaging interaction; **Figure 4B, Table 1**). Mean total plant cover was 52% lower on tip-up mounds versus reference plots both in the salvaged and unsalvaged sites (**Figure 4C, Table 1**). Overall, mounds had an impoverished flora relative to adjacent reference sites and this was particularly true on the unsalvaged side of the blowdowns.

Salvaging caused the formation of different plant communities and tip-up mounds had different communities versus adjacent reference plots (both main effects p=0.001; **Figure 7A**). Salvaging created significantly different communities of herbs, vines, and shrubs (combined) and these communities also differed significantly between tip-up mounds and adjacent reference plots (**Figure 7B**). Salvaging did not, however, significantly change tree communities but tree communities on mounds were significantly different from reference plots (**Figure 7C**).

Indicator species analyses revealed that only three species were consistently associated with one of the four treatment combinations. *Podophyllum peltatum* and *Rosa multiflora* were associated with unsalvaged reference plots and *Robinia pseudoacacia* was associated with salvaged tip-up mounds (**Table 2**). *Podophyllum peltatum* and *Rosa multiflora* were completely absent on the 48 surveyed tip-up mounds and *Robinia pseudoacacia* cover was slightly higher (2%) in salvaged areas than unsalvaged areas (**Table 3**). We found no species that occurred *only* on tip-up mounds.

Mean species richness was significantly higher in reference plots than on either inclined or vertical mounds and Shannon diversity did not differ among vertical mounds, inclined mounds, or reference plots (**Figure 5A,B**). Total plant cover was more than twofold higher in reference plots versus either vertical or inclined mounds (**Figure 5C**). Community composition differed between tip-up mounds and the reference plots (p=0.001, **Figure 6, 7**). Overall, the vegetation on inclined mounds was more similar to vertical mounds than to the reference plots (**Figure 5A,C** and **Figure 6B,C**).

4.4 Discussion

Catastrophic windstorms create a rare opportunity for early successional species to establish within mature forests and for the plant community to reassemble on a large scale. Tip-up mounds can be regeneration hotspots because they add topographic heterogeneity to the landscape and may provide unique regeneration microsites or a refuge from herbivores (Peterson et al. 1990, Long et al. 1998, Webb 1999). We found that after three years, mounds were characterized by different plant communities in comparison to nearby reference sites. Mound communities were moderately impoverished and had much less total plant cover than reference plots likely because these habitats are less stable and experience high levels of desiccation, freezing, and soil slough-off (Beatty 1984, Peterson et al. 1990, Bates et al. 2014). While the communities on mounds and reference sites were different, this was primarily because plants were less abundant on the mounds. We found no species that were unique to mounds and indicator species analyses demonstrated that only three species showed affinity to any one of the four treatment combinations. There are two important implications of these results. First, if sharp differences in community composition do develop on mounds versus reference plots, our results suggest that these differences develop later during forest regeneration. Second, because mounds had much less cover (by as much as 60%), they will remain open for subsequent colonization much later during forest regeneration than sites off mounds. This may be important if mounds stabilize over time and thus provide open habitats with bare soil for colonization and establishment well after the disturbance event.

We quantified whether salvage logging reduced the abundance of mounds on the landscape. Our results show that salvage logging does *not* eliminate tip-up mounds from the landscape or destroy them (cf. Cooper-Ellis et al. 1999, Waldron et al. 2013, 2014) but rather, in our case, salvaging "tips down" approximately 40% of the mounds forming inclined mounds. Thus, salvage logging potentially creates a new intermediate habitat—inclined hillocks that are not as uplifted as vertical tip-up mounds, but have upturned soil and are elevated above reference areas (**Figure 2B**). Salvage logging also contributed to creating shorter vertical mounds (by 0.5m, inclined mounds were excluded), likely because salvaged areas typically have more open canopies, which expose mounds to higher light and direct precipitation thus increasing the rates that mounds decay (see also Schaetzl and Follmer 1990, Lang et al. 2009). We suggest that these hillocks, although only a few years old, resemble pit-and-mound topography after several decades (Lyford and MacLean 1966, Beatty 1984, Ulanova 2000, Šamonil et al. 2009). Salvage logging may therefore accelerate post-windthrow soil development processes on tip-up mounds, but this has scarcely been tested (see mention in Lang et al. 2009, Waldron et al. 2013).

We evaluated not only whether plant assemblages would contrast between vertical tip-up mounds and adjacent reference sites but also whether plant assemblages would be different on the inclined mounds created by salvaging. The plant communities and species richness on inclined mounds were very similar to those on vertical mounds, which were both very different from reference plots. On one hand, the similarity of the inclined mounds to the vertical tip-up mounds may be in part a historic imprint of the time between the tornado and the salvaging operation (in our case, 0-2 growing seasons). Inclined mounds were, in fact, tipped-up for a few months to years before the bole was salvaged and the mound tipped back into the pit. Thus, the vegetation may still reflect this time period a few years later, bearing the legacy (and vegetation characteristics) of the vertical tip-up mound it once was. Nonetheless, we suggest that these inclined mounds, which form a characteristic hillock, are potentially unique microsites that are physically distinct from either vertical mounds or sites off mounds. We predict that over many years, distinct plant communities will develop on these hillocks at least partly because the soil on inclined mounds will stabilize sooner than on vertical mounds yet bare soil will still be present. The rate of soil stabilization and the dynamic nature of tip-up mound topographical degradation are likely important drivers of plant community composition and species turnover over long time periods (Schaetzl and Follmer 1990, Ulanova 2000, Vodde et al. 2011, Phillips et al. 2017). However, if the reason that vertical mounds have unique vegetation is because they serve as a refuge from browsers (Long et al. 1998, Krueger and Peterson 2006), then inclined mounds are likely too short and will instead have vegetation that becomes more similar to reference plots in time. In areas where deer are over abundant, if salvaging tips down the vast majority of mounds, then salvaging may erase an important herbivore refuge across the landscape. Thus, more studies are needed to quantify the percentage of tip-up mounds that tip back down. In addition, it is not clear from other studies the degree that salvaging causes stumps to tip back down completely into the pit; in contrast to our findings, this would *not* create hillocks and could truly “eliminate” mounds. There is likely to be substantial variation in these processes among forest types, disturbance types (e.g., fire versus blowdown), intensity of salvaging, and scale of analysis (Bradford et al. 2012, Kramer et al. 2014, Royo et al. 2016, Lindenmayer et al. 2017, Thorn et al. 2017). Finally, we suggest that it would be fruitful to return to older salvaged sites and locate inclined mounds and compare the vegetation on these mounds to once vertical mounds and to adjacent reference sites.

4.5 Conclusions

Here, we demonstrate that salvaging does not completely erase a signature legacy of a large-scale blowdown, specifically tip-up mounds. Rather, salvaging tips down a substantial percentage of these mounds (~40%), causing the formation of inclined mounds that create novel heterogeneity in the form of numerous hillocks. Most studies that describe post-salvage logging tip-up mounds have referred to mounds that tipped back down as returning to the pre-disturbance state or as completely eliminated (Cooper-Ellis et al. 1999, Waldron et al. 2013, but see mention by Lang et al. 2009). Here, we show that this "tipping down" creates inclined mounds with physical characteristics and vegetation more similar to vertical mounds than to reference sites (**Figures 2B,5,6**). No species were unique to either inclined or vertical mounds; thus, mounds were a slightly impoverished subset of the vegetation found within adjacent reference sites. Our findings suggest that mounds, especially in unsalvaged sites, will remain more open microsites with patches of bare soil available for colonization many years into the future.

4.6 Acknowledgements

Rosa Brandt, Laissa Leonis do Canto, and Austin Brenek assisted in the field and with data entry. The Powdermill Nature Reserve and the University of Pittsburgh Mascaro Center for Sustainable Innovation provided funding. We thank Alejandro Royo, Mike Czypinski, Jake Slyder, and the Powdermill Nature Reserve staff for support and experimental setup. Comments by Yusan Yang, Katie Barry, Chris Peterson, and an anonymous reviewer improved the manuscript.

4.7 Authorship statement

WPC and JWW designed and set up the experiment in 2012. MES and KFS collected data. MES analyzed the data and all authors contributed to writing the manuscript.

4.8 Figures and tables

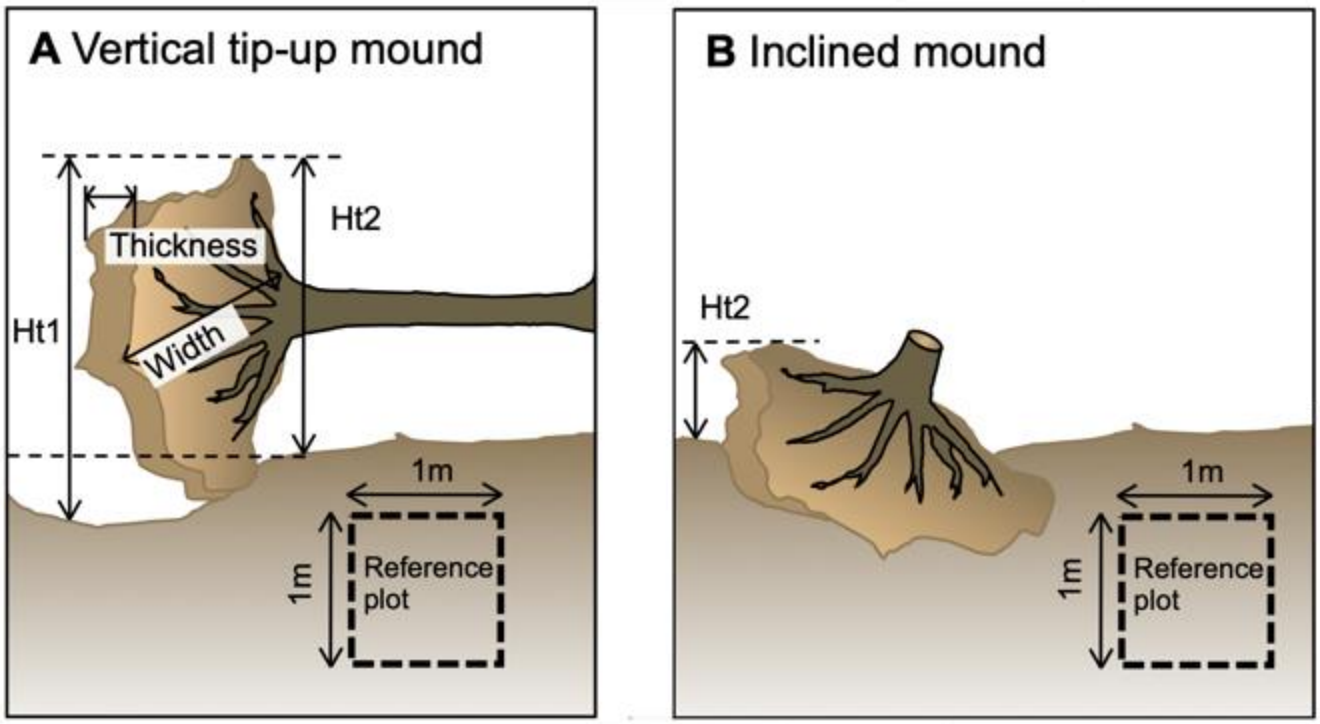


Figure 4-1. Tip-up mounds schematic.

A) Measurements and depiction of a vertical tip-up mound. B) Depiction of a "tipped down" inclined mound post-salvage logging. Randomly selected adjacent reference sites are shown in both A and B. Note how inclined mounds provide a putatively unique microsite or hillock that contrasts with both a vertical mound (which occurs much closer to a 90-degree angle relative to the soil surface) and the adjacent reference site.

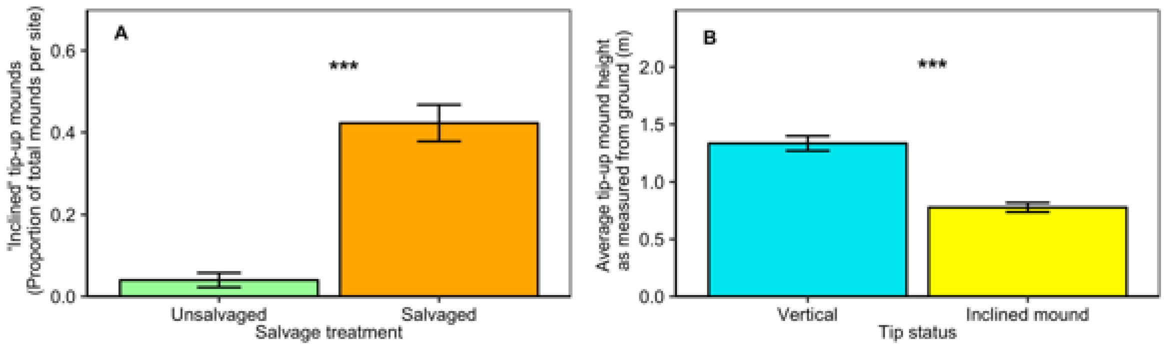


Figure 4-2. Measurements of tip-up mounds.

