

PLANT POPULATION RESPONSES FOLLOWING REINTRODUCTION TO HUMAN-
MODIFIED LANDSCAPES

By

Christopher Russell Warneke

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Plant Biology – Doctor of Philosophy
Ecology, Evolutionary Biology and Behavior – Dual Major

2021

PUBLIC ABSTRACT

PLANT POPULATION RESPONSES FOLLOWING REINTRODUCTION TO HUMAN-MODIFIED LANDSCAPES

By

Christopher Russell Warneke

Ecological restoration, the process of assisting ecosystem recovery following damage by humans, is a critically important practice across the globe. However, the outcomes of restoration actions are notoriously variable, making it challenging to reliably achieve restoration goals. In this dissertation, I focus on plant populations that have been reintroduced as part of restoration in two settings: (1) a landscape affected by a large, human-caused fire and (2) a set of fragmented landscapes. Habitat fragmentation and/or degradation resulting from modified disturbance regimes (like wildfire) are leading causes of plant population decline and local extinctions. In response to these losses, plant population reintroduction efforts are common in ecological restoration. Through four studies, I look at how reintroduced plant populations function in these settings through the processes of plant establishment, seed dispersal, and population growth.

I conducted two studies in a recently-burned forest, in which fire was historically rare, in Hawai'i: (1) a study on plant-soil feedbacks of two locally-abundant tree species and (2) a study on early establishment of one species after the fire. The interactions between plants and microbes, that occur in the soil ("plant-soil feedbacks" or PSFs), can influence where and how plants grow. Although PSFs are known to be ecologically-important and fire is known to affect both plants and microbes, little is known about fire affects PSFs. In study 1, I investigated PSFs for two tree species in the bean family, both inside and outside of a recently burned area. I found that both tree species grew better in soil (and, thus, microbes) from under a tree of the same species, relative to soil from under a different species. Additionally, I found that fire can affect

how these PSFs work between these two tree species, which may lead to one species becoming more abundant than the other after a fire. In study 2, I examined how local environmental conditions modify seedling establishment of one tree species reintroduced by seed after fire. I found that elevation, the amount of shade, and the amount of grass were all important for seedling establishment. Together, these two studies show that restoration should account for soil microbes and local conditions (like amount of grass) in selecting areas for plant reintroduction.

To examine plant reintroduction in fragmented landscapes, I conducted two studies in a habitat fragmentation experiment in South Carolina: (1) a study on seed dispersal via wind and (2) a study on how developing populations grew. For both studies, I examined developing populations at four distances from edges of habitat patches, and I did this in both connected and isolated patches and high and low edge-to-area ratio patches. I found that wind-driven seed dispersal distances are greater in patch centers and that seed dispersal is greater in the direction of the edge of the patch. Patch connectivity and edge-to-area ratio did not affect these dispersal patterns. In the population growth study, I examined populations 7 years after reintroduction and looked at both how the number of plants varied by location and what might be responsible for these differences. I found that, for some plant species, patch edges matter, but that patch connectivity and edge-to-area ratio do not. I found that edges may operate through factors like the amount of shade, which is higher at patch edges than centers. These two studies show that fragmentation modifies plant populations and their processes following reintroduction.

Together, my findings illustrate some ways that habitat fragmentation and fire affect plant reintroduction. My work contributes to the growing field of interpreting variation in ecological restoration outcomes and may help to guide successful restoration going forward.

ABSTRACT

PLANT POPULATION RESPONSES FOLLOWING REINTRODUCTION TO HUMAN-MODIFIED LANDSCAPES

By

Christopher Russell Warneke

Ecological restoration, the process of assisting ecosystem recovery following damage by humans, is a critically important practice across the globe. However, the variability in outcomes of restoration action is notoriously large, making it challenging to reliably achieve restoration goals. In this dissertation, I focus on the responses of plant populations that have been reintroduced as part of restoration in two settings: (1) a landscape affected by a large, human-caused fire and (2) experimentally fragmented landscapes. Habitat fragmentation/degradation resulting from altered disturbance regimes (including fire) are leading causes of biodiversity decline and result in local extirpations. In response to these losses, reintroduction efforts are common in ecological restoration. Through four studies, I evaluate reintroduced plant population responses through the processes of plant establishment, seed dispersal, and population growth.

I conducted two studies in a recently-burned subtropical upland forest system, in which fire was historically infrequent, in Hawai'i: a study on plant-soil feedbacks of two locally-dominant tree species and a study on early establishment of one species post-fire after reintroduction. The interactions between plants and microbes, as mediated by the soil ("plant-soil feedbacks" or PSFs), can influence where and how plants establish from seed. Despite the importance of PSFs and their potential to be altered by fire, little is known about how fire affects PSFs. I investigated PSFs for two nitrogen-fixing leguminous trees inside and outside of a recently burned area. I found that there were largely positive PSF relationships, where both species perform better in soil of conspecifics, relative to heterospecifics. Additionally, I found

that fire can reduce the strength of pairwise PSFs between these species, which may result in altered patterns of local coexistence. In the other study, I examined how local environmental conditions modify seedling establishment of a dominant tree species, reintroduced by seed post-fire. I found that elevation was of overarching importance for plant establishment, with context-dependent effects of tree canopy and grass cover, depending on elevation. Together, these two studies show post-fire restoration in this system should account for the soil microbial community and environmental context when selecting areas for plant reintroduction.

To examine plant reintroduction in fragmented landscapes, I conducted two studies in a habitat fragmentation experiment in South Carolina: (1) a study on abiotic seed dispersal and (2) a study on recruitment patterns of developing populations. For both studies, I examined developing populations at four distances from patch edges in connected and isolated patches and high and low edge-to-area ratio patches. I found that local-scale seed dispersal distances are greater in patch centers and that dispersal is more directional towards patch edges, but that patch connectivity and edge-to-area ratio did not affect these patterns. In the recruitment study, I examined populations 7 years after reintroduction and looked at both how the number of recruited individuals varied and how a suite of mechanisms may drive differences. I found that, for some species, edges mediate recruitment patterns, but that patch connectivity and edge-to-area ratio do not. In terms of mechanisms for these patterns, I found that edges may operate through factors like canopy cover, which is higher at patch edges than centers. These two studies show that fragmentation does modify plant populations and processes following reintroduction.

Together, my findings illustrate how aspects of habitat fragmentation and disturbance affect plant reintroduction efforts. My work contributes to the growing field of interpreting variation in restoration outcomes and may help to guide successful restoration going forward.

To the hope that the world can change. You make so much possible.

ACKNOWLEDGEMENTS

There are so many people and organizations to thank! This dissertation has taken place during ~20% of the time I have been alive to this point, and so many people have been so helpful during that time. I will do my best to thank them here. It takes a village to raise a child, and in some ways, dissertations are like children; they grow and change, they aren't always what you expect they will be, they have a life of their own, and at some point, you let them loose into the world. Thank you to all who have been with me for any part of this journey and for helping me raise this child. Being that life and science overlap, people often fall in multiple categories, but I have only mentioned people here once, so you'll just have to deal with that!

To Lars Brudvig, thanks for being a great advisor. You always managed to find the time to answer any questions and provide feedback on anything I was working on. Your enthusiasm and excitement for science and ecology is contagious. I have grown a lot under your mentorship and appreciate all the work that you have done to facilitate this growth.

To the remaining members of my committee: Marjorie Weber, Doug Landis, and Jen Lau. Marjorie for having a lab that was like a secondary lab for me and for your care for both the science and the non-science parts of being in academia. Doug for always bringing a different perspective to the table and for challenging me on my communication to non-plant-people. Jen for careful feedback on the science and the perspective of how the setup of projects carries through to their end. Committee meetings with you all were something to look forward to.

To the members of the Brudvig Lab group over the years. Lab membership ebbs and flows, and it has been great to science with all of you during the fleeting time we have had together. To Anna Groves, for being a physical manifestation of the importance of community and for finding ways to do all of the things, even if you didn't have time for them. To Chad

Zirbel, for always being up for a discussion, be it about statistics or the catching of digital mice. To Nash Turley for being a role model in how to dabble well in many things. To Jonathan Bauer, for being excited about everything ecological, even the ending of the world. To Emily Conway for all the discussions about baking and for introducing me to the best dumpsters in the Lansing area. To Brandon Latorre for showing me that there is some value to Pokémon. To Toby VCS for being vocal about workplace diversity, equity, and inclusion and for the valuable feedback on presentations. To Riley Pizza for being the most social person in the lab, during a pandemic, and joining all of the grad groups. To the many Michigan-based postdocs, techs, and undergrads, with whom I spent less time, but who nonetheless helped bring the lab to life.

Thanks to Barbara Bloemers, Pat Resler, Elise Zipkin, and most especially to Kay Holekamp, for your work helping the EEB program to be the best it can be; EEB as a program is a great asset to MSU, but more importantly, it is an asset to the students that are members. EEB allows its students to better themselves personally and professionally and your investment in the program is directly responsible for that. EEB is one of the reasons that I came to MSU, and I am glad that I did.

To the Corridor Group, which, among others, contains Ellen Damschen, Nick Haddad, Doug Levey, and Trevor Caughlin, thank you for your intellectual discussion and collegiality. All of the work that we do and have done together has been better because of collaboration.

To the herbaria that I have used for research during my time here. Collections are incredibly important but often underappreciated. I would like to thank them here. These are (listed alphabetically by code): BISH, CHIC, COLO, EMC, F, HAVO, HAW, MICH, MSC, PTBG, SRELH, USCH, WIS. Thanks especially to MSC for being my home herbarium over these past few years.

To all of the people and organizations that have funded my work over the years. During the dissertation, I have received funding or other support from MSU and the College of NatSci, from PLB and Dr. Paul Taylor's Travel Endowment, from the EEB program, and from the DOE, NPS, NSF, USDA-ARS, USDA-FS, and USGS. Thank you to the taxpayers and everyone who has funded both my science and science at large.

To the students I have mentored in an official capacity through the NSF REU program while at MSU. Thanks to Lindsey Kemmerling for your strong work ethic and for helping me to better understand how music can shape lives. Thanks to Paige Barnes for seeing both the importance of large mammals and of plants at the same time. Thanks to Carolyn Graham for your collaborative spirit and for not only listening, but also understanding.

To the ~35 roommates that I have lived with during my time at MSU. It turns out that moving across the country into large field houses, you get to meet a lot of people and you can learn a lot from them! Thanks to Brian St. Aubin for being a constant and grounding presence at the Allen Street house for four years.

To the community of people who I worked with and alongside at SRS. South Carolina, especially in the summer, is not the easiest place to be. The Savannah River Site is both one of the best as well as one of the most challenging places to work. Working and living with you all over the years, I know you will understand the many different layers of feelings that I have about SRS and South Carolina in a way that other people will not. I hope that, as we all continue on in our lives, we will, as the saying goes, have fun, be safe, and stay hydrated. Thanks to Quinn Sorenson being the perfect foil for any situation in which I was also involved and for being the other parental figure in the house with me; your presence provided a balance that made life at the Ranch worth having, and I will miss our conversations, both serious and silly. To Melissa Burt

for having the right words to go with any work situation. Your constant positivity paired with the right amount of cynicism was an asset for any field season. To Sabrie Breland for rocking the double middle name and for the great talks about taxonomy and identification of the southeastern flora. To Josh Zajdel for all of the birds and friendship, even though we disagree on taxonomic issues. To Elise Hanson, for being a peaceful presence in the lives of those around you, even when you don't feel at peace yourself; your kindness is your strength. To the many voices on the radio, for helping to pass the time and allowing us to spin stories about you and your lives on site. To the many undergrads and technicians that worked on the Corridor Project over my time there. We can't do it without you. Meg Kargul introduced me to the best and cutest of the founder species (*Carphephorus bellidifolius*). Matteo Cleary has been a source of constant enthusiasm for all life. Alex Goke has tolerated all of the seed-dispersal-by-poop papers that I have sent over the years. Stephen McCann provided a goofy atmosphere wherever he went. Kai Stewart had genuine curiosity about everything. Michelle Kirchner was there for needed conversations. And, lastly, to the Tar Elves; I told you I would acknowledge your help here, and I keep my promises.

Mahalo to the many people that were there on the project in Hawai'i. Mahalo nui loa to Stephanie Yelenik for all your help with the project, the correct views on work vs life, your views on organizational structures, and for the help with career paths. To Jeff Stallman for the fun conversations about Hawaiian plants and life as a whole; as much as I hate to say that "more work is needed", I am happy that you, at least, are doing some of the work, and it has been a pleasure to do some of that work with you. A Clarice Esch, gracias por tu amistad y por vivir como una ciudadana del mundo. To Gabe Runte for being enthusiastic and accepting of both people and situations as they are. To Taylor Saunders, you may think that Maui nō ka 'oi, but

really, it is the people that make a place the best, and I am glad you joined us in Volcano. To Rosanise Odell for your fight against the powers of the world, be they the people maintaining society's capitalistic structures or the ants in the kitchen; you do make a difference in your endeavors. To the other interns, scientists, and volunteers in HAVO housing, for the community that we had. And, lastly, mahalo also to all of the kama'āina who adopted me into their lives during my time on island; you embody the spirit of aloha.

To Kay Havens and Pati Vitt. Kay, your support through the years has continued to amaze me, and I thank you for being there for all this time. You are still who I want to be when I grow up. Pati, thank you for your continued support and enthusiasm as well. I don't know if you remember the last conversation we had before you drove up to Door County to survey CIPI in 2015, but I have carried it with me through the darker times of this dissertation.

To my MSU Plant Bio Cohort. We have stayed together pretty well, and I have enjoyed our social times. I will also thank Meredith and Ravi here for the formation of our academic triumvirate, which got us through the flaming hoops of comprehensive exams and has been beneficial both personally and professionally.

To the students in the classes that I have taught or TA'd, you have taught me things about teaching and provide inspiration that the world will continue to improve as humanity betters itself. A particular thank you to Alan Prather for giving me the freedom and flexibility to try new teaching methods and techniques and improve the Systematics Lab over the years that I taught it.

To the many friends that have been with me for the different parts of the journey of dissertation, but more importantly, on the reticulately diverging and converging trails that make up the path of life. We may come and go from each other's paths, but the light we give to each other helps shine our way forward, even if we are no longer sharing the same trail. I hope that I

have been as positive a presence in your lives as you have been in mine. To Jessa Finch, for always being forthcoming and helping me to be more so and for paving the dissertation path among our PBC cohort. To Adrienne St. Clair, for being there when I have needed you and showing me a positive path forward. To Shawna Rowe, one of the definitions of “neighbor,” per the incomparable OED, is “fellow human” and I thank you for being a good neighbor, in all of the senses of the word. To Joelyn de Lima for being the world-wise mother of our cohort and helping me to keep us all together. You may not hold the most correct view about tea, but I won’t hold that against you. To Ravi Ranjan for general enthusiasm, both in science and in life, and for providing another home when it was needed. To Meredith Zettlemoyer for being superhuman; I have never known how you do all the things that you do, and I hope that some of your superpowers have rubbed off on me during our time here. To Klara Scharnagl, you are the human personification of the sunflowers on the side of your van, and I hope that you continue to be so. To Robert Logan for understanding the benefits and drawbacks of peregrinations upon the world and for being there to bounce ideas and thoughts off of. A Serena Lotreck, por ser ti misma tan firmemente y constantemente y por los recordatorios de que una vida equilibrada es importante. To Isabela Borges for all the fascinating conversations, despite your fear of bats. To Matt Chansler for all the plant discussions and the general indignation around the various states of the world. To the other members of my PBC cohort and to the friends from Gavin House and the rest of my friends from before I came to MSU, I can’t list you all here, but I do thank you for continuing to be a part of my life. To everyone that I don’t have the space to mention, thank you also for being here. I genuinely appreciate each of you and your existence.

There are groups of people that work in the background so that we can all succeed. Thanks to the campus LBGT Resource Center and CAPS for helping me to persist and thrive

here. To the therapists that I have had at different points over the past six years, and particularly to the therapist I have been with the longest; I won't name you here for privacy reasons, but you have been instrumental in my persistence in grad school and in helping me move through the world as a better person. To the janitorial staff for keeping the building in great shape all the time and for fun conversations on late nights. To the office staff for keeping everything on the rails and ensuring that the department functions properly. To the makers of Tecnu for giving me something to help with the continual poison oak of a South Carolina field season. To the doctors, scientists, and public health experts who worked hard to shepherd the world through the covid-19 pandemic that shaped the last year and a half of this journey and will continue to shape the world for years to come; thank you for your work and for producing a safe vaccine in record time. To public libraries, which hold the keys to the universe. Thanks to the MSU Library and the public library systems of Jefferson County, CO, Aiken, SC, East Lansing and Lansing, MI, and of Hawai'i for keeping me supplied with books and other resources all the time. To the LGBTQ+ people in Michigan, South Carolina, and Hawai'i for being there as we navigate this world together. To the birding and botanical communities in the places I have lived, for creating a ready-made social network that I can join whenever I move anywhere. And thanks especially to the non-human life of the places I have lived and worked, and particularly to the birds and plants; your ability to provide an escape from the pressures of life is worth so much.

I will end with thanking my family, who have been the most integral support for me since the beginning. It is impossible to be succinct when thanking the people who have been with me the longest, so I won't even try to write what I feel in this space. This is only a small token of a much deeper gratitude. Thank you for everything. In so many ways, I would not be here without the four of you.

Land Acknowledgement

The practice of land acknowledgement is a small act in the interest of the increased sovereignty and agency of indigenous and aboriginal peoples, as well as Black people and people of color who have been dispossessed of their land. Even if acknowledgement of past and present injustices perpetuated by land theft and occupation alone is insufficient, it remains a vital part of fighting for rights, reparations, and decolonization of the lands of indigenous and aboriginal peoples.

I carried out my dissertation work in three different places, whose theft and/or occupation I will briefly acknowledge below.

During the majority of the semesters of the academic year during the course of this dissertation (2015-2021), I have worked in the Plant Biology Laboratories building on the campus of Michigan State University. The main campus of Michigan State University occupies the ancestral, traditional, and contemporary lands of the Anishinaabeg – Three Fires Confederacy of Ojibwe, Odawa, and Potawatomi peoples. The university occupies land ceded in the 1819 Treaty of Saginaw. Michigan State University is Michigan’s land-grant university, and under the Morrill Land-Grant Act of 1862 (and related acts), used funds from 235,193 acres of indigenous lands seized within the current boundaries of the State of Michigan and used to form the initial endowment of the university (Lee, 2020).

My fieldwork for Chapters 2 and 3 occurred within Hawai‘i Volcanoes National Park. The portions of the park in which I lived and worked are located in the ahupua‘a of Keauhou and Kapāpala, in the moku of Ka‘ū, on the mokupuni of Hawai‘i. The national park occupies the ancestral, traditional, and contemporary lands of the Hawaiian people. The Kingdom of Hawai‘i was forcibly and illegally overthrown in 1893 by parties of and sympathetic to the United States.

My fieldwork for Chapters 4 and 5 occurred at the Savannah River Site in South Carolina. The Savannah River Site occupies the ancestral, traditional, and contemporary lands of the Westo, Edisto Natchez-Kusso, and Yamassee peoples. The Savannah River Site resides on land coercively ceded to the government of the United Kingdom in a series of treaties concluding in 1763. It is additionally worth acknowledging that, in the formation of the Savannah River Site in 1950-1952, ~6000 people were forcibly displaced, the majority of whom were Black landowners, tenant farmers, and sharecroppers (Reed et al., 2002), who faced and whose descendants continue to face the inequities and injustices perpetrated against them by the racist policies and actions of people and institutions of the past and present.

Literature Cited

Lee, R. 2020. Morrill Act of 1862 Indigenous Land Parcels Database. *High Country News*.

Reed, M. B., M. Swanson, S. Gaither, J. W. Joseph, W. Henry, T. Fedor, and B. S. Strack. 2002. Changing Identity. Savannah River Site at 50, 134–165. U.S. Government Publishing Office, Washington, DC.

PREFACE

Nomenclature and Taxonomy

Because the taxonomy of species is always in flux, and changes with new information, I have presented below a list of the species that are involved in this study, as well as their synonyms and the rationale for their name, as used in this dissertation. Species are presented alphabetically, by genus. Common names are in English and cover the area where we worked with the species.

Hawaiian common names are also provided for the three species that occur in the islands; these names are most often used by both Hawaiian and English-speakers in the islands when referring to these species there, regardless of any English names that may exist for the species.

***Acacia koa* A. Gray**

Synonyms: *Acacia coa* Walp.; *Acacia hawaiiensis* (Rock) O. Degener & I. Degener; *Acacia heterophylla* Hook. & Arn.; *Acacia heterophylla* (Lam.) Willd. var. *latifolia* Benth.; *Acacia kauaiensis* Hillebr.; *Acacia koa* A. Gray var. *hawaiiensis* Rock; *Acacia koa* A. Gray var. *lanaiensis* Rock; *Acacia koa* A. Gray var. *waimeae* Hochr.; *Racosperma kauaiense* (Hillebr.) Pedley; *Racosperma koa* (A.Gray) Pedley

Common

Name(s): koa

Notes: I disagree with Wagner et al. (1999) on their inclusion of *Acacia koa* Hillebr. within a broader-sense *Acacia koa*. The close relative *Acacia heterophylla* (Lam.) Willd., which is found presently only on the island of La Réunion, is very closely related to *Acacia koa* and may be derived from it (Le Roux et al., 2014). If treated as conspecific, *A. heterophylla* (Lam.) Willd. has priority (as it was published in 1806, vs 1854 for *A. koa* A. Gray). However, it seems impractical to treat these two

taxa as conspecific, given the >15,000 kilometers of ocean between them and the fact that there are some morphological differences between the two taxa.

Additionally, given the economic and cultural importance of koa in Hawai‘i, if these two taxa were to be treated as conspecific, a proposal to conserve the *Acacia koa* A. Gray should be presented to the relevant authorities.

***Anthenantia villosa* (Michx.) P. Beauv.**

Synonyms: *Anthenantia villosa* (Michx.) P. Beauv. (orthographic variant); *Panicum Anthenantia* Kuntze; *Panicum ignoratum* Kunth; *Phalaris villosa* Michx.

Common

Name(s): green silkyscale

Notes: Not including *Anthenantia texana* Kral, following Weakley (2020). I follow the comments in Weakley (2020) regarding the correct spelling of the genus. We have deposited a voucher specimen at MSC from one of the source populations for the individuals used in this work (Warneke 274; MSC Accession # 408119).

***Aristida beyrichiana* Trin. & Rupr.**

Synonyms: *Aristida stricta* Michx. var. *beyrichiana* (Trin. & Rupr.) D.B. Ward

Common

Name(s): Beyrich’s threeawn; southern wiregrass; wiregrass

Notes: Whether or not to treat this taxon as a variety of *Aristida stricta* Michx. remains unclear. If treated in that way, the correct name would be *Aristida stricta* Michx. var. *beyrichiana* (Trin. & Rupr.) D.B. Ward. The plants used in this dissertation were sourced from Florida, which is solidly within the range of this taxon. Although it seems likely that the proper treatment of this taxon is as part of *Aristida stricta*

sensu lato (Allred, 2003), rather than at the species level, we have elected to keep this name, as we are generally following Alan Weakley's flora for the region, and he has maintained them as split in the most recent working version of the flora (Weakley, 2020).

***Carphephorus bellidifolius* (Michx.) Torr. & A. Gray**

Synonyms: *Liatris bellidifolia* Michx.

Common

Name(s): sandywoods chaffhead; sandhill chaffhead

Notes: Taxonomically uncomplicated. I have deposited a voucher specimen at MSC from one of the source populations for the individuals used in this work (Warneke 273; MSC Accession # 408120).

***Dodonaea viscosa* (L.) Jacq.**

Synonyms: *Dodonaea eriocarpa* Sm.; *Dodonaea sandwicensis* Sherff; *Dodonaea skottsbergii* (Sherff) O. Degener & I. Degener; *Dodonaea spatulata* Sm.; *Dodonaea stenoptera* Hillebr.; *Dodonaea* × *fauriei* H. Lév. (= *D. viscosa* (L.) Jacq. × *Dodonaea stenoptera* Hillebr.); *Ptelea viscosa* L.

Common

Name(s): 'a'ali'i; common hopbush; varnishleaf

Notes: This is a pantropical species and is taxonomically very messy throughout the entirety of its range. The species (as well as the genus) arose in Australia, and the center of diversity for both the genus and this taxon are on that continent (Wagner et al., 1999; Harrington and Gadek, 2009). *Dodonaea viscosa* dispersed to the Hawaiian Islands a single time, likely from Australia (Harrington and Gadek,

2009). Despite the considerable variation of the complex within the islands, the situation seems extremely messy and complicated, and I agree with the majority of authors that this is best treated broadly, in a very broad *Dodonaea viscosa* (Wagner et al., 1999). The synonyms listed above are only those that are relevant to this taxon as it occurs in Hawai‘i; given the pantropical nature of the taxon, there are many more synonyms in other areas. Additionally, the many varieties described within the species names listed above are left out, for simplicity here. For a comprehensive list of the varietal synonyms, please consult Wagner et al. (1999). Also, in regards to the authority for the species name *Dodonaea viscosa*, sometimes this species is cited as *Dodonaea viscosa* Jacq. and sometimes the equivalent name is *Dodonaea viscosa* (L.) Jacq. The type specimen of *Ptelea viscosa* L. (at BM) matches for *Dodonaea viscosa*, and it seems like Jacq. (in his publication) was referencing names by L., so I have chosen the above form of the authority.

***Liatris earlei* (Greene) K. Schum.**

Synonyms: *Laciniaria ruthii* Alex.

Common

Name(s): Earle’s blazing-star

Notes: This taxon is currently treated as part of the *Liatris squarrulosa* Michx. complex by all relevant authorities. However, both the Weakley and the Flora of North America treatments note that this complex is a challenging group (Nesom, 2006; Weakley, 2020). I here follow the treatment of Radford et al. (1968), which treat this at the species level. I have chosen to maintain this older name so that, if/when taxonomic work is done on the *Liatris squarrulosa* complex, it is clear to future researchers

which part of that complex my plants correspond to. To maintain clarity, at the first mention of this taxon in each component of this dissertation, I also note that it is currently a synonym of *Liatris squarrulosa* Michx., which should enable interested parties to find my work with either (or both) names. I have deposited a voucher specimen at MSC from one of the source populations for the individuals used in this work (Warneke 272; MSC Accession # 408121).

***Sophora chrysophylla* (Salisb.) Seem.**

Synonyms: *Edwardsia chrysophylla* Salisb.; *Edwardsia unifoliata* (Rock) O. Degener; *Sophora chrysophylla* (Salisb.) Seem. var. *unifoliata* Rock, *Sophora grisea* O. Degener & Sherff; *Sophora unifoliata* (Rock) O. Degener & Sherff

Common

Name(s): māmane, mamani

Notes: As with many species in Hawai‘i, variation is visible within this species, which may result in the recognition of formal taxa with additional study (Wagner et al., 1999). All of the individuals I used were from the Mauna Loa Strip portion of Hawai‘i Volcanoes National Park, from Kīpukapuauolu to the top of the road. The list of synonyms, above, ignores the many names proposed by Chock (1956), regardless of the level at which they have or have not been recognized by other authorities. For a more complete list of synonyms, please see Wagner et al. (1999).

***Sorghastrum secundum* (Elliott) Nash**

Synonyms: *Andropogon secundus* Elliott; *Andropogon unilateralis* Hack.; *Chrysopogon secundus* (Elliott) Benth. ex Vasey; *Sorghum nutans* A. Gray subvar. *secundum* (Elliott) Roberty; *Sorghum secundum* (Elliott) Chapm.

Common

Name(s): lopsided indiagrass

Notes: Fairly clear-cut, from a taxonomic perspective. I have deposited a voucher specimen at MSC from one of the source populations for the individuals used in this work (Warneke 275; MSC Accession # 408118).

Literature Cited

- Allred, K. W. 2003. *Aristida*. In Flora of North America Editorial Committee [ed.], Flora of North America north of Mexico vol. 25, 315–342. Oxford University Press, Oxford.
- Chock, A. 1956. A Taxonomic Revision of the Hawaiian Species of the Genus *Sophora* Linnaeus (Family Leguminosae). *Pacific Science* 10: 136–158.
- Harrington, M. G., and P. A. Gadek. 2009. A species well travelled – The *Dodonaea viscosa* (Sapindaceae) complex based on phylogenetic analyses of nuclear ribosomal ITS and ETSf sequences. *Journal of Biogeography* 36: 2313–2323.
- Nesom, G. L. 2006. *Liatris*. In Flora of North America Editorial Committee [ed.], Flora of North America north of Mexico vol. 21, 512–535. Oxford University Press, Oxford.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, North Carolina.
- Le Roux, J. J., D. Strasberg, M. Rouget, C. W. Morden, M. Koordom, and D. M. Richardson. 2014. Relatedness defies biogeography: The tale of two island endemics (*Acacia heterophylla* and *A. koa*). *New Phytologist* 204: 230–242.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawai‘i: revised edition. Bernice Pauahi Bishop Museum Press, Honolulu, Hawai‘i.

Weakley, A. S. 2020. Flora of the Southeastern United States. Edition of 20 October 2020.

University of North Carolina at Chapel Hill Herbarium, Chapel Hill, North Carolina.

TABLE OF CONTENTS

LIST OF TABLES	xxiv
LIST OF FIGURES	xxv
CHAPTER ONE: RESTORATION AND REINTRODUCTION OF PLANTS IN HUMAN-MODIFIED LANDSCAPES	
Introduction.....	1
Plant Populations in Fire-Disturbed Habitats	4
Study System	6
Chapter 2: Fire and Plant-Soil Feedbacks.....	7
Chapter 3: Investigating Factors Influencing Plant Establishment Success Post-Fire	9
Plant Populations in Fragmented Landscapes.....	9
Study System	12
Chapter 4: Local Seed Dispersal in Fragmented Landscapes	13
Chapter 5: Recruitment Patterns of Plants in Fragmented Landscapes	14
LITERATURE CITED	16
CHAPTER TWO: FIRE MODIFIES THE OUTCOME OF PLANT-SOIL FEEDBACKS	
Abstract	25
Introduction.....	26
Methods.....	29
Study Site and Species	29
Soil Sourcing, Set-up, and Data Collection	30
Analysis.....	35
How is plant performance affected by soil source and is this pattern affected by fire?	35
Does nodule formation by rhizobia mediate the effect of soils on plant performance?.....	36
Are net pairwise PSFs between our two focal species affected by fire?	36
Results.....	37
How is plant performance affected by source plant and is this pattern affected by fire?	37
Does nodule formation by rhizobia mediate the effect of soils on plant performance? ..	39
Koa.....	39
Māmane.....	40
Are net pairwise PSFs between our two focal species affected by fire?	41
Discussion	41
Acknowledgements.....	46
LITERATURE CITED	47
CHAPTER THREE: ELEVATION, CANOPY COVER, AND GRASS COVER STRUCTURE PATTERNS OF SEEDLING ESTABLISHMENT IN A SUBTROPICAL POST-FIRE RESTORATION.....	
	53

Abstract	53
Introduction	54
Methods.....	57
Study Site	57
Seed Sowing.....	58
Calculating Māmane Seeding Rate	60
Data Collection	63
Analysis.....	65
Results.....	66
Discussion	70
Acknowledgements.....	74
LITERATURE CITED	75
CHAPTER FOUR: HABITAT FRAGMENTATION ALTERS THE DISTANCE OF ABIOTIC SEED DISPERSAL THROUGH EDGE EFFECTS AND DIRECTION OF DISPERSAL.....	81
Abstract	81
Introduction.....	81
Methods.....	84
Site and Species	84
Seed Dispersal.....	87
Analysis.....	88
Results.....	90
Connectivity and Edge-to-Area Ratio.....	90
Distance from Habitat Edge.....	92
Directionality	95
Relationship between Distance from Edge and Directionality	96
Discussion	97
Acknowledgments.....	100
LITERATURE CITED	101
CHAPTER FIVE: EXPERIMENTAL HABITAT FRAGMENTATION REVEALS THE ROLE OF EDGES FOR PLANT RECRUITMENT	106
Abstract	106
Introduction.....	107
Methods.....	110
Study Site and Focal Species	110
Recruitment Counts	112
Additional Biotic and Abiotic Factors	113
Bare Ground.....	114
Canopy Cover	114
Connectivity, Edge-to-Area Ratio, Edge Distance	114
Germination	114
Number of Recruits.....	115
Reproductive Output.....	115
Herbivory Data.....	115
Seed Predation	116

Analysis.....	116
Results.....	118
Question 1: Effects of Fragmentation on Recruitment	118
Question 2: Factors Mediating Fragmentation Effects	122
<i>Carphephorus</i>	122
<i>Liatris</i>	122
<i>Anthenantia</i>	122
<i>Sorghastrum</i>	123
Discussion.....	124
Acknowledgments.....	127
LITERATURE CITED	128

LIST OF TABLES

Table 2.1. Field soil table.....	33
Table 2.2. Statistical table for biomass models.....	38
Table 2.3. Statistical table for nodulation models.....	38
Table 3.1. Seed weight table	61
Table 3.2. Coordinates and elevation for our 45 study plots	63
Table 3.3. The relationships between different response variables and elevation (m asl).....	69
Table 4.1. The number of individuals and the total number of seeds across all individuals	88
Table 4.2. Mean dispersal distances with percent difference between conditions	96
Table 5.1. Explanation of factors used in constructing the SEMs	114
Table 5.2. Statistics table for the effect of patch type, as obtained from the patch-level GLMM	118
Table 5.3. Statistics table for edge models	120

LIST OF FIGURES

Figure 2.1. Study site location on Hawai‘i Island.....	30
Figure 2.2. Experimental design	31
Figure 2.3. Standardized biomass (g/day) for koa (Panel A) and māmane (Panel B), by source plant crossed with burn.....	39
Figure 2.4. SEM diagrams for each species.....	41
Figure 3.1. Plot and quadrat diagram.....	59
Figure 3.2. The number of seedlings by elevation (with elevation being continuous).....	67
Figure 3.3. Plot of the number of māmane seedlings by canopy cover (number of covered vertices).....	68
Figure 3.4. Plot of the number of māmane seedlings by grass cover	69
Figure 3.5. The relationships between elevation and each of canopy cover, bare ground, grass cover, and fire severity (as measured through char height).....	70
Figure 4.1. Experimental design, showing the location of the eight experimental landscape blocks	86
Figure 4.2. Standardized model coefficients with 50% credible intervals (the light gray lines) and 95% credible intervals (the dark black lines) for five herbaceous plant species in a fragmentation experiment.....	91
Figure 4.3. Seed dispersal kernels (probability density functions) for five herbaceous plant species, located near patch centers (green lines; 37 m from the edge) and near patch edges (blue lines; 1 m from the edge) in a fragmentation experiment.....	92
Figure 4.4. Model results and interpretation.....	93
Figure 4.5. Dispersal kernels with the uncertainty around the mean.....	95
Figure 5.1. Experimental design	111
Figure 5.2. Effects of isolation and shape on recruitment patterns of our four study species	119
Figure 5.3. Interaction plots for the interaction on the number of recruits between distance from the edge of the patch and the patch type	121
Figure 5.4. SEM diagrams for each species.....	123

CHAPTER ONE

RESTORATION AND REINTRODUCTION OF PLANTS IN HUMAN-MODIFIED LANDSCAPES

Introduction

We are living in an era of large-scale, worldwide landscape change (Steffen et al., 2011; Lewis and Maslin, 2015). Habitat loss, fragmentation, and degradation as a result of human land-use conversion and other factors represent the greatest threats to the world's biodiversity (Pereira et al., 2010; Haddad et al., 2015). Our planet has 7.8 billion humans living on it, at the time of this writing (United Nations, 2019b), and conversion to agricultural land to feed all these people and the associated livestock has converted large stretches of native habitats to agricultural land (Nature Editorials, 2010). Additionally, the network of global trade has facilitated the movement of nonnative species to regions where they have not previously occurred, leading to large-scale shifts in the species composition and ecosystem function of essentially all terrestrial habitats, worldwide (Bradley et al., 2012; Chapman et al., 2017). These large-scale changes are resulting in the loss of biodiversity on a scale not seen in planetary history since the Cretaceous–Tertiary extinction event 66 million years ago (Barnosky et al., 2011; Ceballos et al., 2015). There are also large shifts in ecosystem services on which humanity depends for continued existence (Rockström et al., 2009). These losses of species and shifts in ecosystem services require humanity to act, both to save the planet and to save ourselves.

Fortunately, humanity has developed many tools to help address this multifaceted and complex problem. Among them is the tool of ecological restoration, which seeks to increase and maintain species diversity and ecosystem function and to mitigate the negative ecological consequences of human actions (Gann et al., 2019; United Nations, 2020). Ecological restoration

is recognized internationally as a solution to biodiversity decline and ecosystem functioning such that the United Nations has declared this present decade as the Decade on Ecosystem Restoration and has put in motion a set of activities and initiatives aiming to mitigate the ecological devastation caused by humans worldwide (United Nations, 2019a, 2020). Restoration is a multibillion-dollar industry, valued at \$10.5 billion annually in the United States alone (BenDor et al. (2015), adjusted for inflation to 2021 USD). In order to conduct ecological restoration, restoration practitioners often focus on the plant community (Brudvig et al., 2017; Copeland et al., 2018). This approach is often done because plants are relatively easy to manipulate, to grow in large quantities, and because government regulations often focus on plants for defining restoration success (Zedler, 2000; Copeland et al., 2018; Munson et al., 2020). Plants are also thought to provide the scaffolding for other species to then recolonize the restored habitat (Hilderbrand et al., 2005; Frick et al., 2014). However, in order to be successful, the reintroduced populations of these plants must establish in their new habitat, their populations must expand, and they must maintain healthy population levels (Ruiz-Jaen and Aide, 2005; Wortley et al., 2013; Robert et al., 2015). In understanding how and why populations change in the context of ecological restoration, ecologists can then better understand the factors that are driving these restoration outcomes (Brudvig, 2017; Larios et al., 2017; Groves et al., 2020). The factors that influence the success of these restored populations likely vary in the context of where these restoration actions are accomplished and likely depend on the landscape context and the disturbance regime of the site in which the plants are installed (Turley and Brudvig, 2016; Gilby et al., 2018; Zirbel et al., 2019). All of the variability in the factors influencing restoration success make the prediction of restoration outcomes challenging at best (Brudvig, 2017; Brudvig et al., 2017).

Understanding how, when, and where to carry out restoration actions is a pressing concern (Brudvig and Catano *in press*, Munson et al. 2020, United Nations 2020). In recent years, there has been an increasing push to increase the predictability of restoration outcomes and actions (Brudvig, 2017). However, with the prediction aspect of restoration in its infancy, one pressing avenue of investigation that should help address the longer-term goal of better predictability of restoration outcomes, is the understanding of the variation that is present within restoration settings and how that influences the outcomes of restoration actions (Brudvig and Catano *in press*). To better understand this variation, restoration ecologists must and do conduct replicated empirical studies in the field conditions in which restoration actions take place. By conducting these scientific studies in concert with practitioners of ecological restoration, restoration ecologists are better able to assess the mechanisms and reasons that are driving restoration outcomes and then better use that knowledge to understand the variability observed in the field (Beier et al., 2017; Gipple et al., 2020). Eventually, this collective body of knowledge may enable true prediction in ecological restoration.

One important avenue for these research studies to follow is that of the understanding of plant demographic processes and responses in reintroduction settings (Menges, 2008; Larios et al., 2017). Each stage of the plant life cycle can be affected by the different factors present in the restoration setting (Brudvig et al., 2015; Caughlin et al., 2019). Seed dispersal within a population can be changed by landscape context (Soons et al., 2005; Nathan, Schurr, et al., 2008). Seedling establishment following seed arrival is mediated by a host of factors. Seedling location within a landscape can affect that seedling's performance in ways that impact establishment patterns (Bruna, 2002). Interactions with the soil microbial community, which can vary depending on proximity to conspecifics and through the environmental history of the

restoration, can have major effects on plant growth and survival (Kardol and Wardle, 2010; Van der Putten et al., 2013; Crawford et al., 2019). Understanding these processes will enable restoration actions to better manage plant establishment and dispersal, which are key components of population spread, which is often a central goal of plant reintroduction efforts.

In an effort to better understand what drives the success of plant reintroduction efforts, I, along with my coworkers and collaborators, have worked to investigate responses of reintroduced plant populations in a habitat restoration context within fire-disturbed habitats as well as within the context of large-scale habitat fragmentation. Within fire-disturbed habitats, I focused on driving factors influencing early plant establishment. To examine these, I worked in an upland forested system that had recently been burned (in a system that rarely burned, historically). There, I examined the role of the soil microbial community in seedling performance and how this was modified by the context of fire. I also examined seedling establishment and how both biotic and abiotic factors changed rates of establishment, depending on context. In the context of habitat fragmentation, I investigated other population processes from later in the reintroduction process. In that system, I examined seed dispersal and longer-term plant recruitment dynamics. I examined the effects of the landscape and fragmentation on patterns of the direction and distance of seed dispersal. Additionally, I examined the effects of the landscape on longer-term recruitment outcomes, which I tied with factors known to affect population processes, to get at underlying mechanisms.

Plant Populations in Fire-Disturbed Habitats

The disturbance regime of habitats is often important for maintaining the structure and function of that habitat, with frequent disturbance by processes (like fire) being responsible for which species may occur in a given area (Curtis, 1959; D'Antonio and Vitousek, 1992).

However, in this era of global change, humans are causing radical shifts in the disturbance regime of habitats on a global scale (Moritz et al., 2012; Lewis and Maslin, 2015). An important disturbance in many ecosystems is that of fire. Fire is increasing worldwide and causes major changes to the biotic and abiotic components of an ecosystem when it occurs (Flannigan et al., 2000; Moritz et al., 2012). The addition of fire to a landscape where it was historically absent or infrequent is often problematic (D'Antonio and Vitousek, 1992). In habitats where fire was absent but is now a problem, its presence is often driven by shifts in the composition of the plant community, where a suite of nonnative plants provide fuel such that fires are able to carry and establish more than would have been possible in historic conditions (Smith and Tunison, 1992; Ellsworth et al., 2014; Mahood and Balch, 2019). The presence of these nonnative species on the landscape often leads to positive feedback loops that establish a state of nonnative, fire prone grasses that are joined by whatever few native species can exist in this state of frequent fire (D'Antonio and Vitousek, 1992; Smith and Tunison, 1992).

As a result of these fires, and especially in areas that are now experiencing frequent fires, land managers and restoration practitioners often rush to work to restore plant communities after fire events (McDaniel et al., 2008; Peppin et al., 2010; Vallejo and Alloza, 2015; Copeland et al., 2018). This action is done for both the saving of the soil and ecosystem processes and for maintaining the biodiversity of the system. In habitats that were not burned historically, such reintroduction efforts are often done also in an attempt to reduce the dominance of these nonnative grasses in an attempt to break the grass-fire feedback cycle (McDaniel et al., 2008; Davies et al., 2011; Kulpa et al., 2012). However, despite the commonness of this restoration practice, such actions are not always successful (Davies et al., 2011). This persistent uncertainty of success has plagued large-scale post-fire restoration efforts and results in both practitioners

and funding agencies even questioning whether this effort is even worth the cost (Munson et al., 2020). Better understanding of why such outcomes may fail is imperative if restoration practitioners and scientists wish to work together to determine more successful strategies for managing plant populations post-fire.

Study System

In this dissertation, I investigate the response of plants and their populations to a recent disturbance of a fire in the Hawaiian Islands. Fire in this system was historically rare, and has increased through the introduction of nonnative grasses, which facilitate the positive feedback loop between fire and grass that has been observed in many habitats around the world (Smith and Tunison, 1992; Ellsworth et al., 2014). In an effort to break this cycle, following the Keauhou Fire, which burned in August of 2018 (Theune, 2018), land managers sought to restore the native plant community within a burned area through the planting of native seeds to reintroduce native plant biodiversity, following an approach that has been used before in this system (McDaniel et al., 2008). As many of the native species in this system are fire intolerant, the goal would be to allow these species to establish and for the trees and shrubs in the seed mix to perhaps shade the grasses to a sufficient extent to reduce further fires (McDaniel et al., 2008; Loh et al., 2009).

For this Chapters 2 and 3, I worked within the upland forest of the Mauna Loa strip of Hawai‘i Volcanoes National Park, on the Island of Hawai‘i. This forest type is historically dominated primarily by two species: koa (*Acacia koa* A. Gray) and ‘ōhi‘a lehua (*Metrosideros polymorpha* Gaudich.) (Little and Skolmen, 1989). However, within my study site itself, ‘ōhi‘a is less common, resulting in only koa as the dominant tree species (personal observation). At upper elevations, the local dominance pattern of the forest shifts and māmane (*Sophora chrysophylla* (Salisb.) Seem.) and ‘a‘ali‘i (*Dodonaea viscosa* (L.) Jacq.) are more dominant in the canopy with

koa being present, but not as abundant as at lower elevations. The forests and islands of Hawai‘i broadly are species poor, relative to similar land areas of the mainland (Little and Skolmen, 1989), and the diversity of these systems has suffered drastic losses of native biodiversity with the advent of Europeans and Americans to the islands over the last several hundred years (Wagner et al., 1999). Historically, fire was rare to nonexistent within these systems (Smith and Tunison, 1992). However, with the introduction of cattle (*Bos taurus* Linnaeus, 1758) to the islands in 1793, pasture grasses were introduced (Blackmore and Vitousek, 2000; Maly and Wilcox, 2000), which has led to a shift in fire regimes, causing more frequent and larger-scale fires in the remaining forests of the islands (Smith and Tunison, 1992; Loh et al., 2009). This novel fire regime creates the grass-fire feedback loop that reduces the diversity of the system. The area in which I worked is host to 16 species that are federally listed as threatened or endangered, with many unlisted species that are of conservation concern, along with the cultural value of the native biodiversity of the forests, contribute to the pressing need for habitat restoration in the area (Belfield and Pratt 2002; Stephanie Yelenik, personal communication).

Chapter 2: Fire and Plant-Soil Feedbacks

In Chapter 2, I examined how soil legacies, as a result of anthropogenic disturbance, can affect plant reintroduction efforts through their effects on initial seedling performance. I examined this in the context of the restoration effort following the 2018 Keauhou Fire, and in this study, my collaborators and I worked to investigate patterns of feedback between plants, microbes, and soils, termed “plant-soil feedbacks” (PSFs). Plant-soil feedbacks are thought to influence patterns of plant diversity and coexistence (Bever et al., 1997; Crawford et al., 2019). Often, proximity to a conspecific plant results in negative effects on developing seedlings, due to higher abundance of specialized pathogens, resulting in a pattern of negative density dependence

(Kulmatiski et al., 2008; Crawford et al., 2019). However, PSFs may also be positive, if, on balance, the effect of mutualists is stronger than that of pathogens, resulting in a pattern of positive density dependence (Smith and Reynolds, 2012; Crawford and Knight, 2017). These feedbacks, which are often measured in a pairwise fashion, have implications for seedling establishment and for where plants occur on a landscape (Bever et al., 1997, 2015; Mangan et al., 2010; Fukami and Nakajima, 2013).

Despite the importance of fire and of PSFs for early plant establishment, the feedback between fire and PSFs has essentially been unstudied (Van der Putten et al., 2013). With the increasing presence of fires on the terrestrial landscapes of our planet, work on this dynamic can help inform knowledge of how PSFs may function in landscapes that experience fire. To investigate how fire impacts these PSF interactions, I collected soils from under two focal species of interest as well as a standard non-focal plant, to determine whether and how PSFs in this system work. My study species were koa and māmane (both nitrogen-fixing members of the Fabaceae), with the away plant being ‘a‘ali‘i, a non-nitrogen-fixing member of the Sapindaceae. In addition to understanding the PSFs of this system, I crossed my experimental design with the history of fire by replicating the experiment within the area burned by the 2018 fire as well as outside this burned area. I followed common PSF study designs, and inoculated sterile potting media with field soil to focus the results on microbial effects, rather than the myriad other soil factors that influence plant growth (Crawford et al., 2019). I found that PSFs within each species are largely positive, a fact perhaps facilitated by these species being leguminous and benefiting more from specialized bacterial partners than they are harmed by pathogens. I further found that fire seems to reduce the strength of these PSFs, which may result in shifts in the feedback dynamics between these plant species in field conditions and lead to shifts in local patterns of

plant species dominance.

Chapter 3: Investigating Factors Influencing Plant Establishment Success Post-Fire

In Chapter 3, I examined the context dependency of factors that influence early seedling establishment in a restoration setting, following an anthropogenic disturbance. To do this, I conducted fieldwork to look within a replicated system of plots throughout the area of the Keauhou Burn. I surveyed a subset of these plots in an attempt to understand what is driving the patterns of early plant establishment for reintroduced populations of māmane. In doing so, I focused on factors which are known to affect plant establishment in this system, namely abundance of grasses, amount of bare ground, the intensity of the fire, and the amount of canopy cover. I looked at three elevational bands to examine the role of elevation in the success of the seedlings. Elevation is a known driver of plant success both within Hawai‘i and also broadly (D’Antonio et al., 2000; Ainsworth and Kauffman, 2010; Bowles et al., 2011; Davies et al., 2011). I found that the drivers of population establishment in these early stages of the restoration varied by elevation, with cover of grasses and canopy cover being important in some, but not all, elevations. However, the context of elevation was important in shaping what other factors were important, emphasizing that landscape context is likely important for plant establishment. My results show that factors that are known to influence restoration outcomes may not influence restoration outcomes equally, even within the same system

Plant Populations in Fragmented Landscapes

Another factor that affects restoration success (and also affects fire regimes) is that of habitat fragmentation (Huxel and Hastings, 1999; Crouzeilles et al., 2016; Caughlin et al., 2019). Habitat fragmentation is a major factor affecting terrestrial biodiversity (Haddad et al., 2015). Through land use change, formerly contiguous areas of habitat are broken into smaller and more

isolated patches. The landscape between these patches is often a hostile environment to the organisms found in the remaining habitat patches, though the hostility of the between-patch matrix does vary (Templeton et al., 2011; Didham et al., 2012). This process has a diversity of effects on the biotic community and often results in declines of species adapted to the remaining patches (Haddad et al., 2015, 2016). The study of the effects of habitat fragmentation is challenging, in part, due to the simultaneous action of many factors (Haddad et al., 2015), including, among others, patch connectivity, patch edge-to-area ratio, and the effects of edges. I work within a system that allows for the examination of these connectivity, edge-to-area ratio, and edge effects independently, while holding all other effects of habitat fragmentation constant (Sullivan et al., 2011; Brudvig et al., 2015).

A major factor influencing population dynamics and biodiversity in fragmented landscapes is that of patch connectivity (Haddad et al., 2003; Gilbert-Norton et al., 2010; Damschen et al., 2019). Decreased connectivity may prevent movement of individuals between patches, resulting in population declines and potentially local extinction (Krauss et al., 2010). This relationship between connectivity and population persistence has resulted in much expending of effort to create and/or maintain connectivity at landscape scales (Wilson and Willis, 1975; Crooks and Sanjayan, 2006). Connectivity has been shown to help maintain populations and to maintain and/or increase local biodiversity (Crooks and Sanjayan, 2006; Damschen et al., 2019). However, despite the work that has been done on connectivity, much work still remains to be done, especially in the context of population reintroduction, and particularly of plants.

The edge-to-area ratio of habitat patches can have effects on populations and biodiversity, independent of other factors associated with habitat fragmentation (Ewers and

Didham, 2006). Edge-to-area, sometimes called shape or shape complexity is quite variable and, because it is often confounded with area, it is challenging to study (Moser et al., 2002; Ewers and Didham, 2006). However, it is an important trait of landscapes; for instance, if remaining habitat is long and linear, as along riparian corridors, there will be an outsized increase in edge effects, relative to equivalently sized patches with relatively more interior area (e.g., circular patches). These differences in shape can, therefore, have large effects on the structure of communities, independent of the amount of habitat remaining (Moser et al., 2002; Brudvig et al., 2009). Such edge-to-area ratio effects consequently differ from those of edges, yet they may be equally or more important for understanding a population or a process of interest (Ewers and Didham, 2006).

Effects of edges are ubiquitous and pernicious in fragmented landscapes worldwide (Harper et al., 2005; Haddad et al., 2015). Within forested systems alone, 70% of remaining forests worldwide are within 1 km of an edge (Haddad et al., 2015). However, edges do not affect all species equally. Some species may benefit strongly from the presence of edges and have higher populations near edges, while other species may do poorly near edges and may either only be able to persist in the core portions of any remaining habitat patches (Harrison and Bruna, 1999; Vasconcelos and Bruna, 2012). These population changes and resulting local extirpations have consequences for local- and landscape-level patterns of biodiversity (Haddad et al., 2015). Populations of reintroduced species are likely to be affected by edges within the landscapes in which they occur (Bruna, 1999, 2002).

All three of these landscape factors contribute to the need for population reintroduction, following species loss (Haddad et al., 2015; Caughlin et al., 2019). However, despite the ubiquity of habitat fragmentation in the world's terrestrial habitats and the documented loss of biodiversity

that occurs within fragmented landscapes, debate continues to exist about how and why patterns in biodiversity loss emerge (Didham et al., 2012; Fahrig, 2013; Fletcher et al., 2018; Fahrig et al., 2019). Part of this debate stems from the difficulty of empirically studying the different effects of fragmentation (Ewers and Didham, 2006; Didham et al., 2012). This debate has consequences for how and where populations may be reintroduced and how they are managed, as the initial population establishment and growth faces may be influenced by the context of the landscape in ways that are, presently, poorly understood.

In this dissertation, I also investigate the effects of habitat fragmentation on reintroduced populations of a set of plant species in a fragmented landscape in the longleaf pine savanna of South Carolina. Fragmentation of this habitat type has resulted in local losses of many species that are adapted to these savannas (Jose et al., 2006). In the year 2000, my collaborators on this project established a replicated, large-scale system of experimental patches of restored longleaf pine savannas in order to disentangle effects of connectivity, edge-to-area ratio, and edge effects (Damschen et al., 2006). In 2007/2008, my collaborators planted populations of five herbaceous species into these replicated fragmented landscapes (Brudvig et al., 2015; Caughlin et al., 2019). These populations were sown in such a way as to enable study of the mechanistic reasons behind what landscape factors are responsible for driving the observed population responses and patterns. I worked within those reintroduced populations to answer my research questions.

Study System

Longleaf pine savanna is historically a broad-ranging vegetation type which forms the core of the recently-recognized global biodiversity hotspot of the North American Coastal Plain (Jose et al., 2006; Noss et al., 2015). This habitat type has been degraded, fragmented, and converted to agriculture across much of its range, leaving only ~3% of the habitat intact (Jose et al., 2006).