A) Mean percent of tip-up mounds that tipped back down into the pit forming inclined mounds and vertical mounds (N=249). B) Average height of intact vertical and tipped-down inclined mounds. Note that inclined mounds remain elevated 0.8m above the ground. Error bars are standard error.

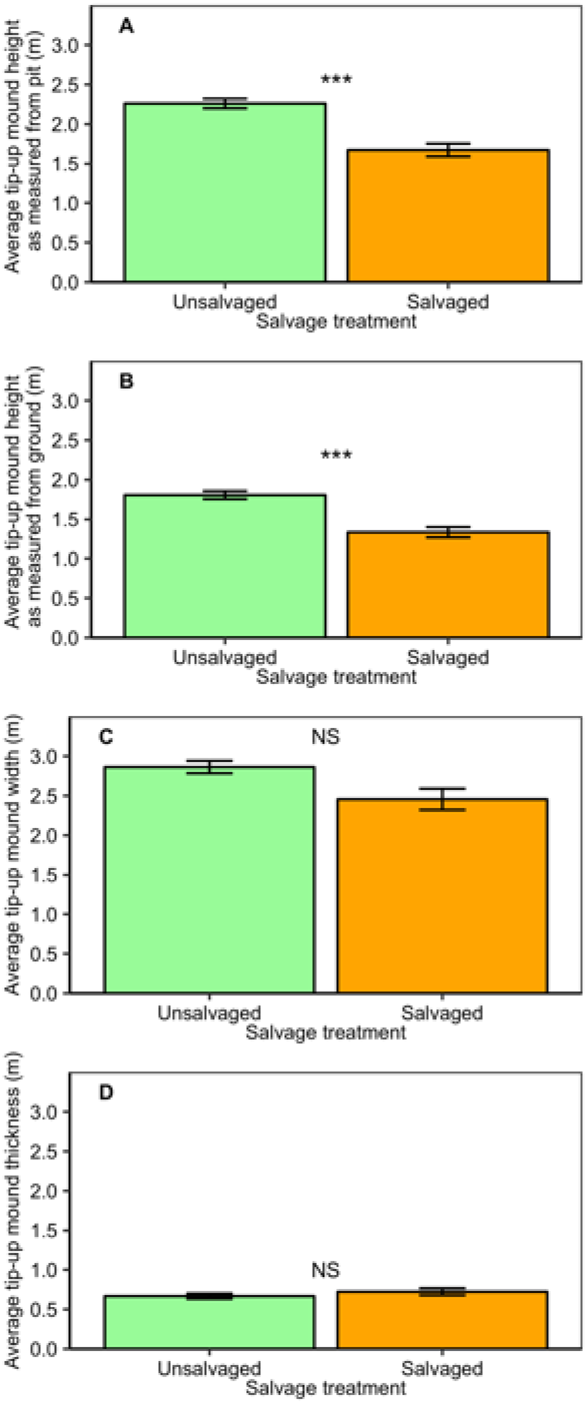


Figure 4-3. Physical characteristics of vertical tip-up mounds between salvaged and unsalvaged areas.

Physical characteristics of vertical tip-up mounds between salvaged and unsalvaged areas (inclined mounds are excluded, N=191): A) Mean height of mounds measured from lowest point of pit to highest point of mound B) height from ground to highest point of mound; C) width of mound; D) thickness of root plate. The cutoff for statistical significance is adjusted for multiple tests (Bonferroni α=0.05/4=0.0125). See Figure 1 for a depiction of these measurements.

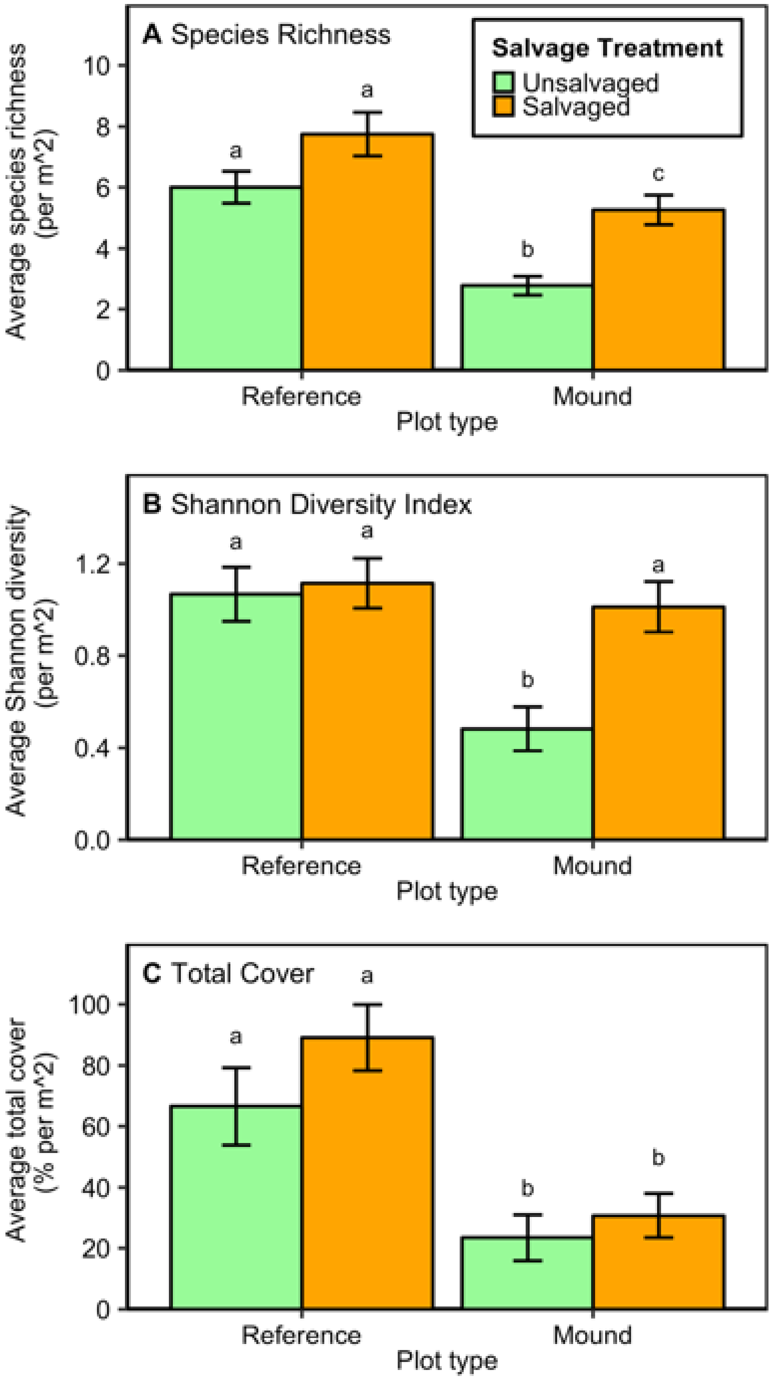


Figure 4-4. Species richness, diversity, and cover: Tip-up mounds versus reference plots.

A) Comparison of species richness, B) Shannon diversity, and C) total cover among tip-up mounds and reference plots in salvage logged and unsalvaged areas (N=96). Lowercase letters above bars indicate significant differences according to post-hoc pairwise comparisons.

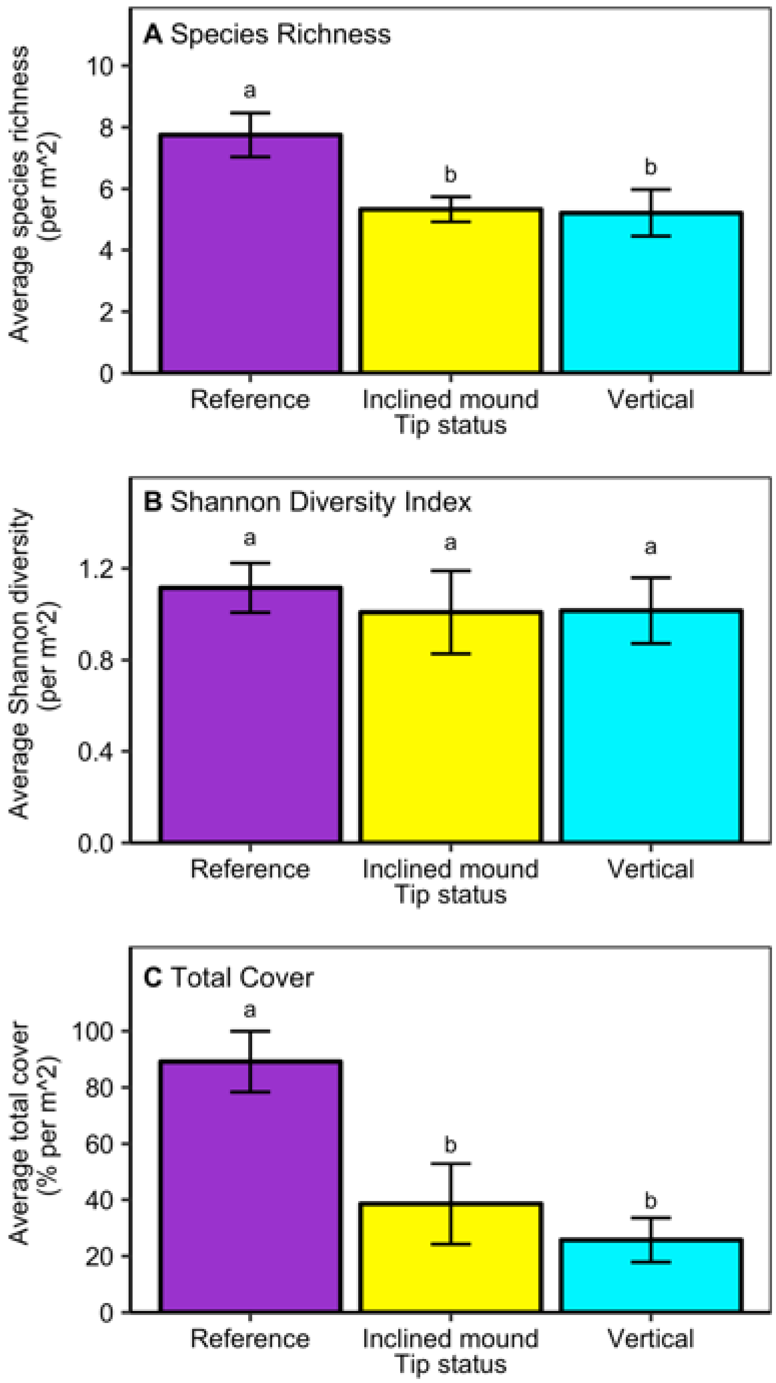
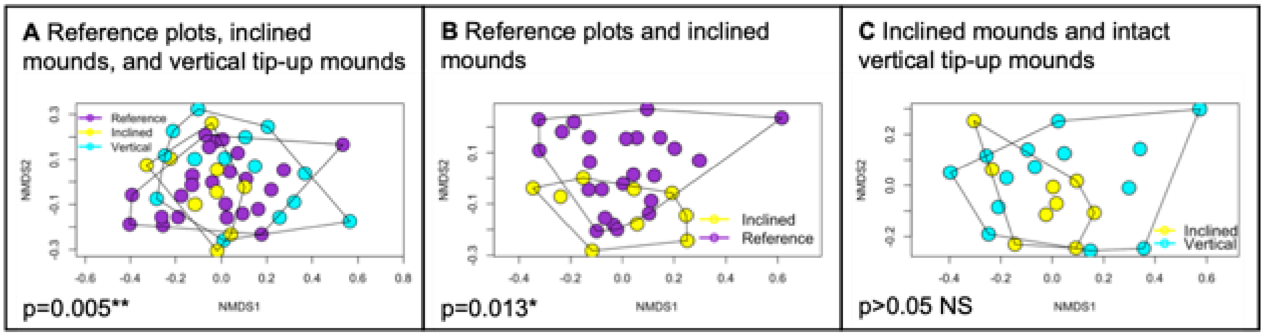


Figure 4-5. Species richness, diversity, and cover: Intact tip-up mounds, inclined mounds, and reference plots within salvaged sites.

Comparison of species richness (A), Shannon diversity (B), and total cover (C) among reference plots, inclined mounds, and intact vertical mounds in salvaged sites (N=48). Letters indicate significant differences according to post-hoc pairwise comparisons.



A Reference plots, inclined mounds, and vertical tip-up mounds

B Reference plots and inclined mounds

C Inclined mounds and intact vertical tip-up mounds

Figure 4-6. Plant community composition differences.

Plant community composition differences among intact vertically oriented tip-up mounds, inclined mounds that have "tipped back down", and reference plots in salvaged logged sites (N=47). Polygons highlight the differences between plant community compositions based on percent cover estimates.

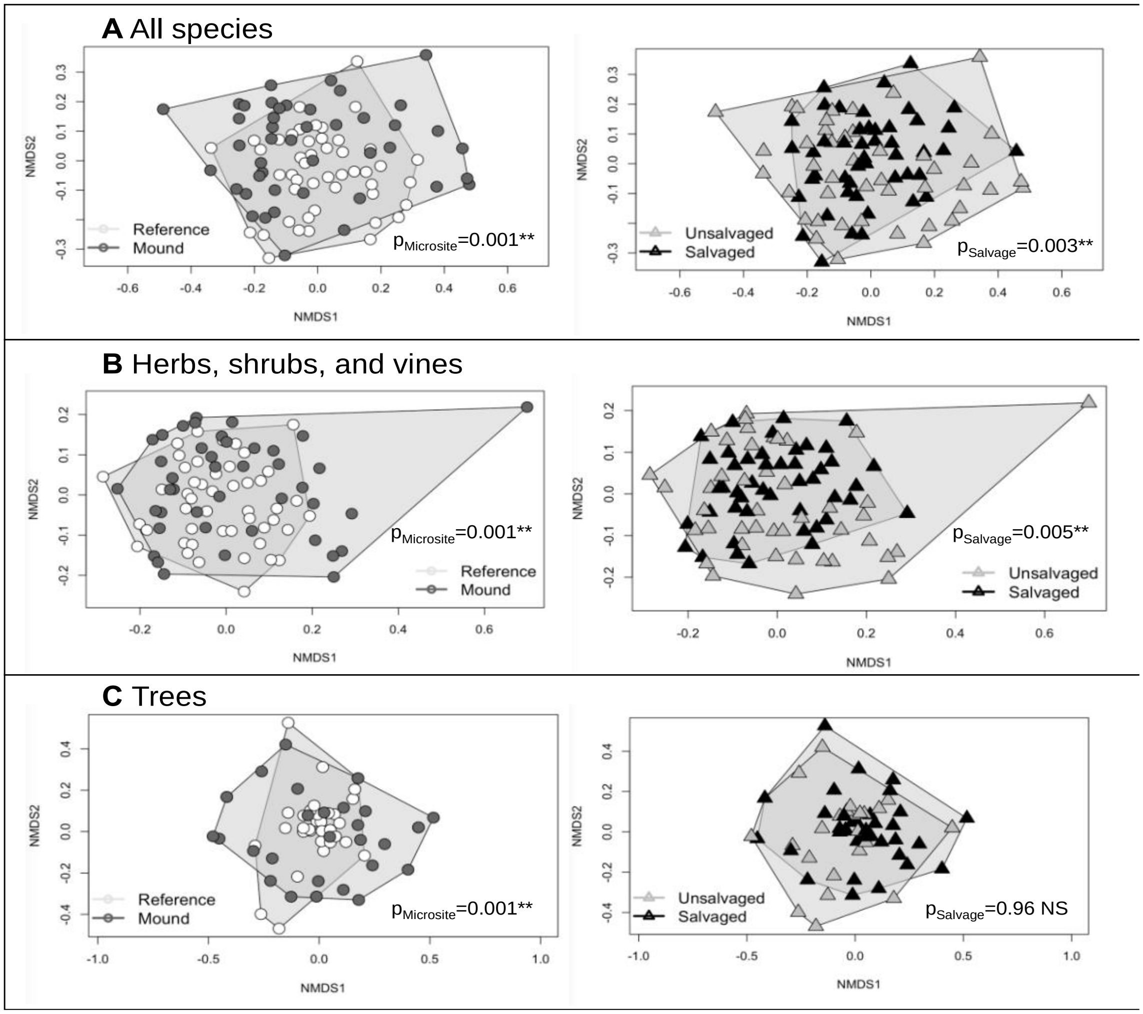


Figure 4-7. Plant community composition differences, by growth-form.

Plant community composition differences among tip-up mounds and reference plots in salvaged logged and unsalvaged sites. In the left panels, polygons highlight the differences between tip-up mound communities and reference communities. Community composition was significantly different for all plant species combined (A), non-tree species (B), and tree species (C). In the right panels, polygons highlight the differences between plant communities in salvaged and unsalvaged areas, which were significant for all plant species combined (A) and non-tree species (B), but were not different for tree species (C).

Table 4-1. Results of (generalized) linear mixed models.

Effects of salvage logging and tip-up mounds on plant species richness, diversity (H'), and total cover (per square meter). Negative values indicate tip-up mound values are lower than reference area values.

N=96	**Species richness**			**Shannon diversity**			**Total cover (%)**		
Treatment	**z**	**SE**	**p**	**t**	**SE**	**p**	**t**	**SE**	**p**
Microsite	-3.21	0.12	**0.0013*****	-0.65	0.15	0.52	-4.35	0.92	**<0.0001*****
Salvaging	1.76	0.14	0.093.	-0.27	0.18	0.79	1.75	0.93	0.094.
M*S	-2.16	0.19	**0.043***	-2.32	0.21	**0.023***	0.83	1.31	0.53

Table 4-2. Results of indicator species analyses.

The three species that are significantly associated with one of the four treatment combinations.

Growth-form	**Species**	**Associated habitat**	**p-value**
Herb	*Podophyllum peltatum*	Unsalvaged reference	**0.005****
Tree	*Robinia pseudoacacia*	Salvaged tip-up mound	**0.003****
Shrub (invasive)	*Rosa multiflora*	Unsalvaged reference	**0.012****

Table 4-3. Mean cover of indicator species.

Mean cover of the three indicator species (% per m_2) in each of the four treatment combinations (first four columns). Results of generalized linear mixed model analyses displaying effects of salvage logging and tip-up mounds on cover of the three indicator species (last three columns). The cutoff for statistical significance is adjusted for multiple tests (Bonferroni α=0.05/3=0.017).

	Reference Plots		**Tip-up Mounds**		**p-values; α=0.017**		
Species	**Salvaged**	**Unsalvaged**	**Salvaged**	**Unsalvaged**	**Microsite**	**Salvage**	**M*S**
Podophyllum peltatum	0.08±0.08	1.09±0.60	0.00±0.00	0.00±0.00	0.67	0.15	0.05
Robinia pseudoacacia	1.04±0.84	0.00±0.00	3.09±1.57	0.14±0.14	**0.014***	0.29	0.15
Rosa multiflora	0.08±0.08	2.61±1.33	0.00±0.00	0.00±0.00	0.79	**0.008***	0.06

4.9 Bibliography

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R Packag. version **1**(7): 1–23.

Beatty, S.W. 1984. Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understory Plants. Ecology **65**(5): 1406–1419.

Bradford, J.B., Fraver, S., Milo, A.M., Amato, A.W.D., Palik, B., and Shinneman, D.J. 2012. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. For. Ecol. Manage. **267**: 209–2014. doi:10.1016/j.foreco.2011.12.010.

Brewer, J.S., Bertz, C.A., Cannon, J.B., and Chesser, J.D. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? Ecol. Appl. **22**(2): 442–458.

De Cáceres, M. 2013. How to use the indicspecies package (ver. 1.7. 1). Cent. Tecnològic For. Catalunya, Catalonia.

Carlton, G.C., and Bazzaz, F.A. 1998. Regeneration of Three Sympatric Birch Species on Experimental Hurricane Blowdown Microsites. Ecol. Monogr. **68**(1): 99–120.

Cooper-Ellis, S., Foster, D.R., Carlton, G., and Lezberg, A. 1999. Forest Response to Catastrophic Wind : Results from an Experimental Hurricane. Ecology **80**(8): 2683–2696. doi:10.2307/177250.doi.

Darabi, S.M., Kooch, Y., and Hosseini, S.M. 2014. Dynamic of Plant Composition and Regeneration following Windthrow in a Temperate Beech Forest. Int. Sch. Res. Not. (421457): 1–9.

Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. **67**(3): 345–366.

Kramer, K., Brang, P., Bachofen, H., Bugmann, H., and Wohlgemuth, T. 2014. Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. For. Ecol. Manage. **331**: 116–128. Elsevier B.V. doi:10.1016/j.foreco.2014.08.002.

Krueger, L.M., and Peterson, C.J. 2006. Effects of White-tailed Deer on Tsuga canadensis Regeneration : Evidence of Microsites as Refugia from Browsing. Am. Midl. Nat. **156**(2): 353–362.

Lang, K.D., Schulte, L.A., and Guntenspergen, G.R. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. For. Ecol. Manage. **259**: 56–64. doi:10.1016/j.foreco.2009.09.042.

Lenth, R. V. 2016. Least-squares means: the R package lsmeans. J Stat Softw **69**(1): 1–33.

Lindenmayer, D., Thorn, S., and Banks, S. 2017. Please do not disturb ecosystems further. Nat. Ecol. Evol. **1**(31). Macmillan Publishers Limited. doi:10.1038/s41559-016-0031.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., and Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science (80-.). **303**: 1303.

Long, Z.T., Carson, W.P., and Peterson, C.J. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J. Torrey Bot. Soc. **125**(2): 165–168.

Lyford, W.H., and MacLean, D.W. 1966. Mound and pit microreleif in relation to soil disturbance and tree distribution in New Bruswick, Canada. Harvard For. Pap.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. *In* 2nd edition. MjM Software Design, Gleneden Beach, Oregon.

McIver, J.D., and Starr, L. 2000. Enviromental Effects of Postfire Logging: Literature Review and Annotated Bibliography. USDA Tech. Rep. PNW-GTR-486: 1–72.

Mitchell, S.J. 2013. Wind as a natural disturbance agent in forests: A synthesis. Forestry **86**(2): 147–157. doi:10.1093/forestry/cps058.

Murphy, S.J., Audino, L.D., Whitacre, J., Eck, J.L., Wenzel, J.W., Queensborough, S.A., and Comita, L.S. 2015. Species associations structured by environment and land-use history promote beta-diversity in a temperate forest. Ecology **96**(3): 705–715.

NOAA. 2012. Confirmed EF-1 Tornado in Ligonier, PA. Available from https://websoilsurvey.sc.egov.usda.gov/WssProduct/bpmela1jf0c1me5qqhiuoqiv/GN_00001/20171128_08343108379_32_Soil_Report.pdf [accessed 11 July 2015].

NRCS. 2017. Custom Soil Resource Report for Westmoreland County, Pennsylvania. Available from https://websoilsurvey.sc.egov.usda.gov/WssProduct/bpmela1jf0c1me5qqhiuoqiv/GN_00001/20171128_08343108379_32_Soil_Report.pdf.

Nuttle, T., Ristau, T.E., and Royo, A.A. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. J. Ecol. **102**(1): 221–228. doi:10.1111/1365-2745.12175.

Nuttle, T., Royo, A.A., Adams, M.B., and Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. **83**(1): 3–17.

Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., R. B. O’hara, R.B., and Simpson, G.L. 2013. Package “vegan.” Community Ecol. Packag. **2**(9).

Peterson, C.J., Carson, W.P., Mccarthy, B.C., and Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos **58**(1): 39–46. doi:10.2307/3565358.

Peterson, C.J., and Leach, A.D. 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecol. Appl. **18**(2): 407–420.

Phillips, J.D., Pavel, Š., Pawlik, Ł., Trochta, J., and Danek, P. 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. Geomorphology **276**: 27–36. doi:10.1016/j.geomorph.2016.10.006.

R Core Development Team, 3.4.1. 2017. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royo, A.A., Peterson, C.J., Stanovick, J.S., and Carson, W.P. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology **97**(6): 1566–1582.

Royo, A.A., Stout, S.L., DeCalesta, D.S., and Pierson, T.G. 2010. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? Biol. Conserv. **143**(11): 2425–2434. Elsevier Ltd. doi:10.1016/j.biocon.2010.05.020.

Šamonil, P., Antolík, L., Svoboda, M., and Adam, D. 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. For. Ecol. Manage. **257**: 1148–1156. doi:10.1016/j.foreco.2008.11.024.