Historically, this longleaf pine savanna was very open and was quite fire prone, burning approximately every 2-3 years (Jose et al., 2006). This frequent fire kept the habitat open and allowed for species found there to be adapted to living in open, sunny habitats (Jose et al., 2006). My study species are all native herbaceous plants of longleaf pine savanna and are in the families Asteraceae and Poaceae. All would have been present historically but are locally uncommon presently and are of conservation concern.

Chapter 4: Local Seed Dispersal in Fragmented Landscapes

In Chapter 4, my collaborators and I examine the process of seed dispersal and how this critical process is impacted by habitat fragmentation. Two years following the introduction of these species to these landscapes, my collaborators on this project marked seeds prior to their dispersal and allowed them to naturally disperse and then relocated the seeds after dispersal had occurred. Seeds of these plant species are abiotically dispersed. Following dispersal, they measured the distance and direction to which the seeds dispersed, within 5m of the parent plant. This short-distance dispersal is not often studied, despite the majority of seed dispersal occurring close to the parent plant (Nathan and Muller-Landau, 2000). Using these data, I built models to examine patterns of seed dispersal and how they are modified by the landscape factors of connectivity, edge effects, and edge-to-area ratio. After all, there cannot be seedlings without seeds having gotten there first (Geisel, 1971; Broadhurst et al., 2008; Reid et al., 2015). To understand populations and their spread following reintroduction to a landscape, it is necessary to understand how their seeds may move across the landscape (Nathan and Muller-Landau, 2000). What I found is that my species, which are all abiotically dispersed, preferentially disperse towards the edges of the habitat patches. I also find that dispersal is farther at greater distances from the edge of that patch. These patterns are largely not affected by the connectivity

or edge-to area ratio of the patch in which the seedlings occur. My results show that, at the local scale, where the vast majority of dispersal events take place, distance to the edge of the patch is the dominant landscape factor that modifies patterns of dispersal and that these patterns may not be intuitive based on the expectations derived from the study of long-distance dispersal.

Chapter 5: Recruitment Patterns of Plants in Fragmented Landscapes

In Chapter 5, I examined the longer-term patterns of recruitment within reintroduced populations and how these recruitment patterns were affected by habitat fragmentation. Unfortunately for these plant populations, as well as for my work, not all of the populations that were sown in 2007 were able to successfully establish within fragmented landscapes. As a result, I worked with a subset of four of the five species that I had used for Chapter 4 and examined how patterns of recruitment were affected by habitat fragmentation. In 2015 and 2016, my collaborators and I surveyed the entirety of the habitat patches for recruits of these four species. Because these species were not present within this experimental system before their reintroduction, all recruits within the habitat patches are derived from the originally sown populations. I examined the responses of these populations to the landscape variables of interest (connectivity, edge-to-area ratio, and edge effects and found that, for some of the study species, edges mediated recruitment patterns, while for the remaining species, they did not have bearing on recruitment patterns. I also examined a variety of mechanisms through which edges may be affecting recruitment patterns and found that factors like canopy cover were important in influencing patterns of recruitment in these species, which are sun-loving herbs of open habitats. My work on this chapter indicates the importance of considering landscape context when assessing patterns of plant reintroduction and demography, as, without doing so, models may not

be accurate for the entirety of a given population of interest, if that population occurs across a varied landscape context.

LITERATURE CITED

LITERATURE CITED

- Ainsworth, A., and J. B. Kauffman. 2010. Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* 42: 647–655.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Beier, P., L. J. Hansen, L. Helbrecht, and D. Behar. 2017. A How-to Guide for Coproduction of Actionable Science. *Conservation Letters* 10: 288–296.
- Belfield, T. R., and L. W. Pratt. 2002. Rare Plants of the Mauna Loa Special Ecological Area, Hawai'i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 130. University of Hawai'i at Mānoa, Department of Botany, Honolulu, Hawai'i.
- BenDor, T. K., A. Livengood, T. W. Lester, A. Davis, and L. Yonavjak. 2015. Defining and evaluating the ecological restoration economy. *Restoration Ecology* 23: 209–219.
- Bever, J. D., S. A. Mangan, and H. M. Alexander. 2015. Maintenance of Plant Species Diversity by Pathogens. *Annual Review of Ecology, Evolution, and Systematics* 46: 305–325.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology* 85: 561–573.
- Blackmore, M., and P. M. Vitousek. 2000. Cattle grazing, forest loss, and fuel loading in a dry forest ecosystem at Pu'u Wa'aWa'a ranch, Hawai'i. *Biotropica* 32: 625–632.
- Bowles, M., S. Apfelbaum, A. Haney, S. Lehnhardt, and T. Post. 2011. Canopy cover and groundlayer vegetation dynamics in a fire managed eastern sand savanna. *Forest Ecology and Management* 262: 1972–1982.
- Bradley, B. A., D. M. Blumenthal, R. Early, E. D. Grosholz, J. J. Lawler, L. P. Miller, C. J. B. Sorte, et al. 2012. Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment* 10: 20–28.
- Broadhurst, L. M., A. Lowe, D. J. Coates, S. A. Cunningham, M. McDonald, P. A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications* 1: 587–597.
- Brudvig, L. A. 2017. Toward prediction in the restoration of biodiversity. *Journal of Applied Ecology* 54: 1013–1017.

- Brudvig, L. A., R. S. Barak, J. T. Bauer, T. T. Caughlin, D. C. Laughlin, L. Larios, J. W. Matthews, et al. 2017. Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology* 54: 1018–1027.
- Brudvig, L. A., and C. P. Catano. *in press*. Prediction and uncertainty in restoration science. *Restoration Ecology* e13380.
- Brudvig, L. A., E. I. Damschen, N. M. Haddad, D. J. Levey, and J. J. Tewksbury. 2015. The influence of habitat fragmentation on multiple plant-animal interactions and plant reproduction. *Ecology* 96: 2669–2678.
- Brudvig, L. A., E. I. Damschen, J. J. Tewksbury, N. M. Haddad, and D. J. Levey. 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America* 106: 9328–9332.
- Bruna, E. M. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* 132: 235–243.
- Bruna, E. M. 1999. Seed germination in rainforest fragments. *Nature* 402: 139.
- Caughlin, T. T., E. I. Damschen, N. M. Haddad, D. J. Levey, C. Warneke, and L. A. Brudvig. 2019. Landscape heterogeneity is key to forecasting outcomes of plant reintroduction. *Ecological Applications* 29: e01850.
- Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* 1: 9–13.
- Chapman, D., B. V. Purse, H. E. Roy, and J. M. Bullock. 2017. Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography* 26: 907–917.
- Copeland, S. M., S. M. Munson, D. S. Pilliod, J. L. Welty, J. B. Bradford, and B. J. Butterfield. 2018. Long-term trends in restoration and associated land treatments in the southwestern United States. *Restoration Ecology* 26: 311–322.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, et al. 2019. When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters* 22: 1274–1284.
- Crawford, K. M., and T. M. Knight. 2017. Competition overwhelms the positive plant–soil feedback generated by an invasive plant. *Oecologia* 183: 211–220.
- Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation: maintaining connections for nature. In K. R. Crooks, and M. Sanjayan [eds.], *Connectivity Conservation*, 1–19.

Cambridge University Press, Cambridge, UK.

- Crouzeilles, R., M. Curran, M. S. Ferreira, D. B. Lindenmayer, C. E. V. Grelle, and J. M. Rey Benayas. 2016. A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications* 7: 1–8.
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin.
- D’Antonio, C. M., J. Timothy Tunison, and R. K. Loh. 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecology* 25: 507–522.
- D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- Damschen, E. I., L. A. Brudvig, M. A. Burt, R. J. Fletcher, N. M. Haddad, D. J. Levey, J. L. Orrock, et al. 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science* 365: 1478–1480.
- Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. *Science* 313: 1284–1286.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144: 2573–2584.
- Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121: 161–170.
- Ellsworth, L. M., C. M. Litton, A. P. Dale, and T. Miura. 2014. Invasive grasses change landscape structure and fire behaviour in Hawaii. *Applied Vegetation Science* 17: 680–689.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117–142.
- Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40: 1649–1663.
- Fahrig, L., V. Arroyo-Rodríguez, J. R. Bennett, V. Boucher-Lalonde, E. Cazetta, D. J. Currie, F. Eigenbrod, et al. 2019. Is habitat fragmentation bad for biodiversity? *Biological Conservation* 230: 179–186.
- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest factors. *The Science of the Total Environment* 262: 221–229.

- Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, et al. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation* 226: 9–15.
- Frick, K. M., A. L. Ritchie, and S. L. Krauss. 2014. Field of dreams: Restitution of pollinator services in restored bird-pollinated plant populations. *Restoration Ecology* 22: 832–840.
- Fukami, T., and M. Nakajima. 2013. Complex plant-soil interactions enhance plant species diversity by delaying community convergence. *Journal of Ecology* 101: 316–324.
- Gann, G. D., T. McDonald, B. Walder, J. Aronson, C. R. Nelson, J. Jonson, J. G. Hallett, et al. 2019. International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27: S1–S46.
- Geisel, T. S. 1971. *The Lorax*. Random House, New York City, New York.
- Gibble, R., L. Miller, and M. C. Harwell. 2020. Using Stakeholder Engagement, Translational Science and Decision Support Tools for Ecosystem-Based Management in the Florida Everglades. In T. G. O’Higgins, M. Lago, and T. H. DeWitt [eds.], *Ecosystem-Based Management, Ecosystem Services and Aquatic Biodiversity: Theory, Tools and Applications*, 517–541. Springer, Cham, Switzerland.
- Gilbert-Norton, L., R. Wilson, J. R. Stevens, and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. *Conservation Biology* 24: 660–668.
- Gilby, B. L., A. D. Olds, R. M. Connolly, C. J. Henderson, and T. A. Schlacher. 2018. Spatial restoration ecology: Placing restoration in a landscape context. *BioScience* 68: 1007–1019.
- Groves, A. M., J. T. Bauer, and L. A. Brudvig. 2020. Lasting signature of planting year weather on restored grasslands. *Scientific Reports* 10: 1–10.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* 84: 609–615.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1: 1–9.
- Haddad, N. M., A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, and E. I. Damschen. 2016. Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography* 125: 336–342.
- Harper, K. A., S. E. Macdonald, P. J. Burton, J. Chen, N. I. E. S. Euskirchen, K. D. Brosofske, S. C. Saunders, et al. 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. 19: 768–782.

- Harrison, S. P., and E. M. Bruna. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography* 22: 225–232.
- Hilderbrand, R. H., A. C. Watts, and A. M. Randle. 2005. The myths of restoration ecology. *Ecology and Society* 10: 19.
- Huxel, G. R., and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. *Restoration Ecology* 7: 309–315.
- Jose, S., E. J. Jokela, and D. Miller eds. . 2006. The longleaf pine ecosystem: Ecology, silviculture, and restoration. Springer, New York City, New York.
- Kardol, P., and D. A. Wardle. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. *Trends in Ecology and Evolution* 25: 670–679.
- Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, et al. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters* 13: 597–605.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: A meta-analytical review. *Ecology Letters* 11: 980–992.
- Kulpa, S. M., E. A. Leger, E. K. Espeland, and E. M. Goergen. 2012. Postfire seeding and plant community recovery in the great basin. *Rangeland Ecology and Management* 65: 171–181.
- Larios, L., L. M. Hallett, and K. N. Suding. 2017. Where and how to restore in a changing world: a demographic-based assessment of resilience. *Journal of Applied Ecology* 54: 1040–1050.
- Lewis, S. L., and M. A. Maslin. 2015. Defining the Anthropocene. *Nature* 519: 171–180.
- Little, E. L. J., and R. G. Skolmen. 1989. Common forest trees of Hawaii (native and introduced). United States Department of Agriculture, Agriculture Handbook No. 679. Washington, DC.
- Loh, R., A. Ainsworth, T. Tunison, and C. D'Antonio. 2009. Testing native species response to fire – a first step towards building fire resilient native plant communities at Hawai'i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 167. University of Hawai'i at Mānoa, Department of Botany, Honolulu, Hawai'i.
- Mahood, A. L., and J. K. Balch. 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). *Ecosphere* 10: 1–19.
- Maly, K., and B. A. Wilcox. 2000. A short history of cattle and range management in Hawai'i. *Rangelands* 22: 21–23.
- 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.
- McDaniel, S., R. K. Loh, S. Dale, K. Smith, and M. Vaidya. 2008. Rehabilitation of ‘ōhi‘a-swordfern (*Metrosideros polymorpha* - *Nephrolepis multiflora*) woodlands following the Kupukupu Fire, Hawai‘i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 160. University of Hawai‘i at Mānoa, Department of Botany, Honolulu, Hawai‘i.
- Menges, E. S. 2008. Restoration demography and genetics of plants: When is a translocation successful? *Australian Journal of Botany* 56: 187–196.
- Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: Art49: 1–22.
- Moser, D., H. G. Zechmeister, C. Plutzer, N. Sauberer, T. Wrba, and G. Grabherr. 2002. Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. *Landscape Ecology* 17: 657–669.
- Munson, S. M., E. O. Yackulic, L. S. Bair, S. M. Copeland, and K. L. Gunnell. 2020. The biggest bang for the buck: cost-effective vegetation treatment outcomes across drylands of the western United States. *Ecological Applications* 30: e02151.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.
- Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution* 23: 638–647.
- Nature Editorials. 2010. How to feed a hungry world. *Nature* 466: 531–532.
- Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Diversity and Distributions* 21: 236–244.
- Peppin, D., P. Z. Fulé, C. H. Sieg, J. L. Beyers, and M. E. Hunter. 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260: 573–586.
- Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, et al. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330: 1496–1502.
- Van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, et al. 2013. Plant-soil feedbacks: The past, the present and future challenges.

- Journal of Ecology* 101: 265–276.
- Reid, J. L., K. D. Holl, and R. A. Zahawi. 2015. Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications* 25: 1072–1082.
- Robert, A., B. Colas, I. Guigon, C. Kerbirou, J. B. Mihoub, M. Saint-Jalme, and F. Sarrazin. 2015. Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. *Animal Conservation* 18: 397–406.
- Rockström, J., W. L. Steffen, K. Noone, Å. Persson, F. Stuart Chapin III, E. Lambin, T. M. Lenton, et al. 2009. Planetary boundaries: exploring the safe operating space for humanity. *Ecology and Society* 14: 32.
- Ruiz-Jaen, M. C., and T. M. Aide. 2005. Restoration success: How is it being measured? *Restoration Ecology* 13: 569–577.
- Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawai‘i: Research and management implications for native ecosystems. *Alien Plant Invasions in Native Ecosystems of Hawai‘i: Management and Research*, 394–408. University of Hawai‘i Cooperative National Park Resources Studies Unit, Honolulu, Hawai‘i.
- Smith, L. M., and H. L. Reynolds. 2012. Positive plant-soil feedback may drive dominance of a woodland invader, *Euonymus fortunei*. *Plant Ecology* 213: 853–860.
- Soons, M. B., J. H. Messelink, E. Jongejans, and G. W. Heil. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology* 93: 1214–1225.
- Steffen, W., J. Grinevald, P. Crutzen, and J. McNeill. 2011. The anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 369: 842–867.
- Sullivan, L. L., B. L. Johnson, L. A. Brudvig, and N. M. Haddad. 2011. Can dispersal mode predict corridor effects on plant parasites? *Ecology* 92: 1559–1564.
- Templeton, A. R., H. Brazeal, and J. L. Neuwald. 2011. The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736–1747.
- Theune, M. 2018. Keauhou Fire Update for August 16. *Hawai‘i Volcanoes National Park News Releases*.
- Turley, N. E., and L. A. Brudvig. 2016. Agricultural land-use history causes persistent loss of plant phylogenetic diversity. *Ecology* 97: 2240–2247.
- United Nations. 2019a. Resolution 73/284: United Nations Decade on Ecosystem Restoration.

United Nations. 2020. The United Nations Decade on Ecosystem Restoration Strategy. United Nations.

United Nations. 2019b. World population prospects 2019: Highlights. United Nations Department of Economic and Social Affairs, Population Division, New York City, New York.

Vallejo, V. R., and J. A. Alloza. 2015. Postfire Ecosystem Restoration. *In* D. Paton, P. T. Buergelt, S. McCaffrey, F. Tedim, and J. F. Shroder [eds.], *Wildfire Hazards, Risks, and Disasters*, 229–246. Elsevier Inc., Oxford, UK.

Vasconcelos, H. L. De, and E. M. Bruna. 2012. Arthropod responses to the experimental isolation of Amazonian forest fragments. *Zoologia* 29: 515–530.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawai‘i: revised edition. Bernice Pauahi Bishop Museum Press, Honolulu, Hawai‘i.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. *Ecology and Evolution of Communities*, 522–534. Harvard University Press, Cambridge, Massachusetts.

Wortley, L., J. M. Hero, and M. Howes. 2013. Evaluating ecological restoration success: A review of the literature. *Restoration Ecology* 21: 537–543.

Zedler, J. B. 2000. Progress in wetland restoration ecology. *Trends in Ecology and Evolution* 15: 402–407.

Zirbel, C. R., E. Grman, T. Bassett, and L. A. Brudvig. 2019. Landscape context explains ecosystem multifunctionality in restored grasslands better than plant diversity. *Ecology* 100: 1–11.

CHAPTER TWO

FIRE MODIFIES THE OUTCOME OF PLANT-SOIL FEEDBACKS

Abstract

Although plant soil feedbacks (the interactions between plants, soil microbes, and soils themselves, abbreviated as PSFs) are widely known to influence patterns of plant diversity at local and landscape scales, these interactions are rarely examined in the context of important environmental factors. This understanding is important because environmental context may alter PSF patterns, by modifying the strength or even direction of PSFs for certain species. One important environmental factor that is increasing in scale and frequency with climate change is fire, though the influence of fire on PSFs remains essentially unexamined. In changing microbial community composition, fire may alter the microbes available to colonize roots of plants and thus seedling growth post-fire. This has potential to change the strength and/or direction of PSFs, depending on how such changes in microbial community composition occur and the plant species with which the microbes interact. We examined how a recent fire altered PSFs of two leguminous, nitrogen-fixing tree species. For both species, growing in conspecific soil resulted in higher plant performance (as measured by biomass production) than growing in heterospecific soil. This pattern was mediated by nodule formation, a critical process for legume species. Fire weakened PSFs for these species and therefore pairwise PSFs were significant outside the burn and tended towards nonsignificant within the burned area. Theory suggests that such positive PSFs in unburned sites would reinforce dominance of these species where they are locally dominant, but this effect might diminish after fire. Our results demonstrate that fire can modify PSFs by weakening the legume-rhizobia symbiosis, which may alter local competitive dynamics between two canopy dominant trees species. These findings illustrate the importance of

considering environmental context when evaluating the role of PSFs for plants, even over relatively small spatial scales.

Introduction

Plants, microbes, and soil interact in diverse ways (termed “plant soil feedbacks” [PSFs]), influencing local biodiversity patterns across the world (Klironomos, 2002; Kardol et al., 2006; Bever et al., 2015). These interactions can shape plant success and survival in both positive (e.g., mutualism) and negative (e.g., pathogens) ways, and this can lead to long-term consequences for biodiversity and coexistence (Chung and Rudgers, 2016). Although it is increasingly evident that the nature of PSFs depends on the environmental context, it remains unclear exactly how and when environmental factors alter the strength or direction of PSFs (Yelenik and Levine, 2011; Crawford et al., 2019). Here, we evaluate how PSFs are modified by a key environmental factor: fire.

Due to the difficulty of assessing effects of environmental factors on PSFs, much attention has been paid to how PSFs influence the survival or performance of a plant living in the space of a conspecific (Kulmatiski et al., 2008; Van der Putten et al., 2013; Crawford et al., 2019). The net outcome of such PSFs is the sum of all the positive, negative, and neutral interactions between plants and microbial communities (Bever et al., 1997). For example, diversity within tropical forests may relate to negative feedbacks between plants and specialist antagonists, including microbial pathogens, which limit the abundance of any one species (Janzen, 1970; Connell, 1971). Such patterns of plant performance being lower when nearer to a mature conspecific (negative density dependence) have been broadly documented across the world’s biomes and in different functional groups, from herbs to trees (Kulmatiski et al., 2008; Crawford et al., 2019). However, PSFs may also increase plant performance, such that proximity

to a mature conspecific may be beneficial (Smith and Reynolds, 2012; Crawford and Knight, 2017). Specialist mutualistic microbes such as mycorrhizae or bacteria, may be more available nearer a mature conspecific, and such mutualistic interactions may balance those of the potential antagonists, resulting in a net positive effect of proximity to a mature conspecific on young plant performance (positive density dependence).

In addition to the PSFs affecting conspecifics, effects on neighboring heterospecifics can lead to pairwise feedbacks that also change patterns of plant performance and where/how plants occur in ecosystems (Bever et al., 1997; Kulmatiski and Kardol, 2008). For example, if one species increases soil-based pathogen loads but these pathogens are more negative for a given heterospecific than for conspecific individuals, then there is a net positive pairwise feedback for that species (Yelenik and Levine, 2011). Additionally, two species of interest may both have positive to neutral PSFs when being grown in both conspecific soil and soil from the other species, relative to heterospecific soils of other species that are not of interest. In that case, the competitive outcome between the two plant species of interest, as mediated by PSFs may depend more on non-PSF-related factors, such as initial abundance of the two species of interest or their relative growth rates. Lastly, an additional possibility is that of a negative net pairwise PSF, where both species are hindered when grown in their own soil, relative to when grown in a heterospecific soil (Crawford et al., 2019). This sort of pairwise PSF can lead to the two species coexisting in the field, all else being equal. All of these pairwise PSFs may also be influenced by environmental context, including that of fire.

Fire is an important disturbance in terrestrial ecosystems worldwide and is forecasted to increase in frequency and extent with climate change (Flannigan et al., 2000; Moritz et al., 2012). In ecosystems where it was historically infrequent, fire can have devastating ecological

consequences and can shift habitats into species-poor stable states where most native diversity is lost (Smith and Tunison, 1992; Ellsworth et al., 2014; Mahood and Balch, 2019). For example, in exotic-grass invaded forests and shrublands, fire can lead to a shift to exotic-dominated landscapes with self-reinforcing short fire return intervals (D'Antonio and Vitousek, 1992; Ellsworth et al., 2014). Typically, fire effects on vegetation are considered through the lens of direct relationships between fire and plants and how fire modifies competitive relationships between plants. Yet, fire may also affect plant communities by altering microbial communities.

Fire is known to alter microbial communities in ways that may then alter plant performance (Pourreza et al., 2014; Hedo et al., 2015; Prendergast-Miller et al., 2017). For example, fire can lead to death of ectomycorrhizal fungi, which may be positive mutualists for plants, leading to a potential shift towards a net negative PSF, if pathogens are then more relatively abundant. However, fire could also eliminate pathogens, which would then favor more positive net PSFs. While it then stands to reason that fire may have strong impacts on PSFs, how fire affects PSFs is poorly understood. Fire may change the direction of PSFs leading from coexistence to competitive exclusion of some species, or it may cause PSFs to vanish altogether (Van der Putten et al., 2013; Senior et al., 2018). Disentangling the complexities of fire on PSFs requires detailed studies that explicitly compare PSFs both with and without fire.

We studied how fire affects PSFs of two tree species in the Fabaceae (the legume family). Like other legumes, these species engage in a mutualism with rhizobial bacteria in the soil (Andrews and Andrews, 2017). Rhizobia fix nitrogen (abbreviated as N, hereafter), which is shared with the plant, while the plant shares carbon and constructs nodules in which the bacteria live. Members of the legume family are ideal for studying PSFs and environmental context because they present a rich set of interactors, both positive (mutualism with rhizobia) and

negative (such as with fungal pathogens) (Jack et al., 2019; Grman, Allen, et al., 2020). How fire might modify the net outcome of these positive and negative interactions remains unknown.

We hypothesized that fire would influence the PSFs of two leguminous tree species found in the Hawaiian Islands. To address this hypothesis, we asked three questions (1) How is plant performance affected by conspecific vs heterospecific soils and is this pattern affected by fire? We predicted that each N-fixer would do better in conspecific soil rather than heterospecific soils, due to the rhizobial mutualism and the relatively low root-associated fungal diversity in Hawai‘i (Hayward and Hynson, 2014). (2) Does nodule formation by rhizobia mediate the effect of soils on plant performance? Given the importance of the rhizobial mutualism to plant performance of legumes, we expected patterns of nodule formation to mediate this relationship. (3) Are net pairwise PSFs between these two species affected by fire? We expected fire to reduce the strength of net pairwise PSFs, as fire may cause death of the microbial members of PSF interactions.

Methods

Study Site and Species

We conducted our work within Hawai‘i Volcanoes National Park on Hawai‘i Island, Hawai‘i. In August of 2018, there was a fire that burned approximately 1500 hectares within the national park, in an area with mostly native upland forest (Figure 2.1). Although fire has not been a significant ecological force in Hawai‘i historically, invasions of exotic grasses, shifting temperatures, and increased ignitions have shortened fire return intervals dramatically (Smith and Tunison, 1992; Trauernicht, 2019). We examined the PSFs of two leguminous tree species endemic to the Hawaiian Islands: koa (*Acacia koa* A. Gray) and māmane (*Sophora chrysophylla* (Salisb.) Seem.). Both of these species are in the family Fabaceae and fix N through a mutualism

with rhizobial bacteria. Additionally, both of these species are able to regenerate after fire, either from seed or from roots, though māmane is, anecdotally, somewhat less fire-tolerant than koa.



Figure 2.1. Study site location on Hawai'i Island.

Soil Sourcing, Set-up, and Data Collection

To examine the effect of fire on PSFs, we performed a factorial experiment using field-collected soils from within and outside the burned area (Figure 2.2). We realize that fires burn heterogeneously, and that fire intensity and fire severity depend on a diverse set of factors, such as slope, aspect, small-scale vegetation patterns, variation in soil organic matter, and small-scale moisture variation (Keeley, 2009; Estes et al., 2017). In our system, old lava flows can form natural barriers of rock, preventing fires from advancing (such as the old flow which forms the upper boundary of the burned area; Figure 2.1). We gathered soils from multiple focal trees

within and outside the burned to attempt to better capture the variation present in the soil microbial community following the fire (or lack thereof).