Schaetzl, R.J., Burns, S.F., Small, T.W., and Johnson, D.L. 1990. Tree uprooting: Review of types and patterns of soil disturbance. Phys. Geogr. **11**(3): 277–291.

Schaetzl, R.J., and Follmer, L.R. 1990. Longevity of treethrow microtopography: implications for mass wasting. Geomorphology **3**: 113–123.

Schaetzl, R.J., Johnson, D.L., Burns, S.F., and Small, T.W. 1989. Tree uprooting: review of terminology, process, and environmental implications. Can. J. For. Res. **19**: 1–11.

Simon, A., Gratzer, G., and Sieghardt, M. 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. For. Ecol. Manage. **262**(7): 1289–1297. Elsevier B.V. doi:10.1016/j.foreco.2011.06.028.

Thompson, J.N. 1980. Treefalls and Colonization Patterns of Temperate Forest Herbs. Am. Midl. Nat. **104**(1): 176–184.

Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.B., Zmihorski, M., and Müller, J. 2017. Impacts of salvage logging on biodiversity: A meta-analysis. J. Appl. Ecol. (May): 1–11. doi:10.1111/1365-2664.12945.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales : a review. For. Ecol. Manage. **135**: 155–167.

Vodde, F., Jõgiste, K., Kubota, Y., Kuuluvainen, T., Köster, K., Lukjanova, A., Metslaid, M., and Yoshida, T. 2011. The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest. J. For. Res. **16**: 155–167. doi:10.1007/10310-011-0273-6.

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. Forest structural attributes after windthrow and consequences of salvage logging. For. Ecol. Manage. **289**: 28–37. Elsevier B.V. doi:10.1016/j.foreco.2012.10.006.

Waldron, K., Ruel, J.-C., Gauthier, S., DeGrandpre, L., and Peterson, C.J. 2014. Effects of post-windthrow salvage logging on microsites, plant composition and regeneration. Appl. Veg. Sci. **17**: 323–337. doi:10.1111/avsc.12061.

Webb, S.L. 1999. Disturbance by wind in temperate-zone forests. *In* Ecosystems of disturbed ground. *Edited by* L.R. Walker. Elsevier, Amsterdam, The Netherlands. pp. 187–222.

5.0 SUBSTRATE TEXTURE MEDIATES VASCULAR EPIPHYTE ESTABLISHMENT: EXPERIMENTAL EVIDENCE FROM A PANAMANIAN CLOUD FOREST

Spicer, M. E., J. Ortega, and W. P. Carson. Substrate texture mediates vascular epiphyte establishment: experimental evidence from a Panamanian cloud forest. *In preparation, intended for submission to Biotropica.*

5.1 Introduction

Epiphytes, or plants that live non-parasitically on other plants, constitute approximately one fifth of Neotropical vascular plant diversity and often account for the majority of all plant species in montane forests (Gentry and Dodson 1987a, 1987b, Kelly et al. 1994, Spicer et al. 2019: Chapter 2). They mediate ecosystem function by enhancing water capture per unit forest area and can contribute nearly four times as much leaf biomass to aboveground biomass than the trees that host them (Nadkarni 1984; Coxson and Nadkarni 1995; Holwerda et al. 2010; Van Stan and Pypker 2015). Epiphytes dramatically increase forest complexity and heterogeneity in the canopy, provide numerous host species for specialist insects (Stuntz et al. 2002), and provide limiting habitat for amphibians and birds (Nadkarni and Matelson 1989, Ellwood and Foster 2004, Scheffers et al. 2014). Despite their clear ecological importance, the ecology of arboreal plant communities is much less well-understood than terrestrial plant ecology. The processes and mechanisms driving epiphyte community assembly and development, for example, remain largely unknown and rarely tested experimentally (Burns 2007; Mendieta-Leiva & Zotz 2015; Woods 2017).

For both epiphytic and terrestrial plants, the earliest life stage transitions are likely key bottlenecks to both individual survival and community development (Harper 1977, Mack and Harper 1977, Ackerman et al. 1996, Gilbert 2002, Zotz and Vollrath 2002, Laube and Zotz 2003, Mondragon and Calvo-Irabien 2006, Sheldon and Nadkarni 2013). Juvenile epiphytes depend upon their microhabitat for water and nutrients more than terrestrial plants, because their roots are adapted for structural stability rather than direct water or nutrient absorption (Benzing 1990, Andrade and Nobel 1997). They also face the unique challenge of adhering to their substrate early on, especially because approximately 84% of epiphyte seeds are anemochorous (Mondragon et al. 2015). Thus, host bark characteristics can be vital to epiphyte establishment and subsequent community development. For example, high bark water absorption rates can enhance epiphytes' access to water, which is particularly important in seasonally dry forests (Callaway et al. 2002, Mehltreter et al. 2005, Mondragon et al. 2015). Bark exfoliation and allelopathic compounds, on the other hand, may inhibit germination, seedling growth or survival (Díaz and Elsa 2007, López-Villalobos et al. 2008, Valencia-Díaz et al. 2010, Cortes-Anzures et al. 2017). Several observational studies have identified a positive association between bark roughness and epiphyte abundance or diversity of epiphytes (Robertson and Platt 2001, Callaway et al. 2002, Wyse and Burns 2011). However, Vergara-Torres *et al.* (2010) and Boelter *et al.* (2014) found that bark texture was less important to epiphyte diversity than broader-scale variables such as nearby hosts and soil nutrients. The results to date remain equivocal, mainly because observational studies cannot separate the effects of bark texture to correlated host traits such as age, size, and nearby epiphyte establishment simultaneously (reviewed in Wagner *et al.* 2015). More experimental work is needed *in situ* to identify the independent contributions of host traits to epiphyte assembly (Wagner et al. 2015).

Here, we use a simple experiment to test the extent to which substrate texture drives vascular epiphyte establishment with an *in situ* experiment in a Neotropical cloud forest. Our experiment is unique in that we sourced all substrates from the same individual tree and experimentally manipulated the roughness, allowing us to control several previously conflated host traits. Moreover, we tracked the cohort survival of epiphyte seedlings every two months for more than a year, providing both a high temporal resolution and a moderately long-term component to *in situ* experiments.

5.2 Methods

5.2.1 Study site

We set up our experiment in the premontane cloud forest of Santa Fé National Park, Veraguas, Panama (8° 31.98’ N, 81° 9.03’W) at an elevation of approximately 750m above sea level. Santa Fé National Park, established in 2001, is a 72,636 hectare National Park located in the mountainous Cordillera Central region of Panama (Ministerio de Economía y Finanzas 2001). The park contains old-growth pre-montane, montane-tropical cloud forest, and lowland tropical seasonal forest with sparse human development (ANAM 2010, Cáceres-González 2013). Because there is no climate station nearby, no local data are available on seasonal or annual precipitation. There is rainfall or heavy mist nearly every night in the higher elevations of Santa Fé National Park where we set up the experiment, and a slightly drier period occurs from February through April (Spicer & Ortega, personal observation). Animal diversity is very high, with an intact fauna containing resident populations of jaguars and pumas, as well as persisting populations of

Critically Endangered Harlequin frogs (Angehr and Dean 2010, Hertz et al. 2012, Meyer et al. 2013, 2019, Moreno and Meyer 2014, Perez et al. 2014, Ortiz and Croat 2016, Barrie et al. 2019, Rázuri-Gonzalez and Armitage 2019). The park has not been well-studied taxonomically, and plant and animal species new to science have recently been described (González Cáceres et al. 2011, Cáceres-González 2013, Cáceres-González and Ibáñez 2014, Flores et al. 2015, Kennedy and Flores 2015, Batista and Mori 2017, Barrie et al. 2019, Ortiz et al. 2019). We report mean annual temperature and relative humidity measured every 4 hours from April 2017 through March 2018 (**Table 1**) using four Hygrochron iButton (Maxim Integrated, D1923).

5.2.2 Artificial substrate construction

We tested the impact of substrate texture on epiphyte establishment by constructing platforms with varying roughness. Each platform was salvaged from the inner wood (without bark) of a native fallen tree of the genus *Pouteria* (donated via permit #SE/AP-1-17). Nine substrates were cut to approximately 10×15×110cm (depth, width, length). Each of the nine platforms were divided into two halves, with at least a 2.5cm buffer between each half and around all edges. Each half is referred to as a *plot*. Each plot was then subdivided into five 10×10cm subplots; these are referred to as *subplots* and are the unit of replication for each experimental treatment (**Figure 1A**). Thus, there are 5 treatments in each of 18 plots for a total of 90 subplots.

We manipulated substrate texture by varying the rugosity (Luckhurst and Luckhurst 1978), or surface complexity or roughness. We hand-sawed grooves to create 5 experimental levels of increasing rugosity. The smoothest subplot (R0) was created using sandpaper to decrease the chainsaw cut texture; the second-most smooth subplot (R1) had no additional grooves because we used the original chainsaw cut of the wood. We created the next two rugosity treatments (R2 &

R3) by hand-sawing four equidistant parallel grooves running the entire length of the subplot. Grooves on R2 were approximately 1mm deep and grooves on R3 were approximately 2mm deep. The most rugose subplot (R4) also had four parallel hand-sawn grooves of approximately 3mm deep, and had two additional grooves sawn from corner-to-corner (**Figure 1A**). The five rugosity treatments were randomly allocated to each subplot. We quantified rugosity by the straight-chain method (Luckhurst and Luckhurst 1978), wherein rugosity equals the length of a fine-chain laid across the surface (encompassing all the surface topography) divided by the straight-line distance (as measured by a ruler). Rugosities in our experiment ranged from 1 (as measured, perfectly smooth) to 1.46. Our goal was to mimic rugosities of nearby Neotropical trees; in Santa Fé, measured tree branch bark rugosities ranged from 1.1 to 2.1 (Spicer unpublished data). We confirmed that the five rugosity treatments increased in measured rugosity (**Figure 8**), although they do not all separate statistically.

We suspended and leveled all platforms 1.3m above the ground throughout the forest using shark-grade fishing line tied to nearby trees, at least 50m from each other. To decrease the potential for colonization of microorganisms or juvenile plants prior to epiphyte seed application, (see below), we sanitized the boards with a 50/50 mix of bleach and water. In a separate study, we have found that epiphytes still readily colonize bleached wood substrates in the absence of seed addition (Spicer unpublished data).

5.2.3 Collection of epiphyte seeds

We collected local seeds from nine different epiphyte species, using one individual of each species (permit SE/AP-1-17). Four individuals were bromeliads and five were orchids. Seed capsules were kept in ambient conditions for less than two months until we used them in the experiment. It is unlikely that storage under ambient conditions would have decreased their viability (Correa and Zotz 2014).

5.2.4 Application of epiphyte seeds and data collection

All epiphyte seeds were removed from capsules and mixed thoroughly. For each subplot, one teaspoon of the seed mix was deposited by hand to a flat glass plate held immediately adjacent to one of the 10×10 cm subplots. We then used five puffs of air from an infant ear cleaner to "wind disperse" the seeds onto the subplot. The glass applicating plate was washed with water and dried between each application. We performed all seed applications in only a few hours when it was not raining, but the substrates were damp from morning rain, which matches ambient conditions. We did not add any water, nutrients, or growth hormones. (*cf*. laboratory germination experiments; Arditti 1967, Arditti and Ghani 2000, Mondragon and Calvo-Irabien 2006). We also did not adhere the seeds to the subplot, unlike other seed field experiments (Mondragon and Calvo-Irabien 2006, Hietz et al. 2012, Ruiz-Cordova et al. 2014, Shao et al. 2017). Our goal was to expose the epiphytes to natural processes *in situ*, including those that would remove seeds. Notably, the local community and indigenous peoples in the Santa Fé region regularly propagate orchids in this way (without any added nutrients or adhesion) (Spicer and Ortega, personal communication). We censused all subplots for epiphytes at approximately two-month intervals for 12 months.

5.2.5 Statistical analyses

First, we tested whether rugosity of the substrate predicted the abundance of germinated epiphytes at the first time point, two months after applying seeds. We analyzed the continuous rugosity measurements as well as the five categorical rugosity treatments. Note that there is variability in measured rugosity within a rugosity treatment (**Figure 8**). We ran a generalized linear mixed model (GLMM) using the continuous rugosity measure to predict the abundance of epiphytes in each subplot (10×10cm). We included a random blocking factor with plots nested within the nine platforms as is appropriate for our split-plot design. We modeled the count data as a Poisson distribution with a log link function. To test how the five categorical rugosity treatments related to the abundance of epiphytes at two months, we used the same model parameters as in the continuous analysis. We followed-up these GLMMs with Tukey's posthoc tests. In addition, we examined the proportion of each of the five treatments that were completely empty (no epiphytes) graphically. Finally, we tested whether the effect of rugosity on epiphyte establishment decreased over time by comparing all time points in another GLMM. In this model, we used the ordinal time points 1-6 as a fixed factor as well as the categorical rugosity treatments to predict epiphyte abundance, and included random blocked plot and pair factors as above. We did not include or statistically evaluate subsequent recruitment that occurred after the first survey (two months) because new colonists could not be distinguished from individuals already present; regardless, our primary interest was mortality. All analyses were run in R version 3.6.0 and models were run using the lme4 package (Bates et al. 2014, R Core Development Team 2017). We calculated the pseudo-R_2 conditional and marginal coefficients for the continuous-predictor test with the package MuMIn (Barton 2019).

5.3 Results

We found a total of 1934 epiphyte seedlings across all plots after two months. Mean epiphyte seedling abundance per 10×10cm subplot was 21 (± 3.5 SE), and ranged from 0 to 173 (**Figure 3**). At two months, epiphyte abundance was positively correlated to rugosity, wherein more rugose substrates had higher epiphyte abundance (z=6.549, p<0.0001***, R_2m=0.013, R_2c=0.976; **Figure 4**). Our categorical analysis confirmed that the higher rugosity treatments caused higher abundance at two months with the two intermediate roughness treatments (R2 & R3) having the most epiphytes (all p<0.0001; **Figure 5**). When averaged together, roughened substrates (R1-R4) had 27 more epiphytes on average than the smoothest substrate (R0). Nearly 80% of the smoothest substrates had no epiphytes present by two months; in contrast, on each of the four rugosity treatments subplots were empty on less than 40% of the subplots. (**Figure 6**). Epiphytes went practically extinct on all treatments over time but this was delayed by months on all the higher-rugosity substrates (Time: z=-3.951, p<0.0001***; Treatments: all p<0.0001***; **Figure 7**).

5.4 Discussion

5.4.1 Substrate rugosity as a regulator of epiphyte establishment

Our results provide the first experimental evidence *in situ* of the direct connection between substrate rugosity and epiphyte establishment. We demonstrated that variation in the texture of a host surface regulates subsequent epiphyte establishment. As predicted, higher rugosity substrates initially had much higher epiphyte abundances (mean of 32 more epiphytes), and also kept more epiphytes for longer (extinction rates declined slower). Interestingly, the main differences we found were between the smoothest (sanded) substrates and all other rougher textures, suggesting that epiphytes may need just a small amount of roughness to adhere. However, we recognize that because we used different approaches to achieve the experimental rugosity gradient (sanding, chainsaw, parallel grooves, and parallel grooves plus angled grooves), we cannot parse apart the effects of experimental approach from resulting rugosity differences.

We observed subsequent recruitment of epiphytes after our first survey point, wherein the abundance of epiphytes *increased* over time. We did not include subsequent recruits in any analyses, but anecdotally observed that 5/13 or 38% of the new recruitment occurred on substrates of the roughest texture (R4) (**Figure 2**). We fully acknowledge that we cannot distinguish between post-seed application natural recruitment and late-germination of experimentally applied seeds, so we leave further exploration of recruitment dynamics to future studies. Supply-side ecology may drive epiphyte establishment, but this remains to be rigorously tested experimentally.

5.4.2 Epiphyte removal processes

Although rugosity explains some of the variation in early epiphyte survival, it is not sufficient to allow for long-term persistence of seedlings. In the end, almost all epiphytes went extinct within a year of dispersal to the substrates. Across all substrates, the survival rate of our epiphyte seedlings over a year was 0.52%, corresponding to a 99.5% mortality rate (comparing the two-month survey to the one-year survey) (**Figure 10**). Relative to the within-treatment two-month abundances, survival rates were still quite high at approximately four months (60%), declined to 35% halfway through the experiment, and reached 12% by seven months (**Figure 11**).

Although the one-year mean is much lower than both the reported mean survival of bromeliads in controlled field experiments (37%) or for bromeliad species in observational studies (9%) (Mondragon *et al.* 2015), there are several notable differences between our study and previous literature. For one, our experiment fits into neither of the study type categories reviewed in Mondragon *et al.* 2015. Field experiments thus far have mostly been highly controlled with respect to adhesion; almost all germination studies use glue or tape to mount epiphytes in the field, ensuring removal processes are not responsible for the epiphyte seedling death (e.g., Zotz & Vollrath 2002). We argue that removal is one of the most important natural processes in this bottleneck stage, so is important to incorporate. Second, our experiment tracks very early on in ontogeny, truly in the first year of an epiphyte seedling's life. Previous seedling mortality literature almost exclusively uses epiphytes that are at least one year old already (e.g., Zotz & Vollrath 2002; Júnior *et al.* 2019). Again, we argue that in nature, the epiphytes likely would not have even made it to that stage, so we did not pre-germinate any of the seeds prior to dispersal. The only other study that we know of which experimentally tests the effects of substrate microsite (and fungal inoculum) on epiphyte germination processes *in situ* is Shao et al. (2017). In that experiment, focused on one orchid species, the authors showed that *without* added fungal inoculum and adherence or protection from removal processes, seeds had a 0% germination rate (Shao et al. 2017). Thus, our experiment serves as an important proof-of-concept for *in situ* epiphyte germination experiments: we show that neither human-aided fungal inoculation, adherence, nor pretreatment are necessary for initial establishment. In fact, *in situ* germination processes *per se* may be less of a bottleneck than previously suggested (Mondragón et al. 2015). Instead, we suggest the more important bottleneck for epiphyte establishment is survival within the first year.

The mechanisms driving the high mortality rate in the field are likely removal via wind and rain. Early in the experiment, we observed several examples of epiphyte seedlings dangling off the edges of the substrates just at the edge of the experimental grooves (**Figure 12**). This pattern, though of course untested, is consistent with heavy rainfall, which would have led to rivulets of water washing across the substrates parallel to the grooves. Rainfall has not previously been identified as a major cause of epiphyte mortality; in fact, drought has been implicated as the major cause of mortality in several experiments (Winkler *et al.* 2005; Benzing 2008; López-Villalobos *et al.* 2008; Zotz 2016; but see Cascante-Marín *et al.* 2008). However, many of these experiments have occurred in seasonally dry or dry forests; our field site not only receives light rain almost daily year-round, including in the “dry season” (Ortega & Spicer pers. obs.), but even in the dry season humidity remains very high (**Table 1**). Epiphyte mortality due to either drought or rainfall likely varies by substrate orientation as well; because all of our substrates were horizontal to the ground, evaluation of this variability is left to future studies. We also observed likely evidence of heavy wind-caused mortality; after a known high-wind and -rain storm (J. Ortega pers. obs.), one of our experimental substrates had broken in half with a large branchfall. All epiphyte seedlings observed on the substrate in the previous survey were gone by the time the next survey occurred. Typhoons are likely a driver of epiphyte community dynamics in Taiwan, as well as Puerto Rico and the southeastern United States (Oberbauer et al. 1996, Robertson and Platt 2001, Hsu et al. 2018). Branchfall and branch break can be a cause of epiphyte mortality, especially because epiphytes do not seem to survive for more than a few months on the forest floor (Matelson *et al.* 1993; López-Villalobos *et al.* 2008; Sarmento Cabral *et al.* 2015; but see Pett-Ridge & Silver 2019). Branchfall has been suggested as an underappreciated potential driver of epiphyte community dynamics, and merits further study (Matelson et al. 1993, Sarmento Cabral et al. 2015, Nadkarni and Kohl 2018). Litterfall, pathogens, and herbivory may all contribute to early epiphyte seedling mortality, but none of these mechanisms have been well-tested experimentally.

5.5 Conclusions

Epiphyte ecology is poorly understood in comparison to terrestrial plant ecology; the early stages of ontogeny are key bottlenecks to the establishment of diverse epiphyte assemblages. Here we experimentally demonstrate, *in situ*, that substrate texture can be an important driver of epiphyte establishment—a difference that lasts at least six months. However, we also show almost 100% mortality of juvenile epiphytes within a year. Thus, we suggest that removal dynamics, rather than germination processes, are more likely to drive patterns of epiphyte community assembly. In particular, we encourage future field experiments to test the mechanisms of mortality in the first year of an epiphyte's life. Epiphyte ecology *in situ* is in need of further exploration to understand the survival and development of diverse epiphyte communities.

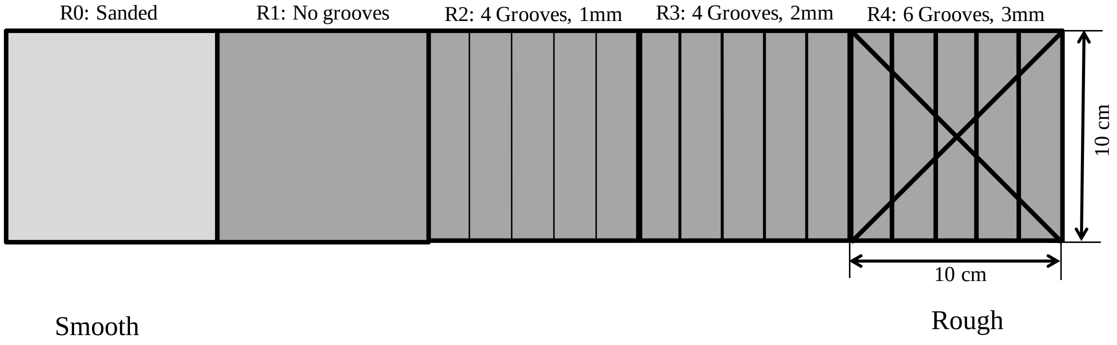
5.6 Acknowledgements

We thank Chefín and Fletcher of Santa Fé, Panama, for their assistance in the field, and Rodolfo Flores or identifying host trees. Initial design of the project was aided by critique from Gerhard Zotz and Joe Wright. We thank the Republic of Panama and MiAmbiente for permitting us to do research in Santa Fé National Park, and the PNSF guardabosques for logistical support.

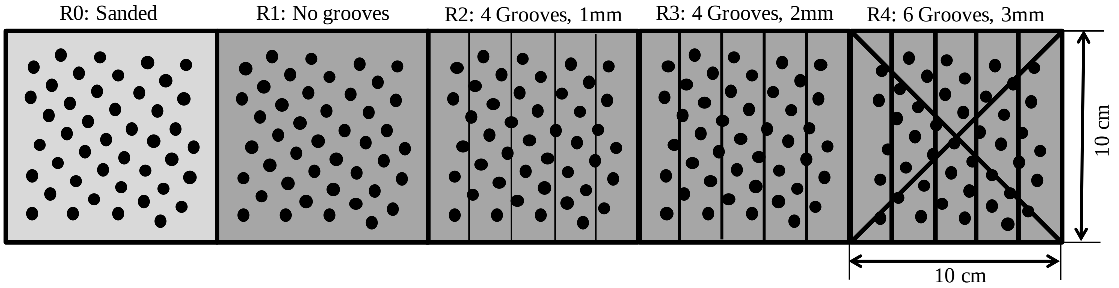
Funding for the research came from the Smithsonian Tropical Research Institute (Short-term fellowship to MES), the University of Pittsburgh Center for Latin American Studies (Fabiola Aguirre Fellowship to MES), Sigma Xi, The Scientific Research Society (Grant-In-Aid-of-Research to MES), and The American Philosophical Society (Lewis and Clark Fund for Exploration and Field Research to MES). We thank Yusan Yang for comments that improved the manuscript.

5.7 Figures and tables

A. Experimental rugosity treatments



B. Epiphyte seed application



C. Predicted relationship between rugosity and epiphyte establishment

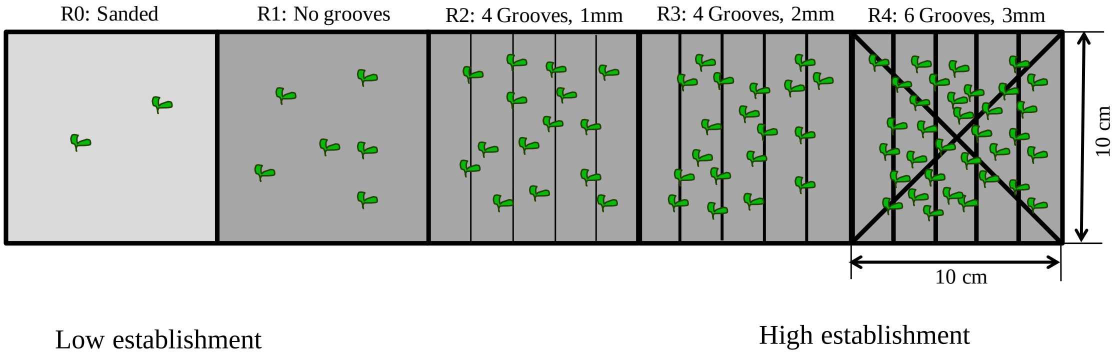


Figure 5-1. Experimental design and predictions for one plot.