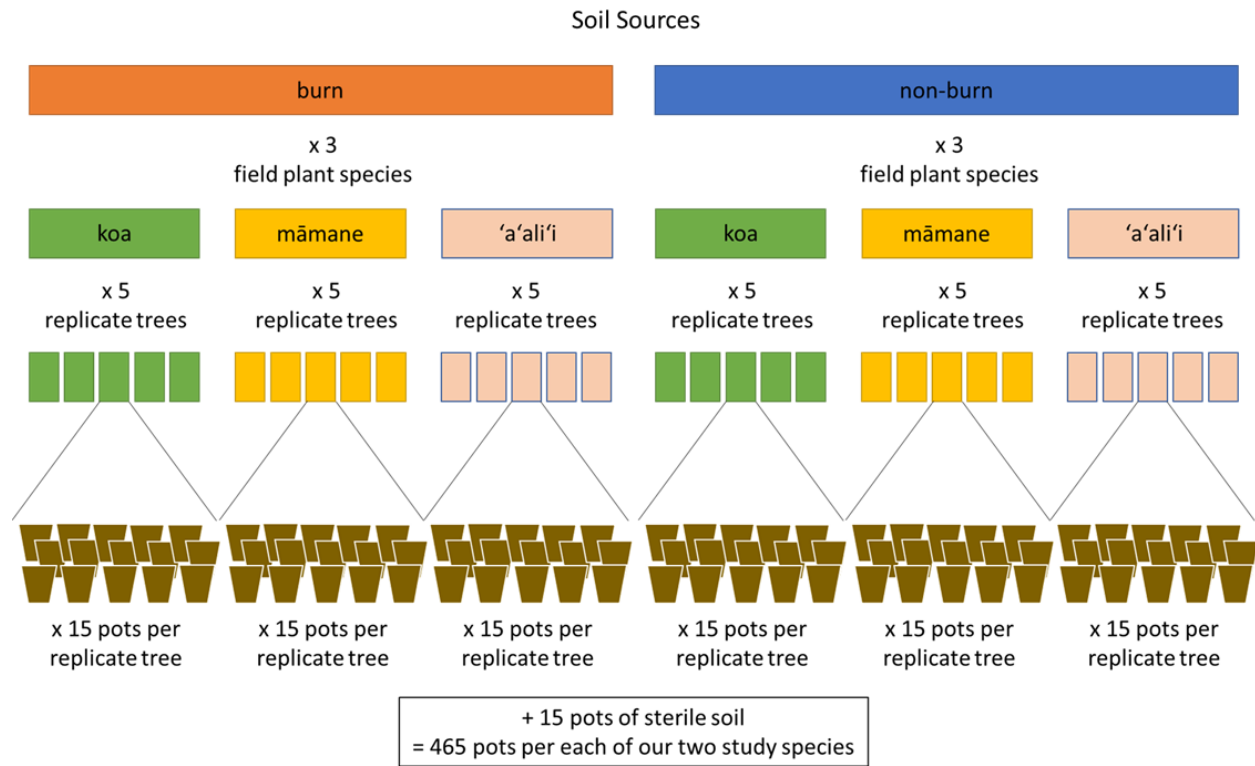


Figure 2.2. Experimental design. We collected soils from within the burned area and outside it. In each location, we collected soils from under koa, māmane, and ‘a‘ali‘i, and we did this with 5 replicate trees of each species. From each of those five replicate trees, we inoculated 15 pots containing a sterile potting medium. We additionally planted seeds in 15 pots containing only the sterile potting medium, for comparison.

In June of 2019, we gathered soils from under both living koa and māmane, as well as from under living ‘a‘ali‘i (*Dodonaea viscosa* (L.) Jacq.), a Hawaiian-native, non-N-fixing member of the Sapindaceae that is common in these sites. We collected soils from under ‘a‘ali‘i so that we would have a consistent “far from conspecific” soil to examine. We collected soils

from under living trees so that effects that we observed were attributable to the burn, rather than to tree death. We termed the species from which we collected soil the “source plant.” We then factorially crossed these three source plants with the burn, by collecting soils from inside the burn and outside the burn ($n = 3 \text{ source plants} \times 2 [\text{burn vs not}] = 6 \text{ possible types of soil inoculum}$). Within each source plant $\times$ burn combination, we collected soils from under 5 replicate trees (Figure 2.2). For the locations and elevations of each of the locations from which we collected soil, please see Table 2.1. The elevation for soil collection location was determined using the Bulk Point Query tool at the United States Geological Survey’s The National Map project (USGS, 2019). We collected soils to a depth of up to ~12 cm, though we generally tried to collect soil from shallow depths as much as possible. The effects of fire on soil biota have been documented to penetrate into the soil profile for up to ~10 cm (Ahlgren, 1974; Pattinson et al., 1999; Mataix-Solera et al., 2009), but are most often documented within the first 3 cm (Ahlgren, 1974; Bradstock and Auld, 1995; Mataix-Solera et al., 2009). Post soil collection, we homogenized soil from within (but not across) each replicate tree in the field. The depth of the soils that we collected likely indicates that the results from this work likely would be conservative, in relation to effects of the fire on the soil microbial community. To minimize any effects of soil nutrients or other non-microbial factors, we used an inoculation approach, whereby we used an inoculum of field soil to pots containing sterilized potting medium (Crawford et al., 2019). We sterilized our potting medium (Professional Growing Mix SS#1, Sungro Horticulture, Agawam, Massachusetts, USA) by autoclaving it for 60 minutes at 121°C. We used a ratio of 85% sterile potting medium to 15% field soil per pot, by volume, following typical inoculation practices (Crawford et al., 2019). Pots were standard 4-inch pots and were surface-sterilized prior to use by submersion in a 0.6% concentration bleach solution for 12-14

hours. Each pot contained a total of 475mL of soil (400mL sterile medium and 75mL field soil inoculum). From each of the 5 replicate trees for each plant species $\times$ burn combination, we inoculated a total of 15 pots filled with sterile potting media ($n = 15 \text{ pots} \times 5 \text{ replicate trees} \times 3 \text{ source plants} \times 2 [\text{burn vs not}] = 450 \text{ pots}$ per each of koa and māmane; see Figure 2.2). We grew a seedling of each species in an additional 15 pots of sterile potting media as a reference for the absence of soil biota for later visual comparisons, though due to the nested nature of our experimental design, we were unable to include these sterile soil seedlings in our statistical analyses. Because some seeds did not germinate, our final sample sizes for each species were 324 inoculated pots and 15 sterile pots for koa and 408 inoculated pots and 13 sterile pots for māmane. Seedlings were grown in a greenhouse located at Kīlauea Field Station, within Hawai‘i Volcanoes National Park, and we randomized placement of the different sorts of inoculum across five benches.

Table 2.1. Field soil table.

Species	Burn?	Latitude	Longitude	Elevation (m asl)
‘a‘ali‘i	burn	19.47594	-155.36295	1705.8
‘a‘ali‘i	burn	19.47566	-155.36301	1701.8
‘a‘ali‘i	burn	19.47627	-155.36180	1700.7
‘a‘ali‘i	burn	19.47611	-155.36170	1699.1
‘a‘ali‘i	burn	19.47603	-155.36277	1705.8
koa	burn	19.47593	-155.36214	1701.2
koa	burn	19.47557	-155.36240	1698.3
koa	burn	19.47570	-155.36212	1698.4
koa	burn	19.47580	-155.36182	1696.9
koa	burn	19.47544	-155.36185	1695.7
māmane	burn	19.47610	-155.36242	1704.2
māmane	burn	19.47555	-155.36271	1699.0
māmane	burn	19.47582	-155.36310	1704.4
māmane	burn	19.47653	-155.36179	1701.3
māmane	burn	19.47637	-155.36184	1701.3
‘a‘ali‘i	nonburn	19.48777	-155.38692	1999.8
‘a‘ali‘i	nonburn	19.48781	-155.38680	1999.4
‘a‘ali‘i	nonburn	19.48793	-155.38695	2004.2
‘a‘ali‘i	nonburn	19.48818	-155.38671	2003.4

Table 2.1 (cont'd)

‘a‘ali‘i	nonburn	19.48779	-155.38661	1997.9
koa	nonburn	19.48840	-155.38653	2002.8
koa	nonburn	19.48848	-155.38689	2008.6
koa	nonburn	19.48863	-155.38684	2008.6
koa	nonburn	19.48865	-155.38660	2006.8
koa	nonburn	19.48773	-155.38609	1989.8
māmane	nonburn	19.48799	-155.38648	1998.8
māmane	nonburn	19.48805	-155.38677	2002.4
māmane	nonburn	19.48792	-155.38657	1998.8
māmane	nonburn	19.48833	-155.38712	2011.8
māmane	nonburn	19.48819	-155.38730	2013.5

Prior to planting, seeds were scarified and surface-sterilized, to enable rapid germination and to eliminate any confounding microbes potentially on the seed coats. The māmane seeds were scarified and sterilized in a solution of 100% sulfuric acid for 1 hour, and then rinsed to remove the acid solution (Sierra McDaniel & Makani Gregg, Pers. Comm.). The koa seeds were scarified in nearly boiling water (~90°C) for 60 seconds, rapidly cooled in a cold water bath, and then soaked in cool water overnight (Elevitch and Wilkinson, 2003), then surface-sterilized in a 0.6% concentration bleach solution for 10 minutes, followed by a sterile water rinse to remove the bleach solution. We planted three seeds of either māmane or koa into the inoculated or sterile pots (n=465 originally, per focal species) to ensure sufficient germination. We thinned to one seedling in each pot at the time of the emergence of the first true leaf. Seedlings were grown for a period of 10 weeks after the emergence of the first true leaf. In the 10 weeks in which the koa seedlings were growing, some plants experienced insect herbivory, which is known to affect biomass production (Bonfil, 1998; Barton, 2016), and we recorded whether a plant experienced herbivory at any time. Māmane seedlings experienced essentially no herbivory, so we did not record this for that species. Following the 10-week growth period, we harvested all individuals and took data on total dry weight biomass (g) and the number of nodules present on the roots of

each seedling. We divided total dry weight biomass (g) by the number of days that a given individual seedling had grown from the emergence of the first true leaf to harvest, to standardize study duration across individuals.

Analysis

All analyses were conducted in R, version 3.6.3 (R Core Team, 2020), through the interface of RStudio, version 1.2.5033 (RStudio, 2019).

How is plant performance affected by soil source and is this pattern affected by fire?

We ran separate linear mixed models for koa and māmane, to examine the effects of the burn. The response variable was total dry biomass, standardized to the number of growing days. The predictor variables were the source plant, the number of nodules present at the time of harvest, and the interaction between the burn and the source plant on biomass. We used two random effects: one for the replicate tree (to account for the 5 replicate trees in each field soil, see Figure 2.2) and the second for the bench in the greenhouse, to account for any effects of where they plants were growing in the greenhouse. We treated the response as following a Gaussian distribution, as the biomass data were normal. Within this model, but only for koa, we included a term for herbivory, due to herbivory on this species in the greenhouse (the māmane plants did not experience herbivory over the study period). We additionally ran separate generalized linear mixed models for koa and māmane, in which the number of nodules was the response, with the predictors of the source plant, the burn, and the interaction of those terms, and treating the response as following a negative binomial distribution (because the number of nodules is overdispersed count data). The random effects of these models followed the same structure as the models with biomass as the response. All four of these models were run through the lme4 package, version 1.1-23 (Bates et al., 2015). We derived the effect size of percent

difference, from estimated marginal means from the model, using emmeans, version 1.4.8 (Lenth, 2020), and using the percent difference formula of: $|\mu_1 - \mu_2| / ((\mu_1 + \mu_2) / 2)$, where μ_i are the estimated marginal means.

Does nodule formation by rhizobia mediate the effect of soils on plant performance?

Based on the results of our linear mixed models, we investigated the direct effect of source plant on biomass and its indirect effect (via nodulation) on biomass, using a structural equation model (SEM) for each of koa and māmane. We constructed SEMs using the piecewiseSEM package, version 2.1.1 (Lefcheck, 2016). We constructed SEMs using both of the models that we used for our linear mixed models, with the modifications that, given that our soil source predictors consisted of three non-ordinal categories, we split soil source into three columns of binary responses (koa or not, ‘a‘ali‘i or not, māmane or not), and removed the focal species binary column from its own model, to avoid rank deficiency of the model. To calculate the standardized effects, in order to facilitate comparison between our variables of interest, we multiplied the beta coefficient of the model by the standard deviation of the independent variables divided by the standard deviation of the dependent variable.

Are net pairwise PSFs between our two focal species affected by fire?

We calculated net pairwise PSF (noted using the interaction coefficient, I_s), following Bever et al. (1997). In this framework, $I_s = G(A)_\alpha - G(A)_\beta - G(B)_\alpha + G(B)_\beta$, where $G(A)$ and $G(B)$ represent growth (biomass, in our case) of species A and B, respectively, and α and β refer to soil sourced from under species A and B, respectively (Bever et al., 1997). Because this feedback is calculated only between pairs of species, we only examined the pairwise feedbacks between koa and māmane, as we did not grow any ‘a‘ali‘i seedlings. First, we determined whether a pairwise PSF between these two species significantly differed inside vs. outside of the

burn. To do this, we ran a linear mixed model in which the response was biomass and the predictor variables were the species (two focal species), the source plant, the burn, and all interactions. Here, a significant three-way interaction between focal species, source plant, and burn would indicate that PSFs differ between burn treatments for these two species. We then calculated I_s within and outside the burn using two linear mixed models, one inside the burn and one outside it. To do this, we ran a linear mixed model in which the response was biomass and the predictor variables were the focal species, the source plant, and their interaction. Here, a significant interaction would indicate a significant PSF between the two species. From this model, we extracted I_s , the coefficient associated with the interaction between the two species, and determined its significance using `summary.lmerModLmerTest`, which uses a Type III ANOVA with Satterthwaite's approximation for degrees of freedom. We ran models in this section in `lmerTest`, version 3.1-2 (Kuznetsova et al., 2017).

Results

How is plant performance affected by source plant and is this pattern affected by fire?

Koa biomass was not affected by source plant (Figure 2.3; Table 2.2). However, more nodules resulted in higher koa biomass and nodulation was affected by source plant, with more nodules in conspecific soil (Table 2.3). There were 5.2% more nodules on koa in koa soil than in māmane soil and 10.5% more nodules on koa in koa soil than in 'a'ali'i soil (calculated as percent difference).

For māmane, biomass was affected by source plant (Figure 2.3; Table 2.2), with higher biomass in conspecific soil. Māmane biomass was 33.0% higher in conspecific soil than in koa soil and 13.9% higher when grown in conspecific soil than in 'a'ali'i soil (percent difference). However, for māmane, nodulation patterns were not affected by soil source (Table 2.3).

The recent fire did not affect biomass or nodulation for koa (Tables 2.2 and 2.3), nor for biomass of māmane (Table 2.2) (see Figure 2.3 for biomass data). Fire had an interactive effect on the nodulation of māmane, where māmane seedlings grown in māmane soil had more nodules outside the burn than māmane seedlings in any other treatment (Table 2.3; range of 5.1%-37.8% more nodules than other source plant $\times$ burn combinations [percent difference]).

Table 2.2. Statistical table for biomass models

	Predictor	Chi.sq	df	p-value
Koa	Burn	0.20	1	0.65
	Source Plant	4.12	2	0.13
	Number of Nodules	58.71	1	<0.0001
	Interaction between Source Plant and Burn	0.45	2	0.80
Māmane	Burn	0.87	1	0.35
	Source Plant	9.33	2	0.0094
	Number of Nodules	68.42	1	<0.0001
	Interaction between Source Plant and Burn	5.18	2	0.075

Table 2.3. Statistical table for nodulation models

	Predictor	Chi.sq	df	p-value
Koa	Burn	1.35	1	0.25
	Source Plant	11.63	2	0.0030
	Interaction between Source Plant and Burn	1.69	2	0.43
Māmane	Burn	12.84	1	0.00034
	Source Plant	3.87	2	0.14
	Interaction between Source Plant and Burn	20.42	2	<0.0001

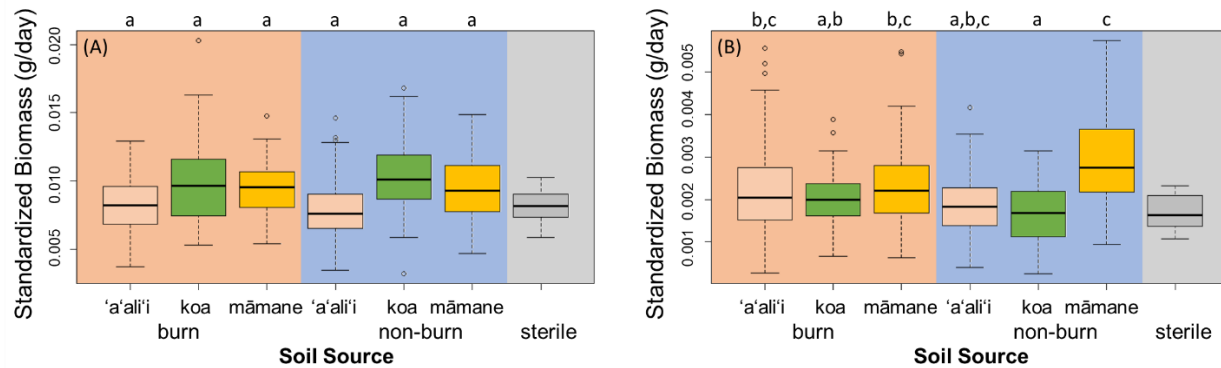


Figure 2.3. Standardized biomass (g/day) for koa (Panel A) and māmane (Panel B), by source plant crossed with burn. Background color indicates burn (light orange; left) or nonburn (light blue; middle), and bar color is color coded by source plant species. Letters above the plot indicate groups, determined by post-hoc comparisons. Biomass tends to be higher in soil from conspecifics and N-fixing species. Sterile soil (gray bar with a gray background; right) is included for a visual comparison and was not included in statistical analyses.

Does nodule formation by rhizobia mediate the effect of soils on plant performance?

Koa

Koa tended to obtain greater biomass in its own soils than in heterospecific soils ('a'ali'i and māmane), leading to a positive single species PSF. Biomass differences were indirectly mediated through number of nodules. Biomass was positively affected by the number of nodules ($r = 0.38$, $p < 0.0001$). Koa produced more nodules when grown in its own soil compared to 'a'ali'i soil ($r = -0.0053$, $p < 0.0001$), with the indirect effect of growing in 'a'ali'i soil being $r = -0.0020$. Koa also produced more nodules when grown in its own soil compared to māmane soil ($r = -0.0027$, $p=0.022$), with the standardized indirect effect of growing in māmane soil

being $r = -0.0010$. Biomass was negatively affected by herbivory ($r = -0.19$, $p = 0.0001$). The SEM fit the data well (Fisher's $C = 0.035$; $p = 0.98$; Figure 2.4).

Māmane

Māmane, similar to koa, obtained greater biomass in its own soils than in heterospecific soils ('a'ali'i and koa) leading to a positive single species PSF. Unlike koa, however, this was only indirectly mediated through nodule biomass with one of the away soils: 'a'ali'i. Māmane biomass was higher when grown in its own soil than when grown in 'a'ali'i soil ($r = -0.15$, $p = 0.019$), with the indirect effect of growing in 'a'ali'i soil being $r = -0.0083$. Māmane biomass was also higher when grown in its own soil than when grown in koa soil ($r = -0.35$, $p < 0.0001$), with the indirect effect of growing in koa soil being $r = -0.0016$. Biomass was positively affected by the number of nodules ($r = 0.39$, $p < 0.0001$). The number of nodules was negatively affected by being grown in 'a'ali'i soil ($r = -0.021$, $p = 0.0002$). The SEM fit the data well (Fisher's $C = 0$; $p = 1$; Figure 2.4).

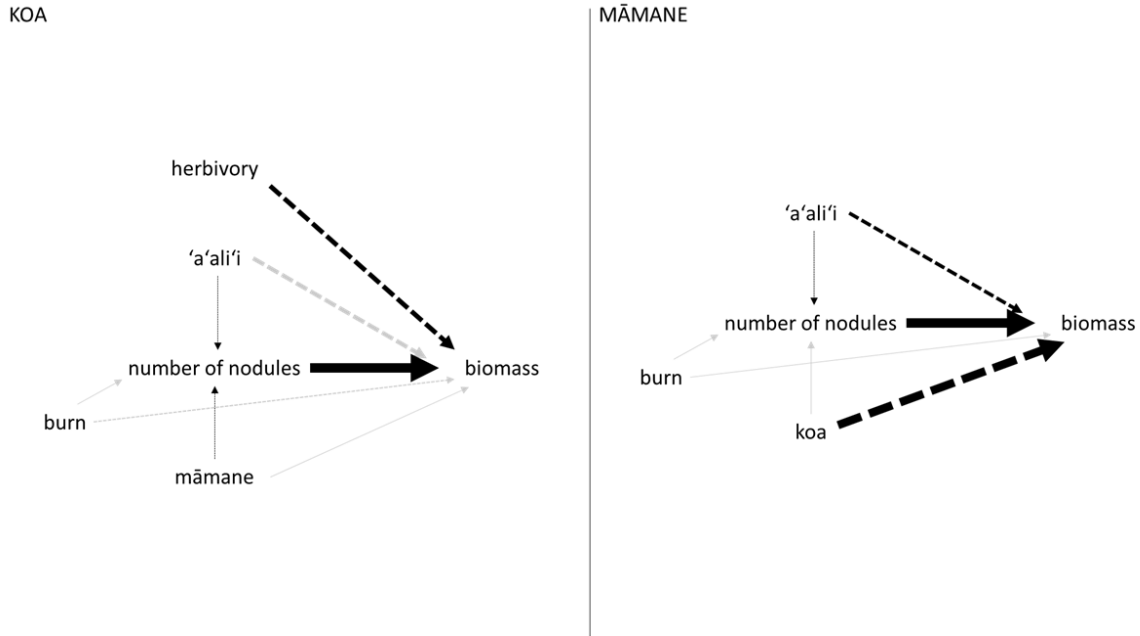


Figure 2.4. SEM diagrams for each species. Solid arrows indicate positive relationships, while dashed arrows indicate negative relationships. Black arrows indicate significant relationships ($p < 0.05$), while gray arrows indicate nonsignificant relationships ($p > 0.05$). Line size is scaled to standardized effect size.

Are net pairwise PSFs between our two focal species affected by fire?

Burning trended towards reducing the strength of otherwise positive PSFs between koa and māmane ($F_{1,457} = 2.96$; $p = 0.086$). Outside the burn, PSFs are significantly positive ($I_s = 0.0016$, $p = 0.00027$). However, within the burn, I_s is 0.00061, and this is not significant ($p = 0.16$).

Discussion

Our study is one of the first experimental studies to explicitly test the effects of fire on PSFs, and, in doing so, we found that fire can alter net pairwise PSFs with important implications for post-fire succession. Mechanistically, this may have been due to a breakdown in

the positive effects of conspecific soils, suggesting that positive benefits from rhizobia were weakened with the fire. Specifically, in māmane, root nodulation was lower in soils from burned sites. Our results illustrate the importance of considering how environmental context, and specifically fire, alters PSFs.

Nodule formation positively affected seedling performance, and this is likely a major factor for the positive relationship that we see with our seedlings when they are grown in conspecific soil (Crawford and Knight, 2017; Siefert et al., 2018). The patterns that we observe with nodulation may indicate that the rhizobial bacteria associated with our species are at least somewhat host-specific, as has been shown with rhizobial bacteria in other systems (Fauvert and Michiels, 2008; Andrews and Andrews, 2017). In our system, nodulation of koa was higher when grown in conspecific soil, while nodulation in heterospecific soil of another legume was similar to heterospecific soil from a non-N-fixer, which further demonstrates that koa rhizobia may be somewhat host-adapted. For māmane, although not significant, nodulation trended toward being higher in conspecific soil than heterospecific soil and higher in N-fixer soil than non-N-fixer soil. These patterns indicating potential host-specificity of rhizobia may be part of the reason that PSFs are positive in conspecific soil in our system and suggest a mechanism for positive PSFs elsewhere.

For one of our study species (māmane) the pattern of nodulation was affected by fire, indicating that fire can change positive PSF interactions (Carvalho et al., 2010; Jesus et al., 2020). Nodulation was higher in conspecific, non-burned soil than any other combination of burn and soil source, indicating that fire negatively impacts the ability of this species to form nodules. How fire affects PSFs and patterns of nodulation in legumes is poorly understood (De Long et al., 2019). PSFs broadly have only rarely been studied in the context of environmental factors.

However, fire has been shown to lead to large-scale changes in bacterial and fungal communities, independent of plants (Dooley and Treseder, 2012; Whitman et al., 2019), and we show how these types of impacts can shape PSFs. Within the legume-rhizobial symbiosis, it is increasingly recognized that nodulation can be modified by fire, especially with shifts in the bacterial community involved in this interaction (Jesus et al., 2020), but this has not been studied outside just a few systems. Our work shows that fire can modify nodulation patterns and as a result reduce the strength of positive PSF.

While our results do demonstrate the importance of incorporating the effects of fire when considering PSFs, our findings are also nuanced. It is possible that some of this nuance in our results is potentially due to fire severity. Fire severity is known to affect the soil microbial community, with more severe fires having correspondingly larger impacts on soil microbes (Reazin et al., 2016; Adkins et al., 2020), and this may then also reflect back on the microbes that participate in PSFs. We sampled from beneath trees that survived the fire (to not confound our results with death of an individual in the field), and it is possible that, by selecting from these trees, we selected for microsites of lower fire severity, which potentially muted our findings, relative to that which may occur in microsites with higher fire severity. In addition, there could be a temporal effect, where fire's effects on PSFs become more muted over time. We collected soils ~10 months following the burn. Although some effects of fire on soil microbes have been shown to last for ~20 years (Pérez-Valera et al., 2018) and PSFs may carry on after the death of an individual (Kardol et al., 2007; Mueller et al., 2019), these effects do become less with time, and effects on PSFs are likely most pronounced immediately following the fire itself.

There are additional caveats due to the nature of our experimental design. We worked within and outside of a single wildfire event, meaning that, on the scale of fire events, $n=1$. We

sampled from both within and outside of the burned area. Due to the way that the burn occurred and the fact that the uphill border of the burn was an old lava flow, our samples from within the burned area and outside of the burned area occurred at different elevations. The burned soil samples were taken from 1695 m asl to 1705 m asl and the non-burned samples were taken from 1989 m asl to 2013 m asl. Despite the difference in elevation between these areas, the pre-fire vegetation community is broadly similar at both elevations.

Although pairwise PSFs between species are the most frequent way to examine PSFs, such studies rarely incorporate environmental context and almost never incorporate the relationship with fire (Kulmatiski and Kardol, 2008; Van der Putten et al., 2013; Senior et al., 2018; Crawford et al., 2019; Beals et al., 2020). We see that there is a significant pairwise feedback between two species in non-burned areas, and while not significantly different from the lack of feedback within the burned area, the trend is towards stronger feedbacks before fire. This means that, likely, prior to fires, neighbor identity matters for koa and māmane, while after fire, this PSF pattern disappears. Similar patterns have been seen in the only other study of this sort of which we are aware (Senior et al., 2018). Such weakening of PSFs with fire follows from a priori assumptions where the abundance and richness of soil microbes decreases after fire (Dooley and Treseder, 2012; Reazin et al., 2016). Given this assumption, our results, and those of Senior et al (2018), it is possible that such patterns may be occurring in fire-impacted systems more generally.

Changes to PSFs may influence patterns of plant diversity, and understanding of the pairwise PSFs of our two focal species can help understand the interactions between these two plant species in the field. Forests in the Hawaiian Islands are relatively species poor, in terms of tree diversity (Little and Skolmen, 1989), and our two focal species make up the vast majority of

trees within our study site (C. Warneke, S. Yelenik, personal observation). In areas near our field site, koa abundance seem to rapidly increase in previously māmane-dominated habitats after successive fires (Rick Warshauer, personal communication). Based on our findings, it seems likely that, before fire, PSFs would reinforce each species where it is already locally dominant. However, after fire, when PSFs break down, it may be more likely for the two N-fixers to shift in their local dominance patterns towards more coexistence or a change in local dominance towards koa. Koa growth rates are higher than those of māmane (Barton and Shiels, 2020), and it is possible that this trend of weaker pairwise feedbacks that we observed in burned areas may enable koa to better outcompete māmane, post-fire. Although this is a trend in our data, and is nonsignificant, it does support the anecdotal field observation of these species in field conditions.