One of five rugosity treatments, in random order, were applied to each 10x10cm subplot of salvaged native wood (A). We used a standardized protocol to artificially wind-disperse seeds onto all substrates (B) and predicted higher epiphyte establishment at higher rugosities (more rough substrates) (C).

Figure 5-2. Seed photographs.

Photographs of a subsample of epiphyte seeds used in the experiment, under a Nikon Eclipse 80i microscope at 10x magnification.

Figure 5-3. Epiphyte seedling photograph.

Photographs one of the subplots with a high abundance of epiphytes two months after the seeds were experimentally dispersed.

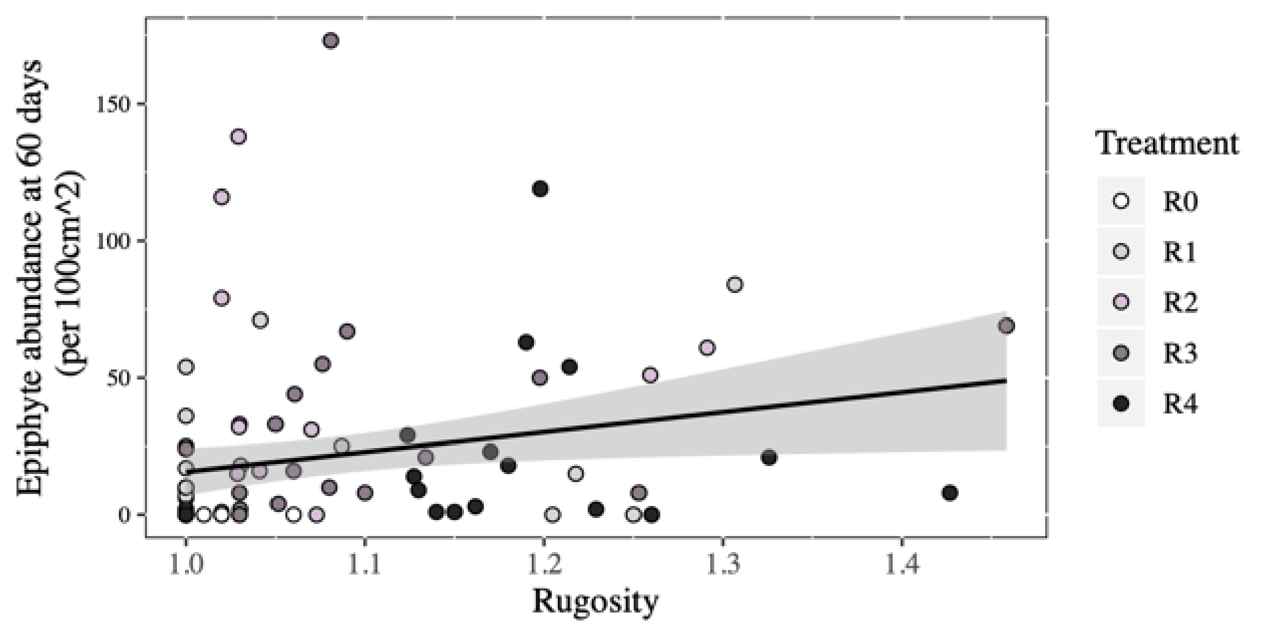


Figure 5-4. Epiphyte establishment versus continuous measured substrate rugosity.

Higher (continuous) rugosity substrates had higher epiphyte establishment after two months.

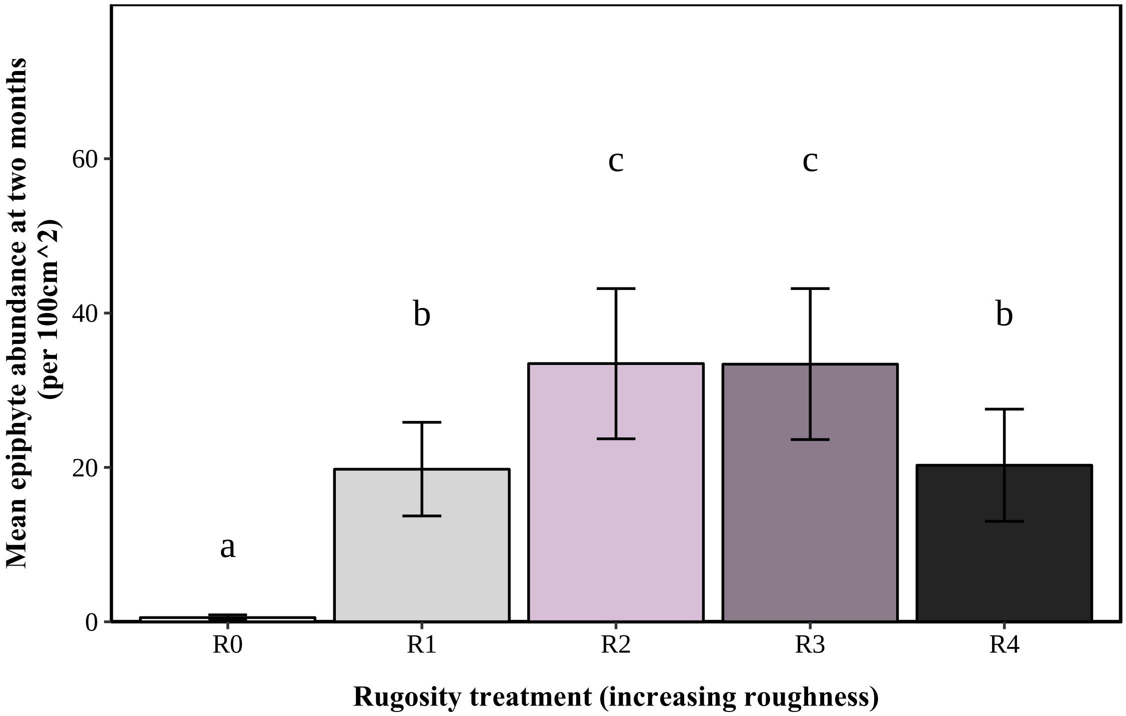


Figure 5-5. Epiphyte establishment versus categorical substrate rugosity treatments.

Higher (categorical) rugosity substrates had higher epiphyte establishment after two months. Letters refer to statistical difference from posthoc Tukey's HSD tests.

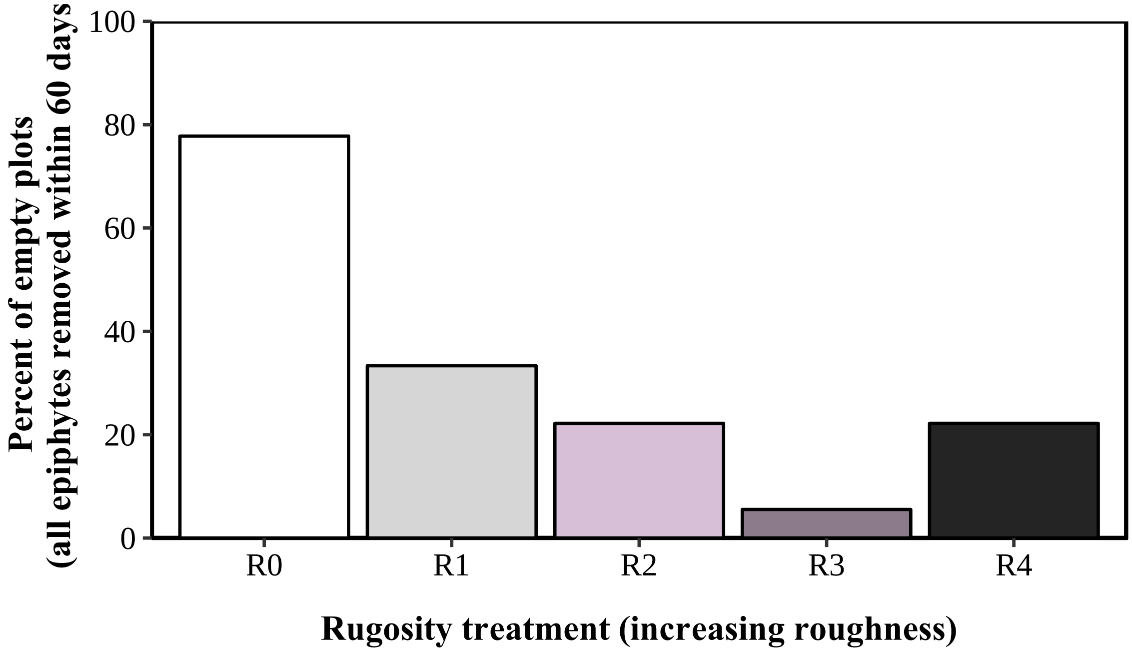


Figure 5-6. Complete epiphyte removal at two months.

Proportion of subplots with zero epiphytes. After two months, completely vacant substrates were most common in the smoothest (R0) substrates.

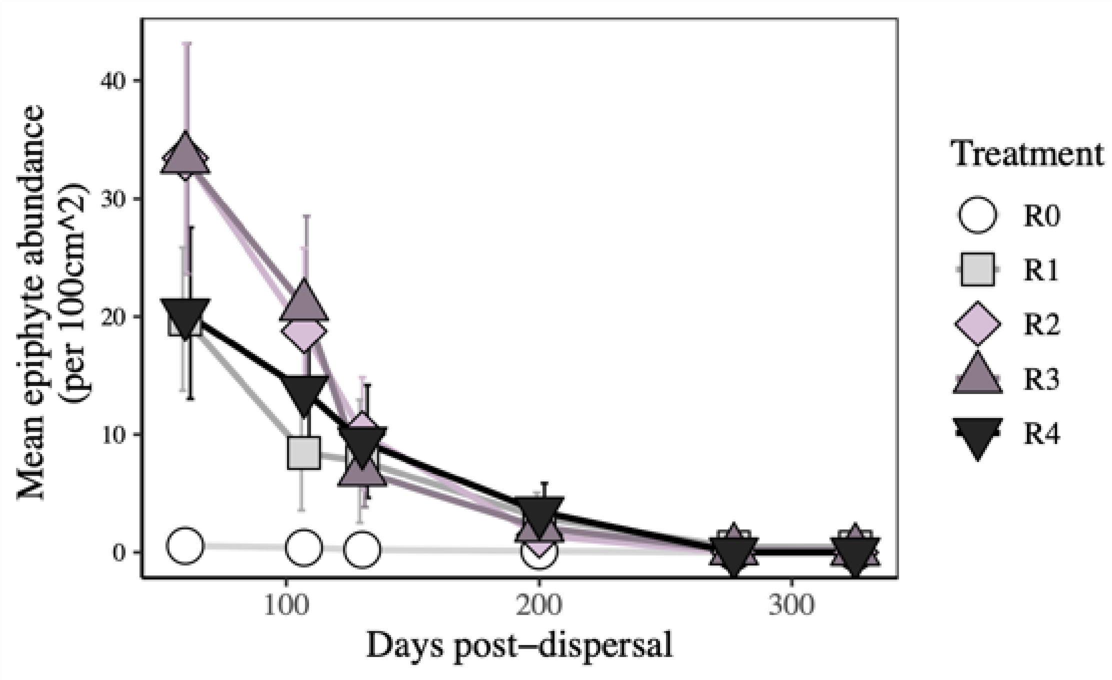


Figure 5-7. Cohort epiphyte abundances through time.

Almost all epiphytes were removed from the substrates or died in one year, but epiphytes on rougher substrates survived longer than those on the smoothest substrates.

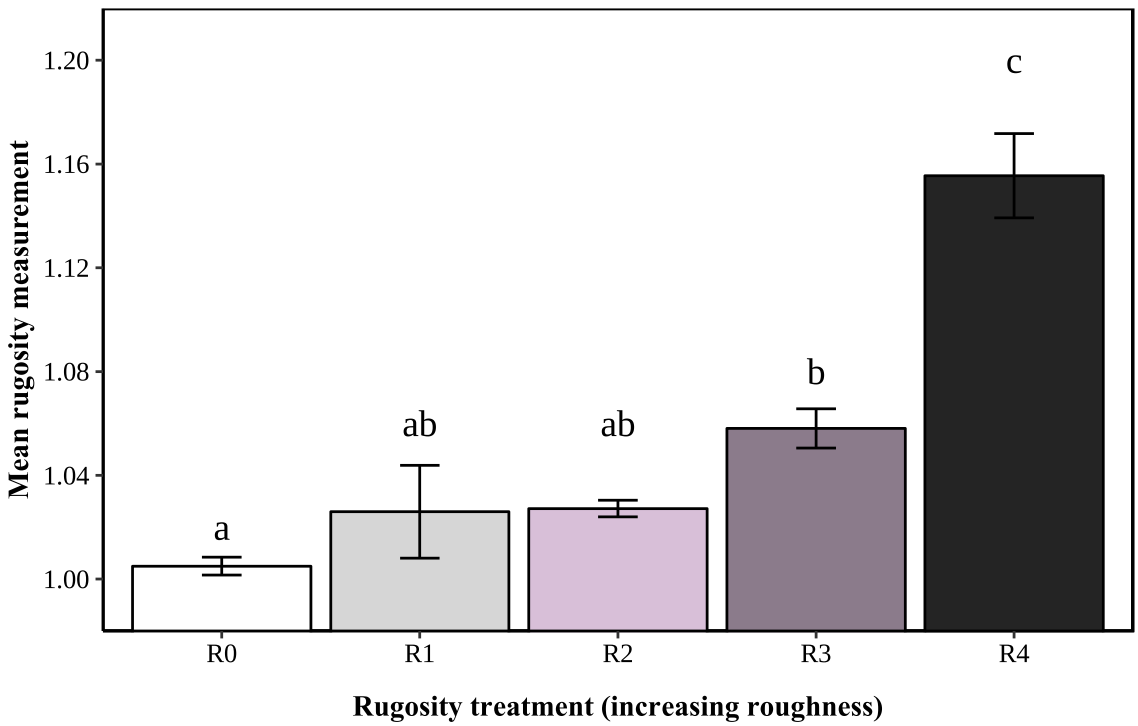


Figure 5-8. Affirmation that rugosity treatments corresponded to increasing measured rugosity.

Rugosity bins reflected measured rugosities, as measured by the straight-chain approach. Letters correspond to differences by post-hoc Tukey HSD tests.

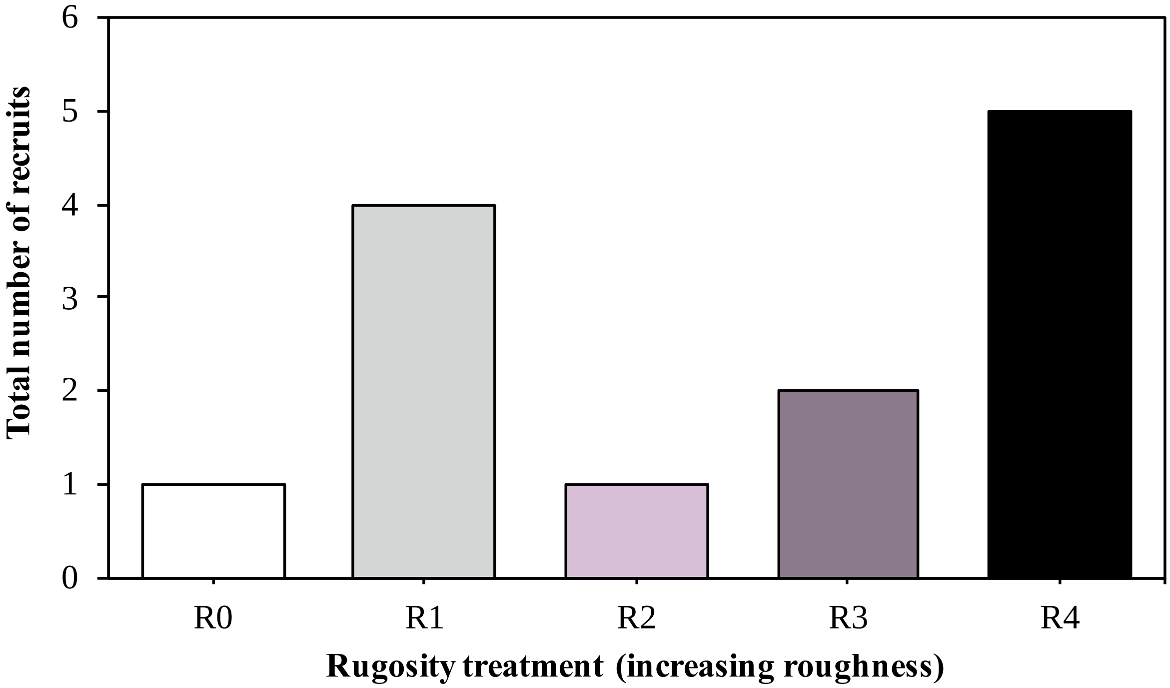


Figure 5-9. Epiphyte recruits.

Total abundance of epiphyte recruits recorded throughout the year, per experimental rugosity treatment. Recruits were recorded if there was an increase in the total abundance of epiphytes on a subplot in comparison to the first survey (day 60). A total of 13 recruits were recorded, and the highest number of recruits (5) were found on the roughest substrates (R4).

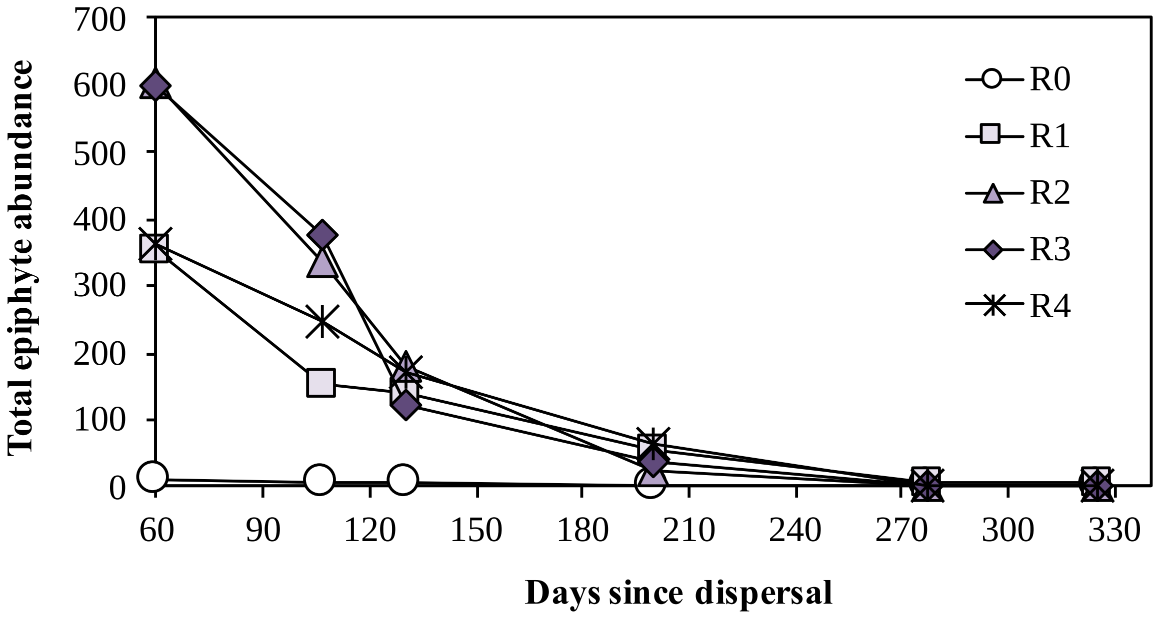


Figure 5-10. Total epiphyte abundance through time, separated by rugosity treatment.

Total epiphyte abundance, through time. Note that the last two points are both above zero (11 and 10 total epiphytes, respectively).

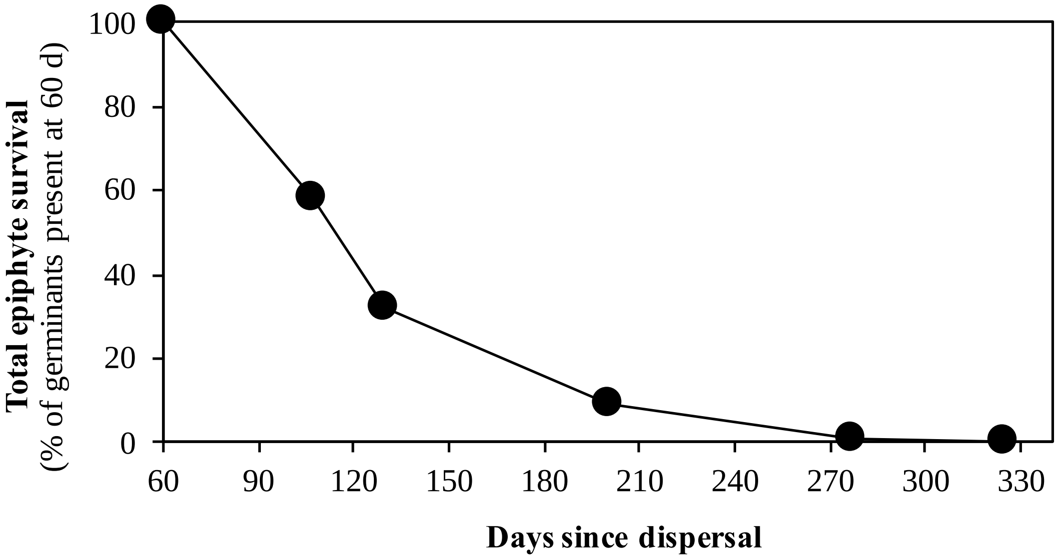


Figure 5-11. Pooled epiphyte survival, based on first survey period.

Total epiphyte survival rate through time, as a percentage of total number of seedlings counted at the first survey point (two months). Note that the last two points are both above zero (0.6% and 0.5%, respectively).

Figure 5-12. Seedling removal photograph.

Photograph of one example of epiphyte seedlings barely attached to the edge of the substrate, likely swept away by heavy rainfall.

Table 5-1. Mean temperature and relative humidity.

Mean temperature and relative humidity measures in Santa Fé National Park, April 19th, 2018-March 26th, 2019. Readings were taken every two hours and relative humidities were truncated at 100%.

	Relative Humidity (%)	**Temperature (℃)**
Minimum	64.22	16.58
Maximum	100	29.08
Mean	99.44	19.8

5.8 Bibliography

Ackerman, J. D., A. Sabat, and J. K. Zimmerman. 1996. Seedling Establishment in an Epiphytic Orchid : An Experimental Study of Seed Limitation. Oecologia 106:192–198.

ANAM. 2010. Atlas Ambiental de la República de Panamá. Editora Novo Art, S.A., Panamá.

Andrade, J. L., and P. S. Nobel. 1997. Microhabitats and Water Relations of Epiphytic Cacti and Ferns in a Lowland Neotropical Forest. Biotropica 29:261–270.

Angehr, G. R., and R. Dean. 2010. The Birds of Panama: A Field Guide. Comstock Publishing Associates.

Arditti, J. 1967. Factors affecting the germination of orchid seeds. Review Literature And Arts Of The Americas 33:1–97.

Arditti, J., and A. K. A. Ghani. 2000. Tansley Review No. 110: Numerical and physical properties of orchid seeds and their biological implications. New Phytologist 145:367–421.

Barrie, F. R., C. Ramos, O. O. Ortiz, I. Pérez, and G. Mcpherson. 2019. Five New Species of Eugenia (Myrtaceae) from Panama. Novon: A Journal for Botanical Nomenclature 24:333–342.

Barton, K. 2019. MuMIn: Multi-Model Inference, Version 1.43.6:1–75.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1:1–23.

Batista, J. E. G., and S. A. Mori. 2017. Eschweilera correae (Lecythidaceae), a new species from the cloud forests of Panama and Costa Rica. Brittonia 69:340–346.

Benzing, D. H. 1990. Vascular epiphytes: general biology and related biota. Cambridge University Press, Cambridge, UK.

Benzing, D. H. 2008. Vascular epiphytes: General biology and related biota. Cambridge University Press.

Boelter, C. R., C. S. Dambros, H. E. M. Nascimento, and C. E. Zartman. 2014. A tangled web in tropical tree-tops: Effects of edaphic variation, neighbourhood phorophyte composition and bark characteristics on epiphytes in a central Amazonian forest. Journal of Vegetation Science 25:1090–1099.

Burns, K. C. 2007. Network properties of an epiphyte metacommunity. Journal of Ecology 95:1142–1151.