Our results suggest that managers may need to consider changes in microbial communities after fire when considering management actions (Dooley and Treseder, 2012; Pérez-Valera et al., 2018; Grman, Allen, et al., 2020). Due to the increase in fire frequency in the Hawaiian Islands in recent years and going forward, land managers often plant seeds and seedlings of our study species into recently burned habitats to reestablish the native plant community (McDaniel et al., 2008). By adding conspecific soil or rhizobial inoculum to growing media, restoration practitioners may help grow bigger, more successful koa and māmane in the greenhouse, which, in turn may allow for better success of seedlings when outplanted into field conditions (Elevitch and Wilkinson, 2003). Decreases in nodule formation may alter growth rates of these species in post-fire reseeding and planting efforts, and countering that through inoculation may benefit restoration efforts. This is likely to more strongly benefit māmane, which has a slower growth rate than koa (Yelenik et al., 2017; Barton and Shiels, 2020), making restoring populations of this species a challenge in degraded habitat conditions.

Overall, our results demonstrate that fire has the potential to modify PSFs and the legume-rhizobial symbiosis. The relationship between fire and PSFs has been unclear; yet, advancing knowledge around this topic is critical at a time when fire is increasing worldwide. Our work demonstrates the importance of considering environmental context for PSFs.

Acknowledgements

We thank staff and managers at Hawai‘i Volcanoes National Park and the Pacific Cooperative Studies Unit for their assistance, coordination, and resources (including greenhouse space), and we particularly thank Heather Quintana, Makani Gregg, and Sierra McDaniel for their thoughts, time, and enthusiasm for this work. We thank USGS-PIERC and particularly Gordon Tribble and Nina Zárate for logistical support and PIERC/HAVO for providing housing and office space for C. Warneke while this work was being conducted. We thank the USDA-FS and USDA-ARS for letting us use their autoclaves to sterilize our potting media. We thank Kim Freeman, Rosanise Odell, Gabe Runte, Taylor Saunders, and Jeff Stallman for assistance in different parts of the setup and/or harvest of this experiment. We thank Jonathan Bauer, Clarice Esch, Meredith Zettlemoyer, and Chad Zirbel for thoughts and feedback about different aspects of this experiment and/or manuscript. Funding for this project was provided by the USGS Environments Program and USGS-NPS Natural Resources Preservation Program (NRPP), and by the National Science Foundation (Awards 1354085, 1913501, 1921769).

LITERATURE CITED

LITERATURE CITED

- Adkins, J., K. M. Docherty, J. L. M. Gutknecht, and J. R. Miesel. 2020. How do soil microbial communities respond to fire in the intermediate term? Investigating direct and indirect effects associated with fire occurrence and burn severity. *Science of the Total Environment* 745: 140957.
- Ahlgren, I. F. 1974. The effect of fire on soil organisms. In T. T. Kozlowski, and C. E. Ahlgren [eds.], *Fire and Ecosystems*, 47–72. Academic Press, Cambridge, Massachusetts.
- Andrews, M., and M. E. Andrews. 2017. Specificity in legume-rhizobia symbioses. *International Journal of Molecular Sciences* 18.
- Barton, K. E. 2016. Low tolerance to simulated herbivory in Hawaiian seedlings despite induced changes in photosynthesis and biomass allocation. *Annals of Botany* 117: 1053–1062.
- Barton, K. E., and A. B. Shiels. 2020. Additive and non-additive responses of seedlings to simulated herbivory and drought. *Biotropica* 52: 1217–1228.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48.
- Beals, K. K., J. A. M. Moore, S. N. Kivlin, S. L. J. Bayliss, C. Y. Lumibao, L. C. Moorhead, M. Patel, et al. 2020. Predicting plant-soil feedback in the field: Meta-analysis reveals that competition and environmental stress differentially influence PSF. *Frontiers in Ecology and Evolution* 8.
- Bever, J. D., S. A. Mangan, and H. M. Alexander. 2015. Maintenance of Plant Species Diversity by Pathogens. *Annual Review of Ecology, Evolution, and Systematics* 46: 305–325.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology* 85: 561–573.
- Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany* 85: 79–87.
- Bradstock, R. A., and T. D. Auld. 1995. Soil Temperatures During Experimental Bushfires in Relation to Fire Intensity: Consequences for Legume Germination and Fire Management in South-Eastern Australia. *The Journal of Applied Ecology* 32: 76.
- Carvalho, L. M., P. M. Antunes, M. A. Martins-Loução, and J. N. Klironomos. 2010. Disturbance influences the outcome of plant-soil biota interactions in the invasive *Acacia*

- longifolia* and in native species. *Oikos* 119: 1172–1180.
- Chung, Y. A., and J. A. Rudgers. 2016. Plant–soil feedbacks promote negative frequency dependence in the coexistence of two aridland grasses. *Proceedings of the Royal Society B: Biological Sciences* 283.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer, and G. R. Gradwell [eds.], *Dynamics of Populations*, 298–312. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, et al. 2019. When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters* 22: 1274–1284.
- Crawford, K. M., and T. M. Knight. 2017. Competition overwhelms the positive plant–soil feedback generated by an invasive plant. *Oecologia* 183: 211–220.
- D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- Dooley, S. R., and K. K. Treseder. 2012. The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry* 109: 49–61.
- Elevitch, C. R., and K. M. Wilkinson. 2003. Growing koa: A Hawaiian legacy tree. Permanent Agriculture Resources, Hōlualoa, Hawai‘i.
- Ellsworth, L. M., C. M. Litton, A. P. Dale, and T. Miura. 2014. Invasive grasses change landscape structure and fire behaviour in Hawaii. *Applied Vegetation Science* 17: 680–689.
- Estes, B. L., E. E. Knapp, C. N. Skinner, J. D. Miller, and H. K. Preisler. 2017. Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA. *Ecosphere* 8.
- Fauvert, M., and J. Michiels. 2008. Rhizobial secreted proteins as determinants of host specificity in the rhizobium-legume symbiosis. *FEMS Microbiology Letters* 285: 1–9.
- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest factors. *The Science of the Total Environment* 262: 221–229.
- Grman, E., J. Allen, E. Galloway, J. McBride, J. T. Bauer, and P. A. Price. 2020. Inoculation with remnant prairie soils increased the growth of three native prairie legumes but not necessarily their associations with beneficial soil microbes. *Restoration Ecology* 28: S393–S399.
- Hayward, J., and N. A. Hynson. 2014. New evidence of ectomycorrhizal fungi in the Hawaiian

- Islands associated with the endemic host *Pisonia sandwicensis* (Nyctaginaceae). *Fungal Ecology* 12: 62–69.
- Hedo, J., M. E. Lucas-Borja, C. Wic, M. Andrés-Abellán, and J. De Las Heras. 2015. Soil microbiological properties and enzymatic activities of long-term post-fire recovery in dry and semiarid Aleppo pine (*Pinus halepensis* M.) forest stands. *Solid Earth* 6: 243–252.
- Jack, C. N., K. J. Wozniak, S. S. Porter, and M. L. Friesen. 2019. Rhizobia protect their legume hosts against soil-borne microbial antagonists in a host-genotype-dependent manner. *Rhizosphere* 9: 47–55.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.
- Jesus, J. G. de, R. Tenreiro, C. Máguas, and H. Trindade. 2020. *Acacia longifolia*: A host of many guests even after fire. *Diversity* 12.
- Kardol, P., N. J. Cornips, M. M. L. Van Kempen, J. M. T. Bakx-Schotman, and W. H. Van Der Putten. 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs* 77: 147–162.
- Kardol, P., T. Martijn Bezemer, and W. H. Van Der Putten. 2006. Temporal variation in plant-soil feedback controls succession. *Ecology Letters* 9: 1080–1088.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire* 18: 116–126.
- Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67–70.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: A meta-analytical review. *Ecology Letters* 11: 980–992.
- Kulmatiski, A., and P. Kardol. 2008. Getting Plant—Soil Feedbacks out of the Greenhouse: Experimental and Conceptual Approaches. In U. Lüttge, W. Beyschlag, and J. Murata [eds.], *Progress in Botany*, vol 69, 449–472. Springer Berlin Heidelberg, Berlin.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Brockhoff. 2017. lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software* 82: 1–26.
- Lefcheck, J. S. 2016. piecewiseSEM : Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7: 573–579.
- Lenth, R. V. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Little, E. L. J., and R. G. Skolmen. 1989. Common forest trees of Hawaii (native and

- introduced). United States Department of Agriculture, Agriculture Handbook No. 679. Washington, DC.
- De Long, J. R., E. L. Fry, G. F. Veen, and P. Kardol. 2019. Why are plant–soil feedbacks so unpredictable, and what to do about it? *Functional Ecology* 33: 118–128.
- Mahood, A. L., and J. K. Balch. 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). *Ecosphere* 10: 1–19.
- Mataix-Solera, J., C. Guerrero, F. García-Orenes, G. M. Bárcenas, and M. P. Torres. 2009. Forest fire effects on soil microbiology. In A. Cerdà, and P. R. Robichaud [eds.], *Fire effects on soil and restoration strategies*, 133–175. Science Publishers, Enfield, New Hampshire.
- McDaniel, S., R. K. Loh, S. Dale, K. Smith, and M. Vaidya. 2008. Rehabilitation of ‘ōhi‘a-swordfern (*Metrosideros polymorpha* - *Nephrolepis multiflora*) woodlands following the Kupukupu Fire, Hawai‘i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 160. University of Hawai‘i at Mānoa, Department of Botany, Honolulu, Hawai‘i.
- Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: Art49: 1–22.
- Mueller, R. C., C. M. Scudder, T. G. Whitham, and C. A. Gehring. 2019. Legacy effects of tree mortality mediated by ectomycorrhizal fungal communities. *New Phytologist* 224: 155–165.
- Pattinson, G. S., K. A. Hammill, B. G. Sutton, and P. A. Mcgee. 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research* 103: 491–496.
- Pérez-Valera, E., M. Verdú, J. A. Navarro-Cano, and M. Goberna. 2018. Resilience to fire of phylogenetic diversity across biological domains. *Molecular Ecology* 27: 2896–2908.
- Pourreza, M., S. M. Hosseini, A. A. Safari Sinegani, M. Matiniazadeh, and W. A. Dick. 2014. Soil microbial activity in response to fire severity in Zagros oak (*Quercus brantii* Lindl.) forests, Iran, after one year. *Geoderma* 213: 95–102.
- Prendergast-Miller, M. T., A. B. de Menezes, L. M. Macdonald, P. Toscas, A. Bissett, G. Baker, M. Farrell, et al. 2017. Wildfire impact: Natural experiment reveals differential short-term changes in soil microbial communities. *Soil Biology and Biochemistry* 109: 1–13.
- Van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, et al. 2013. Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology* 101: 265–276.

- R Core Team. 2020. R: a language and environment for statistical computing.
- Reazin, C., S. Morris, J. E. Smith, A. D. Cowan, and A. Jumpponen. 2016. Fires of differing intensities rapidly select distinct soil fungal communities in a Northwest US ponderosa pine forest ecosystem. *Forest Ecology and Management* 377: 118–127.
- RStudio. 2019. RStudio.
- Senior, J. K., J. M. O'Reilly-Wapstra, J. A. Schweitzer, J. K. Bailey, and B. M. Potts. 2018. Forest fire may disrupt plant–microbial feedbacks. *Plant Ecology* 219: 497–504.
- Siefert, A., K. W. Zillig, M. L. Friesen, and S. Y. Strauss. 2018. Soil microbial communities alter conspecific and congeneric competition consistent with patterns of field coexistence in three *Trifolium* congeners. *Journal of Ecology* 106: 1876–1891.
- Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawai'i: Research and management implications for native ecosystems. *Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research*, 394–408. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu, Hawai'i.
- Smith, L. M., and H. L. Reynolds. 2012. Positive plant-soil feedback may drive dominance of a woodland invader, *Euonymus fortunei*. *Plant Ecology* 213: 853–860.
- Trauernicht, C. 2019. Vegetation—Rainfall interactions reveal how climate variability and climate change alter spatial patterns of wildland fire probability on Big Island, Hawaii. *Science of the Total Environment* 650: 459–469.
- USGS. 2019. TNM Elevation. The National Map. Website <https://apps.nationalmap.gov/elevation/> [accessed 15 July 2021].
- Whitman, T., E. Whitman, J. Woolet, M. D. Flannigan, D. K. Thompson, and M. A. Parisien. 2019. Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. *Soil Biology and Biochemistry* 138: 107571.
- Yelenik, S. G., C. M. D'Antonio, and E. August-Schmidt. 2017. The influence of soil resources and plant traits on invasion and restoration in a subtropical woodland. *Plant Ecology* 218: 1149–1161.
- Yelenik, S. G., and J. M. Levine. 2011. The role of plant-soil feedbacks in driving native-species recovery. *Ecology* 92: 66–74.

CHAPTER THREE

ELEVATION, CANOPY COVER, AND GRASS COVER STRUCTURE PATTERNS OF SEEDLING ESTABLISHMENT IN A SUBTROPICAL POST-FIRE RESTORATION

Abstract

Ecological restoration is increasingly critical in this era of large-scale landscape change.

However, restoration outcomes are notoriously variable, which makes fine-scale decision making challenging. This is true for restoration efforts that follow large fires, which are increasingly common as the climate changes. Post-fire restoration efforts, like tree planting and seeding have shown mixed success, though the causes of the variation in restoration outcomes remain unclear.

Abiotic factors such as elevation and fire severity, as well as biotic factors, such as residual canopy cover and abundance of competitive understory grasses, can vary across a burned area and all influence the success of restoration efforts to re-establish trees. We examined the effect of these factors on early seedling establishment of a tree species (māmane [*Sophora chrysophylla* (Salisb.) Seem.]) in a subtropical montane woodland in Hawai‘i. Following a human-caused wildfire, land managers sowed seeds of māmane as part of a restoration effort. We examined māmane seedling establishment and found that elevation was of overriding importance, structuring total levels of plant establishment, with fewer seedlings found at higher elevations. Cover by exotic, competitive understory grasses very weakly positively correlated with increased seedling establishment, and while residual canopy cover was positively correlated with seedling establishment. Our results point to specific factors structuring plant establishment following a large fire and suggest additional targeted restoration actions within this subtropical system, such as more targeted seed placement and grass removal.

Introduction

Large-scale changes in land use and ecosystem disturbance regimes are happening worldwide (Steffen et al., 2011; Lewis and Maslin, 2015). These changes lead to loss of biodiversity with the associated consequences that that entails (Pereira et al., 2010; Haddad et al., 2015). A tool that is used to address the concerns of biodiversity decline is that of ecological restoration (Gann et al., 2019; United Nations, 2020). However, the outcomes of ecological restoration are notoriously unpredictable (Brudvig et al., 2017; Barnard et al., 2019). Understanding the reasons behind the variability of restoration outcomes is critical for moving the field of ecological restoration forward and enabling higher success of restoration actions (Brudvig, 2017).

Variability in outcomes is prevalent in restoration efforts, such as revegetation efforts, following wildfire (Engel and Abella, 2011; Bates et al., 2014; Brudvig et al., 2017). Wildfire, both natural and anthropogenic, is increasing in frequency and scale and is expected to continue increasing worldwide, due partially to the changing climate (Flannigan et al., 2000; Moritz et al., 2012). Fire, especially in ecosystems where it may have historically been infrequent, can change ecosystem composition and function (D'Antonio and Vitousek, 1992). Species diversity is often lost following large fires which can change community functioning and ecosystem services for humans (such as changes to water quality) (D'Antonio and Vitousek, 1992; Smith et al., 2011). As a result of these effects on the ecological community and human wellbeing, land managers often take large and often costly actions to try to mitigate disturbance by fire, often involving revegetation of the burned area via planting of native species, and, in forested systems, of trees (McDaniel et al., 2008; Peppin et al., 2010; Vallejo and Alloza, 2015; Copeland et al., 2018). However, these efforts have varied success in terms of reestablishment of desired vegetation

(Bates et al., 2014; Munson et al., 2020). Better understanding of the context dependency of what is driving success or failure of revegetation action could allow land managers, who often have limited funds, personpower, and time, to direct their efforts to focus on areas that are more likely to have successful restoration outcomes as well as what additional techniques may be needed to enhance success across contexts (Brudvig and Catano *in press*, Gann et al. 2019).

One factor that leads to more frequent fire in systems where fire was infrequent historically is that of non-native grasses (D’Antonio and Vitousek, 1992; D’Antonio et al., 2011). These grasses may form self-reinforcing positive feedback loops with fire, in which fire size increases and return interval decreases as a result of increased fuel (provided by the grasses), which then benefits grasses relative to native plant species that may not be as well adapted to fire (Smith and Tunison, 1992; Ellsworth et al., 2014; Mahood and Balch, 2019). This feedback loop may result in species-poor alternative stable states where one of the major components is the cover of nonnative grasses (Smith and Tunison, 1992; D’Antonio et al., 2011; Yelenik and D’Antonio, 2013). In addition to their effects on fire regimes with their associated impacts on biodiversity, nonnative grasses are a major competitor with native plants. Grasses are often strong competitors for resources and in systems like ours, in the upland forests of Hawai‘i, where monoculture-forming grasses were historically absent, introduced grasses can consistently suppress natural regeneration of the native flora, even in the absence of the relationship of grasses with fire (Smith and Tunison, 1992; Yelenik and D’Antonio, 2013). Indeed, past work has shown that exotic pasture grasses in the understory of forests can create priority effects that stall succession to a more diverse forest system (Yelenik, 2017; Rehm et al., 2019). In sites where fire has occurred, these forests tend to reestablish as similar, species-depauperate systems with a native monotypic canopy and exotic grass understory (Hughes and Vitousek, 1993;

Yelenik, 2017). A tool that may work to increase native diversity, lower grass dominance, and break grass-fire cycles is seed-based restoration, where diverse seeds of native species are sown immediately after the fire event has occurred (McDaniel et al., 2008; Copeland et al., 2018). Work, both in systems similar to our own, as well as more broadly, has shown that this approach, while it may help with maintenance of biodiversity, does not always break this cycle (McDaniel et al., 2008; Yelenik, 2017; Munson et al., 2020).

There are myriad factors that may affect success of restoration via revegetation following a fire. Factors like patterns of residual canopy cover, fire severity, abiotic aspects of the soil, invasive plant species responses, and more have all been shown to change plant-based restoration outcomes (Díaz-Delgado et al., 2003; Bowles et al., 2011; Kulpa et al., 2012). Abiotic factors such as landscape position and fire severity can impact how restoration and revegetation proceeds, post-fire (Díaz-Delgado et al., 2003; Kulpa et al., 2012). Elevation, especially in topographically-diverse systems, can change local habitat characteristics in profound ways, and is known to affect restoration success and revegetation patterns (D'Antonio et al., 2000; Ainsworth and Kauffman, 2010; Bowles et al., 2011; Davies et al., 2011). Additionally, fire severity may affect the outcome of restoration actions that are undertaken post-fire through changes to soil aggregate properties, organic matter and nutrients, the microbial community, and many other factors (Dooley and Treseder, 2012; Vallejo and Alloza, 2015). Biotic factors, such as competition with invasive species and residual canopy cover following fire, which are often heterogeneous across burned landscapes, are likely to change patterns of revegetation in restoration settings (D'Antonio et al., 2000; Davies et al., 2011). Canopy cover may have positive or negative effects, depending on the system in question, and may positively correlate with success of forest interior species but negatively correlate with success of open-habitat

species. Invasive species, such as nonnative grasses, may compete with desired native species in ways that reduce the germination, survival, and growth of those native plants and thus negatively impact the resulting restoration outcome (D'Antonio and Vitousek, 1992; Smith and Tunison, 1992; Davies et al., 2011).

To better understand the factors that lead to differences in revegetation following wildfire, we used a replicated system of 45 seed addition plots in a recently burned area on the Island of Hawai'i. In this system, fire has been historically rare, but has increased due to the presence of a suite of nonnative pasture grasses and increased anthropogenic ignition events. In the upland forests of Hawai'i, restoration action seeks to maintain and reestablish native vegetation post-fire, while creating resistance to exotic species and resilience to fire (McDaniel et al., 2008). However, restorations in these systems are not always successful. We investigated a suite of factors that are known to affect restoration success in an effort to determine which were the most important in structuring the early plant establishment in field conditions. One common measure of success and one we are using here is that of seedling establishment. Our question was: How do biotic factors (e.g., canopy cover, grass abundance) and abiotic factors (e.g., elevation, fire severity) affect seedling establishment across the landscape?

Methods

Study Site

We conducted this study within Hawai'i Volcanoes National Park on Hawai'i Island, Hawai'i. A fire that started by human activity took place in August of 2018, burning approximately 1500 hectares of land, mostly within the national park (in the area known as the Mauna Loa Strip) (Theune, 2018; West Hawaii Today Staff, 2018). This area contains mostly native upland forest and is dominated at lower elevations by koa (*Acacia koa* A. Gray), while at

higher elevations māmane (*Sophora chrysophylla* (Salisb.) Seem.) and ‘a‘ali‘i (*Dodonaea viscosa* (L.) Jacq.) are canopy dominant and koa, though still present, is less abundant. Within the area burned by this fire, there was mortality of trees and understory plants on a large scale, as is typical in fires in this system (Ainsworth and Kauffman, 2010). The large-scale mortality of native species, in conjunction with the abundance of nonnative grasses led the National Park Service to engage in a restoration effort to attempt to reestablish the native plant community and to attempt to reduce the ability of the nonnative grasses to form a monoculture in the understory (McDaniel et al., 2008).

Seed Sowing

Between November of 2018 and March of 2019, within the burned area, members of the Hawai‘i Volcanoes National Park Natural Resources Management team seeded ~700 plots (of a planned 1180 plots) with seeds of native species, including māmane, to promote forest regrowth (Figure 3.1). Māmane and other seeded species were chosen as they are native, are competitively disadvantaged by weedy species, and have some resilience to fire (Loh et al., 2009). We worked with māmane because it was sown in all plots across all elevations and had relatively high germination, allowing for more statistically rigorous comparisons than if we were to use any other species. Circular (5m radius) plots were located 50m apart along transects, with transects being 200m apart, from 1340-1710 m asl. Plots with >50% cover of nonnative grasses were not selected for restoration, nor for our work here, as high grass covers are expected to decrease native species establishment (i.e., they would require additional forms of management before sowing could take place, and resources did not allow for that). In preparation for seeding, plots were raked to disturb the soil surface. Seeds were sown along raking lines within the plot and

loosely covered with soil. Māmane was seeded at a rate of 49.2 g/plot, which is approximately 730 seeds/plot or roughly 9.3 seeds/m² (see “Calculating Māmane Seeding Rate,” below).

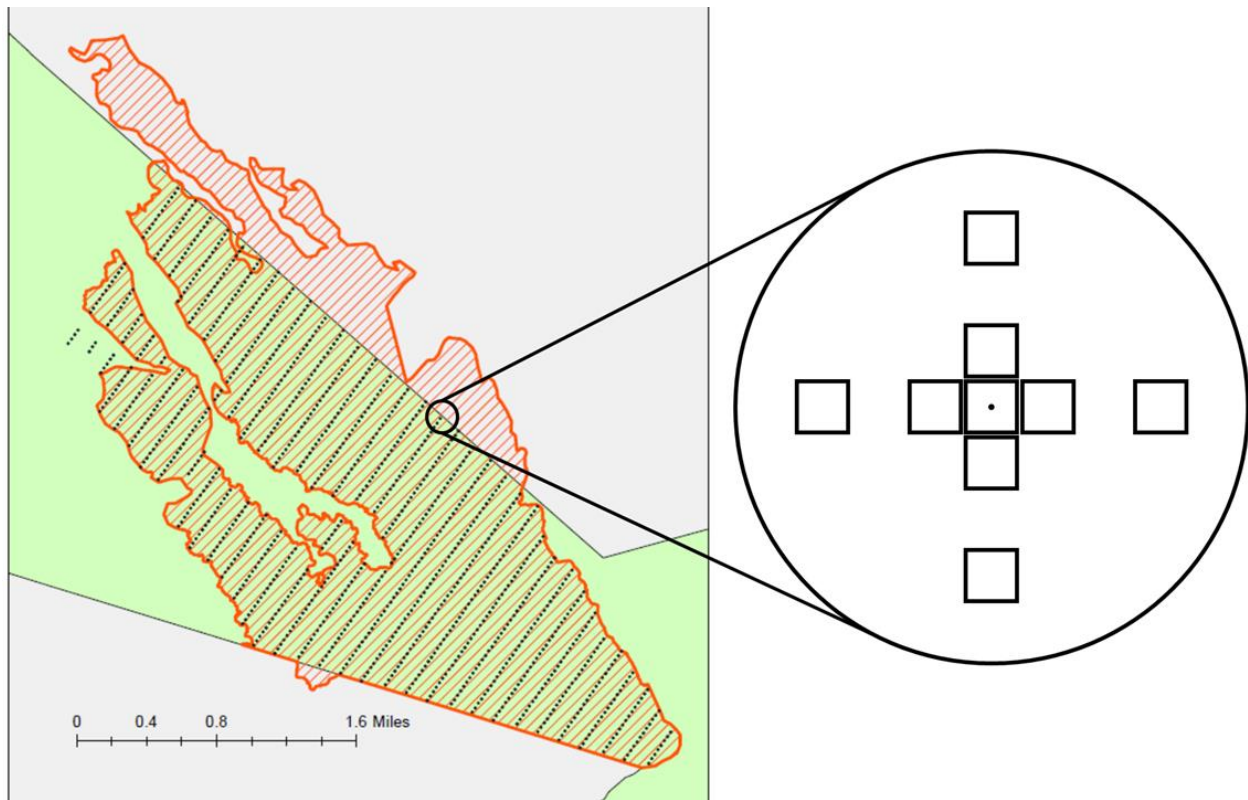


Figure 3.1. Plot and quadrat diagram. The black point in the circular plot represents the plot center, with the quadrats arrayed from there. Quadrats are 1m² and are to scale, within the circular plot.

Seed predation on seeds of māmane is exceedingly unlikely once seeds have been sown. Māmane seeds contain quinolizidine alkaloids that are toxic to vertebrates and may deter insects that lack adaptations to these compounds (Banko et al., 2002). At least one introduced potential seed predator insect was unable to complete its lifecycle on māmane seed (Medeiros et al., 2008). Additionally, the native seed predators of the Palila (*Loxioides bailleui* Oustalet, 1877; an endemic bird species) and several Hawaiian endemic moths in the genus *Cydia* Hübner, 1825, all

predate seeds pre-dispersal, and do not consume seeds after dispersal has occurred (Brenner et al., 2002; Hess et al., 2014). Also, Palila do not presently occur in our study area (Hess et al., 2014).

Depending on elevation, a subset of the māmane seeds were scarified prior to seeding, to increase the rate and evenness of germination. In plots below 1500 m asl, where fast-growing exotic grasses are more prevalent, all māmane seeds were scarified to facilitate māmane germination in the short, post-fire, grass-free window. In plots of higher elevations, where exotic grasses are less abundant, half of the māmane seeds were scarified and the other half were not to increase the length of time over which māmane might germinate, a practice similar to that seen in other systems that allows for bet hedging of germination and establishment success by spreading germination over multiple years (Madsen et al., 2016). For our analyses, we corrected for these differences in the amount of scarified seeds, as described in the *Analysis* section, below. For the seeds of māmane that were scarified prior to seeding, this was done in a solution of 100% sulfuric acid for 1 hour, and then rinsed to remove the acid solution (Sierra McDaniel & Makani Gregg, personal communication).

Calculating Māmane Seeding Rate

The māmane seeds that were used in this restoration effort and this research were collected in the field, within Hawai‘i Volcanoes National Park on Hawai‘i Island, Hawai‘i. Each collection was given a unique collection ID. There were two collection areas: Hilina Pali and the Mauna Loa strip, both within the boundaries of the park. The Hilina Pali collection area runs from 960–1040 m asl in elevation, while the Mauna Loa strip collection area runs from 1200–1900 m asl in elevation. In the past, māmane plants from a variety of locations were planted at Hilina Pali, and this may have included sources from outside the park. To use local seed of

known provenance, the Natural Resources Management team only used seed that was collected on the Mauna Loa strip for the restoration effort of this study (Sierra McDaniel, personal communication).

Some seeds were acid washed as a scarification treatment. The acid wash consisted of 100% sulfuric acid for 1 hour, after which time they were rinsed to remove any acid residue.

To obtain average seed weight, seeds from each collection were weighed in 5 batches. Each batch contained one US tablespoon of seeds, which was weighed. Following weighing, the number of seeds were counted, and from that, an average mass was calculated (Table 3.1). To then convert the weight of seeds used by the Natural Resources Management team into a number of seeds, we used the average weight of the Mauna Loa collections, and did not include data from the Hilina Pali collections, as no seeds from Hilina Pali were used in this restoration effort. The Hilina Pali data are presented here simply to show the variation in seed weight that exists within māmane.

Table 3.1. Seed weight table

Acid Wash	Location	Collection Date	Collection ID	Sample Weight (g) ¹	N Seeds ²	Avg. Weight (g) ³
No	Hilina Pali	July 2014	0714-17	10.62	186	0.05710
No	Hilina Pali	July 2014	0714-17	10.59	207	0.05116
No	Hilina Pali	July 2014	0714-17	10.71	193	0.05549
No	Hilina Pali	July 2014	0714-17	11.18	223	0.05013
No	Hilina Pali	July 2014	0714-17	11.55	213	0.05423
No	Hilina Pali	April 2019	0419-74	11.17	190	0.05879
No	Hilina Pali	April 2019	0419-74	11.62	189	0.06148
No	Hilina Pali	April 2019	0419-74	11.42	197	0.05797
No	Hilina Pali	April 2019	0419-74	11.15	181	0.06160
No	Hilina Pali	April 2019	0419-74	11.09	192	0.05776
No	Hilina Pali	August 2019	0819-146	11.3	224	0.05045
No	Hilina Pali	August 2019	0819-146	10.57	203	0.05207
No	Hilina Pali	August 2019	0819-146	11.51	226	0.05093
No	Hilina Pali	August 2019	0819-146	11.39	224	0.05085
No	Hilina Pali	August 2019	0819-146	11.36	232	0.04897
No	Hilina Pali	August 2019	0819-147	11.44	226	0.05062

Table 3.1 (cont'd)

No	Hilina Pali	August 2019	0819-147	10.46	214	0.04888
No	Hilina Pali	August 2019	0819-147	10.11	202	0.05005
No	Hilina Pali	August 2019	0819-147	10.76	209	0.05148
No	Hilina Pali	August 2019	0819-147	11.08	223	0.04969
No	Mauna Loa	August 2019	0819-140	10.2	158	0.06456
No	Mauna Loa	August 2019	0819-140	10.01	143	0.07000
No	Mauna Loa	August 2019	0819-140	10.05	150	0.06700
No	Mauna Loa	August 2019	0819-140	8.56	117	0.07316
No	Mauna Loa	August 2019	0819-140	10.5	167	0.06287
Yes	Mauna Loa	June 2011	0611-03B	11.69	181	0.06459
Yes	Mauna Loa	June 2011	0611-03B	10.13	153	0.06621
Yes	Mauna Loa	June 2011	0611-03B	10.8	155	0.06968
Yes	Mauna Loa	June 2011	0611-03B	9.23	137	0.06737
Yes	Mauna Loa	June 2011	0611-03B	10.78	168	0.06417
Yes	Mauna Loa	June 2011	0611-296	10.2	138	0.07391
Yes	Mauna Loa	June 2011	0611-296	10.55	154	0.06851
Yes	Mauna Loa	June 2011	0611-296	10.57	149	0.07094
Yes	Mauna Loa	June 2011	0611-296	10.97	154	0.07123
Yes	Mauna Loa	June 2011	0611-296	11.2	151	0.07417
Yes	Mauna Loa	August 2019	0819-151	10.58	164	0.06451
Yes	Mauna Loa	August 2019	0819-151	10.87	176	0.06176
Yes	Mauna Loa	August 2019	0819-151	11.25	174	0.06466
Yes	Mauna Loa	August 2019	0819-151	10.66	154	0.06922
Yes	Mauna Loa	August 2019	0819-151	10.72	160	0.06700
Yes	Mauna Loa	August 2019	0819-152	10	156	0.06410
Yes	Mauna Loa	August 2019	0819-152	11.05	154	0.07175
Yes	Mauna Loa	August 2019	0819-152	9.55	147	0.06497
Yes	Mauna Loa	August 2019	0819-152	10.09	154	0.06552
Yes	Mauna Loa	August 2019	0819-152	10.26	157	0.06535
Yes	Mauna Loa	August 2019	0819-154	10.93	170	0.06429
Yes	Mauna Loa	August 2019	0819-154	10.84	163	0.06650
Yes	Mauna Loa	August 2019	0819-154	10.55	160	0.06594
Yes	Mauna Loa	August 2019	0819-154	10.39	154	0.06747
Yes	Mauna Loa	August 2019	0819-154	10.49	156	0.06724

¹Sample Weight refers to the weight of a US tablespoon of seeds

²N Seeds refers to the number of seeds present in that US tablespoon of seeds

³Avg. Weight refers to the average weight of a seed, using the previous two columns

Data Collection

In late October to early November 2019, we randomly selected a subset of 15 of the plots, within each of the three elevational bands (n=45 total plots). The fire burned land across a range of elevations from 1170-1710 m asl. The three elevational bands were low elevation (1338-1400 m asl), middle elevation (1427-1487 m asl) and upper elevation (1578-1652 m asl). For the coordinates and elevations of each plot, please see Table 3.2. The elevation for each plot was determined using the Bulk Point Query tool at the United States Geological Survey's The National Map project (USGS, 2019). The elevational bands were chosen both to capture the breadth of elevational change that is present in the burned area and based on where the 700 sown plots were, across the burned area.

Table 3.2. Coordinates and elevation for our 45 study plots.

Plot	Longitude	Latitude	Elevation (m asl)	Elevational Band
V3	-155.331	19.4519	1403.46	low
V4	-155.331	19.4516	1402.83	low
V10	-155.333	19.4494	1402.38	low
V12	-155.333	19.4486	1400.6	low
W6	-155.33	19.4498	1391	low
W11	-155.331	19.4479	1388.01	low
W32	-155.337	19.4403	1363.5	low
X6	-155.33	19.4472	1379.6	low
X7	-155.33	19.4469	1376.85	low
X22	-155.334	19.4414	1356.17	low
X28	-155.336	19.4392	1353.18	low
Y11	-155.33	19.4436	1354.63	low
Y14	-155.331	19.4425	1349.91	low
Z13	-155.329	19.4418	1338.06	low
AA6	-155.326	19.4426	1338.26	low
O18	-155.345	19.4554	1471.47	mid
P4	-155.339	19.4594	1486.64	mid
P7	-155.34	19.4583	1479.48	mid
P13	-155.342	19.4562	1472.98	mid
Q5	-155.338	19.4576	1469.04	mid
Q8	-155.339	19.4565	1464.08	mid
Q11	-155.34	19.4555	1463.93	mid
Q15	-155.341	19.454	1457.43	mid

Table 3.2 (cont'd)

Q16	-155.341	19.4536	1454.58	mid
R2	-155.336	19.4577	1461.19	mid
R5	-155.337	19.4566	1459.48	mid
R6	-155.337	19.4562	1458.52	mid
S9	-155.336	19.4537	1443.47	mid
S20	-155.34	19.4497	1427.41	mid
S21	-155.34	19.4493	1426.93	mid
D4	-155.356	19.4741	1649.22	upper
D8	-155.357	19.4726	1651.4	upper
D9	-155.357	19.4723	1647.25	upper
D11	-155.358	19.4715	1649.4	upper
D12	-155.358	19.4712	1652.23	upper
D14	-155.359	19.4705	1645.55	upper
E4	-155.355	19.4727	1636.23	upper
E7	-155.356	19.4716	1634.86	upper
E8	-155.356	19.4712	1633.23	upper
F9	-155.355	19.4698	1620.12	upper
G17	-155.355	19.4658	1599.2	upper
G19	-155.356	19.4651	1594.49	upper
H16	-155.354	19.4647	1582.02	upper
H17	-155.354	19.4644	1581.96	upper
H19	-155.355	19.4636	1577.61	upper

Within each plot, we collected several types of data, using a subsample of nine 1m x 1m quadrats (Figure 3.1). Within each quadrat, we recorded the number of māmane seedlings, grass abundance (as a percent cover), and the percent cover of bare soil (a proxy for microsite availability). The cover of grass and of bare soil was recorded to the nearest whole percent for values greater than one, to the nearest 0.1% for values between 0.1-1% and to the nearest 0.01 for values between 0-0.1%.

Additionally, at the level of each plot, we took data on canopy cover (taken in June/July 2019) and fire severity. We measured canopy cover using densiometers (Robert E. Lemmon Forest Densiometers, Rapid City, South Dakota). For each plot, we took four readings (one for each of the cardinal directions) and summed them to obtain a reading for the plot. Each reading

consisted of a count of the number of vertices of the densiometer that were covered by the canopy, and followed the subsetting methods of Strickler (1959). We measured fire severity using char height, which is the estimated average height, in meters, that char is left on the trees in or immediately adjacent to the plot. We realize that fire severity is a complex variable to measure and that other and better proxies for this measure exist (Keeley, 2009); however, due to logistical constraints, char height was the proxy we had the ability to collect at the time.

Analysis

In early model selection, we had run all the pairwise interactions with elevation, but when these interactions are included, only elevation was significant. We therefore decided to remove the nonsignificant interaction terms, focusing only on main effects.

We ran our analyses in two ways. We ran two generalized linear mixed effects models; in both of these, the response was the number of seedlings, and the fixed effects were canopy cover, grass cover, bare ground, fire severity, and elevation, and the random effect was plot. These models had the response following a negative binomial distribution, as is typical for overdispersed count data and were run through the lme4 package, version 1.1-23 (Bates et al., 2015). Because only half of māmane seeds that were sown in the upper elevation band were scarified and it is unlikely that any non-scarified seeds germinated on the timescale of this project (Scowcroft, 1981), we halved the number of seedlings in the lower and middle elevation bands, to enable comparability between the elevational bands. The difference between the two models was that in one, elevation was categorical (as originally collected) and in the other, elevation was continuous. The overall results were qualitatively the same between the models, in terms of which variables were significant and the direction of the effect, and so we present the results of the model using continuous elevation, below. We checked all models for collinearity

using the function `check_collinearity` within the `performance` package, version 0.4.5 (Lüdtke et al., 2020). Collinearity was not a problem in our models (all variance inflation factors < 2.6).

To see how our several of our predictor variables vary across elevation, we also ran statistics on the pairwise relationships between elevation (continuous, in m asl) and each of canopy cover, bare ground, grass cover, and fire severity. These generalized linear models consisted of the factor of interest as the response variable, elevation as the predictor variable, and each was run at the level of the plot (n=45). We ran all four of these models following a gamma distribution, with a negligible offset of 1×10^{-14} , so that there were not zeros in the data. These models did not have a random effect, as they were run at the level of the plot. Additionally, we calculated Pearson's *r* for each of these four relationships, using the data at the plot level for canopy cover and fire severity (which were measured at the plot level) and the data at the quadrat level for grass cover and bare ground (which were measured at the quadrat level).

All analyses were performed in R, version 3.6.3 (R Core Team, 2020) through the interface of RStudio version 1.2.5033 (RStudio, 2019).

Results

Elevation structured recruitment ($p=0.0035$), with a Pearson's *r* of -0.217, indicating fewer seedlings at higher elevations. (Figure 3.2). Recruitment was also structured by canopy cover, which positively correlated with the number of seedlings ($p=0.0062$; Pearson's *r* = 0.214; Figure 3.3) and grass cover, which counterintuitively trended towards a positive correlation between grass cover and the number of seedlings ($p=0.038$; Pearson's *r* = 0.005; Figure 3.4). Bare ground did not affect the number of seedlings ($p=0.51$) nor did fire severity ($p=0.31$).

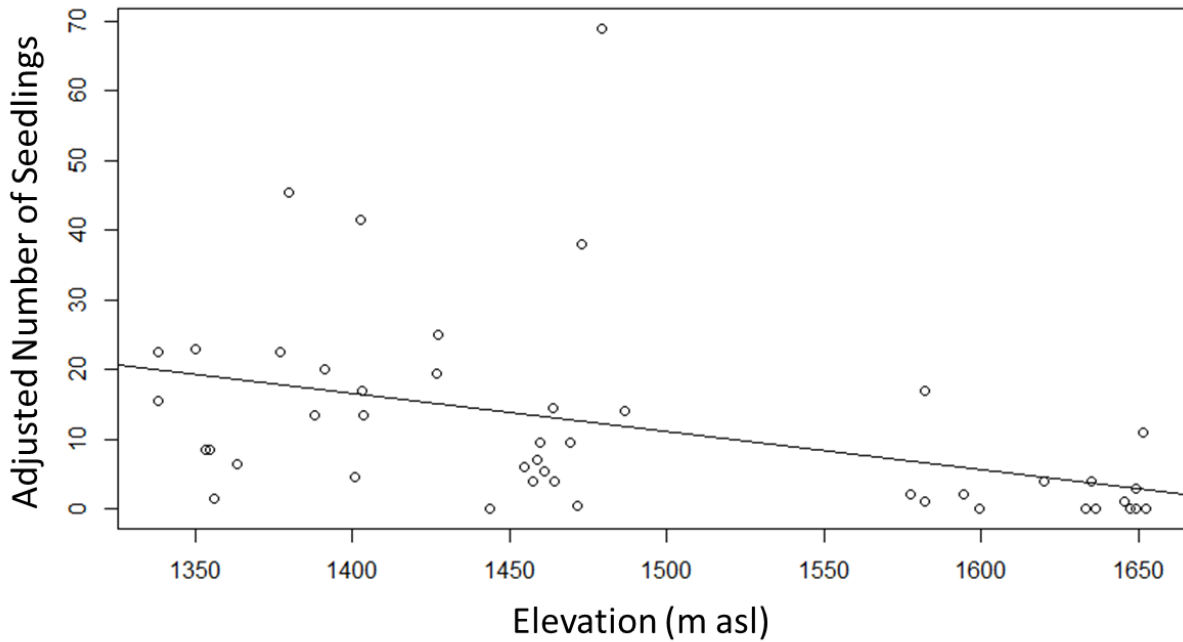


Figure 3.2. The number of seedlings by elevation (with elevation being continuous). The data shown here are the adjusted number of seedlings, obtained by halving the number of seedlings at the two lower elevational bands. The data presented here are sums of the number of seedlings at the plot level (n=45). The trendline is for visual comparison only.

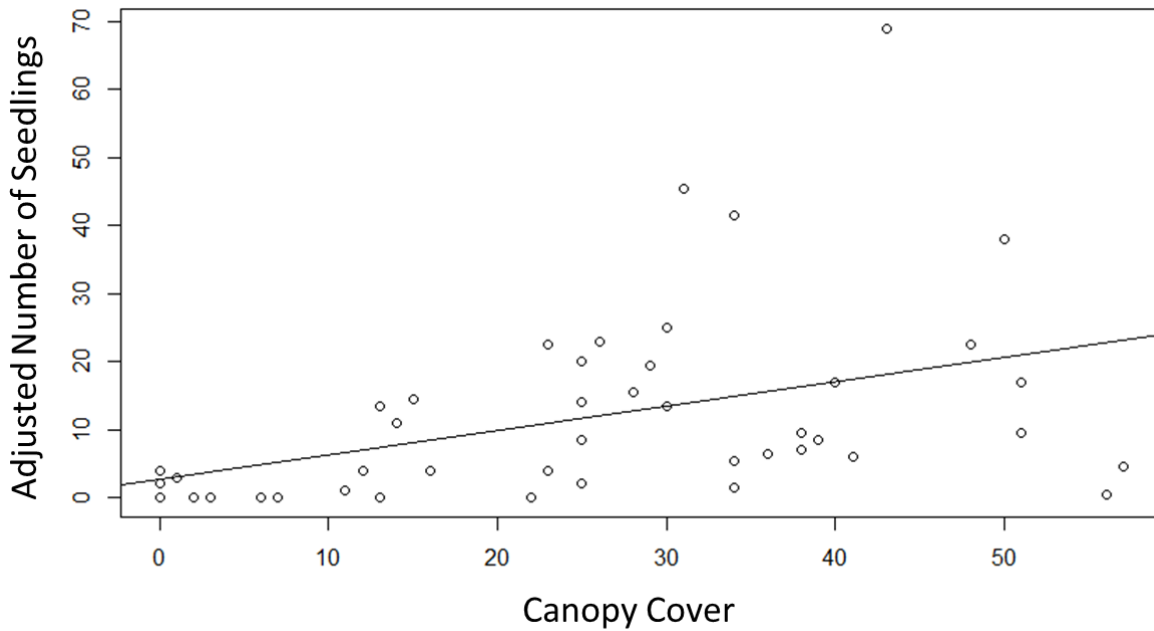


Figure 3.3. Plot of the number of māmane seedlings by canopy cover (number of covered vertices). Canopy cover was taken at the plot level, rather than the quadrat level, and is plotted here accordingly. The trendline is for visual comparisons only.

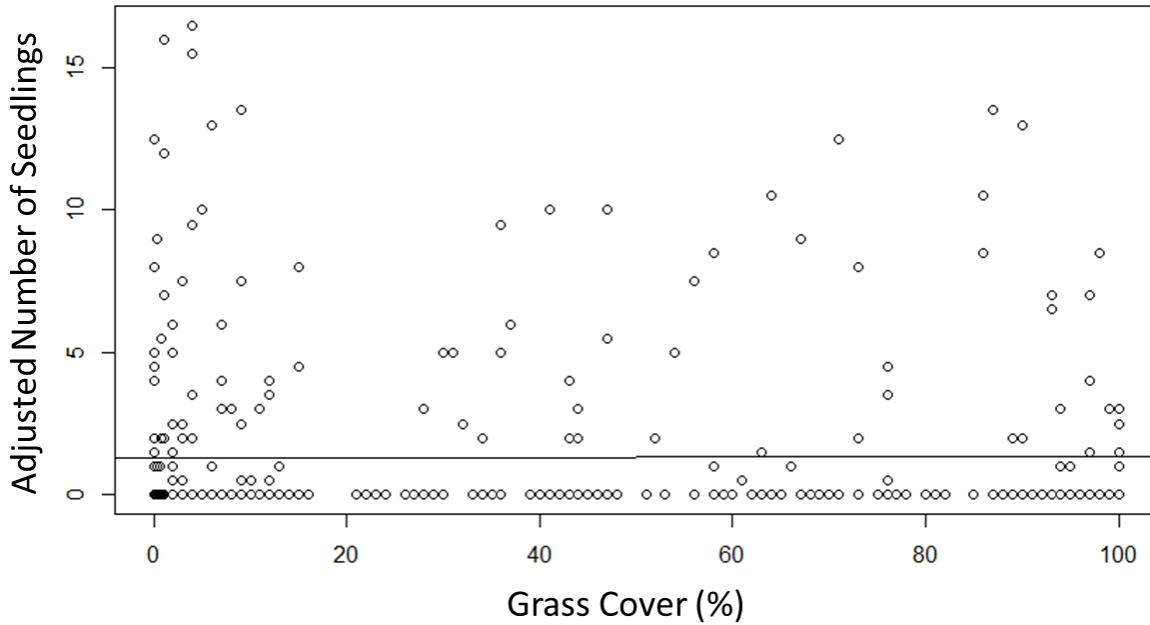


Figure 3.4. Plot of the number of māmane seedlings by grass cover. Grass cover was taken at the level of the quadrat (n=405), as was the number of seedlings, and is presented here accordingly. The trendline is for visual comparisons only.

The relationships of canopy cover, bare ground, grass cover, and fire severity with elevation are summarized in Table 3.3 and are shown in Figure 3.5.

Table 3.3. The relationships between different response variables and elevation (m asl).

Response	p-value	Pearson's r
canopy cover	<0.0001	-0.63
bare ground	0.35	0.098
grass cover	<0.0001	-0.46
char height	<0.0001	0.49

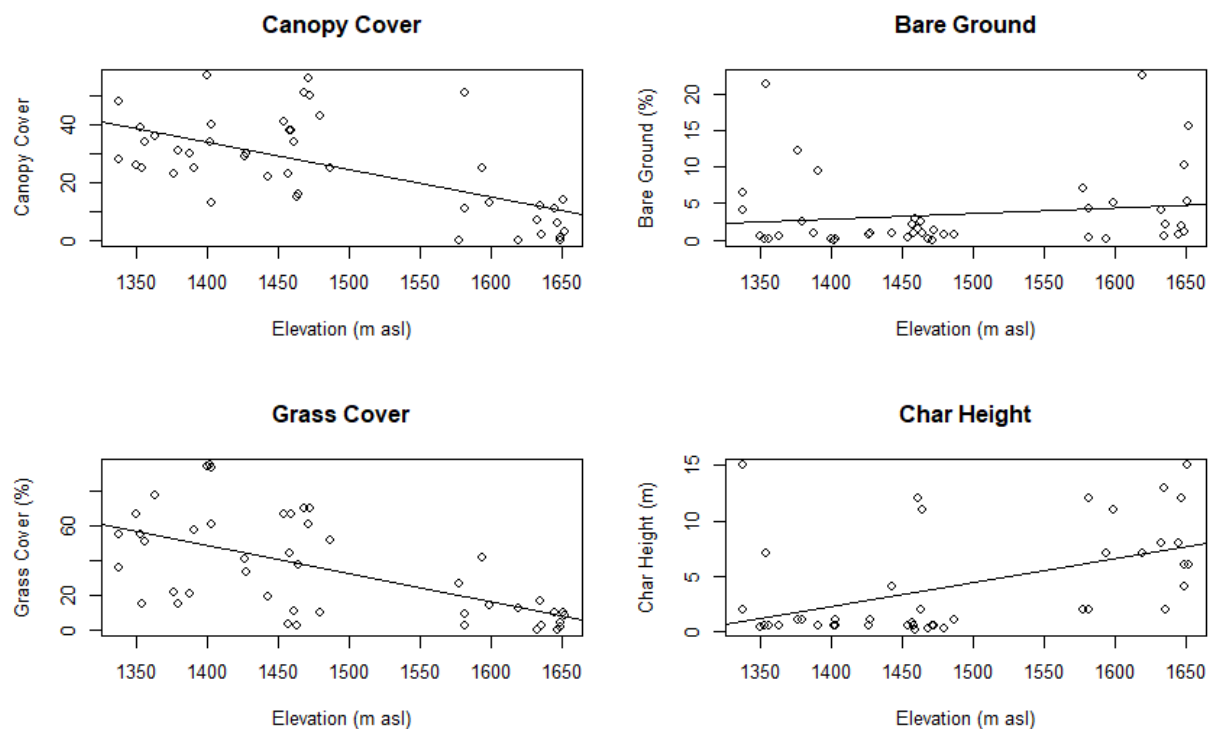


Figure 3.5. The relationships between elevation and each of canopy cover, bare ground, grass cover, and fire severity (as measured through char height). Canopy cover is measured as the number of covered vertices.

Discussion

We found that elevation was a critical factor behind patterns of seedling establishment. We found that fewer seedlings were at higher elevations. In montane systems, such as ours, elevation is of overriding importance in structuring plant communities and their dynamics (Ainsworth and Kauffman, 2010). Elevation additionally influences other biotic and abiotic factors that affect seedling establishment patterns because it covaries with a host of factors, including precipitation, temperature, plant competitive interactions, and others (D'Antonio et al., 2000; Davies et al., 2011). These relationships between elevation on other factors that influence

plant recruitment may necessitate different restoration actions at different elevations (Davies et al., 2011; Yelenik and D'Antonio, 2013).

Cover by invasive exotic grasses affected plant establishment, where higher grass cover was weakly, but significantly correlated with number of seedlings (Pearson's $r = 0.005$). Grass cover is known to be a major driver of restoration success in this system (Yelenik, 2017), so the very weak correlation was unexpected. There are several reasons why we might be seeing this pattern. One potential reason is that grass cover could be interacting with factors that we did not measure to influence seedling establishment (D'Antonio et al., 2000; Ainsworth and Kauffman, 2010). It is possible that, for example, higher moisture availability in lower elevations (Giambelluca et al., 2013) facilitates establishment of both māmane and of grass, which may then result in patterns similar to those that we observe. A second reason could be a temporal delay (Matthews and Spyreas, 2010; Crouzeilles et al., 2016). We collected our data 7-11 months following seeding and 14-15 months post-fire. It is possible that seedling establishment on this timescale is less structured by grasses, but that an effect of grass cover may become more clear over time (Yelenik and D'Antonio, 2013; Stricker et al., 2015; Grman, Zirbel, et al., 2020). Given the effects of grasses on seedling establishment in our system, breaking the grass-fire cycle with seed-based restoration alone is likely to be challenging and may not be possible, under some circumstances.

Additionally, we found evidence that establishment increased with higher canopy cover. This may be due to a facilitative relationship, as occurs in moderately to strongly harsh environments (Callaway et al., 2002; Holmgren and Scheffer, 2010; Yelenik et al., 2015), and may be achieved here through the canopy species in fostering seedling survival, by shading seedlings from harsh sun, lowering soil evaporation, and/or through the addition of soil organic

matter and nutrients. These potential facilitative interactions may be more consequential than grasses, within these abiotically harsher areas (Badano et al., 2015). Using effective proxies for plant establishment success may help managers make resource-saving decisions by focusing effort in locations where success may be higher. In abiotically harsher systems, such as our upper elevation plots, using other plants as a guide may be helpful (Gómez-Aparicio et al., 2004). Determining these, and similar, factors will require knowledge of the system and is an argument for an adaptive management approach, where further management actions are determined based on results of earlier actions.

The seed-sowing strategies employed in the setup of our study plots likely influenced our findings in some ways. The scarification of only half of the māmane seeds in the upper elevation band resulted in our need to recalibrate our data in order to effectively compare the elevations. However, after recalibrating the data, we found the same results, which is to say that elevation was still a significant factor in structuring seedling establishment patterns. This shows that, even after adjusting for number of seeds sown, fewer māmane germinate at higher elevations, relative to lower elevations. This difference may be indicative of the local environment being harsher at upper elevations, indicating that the choice to scarify only half of the seeds as a bet-hedging technique for the harsh environment is likely an effective method for ensuring restoration success in these areas (Madsen et al., 2016). Additionally, the sowing of seeds in clusters, rather than uniformly, which was done to expedite plot preparation and allow more plots to be seeded in less time, resulted in a clustered pattern of seedlings. This clumped pattern of the seedlings may have made our results more variable and thus our ability to determine the driving factors of plant establishment more challenging. Such clustering may also have long-term effects on

seedlings survival, due to potentially increased microscale intraspecific competition within clusters (Murrell, 2009).