Cáceres-González, D. A. 2013. Guzmania panamensis (Bromeliaceae) – a new species from Talamanca Mountain in Veraguas province, Western Panama. PhytoKeys 25:69–74.

Cáceres-González, D. A., and A. Ibáñez. 2014. Pitcairnia albifolia (Bromeliaceae), a new species from the Talamanca Mountains in Veraguas Province, Panama. Phytotaxa 172:46–50.

Callaway, R. M., K. O. Reinhart, G. W. Moore, D. J. Moore, and S. C. Pennings. 2002. Epiphyte host preferences and host traits : mechanisms for species-specific interactions:221–230.

Cascante-Marín, A., J. H. D. Wolf, J. G. B. Oostermeijer, and J. C. M. Den Nijs. 2008. Establishment of Epiphytic Bromeliads in Successional Tropical Premontane Forests in Costa Rica. Biotropica 40:441–448.

Correa, S., and G. Zotz. 2014. The influence of collecting date, temperature and moisture regimes on the germination of epiphytic bromeliads. Seed Science Research 24:353–363.

Cortes-Anzures, B., A. Corona-López, V. H. Toledo-Hernández, S. Valencia Díaz, and A. Flores-Palacios. 2017. Branch mortality influences phorophyte quality for vascular epiphytes. Botany.

Coxson, D. S., and N. M. Nadkarni. 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. Pages 495–543 Forest Canopies.

Díaz, S. V., and V. Elsa. 2007. Factores ambientales que influyen en la germinación de semillas de orquídeas y bromelias epifitas.

Flores, E. E., J. De la Cruz, B. Peña, V. De Gracia, I. Cisneros, and J. Ortega. 2015. Geographic distribution: Craugastor bransfordii. Herpetological Review 46:376.

Gentry, A. H., and C. Dodson. 1987a. Contribution of nontrees to species richness of a tropical rainforest. Biotropica 19:149–156.

Gentry, A. H., and C. H. Dodson. 1987b. Diversity and biogeography of Neotropical vascular epiphytes. Annals of the Missouri Botanical Garden 74:205–233.

Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. Annual Review of Phytopathology 40:13–43.

González Cáceres, D. A., K. Schulte, M. Schmidt, and G. Ziz-Ka. 2011. A synopsis of the Bromeliaceae of Panama, including new records for the country. Willdenowia 41:357–369.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York, NY.

Hertz, A., S. Lotzkat, A. Carrizo, M. Ponce, G. Köhler, and B. Streit. 2012. Field notes on findings of threatened amphibian species in the central mountain range of western Panama. Amphibian and Reptile Conservation 6:9–30.

Hietz, P., M. Winkler, S. Scheffknecht, and K. Hülber. 2012. Germination of Epiphytic Bromeliads in Forests and Coffee Plantations : Microclimate and Substrate Effects. Biotropica 44:197–204.

Holwerda, F., L. A. Bruijnzeel, L. E. Muñoz-Villers, M. Equihua, and H. Asbjornsen. 2010. Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. Journal of Hydrology 384:84–96.

Hsu, R. C. C., J. H. D. Wolf, J. M. Tsai, and Y. C. Lin. 2018. The long-term effect of typhoons on vascular epiphytes in Taiwan. Journal of Tropical Ecology 34:308–315.

Júnior, D. E., M. H. Sasamori, C. T. Petry, S. Santos, and A. Droste. 2019. Original Paper / Artigo Original Host tree bark traits and development of reintroduced Cattleya intermedia (Orchidaceae) plants in Southern Brazil Abstract The traits of the bark of host trees can influence the distribution and development of epiphytes .

Kelly, D. L., E. V. J. Tanner, E. M. Nic Lughadha, and V. Kapos. 1994. Floristics and Biogeography of a Rain Forest in the Venezuelan Andes. Journal of Biogeography 21:421–440.

Kennedy, H., and R. Flores. 2015. Calathea galdamesiana (Marantaceae), a new endemic Panamanian species. Journal of the Botanical Research Institute of Texas 9:319–323.

Laube, S., and G. Zotz. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte? Functional Ecology 17:598–604.

López-Villalobos, A., A. Flores-Palacios, and R. Ortiz-Pulido. 2008. The relationship between bark peeling rate and the distribution and mortality of two epiphyte species. Plant Ecology 198:265–274.

Luckhurst, E., and K. Luckhurst. 1978. Analysis of the Influence of Substrate Variables on Coral Reef Fish Communities. Marine Biology 323:317–323.

Mack, R. N., and J. L. Harper. 1977. Interference in Dune Annuals: Spatial Pattern and Neighbourhood Effects. Journal of Ecology 65:345–363.

Matelson, T. J., N. M. Nadkarni, and J. T. Longino. 1993. Longevity of Fallen Epiphytes in a Neotropical Montane Forest. Ecology 74:265–269.

Mehltreter, K., A. Flores-Palacios, and J. G. García-Franco. 2005. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. Journal of Tropical Ecology 21:651–660.

Mendieta-Leiva, G., and G. Zotz. 2015. A conceptual framework for the analysis of vascular epiphyte assemblages. Perspectives in Plant Ecology, Evolution and Systematics 17:510–521.

Meyer, N. F. V, R. Moreno, C. Sutherland, J. A. De, R. Reyna-hurtado, S. Valdes, and P. A. Jansen. 2019. Effectiveness of Panama as an intercontinental land bridge for large mammals 0:1–13.

Meyer, N., R. Moreno, and P. A. Jansen. 2013. Distribution and conservation status of Baird's tapir in Panama. Tapir Conservation 22:10–13.

Ministerio de Economía y Finanzas. 2001. Por el cual se declara el Parque Nacional Santa Fe, en el distrito de Santa Fe, provincia de Veraguas. Page 28 diciembre. Panama.

Mondragon, D., and L. M. Calvo-Irabien. 2006. Seed Dispersal and Germination of the Epiphyte Tillandsia Brachycaulos (Bromeliaceae) in a Tropical Dry Forest, Mexico. The Southwestern Naturalist 51:462–470.

Mondragon, D., T. Valverde, and M. Hernandez-Apolinar. 2015. Population ecology of epiphytic angiosperms: A review. Tropical Ecology 56:1–39.

Moreno, R., and N. Meyer. 2014. Distribution and conservation status of the White-lipped peccary (Tayassu pecari) in Panama. Suiform Soundings Newsletter of the IUCN / SSC Wild Pig 13.

Nadkarni, N. M. 1984. Biomass and mineral capital of epiphytes in an Acer macrophyllum community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Canadian Journal of Botany 62:2223–2228.

Nadkarni, N., and K. D. Kohl. 2018. Elements of disturbance that affect epiphyte vitality in a temperate rainforest: an experimental approach. Journal of Plant Ecology 26:62–71.

Nadkarni, N. M., and T. J. Matelson. 1989. Bird Use of Epiphyte Resources in Neotropical Trees. Condor 91:891–907.

Oberbauer, A. S. F., K. Von Kleist, K. R. T. Whelan, and S. Koptur. 1996. Effects of Hurricane Andrew on epiphyte communities within cypress domes of Everglades National Park. Ecology 77:2–4.

Ortiz, O. O., and T. B. Croat. 2016. New species of Anthurium section Calomystrium from costa rica and Panama. Phytotaxa 257:34–50.

Ortiz, O. O., R. Flores, G. Mcpherson, J. F. Carrión, E. Campos-Pineda, and R. M. Baldini. 2019. Additions to the flora of Panama, with comments on plant collections and information gaps. Check List 15:601–627.

Perez, R., C. L. Richards-zawacki, A. R. Krohn, M. Robak, E. J. Griffith, H. Ross, B. Gratwicke, R. Ibáñez, and J. Voyles. 2014. Short Communication Field surveys in Western Panama indicate populations of Atelopus varius frogs are persisting in regions where Batrachochytrium dendrobatidis is now enzootic 8:30–35.

Pett-Ridge, J., and W. L. Silver. 2002. Survival, Growth, and Ecosystem Dynamics of Displaced Bromeliads in a Montane Tropical Forest. Biotropica 34:211–224.

R Core Development Team, 3.6.0. 2019. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RStudio Team, 1.0.153. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rázuri-Gonzalez, E., and B. J. Armitage. 2019. The Trichoptera of Panama. XI. Three new species of caddisflies in the genus Smicridea McLachlan (Trichoptera: Hydropsychidae) from Omar Torrijos and Santa Fe National Parks. Insecta Mundi 710.

Robertson, K. M., and W. J. Platt. 2001. Effects of Multiple Disturbances (Fire and Hurricane) on Epiphyte Community Dynamics in a Subtropical Forest, Florida, U.S.A.1. Biotropica 33:573.

Ruiz-Cordova, J. P., V. H. Toledo-Hernández, and A. Flores-Palacios. 2014. The effect of substrate abundance in the vertical stratification of bromeliad epiphytes in a tropical dry forest (Mexico). Flora: Morphology, Distribution, Functional Ecology of Plants 209:375–384.

Sarmento Cabral, J., G. Petter, G. Mendieta-Leiva, K. Wagner, G. Zotz, and H. Kreft. 2015. Branchfall as a Demographic Filter for Epiphyte Communities: Lessons from Forest Floor-Based Sampling. Plos One 10:e0128019.

Scheffers, B. R., B. L. Phillips, and L. P. Shoo. 2014. Asplenium bird’s nest ferns in rainforest canopies are climate-contingent refuges for frogs. Global Ecology and Conservation 2:37–46.

Shao, S. C., K. S. Burgess, J. M. Cruse-Sanders, Q. Liu, X. L. Fan, H. Huang, and J. Y. Gao. 2017. Using in situ symbiotic seed germination to restore over-collected medicinal orchids in Southwest China. Frontiers in Plant Science 8:1–10.

Sheldon, K. S., and N. M. Nadkarni. 2013. Spatial and temporal variation of seed rain in the canopy and on the ground of a tropical cloud forest. Biotropica 45:549–556.

Spicer, M. E., H. Mellor, and W. P. Carson. 2019. Seeing beyond the trees: a comparison of tropical and temperate plant growth-forms and their vertical distribution. Ecology in press.

Van Stan, J. T., and T. G. Pypker. 2015. A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. Science of The Total Environment 536:813–824.

Stuntz, S., C. Ziegler, U. Simon, and G. Zotz. 2002. Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. Journal of Tropical Ecology 18:161–176.

Valencia-Díaz, S., A. Flores-Palacios, V. Rodríguez-López, E. Ventura-Zapata, and A. R. Jiménez-Aparicio. 2010. Effect of host-bark extracts on seed germination in Tillandsia recurvata, an epiphytic bromeliad. Journal of Tropical Ecology 26:571–581.

Vergara-Torres, C. A., M. C. Pacheco-Álvarez, and A. Flores-Palacios. 2010. Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. Journal of Tropical Ecology 26:563–570.

Wagner, K., G. Mendieta-Leiva, and G. Zotz. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. AoB PLANTS 7:plu092–plu092.

Winkler, M., K. Hulber, P. Hietz, K. Hülber, and P. Hietz. 2005. Effect of canopy position on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. Annals of Botany 95:1039–1047.

Woods, C. L. 2017. Primary ecological succession in vascular epiphytes: The species accumulation model. Biotropica 49:452–460.

Wyse, S. V., and B. R. Burns. 2011. Do host bark traits influence trunk epiphyte communities? New Zealand Journal of Ecology 35:296–301.

Zotz, G. 2016. Plants on Plants – The Biology of Vascular Epiphytes. Springer International Publishing, Switzerland.

Zotz, G., and B. Vollrath. 2002. Substrate preferences of epiphytic bromeliads: an experimental approach. Acta Oecologica 23:99–102.

APPENDIX A: CHAPTER 2 SUPPLEMENTAL REVIEW METHODS

We chose two prominent temperate forest research journals to test for growth-form publication bias in the Eastern Deciduous Forest Biome: the *Canadian Journal of Forest Research* (CJFR) and *Forest Ecology and Management* (FEM). We searched directly on each journals' press site and narrowed the study by 1) selecting only articles published between January 1st, 2000, and January 1st, 2017; 2) key word searching eastern OR deciduous AND North America; 3) excluding articles that did not collect or analyze data from North America; and 4) excluding articles with no plant data. This yielded 737 articles from CJFR and 1337 articles from FEM. We read the abstract and title of each article and determined which of four major growth-forms common in temperate forests (tree, shrub, herb, or vine) was the focus of the article. If the focus could not be determined immediately from the abstract and title, we searched the results, introduction, and methods. For each article, we noted: 1) whether data were included for each of the four growth-forms (present/absent); 2) whether the data were qualitative or quantitative; and 3) which growth-form, if any, was the primary focus of the paper.