Altogether, our results offer several potential recommendations for restoration practice. Due to the positive relationship with canopy cover that we observe, it may be beneficial to plant under canopy cover when possible, in this system. Additionally, seeding more seeds at higher elevations may help to increase the number of surviving seedlings at those elevations, given the generally lower seedling success at higher elevations. Furthermore, despite the weak correlation that we observed between grass cover and the number of seedlings in this study, due to the known dynamics of grass cover on long-term restoration success in this system (Yelenik, 2017), removing grass when feasible and seeding into areas with lower grass cover is likely to increase the number of established seedlings over time.

Our results illustrate factors leading patterns of plant reestablishment during post-fire restoration. Both biotic and abiotic pressures are known to be important drivers of restoration outcomes, but the relative importance of these, as well as other factors, is dependent on context (Ainsworth and Kauffman, 2010; Davies et al., 2011; Munson et al., 2011). Elevation clearly played a role in our system, as did grass cover and canopy cover. The diversity of factors that influence restoration outcomes continues to be a challenge for the field of restoration ecology and is a major barrier in helping ecological restoration to fulfill its aims in service to humanity and the world. Our results here help address this challenge by clarifying the nuanced relationships between the drivers of early seedling establishment success in a post-fire restoration setting.

Acknowledgements

We would like to acknowledge the staff and managers at Hawai‘i Volcanoes National Park and the Pacific Cooperative Studies Unit for preparing the plots and sowing the seeds for this work and allowing us to collaborate with them and for their thoughts and feedback on this project; we would particularly like to thank Makani Gregg and Sierra McDaniel. We would also like to thank Gordon Tribble and Nina Zárata at USGS-PIERC for logistical support and PIERC/HAVO for providing housing and office space for C. Warneke while this work was being conducted. We would also like to thank Rosanise Odell, Gabe Runte, and Jeff Stallman for field assistance. We would also like to thank Stephen Bechtel, Clara Smith, and Corie Yanger for weighing māmane seeds to help establish the number of māmane seeds that were sown, based on the mass of seeds sown. Funding for this project came from several sources, namely the USGS Environments Program, the USGS-NPS Natural Resources Preservation Program (NRPP), and the National Science Foundation (Awards 1354085, 1913501, 1921769).

LITERATURE CITED

LITERATURE CITED

- Ainsworth, A., and J. B. Kauffman. 2010. Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* 42: 647–655.
- Badano, E. I., R. O. Bustamante, E. Villarroel, P. A. Marquet, and L. A. Cavieres. 2015. Facilitation by nurse plants regulates community invasibility in harsh environments. *Journal of Vegetation Science* 26: 756–767.
- Banko, P. C., M. L. Cipollini, G. W. Breton, E. Paulk, M. Wink, and I. Izhaki. 2002. Seed chemistry of *Sophora chrysophylla* (mamane) in relation to diet of specialist avian seed predator *Loxioides bailleui* (palila) in Hawaii. *Journal of Chemical Ecology* 28: 1393–1410.
- Barnard, D. M., M. J. Germino, D. S. Pilliod, R. S. Arkle, C. Applestein, B. E. Davidson, and M. R. Fisk. 2019. Cannot see the random forest for the decision trees: selecting predictive models for restoration ecology. *Restoration Ecology* 27: 1053–1063.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48.
- Bates, J. D., R. N. Sharp, and K. W. Davies. 2014. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *International Journal of Wildland Fire* 23: 117–130.
- Bowles, M., S. Apfelbaum, A. Haney, S. Lehnhardt, and T. Post. 2011. Canopy cover and groundlayer vegetation dynamics in a fire managed eastern sand savanna. *Forest Ecology and Management* 262: 1972–1982.
- Brenner, G. J., P. T. Oboyski, and P. C. Banko. 2002. Parasitism of *Cydia* spp. (Lepidoptera: Tortricidae) on *Sophora chrysophylla* (Fabaceae) along an elevation gradient of dry subalpine forest on Mauna Kea, Hawaii. *Pan-Pacific Entomologist* 78: 101–109.
- Brudvig, L. A. 2017. Toward prediction in the restoration of biodiversity. *Journal of Applied Ecology* 54: 1013–1017.
- Brudvig, L. A., R. S. Barak, J. T. Bauer, T. T. Caughlin, D. C. Laughlin, L. Larios, J. W. Matthews, et al. 2017. Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology* 54: 1018–1027.
- Brudvig, L. A., and C. P. Catano. *in press*. Prediction and uncertainty in restoration science. *Restoration Ecology* e13380.
- Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et

- al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.
- Copeland, S. M., S. M. Munson, D. S. Pilliod, J. L. Welty, J. B. Bradford, and B. J. Butterfield. 2018. Long-term trends in restoration and associated land treatments in the southwestern United States. *Restoration Ecology* 26: 311–322.
- Crouzeilles, R., M. Curran, M. S. Ferreira, D. B. Lindenmayer, C. E. V. Grelle, and J. M. Rey Benayas. 2016. A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications* 7: 1–8.
- D’Antonio, C. M., R. F. Hughes, and J. T. Tunison. 2011. Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecological Applications* 21: 1617–1628.
- D’Antonio, C. M., J. Timothy Tunison, and R. K. Loh. 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecology* 25: 507–522.
- D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144: 2573–2584.
- Díaz-Delgado, R., F. Lloret, and X. Pons. 2003. Influence of fire severity on plant regeneration by means of remote sensing imagery. *International Journal of Remote Sensing* 24: 1751–1763.
- Dooley, S. R., and K. K. Treseder. 2012. The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry* 109: 49–61.
- Ellsworth, L. M., C. M. Litton, A. P. Dale, and T. Miura. 2014. Invasive grasses change landscape structure and fire behaviour in Hawaii. *Applied Vegetation Science* 17: 680–689.
- Engel, E. C., and S. R. Abella. 2011. Vegetation recovery in a desert landscape after wildfires: Influences of community type, time since fire and contingency effects. *Journal of Applied Ecology* 48: 1401–1410.
- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest factors. *The Science of the Total Environment* 262: 221–229.
- Gann, G. D., T. McDonald, B. Walder, J. Aronson, C. R. Nelson, J. Jonson, J. G. Hallett, et al. 2019. International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27: S1–S46.

- Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y. L. Chen, P. S. Chu, J. K. Eischeid, and D. M. Delaporte. 2013. Online rainfall atlas of Hawai‘i. *Bulletin of the American Meteorological Society* 94: 313–316.
- Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.
- Grman, E., C. R. Zirbel, J. T. Bauer, A. M. Groves, T. Bassett, and L. A. Brudvig. 2020. Super-abundant C4 grasses are a mixed blessing in restored prairies. *Restoration Ecology*: 1–8.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1: 1–9.
- Hess, S. C., P. C. Banko, L. J. Miller, and L. P. Laniawe. 2014. Habitat and food preferences of the endangered Palila (*Loxioides bailleui*) on Mauna Kea, Hawai‘i. *Wilson Journal of Ornithology* 126: 728–738.
- Holmgren, M., and M. Scheffer. 2010. Strong facilitation in mild environments: The stress gradient hypothesis revisited. *Journal of Ecology* 98: 1269–1275.
- Hughes, F., and P. M. Vitousek. 1993. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawai‘i. *Oecologia* 93: 557–563.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire* 18: 116–126.
- Kulpa, S. M., E. A. Leger, E. K. Espeland, and E. M. Goergen. 2012. Postfire seeding and plant community recovery in the great basin. *Rangeland Ecology and Management* 65: 171–181.
- Lewis, S. L., and M. A. Maslin. 2015. Defining the Anthropocene. *Nature* 519: 171–180.
- Loh, R., A. Ainsworth, T. Tunison, and C. D’Antonio. 2009. Testing native species response to fire – a first step towards building fire resilient native plant communities at Hawai‘i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 167. University of Hawai‘i at Mānoa, Department of Botany, Honolulu, Hawai‘i.
- Lüdecke, D., D. Makowski, P. Waggoner, and I. Patil. 2020. performance: Assessment of Regression Models Performance. R package version 0.4.5.
- Madsen, M. D., K. W. Davies, C. S. Boyd, J. D. Kerby, and T. J. Svejcar. 2016. Emerging seed enhancement technologies for overcoming barriers to restoration. *Restoration Ecology* 24: S77–S84.

- Mahood, A. L., and J. K. Balch. 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). *Ecosphere* 10: 1–19.
- Matthews, J. W., and G. Spyreas. 2010. Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. *Journal of Applied Ecology* 47: 1128–1136.
- McDaniel, S., R. K. Loh, S. Dale, K. Smith, and M. Vaidya. 2008. Rehabilitation of ‘ōhi‘a-swordfern (*Metrosideros polymorpha* - *Nephrolepis multiflora*) woodlands following the Kupukupu Fire, Hawai‘i Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 160. University of Hawai‘i at Mānoa, Department of Botany, Honolulu, Hawai‘i.
- Medeiros, A. C., E. Vonallmen, M. Fukada, A. Samuelson, and T. Lau. 2008. Impact of the newly arrived seed-predating beetle *Specularius impressithorax* (Coleoptera: Chrysomelidae: Bruchinae) in Hawai‘i. *Pacific Conservation Biology* 14: 7–12.
- Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: Art49: 1–22.
- Munson, S. M., J. Belnap, C. D. Schelz, M. Moran, and T. W. Carolin. 2011. On the brink of change: plant responses to climate on the Colorado Plateau. *Ecosphere* 2: art68.
- Munson, S. M., E. O. Yackulic, L. S. Bair, S. M. Copeland, and K. L. Gunnell. 2020. The biggest bang for the buck: cost-effective vegetation treatment outcomes across drylands of the western United States. *Ecological Applications* 30: e02151.
- Murrell, D. J. 2009. On the emergent spatial structure of size-structured populations: When does self-thinning lead to a reduction in clustering? *Journal of Ecology* 97: 256–266.
- Peppin, D., P. Z. Fulé, C. H. Sieg, J. L. Beyers, and M. E. Hunter. 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260: 573–586.
- Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, et al. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330: 1496–1502.
- R Core Team. 2020. R: a language and environment for statistical computing.
- Rehm, E. M., M. K. Thomas, S. G. Yelenik, D. L. Bouck, and C. M. D’Antonio. 2019. Bryophyte abundance, composition and importance to woody plant recruitment in natural and restoration forests. *Forest Ecology and Management* 444: 405–413.
- RStudio. 2019. RStudio.

- Scowcroft, P. G. 1981. Regeneration of mamane: Effects of seedcoat treatment and sowing depth. *Forest Science* 27: 771–779.
- Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawai‘i: Research and management implications for native ecosystems. *Alien Plant Invasions in Native Ecosystems of Hawai‘i: Management and Research*, 394–408. University of Hawai‘i Cooperative National Park Resources Studies Unit, Honolulu, Hawai‘i.
- Smith, H. G., G. J. Sheridan, P. N. J. Lane, P. Nyman, and S. Haydon. 2011. Wildfire effects on water quality in forest catchments: A review with implications for water supply. *Journal of Hydrology* 396: 170–192.
- Steffen, W., J. Grinevald, P. Crutzen, and J. McNeill. 2011. The anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 369: 842–867.
- Stricker, K. B., D. Hagan, and S. L. Flory. 2015. Improving methods to evaluate the impacts of plant invasions: Lessons from 40 years of research. *AoB PLANTS*: 1–10.
- Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. Portland, Oregon.
- Theune, M. 2018. Keauhou Fire Update for August 16. *Hawai‘i Volcanoes National Park News Releases*.
- United Nations. 2020. The United Nations Decade on Ecosystem Restoration Strategy. United Nations.
- USGS. 2019. TNM Elevation. The National Map. Website <https://apps.nationalmap.gov/elevation/> [accessed 15 July 2021].
- Vallejo, V. R., and J. A. Alloza. 2015. Postfire Ecosystem Restoration. In D. Paton, P. T. Buergelt, S. McCaffrey, F. Tedim, and J. F. Shroder [eds.], *Wildfire Hazards, Risks, and Disasters*, 229–246. Elsevier Inc., Oxford, UK.
- West Hawaii Today Staff. 2018. Keauhou Fire 90% contained. *West Hawaii Today*.
- Yelenik, S. G. 2017. Linking dominant Hawaiian tree species to understory development in recovering pastures via impacts on soils and litter. *Restoration Ecology* 25: 42–52.
- Yelenik, S. G., and C. M. D’Antonio. 2013. Self-reinforcing impacts of plant invasions change over time. *Nature* 503: 517–20.
- Yelenik, S. G., N. Dimanno, and C. M. D’Antonio. 2015. Evaluating nurse plants for restoring native woody species to degraded subtropical woodlands. *Ecology and Evolution* 5: 300–313.

CHAPTER FOUR

HABITAT FRAGMENTATION ALTERS THE DISTANCE OF ABIOTIC SEED DISPERSAL THROUGH EDGE EFFECTS AND DIRECTION OF DISPERSAL

Abstract

Habitat loss and fragmentation are leading causes of species declines, driven in part by reduced dispersal. Isolating the effects of fragmentation on dispersal, however, is daunting because the consequences of fragmentation are typically intertwined, such as reduced connectivity and increased prevalence of edge effects. We used a large-scale landscape experiment to separate consequences of fragmentation on seed dispersal, considering both distance and direction of local dispersal. We evaluated seed dispersal for five wind- or gravity-dispersed, herbaceous plant species that were planted at different distances from habitat edges, within fragments that varied in their connectivity and shape (edge-to-area ratio). Dispersal distance was affected by proximity and direction relative to the nearest edge. For 4 of 5 species, dispersal distances were greater further from habitat edges and when seeds dispersed in the direction of the nearest edge. Connectivity and patch edge-to-area ratio had minimal effects on local dispersal. Our findings illustrate how some, but not all, landscape changes associated with fragmentation can affect the key population process of seed dispersal.

Introduction

Habitat loss and fragmentation are leading causes of biodiversity decline (Haddad et al., 2015; Newbold et al., 2015), yet the mechanisms linking such landscape changes to biodiversity loss remain unresolved. This uncertainty results from the highly interrelated patterns and processes that accompany habitat loss and fragmentation (Didham et al., 2012). For example, dispersal is a key process impacted by fragmentation, mediating immigration and emigration rates and affecting population persistence in fragmented landscapes (Templeton et al., 2001;

Soons et al., 2005). However, fragmentation may influence dispersal through a variety of intertwined landscape changes, such as reductions to patch connectivity and alterations to patch edge-to-area ratios (Levey et al., 2005; Damschen et al., 2014), making it difficult to know how dispersal is affected by fragmentation.

Understanding fragmentation effects on seed dispersal requires consideration of how the processes that mediate seed dispersal are themselves modified by fragmentation (Nathan, Getz, et al., 2008). For example, in wind-dispersed plants of open habitats, the focus of this study, changes to wind patterns as a result of habitat fragmentation have consequences for seed dispersal (Soons et al., 2005; Damschen et al., 2014; Herrmann et al., 2016). Broadly, modifications to wind patterns by habitat fragmentation can affect seed dispersal distance (Nathan and Katul, 2005; Bohrer et al., 2008; Damschen et al., 2014). For example, seeds disperse further when open habitat fragments surrounded by forest have greater edge-to-area ratio or when they are connected by corridors, due to greater wind speeds in these situations (Damschen et al., 2014).

Because the distance of dispersal is often assumed to be the most important aspect of dispersal, the direction of dispersal is rarely considered, especially in the context of fragmentation (van Putten et al., 2012; Rogers et al., 2019). However, fragmentation might influence dispersal directionality through similar mechanisms to effects on dispersal distance. For example, in open habitats surrounded by forest, wind-dispersed seeds may disperse directionally and to greater distances along the long axis of a fragment or towards the edges, due to fragmentation and edges redirecting and accelerating wind in these directions (Detto et al., 2008; Damschen et al., 2014). The direction in which a seed disperses can influence both how far it travels (Nathan and Muller-Landau, 2000) and its probability of finding a suitable site to

establish and grow (Greene et al., 2008; Horvitz et al., 2014). Directional dispersal is likely to influence where plants occur in fragmented landscapes (Nathan and Muller-Landau, 2000; Levine, 2003) because seeds that disperse into unsuitable habitat, such as into an inhospitable matrix, result in lower population persistence (Rand, 2000; Levine and Murrell, 2003).

Virtually all fragmentation research has focused on long-distance dispersal (e.g., Rodríguez-Cabala et al. 2007, Uriarte et al. 2011), yet, it remains unclear if or how habitat fragmentation alters dispersal patterns at a local scale (i.e., short-distance dispersal). Resolving these effects is important because the vast majority of seeds disperse short distances with consequences for population and community dynamics; for example, by altering neighborhood densities and the arrival to suitable microsites in heterogeneous environments (Nathan and Muller-Landau, 2000; Law et al., 2003; Caughlin et al., 2014).

To understand how fragmentation affects local seed dispersal, we studied dispersal distances of five wind and gravity-dispersed herbaceous species. We did so within a replicated, large-scale fragmentation experiment that overcomes the confounding effects of observational fragmentation studies by experimentally disentangling patch connectivity, patch edge-to-area ratio (patch shape), and edge proximity, while controlling for habitat amount, matrix type, and patch area (Tewksbury et al., 2002). Our study system is comprised of open savanna fragments, surrounded by a matrix of pine plantation. We frame hypotheses based on how wind is affected by the landscape structure of our experiment (Damschen et al., 2014). We studied local-scale seed dispersal (to 5m; hereafter “seed dispersal”) and asked five questions:

- (1) How does patch connectivity affect seed dispersal distance? We hypothesized that patch connectivity would increase dispersal distances, due to higher wind speeds in connected patches.
- (2) How does patch edge-to-area ratio affect seed dispersal distance? We hypothesized that

patches with higher edge-to-area ratios would have greater dispersal distances, due to relatively higher windspeeds in those patches.

(3) How does distance to a habitat edge influence seed dispersal distance? We hypothesized that individuals farther from an edge would have greater dispersal distances, due to higher wind speeds at the center of habitat patches.

(4) How does the direction of dispersal influence dispersal distance? We hypothesized that seeds would disperse further along the long axis of patches, due to higher wind speeds in that direction.

(5) How are relationships between seed dispersal direction and distance affected by proximity to edge? We had two non-mutually exclusive hypotheses. First, the effect of dispersal direction may be stronger near open patch centers, because both wind speed and direction are higher and more directional away from forested edges (Damschen et al. 2014). Alternately, the effect of dispersal direction may be stronger near edges, due to winds eddying back toward the edge after entering a patch from above the adjacent tree canopy (Detto et al., 2008).

Methods

Site and Species

We conducted this experiment within eight experimentally-fragmented landscapes, designed to test effects of patch connectivity and differences in edge-to-area ratio. These experimental landscapes (hereafter “blocks”) are located at the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. SRS is US Department of Energy land that is managed under agreement by the US Forest Service. Each block contains five open-habitat patches, created by clearing mature pine plantation, that differ in their edge-to-area ratio and connectivity (Figure 4.1). All blocks have a 100m × 100m center patch and a connected patch, which is 100m × 100m and connected to the

center patch via a $150\text{m} \times 25\text{m}$ corridor. Additionally, all blocks have two types of isolated patches, rectangular and winged, which are not connected to the center patch, but are of equivalent area to the connected patch plus the corridor. The rectangular patch is $100\text{m} \times 137.5\text{m}$ and the winged patch is $100\text{m} \times 100\text{m}$ plus two $75\text{m} \times 25\text{m}$ "wings", which extend from opposite sides of the patch. Winged patches have similar edge-to-area ratio as the connected patch plus the corridor and have a higher edge-to-area ratio than the rectangular patch. Four blocks have two rectangular patches and four have two winged patches. All patch types were randomly assigned. Following initial clearing in the winter of 1999-2000, each patch is being restored to longleaf pine savanna, the historically dominant ecosystem of our study area (Jose et al., 2006). Surrounding and between each patch of open habitat is a matrix of mature pine plantation.

We planted populations of five herbaceous plant species into each patch, at four distances from edge (Figure 4.1). These wind and gravity-dispersed perennial species did not previously occur within our experimental landscapes, but are native components of longleaf pine savannas. Two were forbs in the Asteraceae: *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray and *Liatris squarrulosa* Michx. Three were grasses in the Poaceae: *Aristida beyrichiana* Trin. & Rupr., *Sorghastrum secundum* (Elliott) Nash, and *Anthenantia villosa* (Michx.) P. Beauv. We hereafter refer to all species by their genus name. Mean seed masses based on 5-15 individuals/species were: *Anthenantia* (22 mg), *Aristida* (7 mg), *Carphephorus* (21 mg), *Liatris* (20 mg), and *Sorghastrum* (28 mg) (Damschen, unpublished data). All five of these species flower and fruit in the fall, from October-December. We started founder populations from seed gathered from SRS, with the exception of *Aristida*, which we sourced as plugs from north Florida. Within the seed collections for each species, we mixed all seeds together, to randomize any maternal effects and minimize their potential effects on the later results of the experiment.

These seeds were then propagated into seedlings in greenhouses.

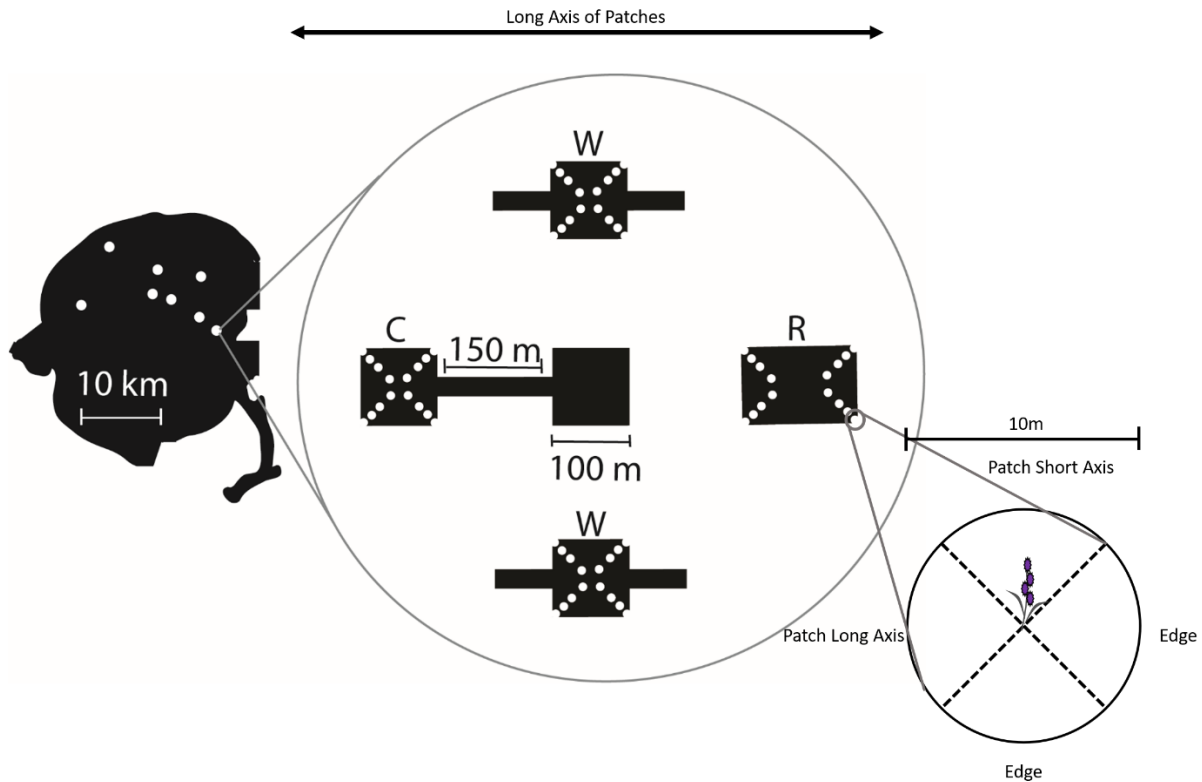


Figure 4.1. Experimental design, showing the location of the eight experimental landscape blocks. Each block has five open habitat patches within a forested matrix: a central patch, a connected patch that is connected to the center patch by a 150m corridor (C, above), and two types of isolated patches, a winged patch (high edge:area ratio; W, above) and a rectangle patch (low edge:area ratio; R, above). Each patch has 16 plots, arranged from edge to center along each of four transects. Each plot contained a single individual of each of our five study species, with an example individual shown here. The long and short axes noted on the search area are in reference to the overall habitat patch.

We planted one individual seedling of each species into each of 16 plots/patch in spring

2007 (N=3200 plants). In fall 2007/spring 2008, we replaced individuals that had died following initial planting. Prior to transplanting, we prepared plots by removing all vegetation and, afterwards, we weeded plots through the duration of this study. We arranged these plots along transects (Figure 4.1), with plots at four distances from each corner of each patch (1, 10.5, 20, 37m from the nearest edge). In each plot, we planted one seedling of each species at least 0.5 m from any other transplant (Figure 4.1). For more details on plot setup, see Levey et al. (2016).

Seed Dispersal

In fall 2009, we visited each reproductive plant (796 individuals across the five species; Table 4.1). On each individual we airbrushed fluorescent paint onto the seeds while the seeds were on the plant. This procedure minimally affects seed dispersal (Lemke et al., 2009). Following seed dispersal, we visited each parent plant a single time (after most or all seeds had dispersed), relocated the marked seeds within 5m of each parent plant with a blacklight at night, and flagged all marked seeds (see Table 4.1 for the number of seeds). We then determined the distance that each seed dispersed from its parent (in cm), as well as the direction in which the seed dispersed within four 90° directional bins, with the bins representing each of the four factorial combinations of being in-line/out-of-line with the long axis of the patch and towards/away from the edge (see Figure 4.1). We measured seeds within 5m of the parent plant because 7.5m is the halfway point between plots and we wanted to minimize ambiguity as to the parentage of a given seed. Across species, 94-98% of recovered seeds were within 2m of a conspecific adult, which we assumed to be the parent plant. We also measured the height of all seed dispersal structures and averaged for each individual, as height is known to be important in seed dispersal patterns (Thomson et al., 2011).

Table 4.1. The number of individuals and the total number of seeds across all individuals.

Species	Number of Individuals	Number of Seeds
<i>Aristida</i>	104	2576
<i>Anthenantia</i>	271	10997
<i>Carphephorus</i>	144	4126
<i>Liatris</i>	130	5897
<i>Sorghastrum</i>	147	16831

Analysis

Our analysis had three stages. In step 1, we performed model selection to identify the set of fixed and random effects and interactions to include in our final models. To facilitate interspecific comparisons and because our goal was inference rather than prediction, our model selection objective was to develop a single model for all species, rather than to identify the best-fit model for each species. We were able to find a common model for all species, with the exception of a directionality term for one species (see step 2). In step 2, within the random effects structure identified in step 1, we conducted a second phase of model selection to determine which set of seed dispersal directions to include in our final models. In step 3, to conduct statistical inference on the effects of directionality, patch type, and distance from edge on seed dispersal distances, we compared parameter estimates between our final models for each species. We conducted all statistical analyses in R, version 3.1.3 (R Core Team, 2020). We did not use a single model with species identity as a fixed or random effect because our goal was not to make comparisons between species, but rather to see how the landscape influenced our different focal species.

Our first step was to determine which fixed and random effects and interactions to include in our model. Our initial list included the experimental factors of patch type (a three-level unitless factor, which allows us to test for connectivity and edge-to-area ratio), distance from the edge (measured in meters), as well as dispersal direction (as a four-directional or as a

two-directional), and plant height (measured in centimeters). The continuous numeric variables of distance from the edge and plant height were standardized to allow for comparison of effect sizes, using the standardization formula where the observed value minus the mean is then divided by twice the standard deviation. We forced inclusion of patch type (connectivity and edge-to-area ratio), distance from edge, and one of the dispersal directions factors, since these were all related to focal research questions. The interactions that were considered were the pairwise interactions between our fixed effects, if there was a biological rationale that such an interaction might exist. We retained interactions between these factors if there was a biological rationale to warrant the interaction and random effects of experimental block and parent plant identity if they were selected. We performed initial model selection using generalized linear mixed effects models, in the *rstanarm* package, version 2.19.3 (Goodrich et al., 2020). We performed model selection for each species and compared among models within species using LOOIC, an information criterion similar to AIC, for models that are fit using MCMC and leave-one-out cross-validation (Magnusson et al., 2020), found within the *loo* package, version 2.2.0 (Vehtari et al., 2019). Based on these results, we selected a single model that had the best fit for two species and was a good fit for the remaining three species.

Our final model used the distance to which a seed dispersed as the response variable and the direction of dispersal, patch type (categorical; testing connectivity [connected vs. winged] and edge-to-area ratio [winged vs. rectangle]), distance from nearest edge (continuous, in m), plant height, and the interaction of direction and distance from edge as predictor variables. During model selection (step 1), we selected the parent plant as a random effect; we dropped other random effects (e.g., experimental block), as they did not improve predictive fit of models.

We next determined which direction of dispersal to model for each species, maintaining

the random effects and interactions from our selected model (step 2). We retained one dispersal direction factor, selecting either the two-directional factor (in which we collapsed the original four directions to two, which were “away from edge” and “towards edge”) or the original four-directional factor. The models using the two-directional factor had a better fit than the models with four-directional factor for all species, except for *Anthenantia* (for which we used the four-directional model).

Finally, we ran selected models in a Bayesian framework (step 3), though the *rstanarm* package, version 2.19.3 (Goodrich et al., 2020). We checked model convergence through visual examination of chains, by checking that R-hat values were <1.1 , and by ensuring models provided a reasonable number of effective samples. The Bayesian framework facilitated propagation of parameter uncertainty, including random effects, to model predictions.

Results

Overall, we found that distance from the edge of the habitat and the direction in which seeds disperse, as well as their interaction, influence the distance to which seeds disperse. The larger landscape factors of connectivity and edge-to-area ratio largely did not affect seed dispersal distance.

Connectivity and Edge-to-Area Ratio

Connectivity had no effect on dispersal distance for any species, although for *Liatris* there was a trend of greater dispersal distance in isolated patches, compared to connected patches (Figure 4.2). Patch edge-to-area ratio affected dispersal distance of *Liatris*, with greater dispersal distances in high edge-to-area ratio (winged) patches, compared to low edge-to-area ratio (rectangle) patches (Figure 4.2).

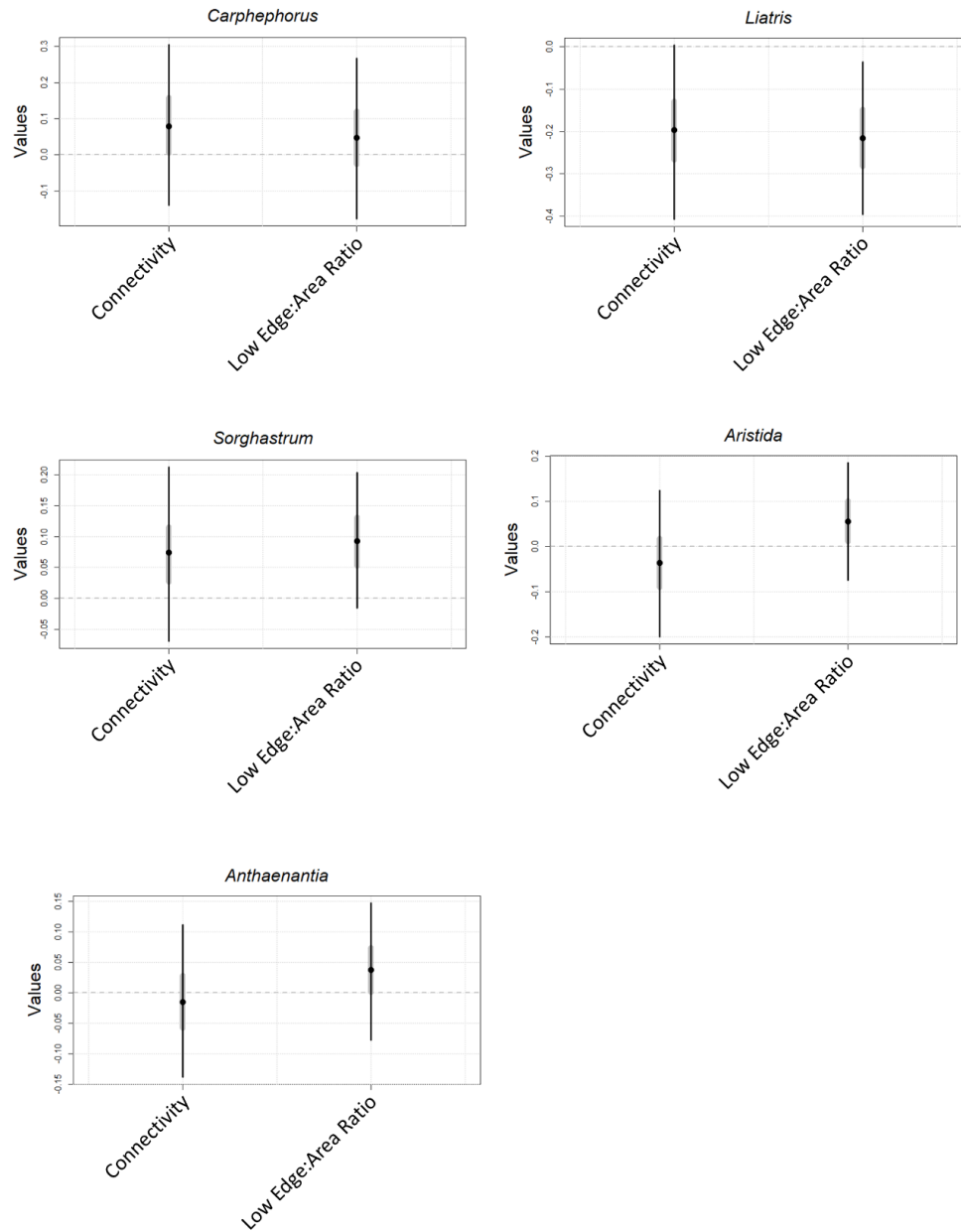


Figure 4.2. Standardized model coefficients with 50% credible intervals (the light gray lines) and 95% credible intervals (the dark black lines) for five herbaceous plant species in a fragmentation experiment. Values above the 0 line mean greater dispersal than the intercept, while values below mean less dispersal than the intercept. For instance, an effect of low edge-to-area ratio below the zero line would indicate that high edge-to-area patches have greater dispersal distances.

Distance from Habitat Edge

Distance from edge affected seed dispersal distance in four of five species (Figure 4.3, Figure 4.4; Table 4.2). For *Carphephorus*, *Anthenantia*, and *Sorghastrum*, seed dispersal distance was greater away from edge, while for *Aristida*, seed dispersal distance was greater when close to edge. For *Liatris*, there was no effect of distance from edge.

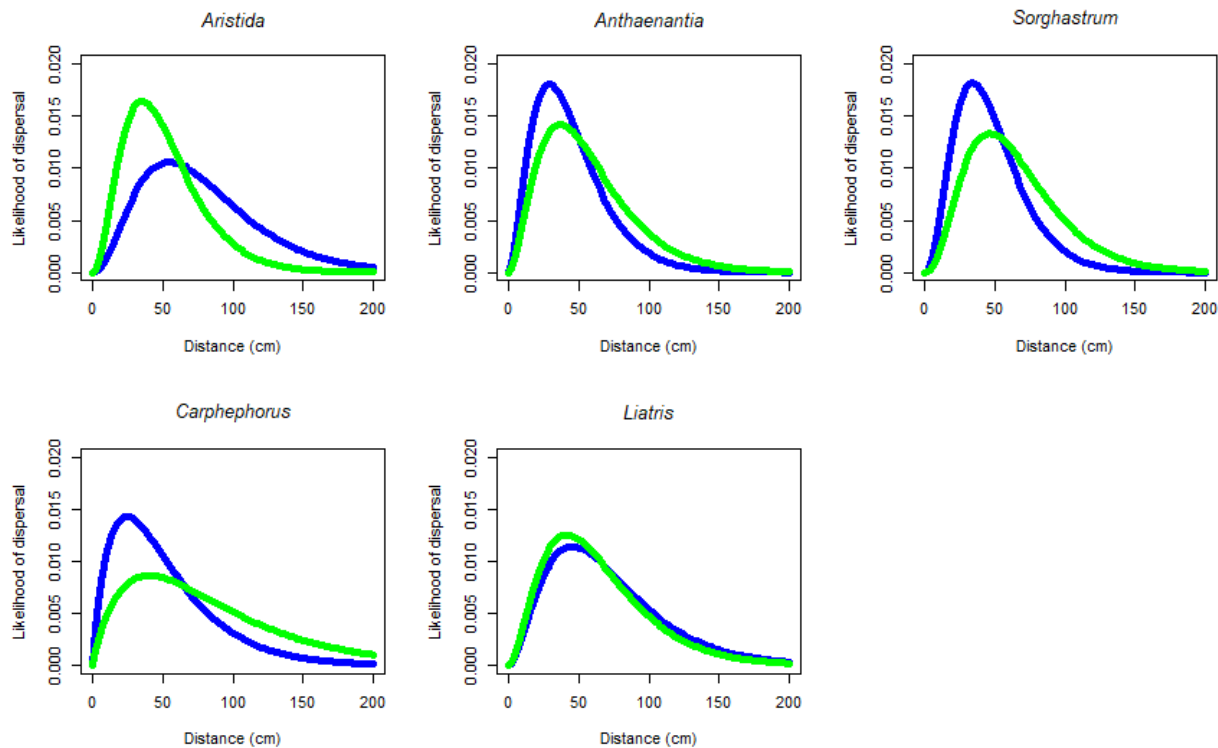


Figure 4.3. Seed dispersal kernels (probability density functions) for five herbaceous plant species, located near patch centers (green lines; 37 m from the edge) and near patch edges (blue lines; 1 m from the edge) in a fragmentation experiment. For an example with a visual depiction of the uncertainty around the mean, see Figure 4.5.

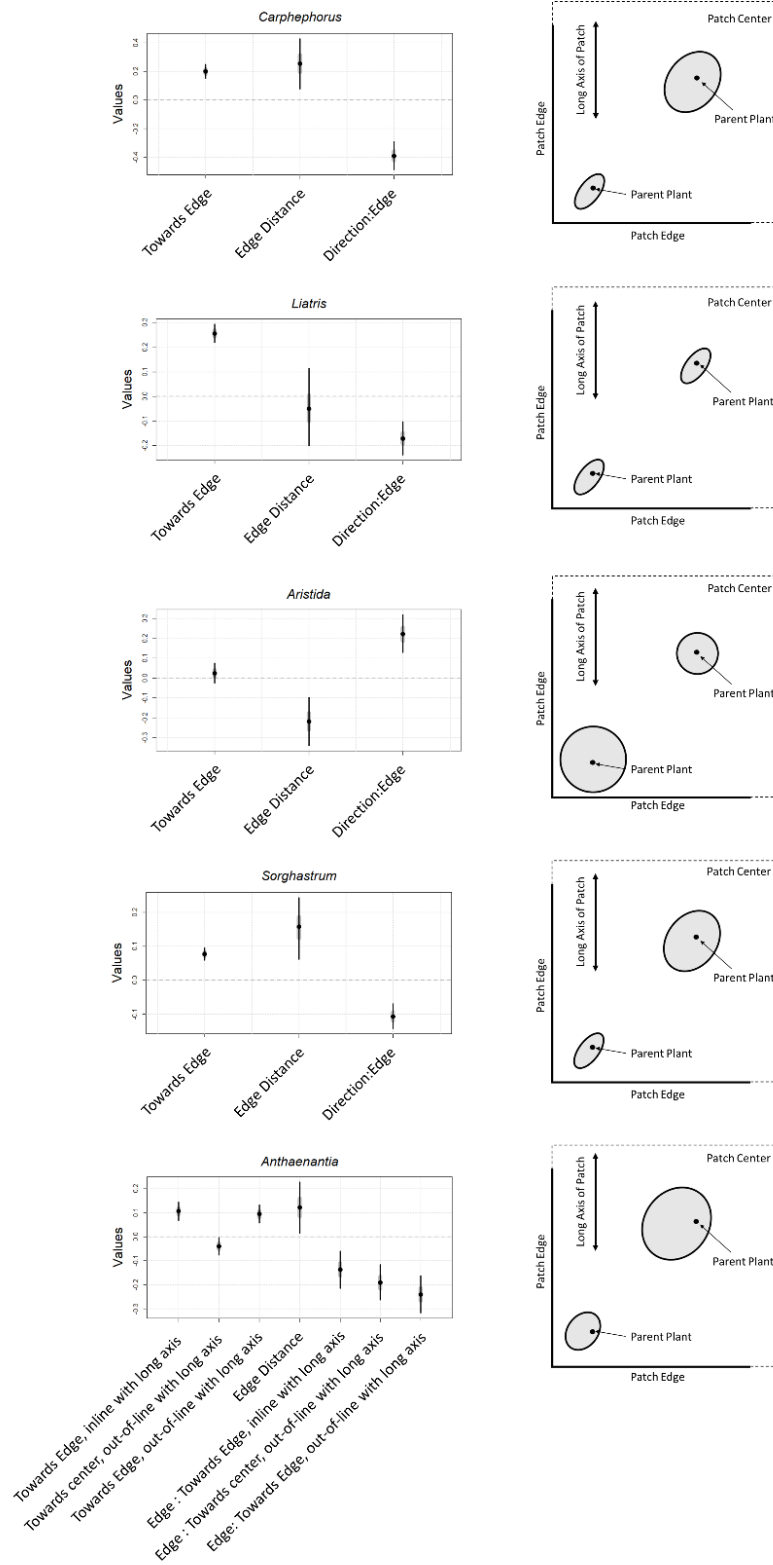


Figure 4.4. Model results and interpretation. *Left Panels:* Standardized model coefficients

with 50% credible intervals (the light gray lines) and 95% credible intervals (the dark black lines) for five herbaceous plant species in a fragmentation experiment. Values above the 0 line mean greater dispersal than the intercept, while values below mean less dispersal than the intercept. For instance, an effect of edge distance below the zero line would indicate that areas closer to edges have shorter dispersal distances. For the x-axis of the *Anthenantia* panel, the labels correspond to the analogous label on the other panels as follows: The first three labels correspond to directionality (analogous to “Towards Edge.” The “Edge Distance” is exactly the same for this species as the others. The remaining three labels correspond to the “Direction:Edge” interaction term, as this term is more complicated for *Anthenantia* (see Methods). *Right Panels:* The right-hand panel in each species row is a stylized representation of our interpretation of these results. The gray zone surrounding each parent plant is a stylized representation of mean seed dispersal patterns.

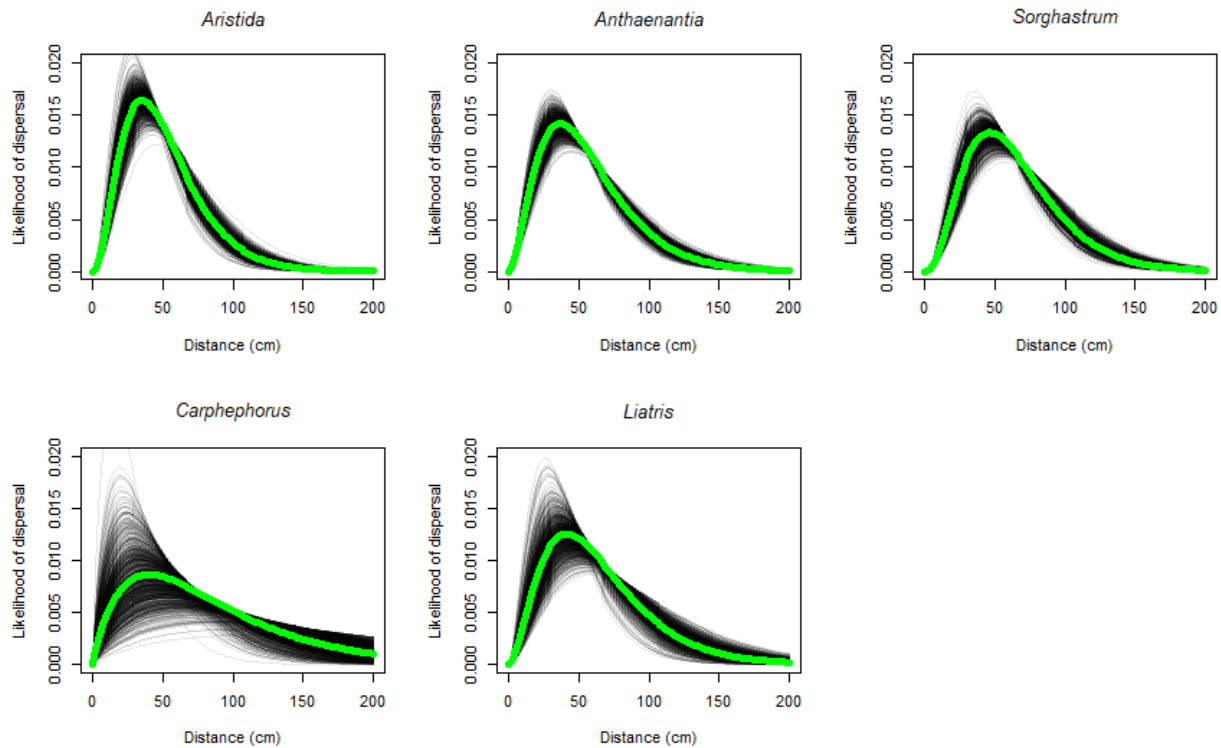


Figure 4.5. Dispersal kernels with the uncertainty around the mean. The means depicted here are those from near the centers of patches.

Directionality

Seed dispersal direction was correlated with the distance of dispersal for four of five species (Figure 4.4, Table 4.2). For *Carphophorus*, *Liatris*, and *Sorghastrum*, seeds that dispersed towards the center of the patch dispersed shorter distances than seeds that dispersed towards the edge of the patch. For *Aristida*, there was no effect of directionality on distance of seed dispersal. For *Anthenantia*, for which the model supported four-directional bins (the bins noted in Figure 4.1), seeds in the two bins oriented towards the edge dispersed further than seeds in the two bins oriented towards the center. However, for *Anthenantia*, in the two bins with seeds that dispersed towards the center of patches, dispersal distances were greater in the direction in-

line with the long axis of the patch (Figure 4.4).

Relationship between Distance from Edge and Directionality

Dispersal was less directional at locations closer to the center of the patch for all species except *Aristida* (Figure 4.4, Table 4.2). So, for most species, the pattern of greater dispersal distances towards the edge was stronger for plants located nearer to patch edges. For *Aristida*, seed dispersal was less directional closer to patch edges.

Table 4.2. Mean dispersal distances with percent difference between conditions.

Comparison	Species	Condition	Mean Dispersal Distance (cm)	Percent Difference
Edge vs Center	<i>Anthenantia</i>	edge	55.3	4.7 ^a
	<i>Anthenantia</i>	center	58.0	
	<i>Aristida</i>	edge	80.2	-22.4 ^a
	<i>Aristida</i>	center	64.0	
	<i>Carphephorus</i>	edge	49.9	8.5 ^a
	<i>Carphephorus</i>	center	54.3	
	<i>Liatris</i>	edge	101.8	-25.8 ^a
	<i>Liatris</i>	center	78.5	
	<i>Sorghastrum</i>	edge	70.4	12.6 ^a
	<i>Sorghastrum</i>	center	79.8	
Dispersal Direction	<i>Anthenantia</i>	towards center	57.2	14.5 ^b
	<i>Anthenantia</i>	towards edge	66.1	
	<i>Aristida</i>	towards center	62.8	6.3 ^b
	<i>Aristida</i>	towards edge	66.9	
	<i>Carphephorus</i>	towards center	45.1	19.4 ^b
	<i>Carphephorus</i>	towards edge	54.8	
	<i>Liatris</i>	towards center	76.4	21.2 ^b
	<i>Liatris</i>	towards edge	94.6	
	<i>Sorghastrum</i>	towards center	71.6	10.5 ^b
	<i>Sorghastrum</i>	towards edge	79.5	

Table 4.2 (cont'd)

Distance from edge x Direction Interaction	<i>Anthenantia</i>	at edge towards edge	59.0	13.9 ^c
	<i>Anthenantia</i>	at edge towards center	51.3	
	<i>Anthenantia</i>	at center towards edge	61.2	9.7 ^c
	<i>Anthenantia</i>	at center towards center	55.5	
	<i>Aristida</i>	at edge towards edge	83.8	16.5 ^c
	<i>Aristida</i>	at edge towards center	71.0	
	<i>Aristida</i>	at center towards edge	71.5	23.7 ^c
	<i>Aristida</i>	at center towards center	56.3	
	<i>Carphephorus</i>	at edge towards edge	68.0	60.2 ^c
	<i>Carphephorus</i>	at edge towards center	36.5	
	<i>Carphephorus</i>	at center towards edge	49.3	-16.8 ^c
	<i>Carphephorus</i>	at center towards center	58.4	
	<i>Liatris</i>	at edge towards edge	141.6	57.3 ^c
	<i>Liatris</i>	at edge towards center	78.5	
	<i>Liatris</i>	at center towards edge	88.5	23.0 ^c
	<i>Liatris</i>	at center towards center	70.3	
	<i>Sorghastrum</i>	at edge towards edge	74.7	13.6 ^c
	<i>Sorghastrum</i>	at edge towards center	65.2	
	<i>Sorghastrum</i>	at center towards edge	81.3	4.3 ^c
	<i>Sorghastrum</i>	at center towards center	77.9	

^aPositive values indicate greater distances of dispersal at patch centers, relative to patch edges.

^bPositive values indicate greater distances of dispersal towards edges, relative to towards patch centers.

^cPositive values indicate greater distances of dispersal towards edges, relative to towards patch centers.

Discussion

We found that habitat fragmentation affects local seed dispersal primarily through the creation of edges. Dispersal distance was generally greater in patch centers and in the direction of an edge, with this directionality pattern typically stronger closer to patch edges. Our consideration of directionality afforded key insights about how fragmentation affects seed dispersal, which would have been missed under the common approach of assuming seed dispersal is equal in all directions. Our results illustrate consequences of fragmentation on dispersal that may have ramifications for plant population dynamics (Levine and Murrell 2003; discussed below).

Two mechanisms might explain how patch edges influenced dispersal. First, wind is stronger away from edges in open habitats (Damschen et al., 2014), likely resulting in greater seed dispersal distances away from edge for three species. Second, as wind travels over forest canopy into a clearing, it can eddy backwards (Detto et al., 2008), likely resulting in three species dispersing to greater distances toward edges, particularly at close proximity to edges.

Conversely, we saw little effect of patch connectivity or edge-to-area ratio on seed dispersal, in spite of our expectations. This difference may be related to how wind behavior at higher altitudes (smoother, more predictable), rather than at the more chaotic lower levels (which nonetheless may show trends), as we observe in our data (Bohrer et al., 2008; Detto et al., 2008).

An important consequence of our findings is that fragmentation may influence seed dispersal differently at long-distance and local scales. Most previous work has focused on only one scale, without considering differences between them (Nathan and Muller-Landau, 2000; Rogers et al., 2019). While we find that local seed dispersal is influenced by edge proximity, past work in our system has illustrated how larger-scale fragmentation effects, such as patch connectivity and edge-to-area ratio, modify long-distance seed dispersal for both biotically and abiotically dispersed species, albeit of different species (Levey et al., 2005; Damschen et al., 2014; Herrmann et al., 2016). Together, these findings suggest that edge proximity may affect seeds dispersing locally, with patch connectivity and edge-to-area ratio influencing only those seeds that reach above-boundary layer heights (e.g., >5m above the ground surface).

In spite of their different adaptations to dispersal by wind, our study species showed remarkably similar dispersal responses to fragmentation. Two of our species (*Carphephorus* and *Liatris*) have clear morphological adaptations to wind dispersal (the pappus), while the three grasses do not. Adaptations to dispersal could vary with scale of dispersal (Murrell et al., 2002;

Muller-Landau et al., 2003). The presence of a pappus almost certainly facilitates long-distance dispersal in *Liatris* and *Carphephorus* and the presence of awns may facilitate short-distance dispersal in *Sorghastrum* and *Aristida*. Local dispersal by wind may even occur without any obvious morphological adaptations, as we see in *Anthenantia* (Murrell et al., 2002; Riba et al., 2009). How traits affect dispersal patterns at different scales is an avenue for future research.

Creation of edges through fragmentation affected seed dispersal distance, which in turn may influence plant population dynamics in several ways. First, plants close to edges typically dispersed shorter distances than plants away from edges. As a consequence, seedlings closer to edges may experience higher levels of intraspecific competition with other seedlings originating from the same parent plant (Comita et al., 2014). Shorter dispersal distances near edges may also lead to negative demographic consequences through Janzen-Connell effects (Janzen, 1970; Connell, 1971; Hovanes et al., 2018) on seedlings close to their parent plants, which may reduce population growth rates near patch edges. Second, near patch edges, dispersal was more strongly directed towards the edge, which could exacerbate negative density-dependent processes caused by shorter dispersal distances. Third, in our longleaf pine study system, edge proximity is associated with increased leaf litter and shading, which are detrimental to longleaf pine understory herbs (Hiers et al., 2007; Veldman et al., 2013), such as our study species.

We show that the relationship between the distance and direction of dispersal can be important for abiotically dispersed species, even at local scales. Many terrestrial plants are abiotically dispersed (e.g., wind, gravity), and may disperse in a directional manner (Nathan et al., 2002; van Putten et al., 2012). Despite this, relatively few studies have examined directional seed dispersal for abiotically dispersed species, with past work focusing on riparian systems and for long-distance dispersal by wind (Levine, 2003; Wright et al., 2008; Damschen et al., 2014;

Horvitz et al., 2014). We show how novel insights can emerge through consideration of seed dispersal directionality, in ways that may influence plant populations.

In summary, we show how fragmentation affects seed dispersal at local scales. Our experimental design allowed us to tease apart influences of patch isolation, edge-to-area ratio, and edge effects — factors that are often conflated in observational studies of habitat fragmentation (Didham et al., 2012; Fletcher et al., 2018). Our finding that edges are most important for local seed dispersal while the large-scale factors of connectivity and edge-to-area ratio matter less for this process illustrate how experiments can parse out the scale-dependent influence of fragmentation on key ecological processes, such as seed dispersal.

Acknowledgments

We thank the USDA-Forest Service for the creation and much of the maintenance of our experimental blocks, particularly John Blake, Ed Olson, Andy Horcher, Jim Segar, and the fire management team. In addition, we thank the people who contributed to fieldwork, including John Orrock, Melissa Burt, Melissa Habenicht, Elizabeth Long, Marilena Nunez, Julian Resasco, Lauren Sullivan, and Stephanie Wagner. Funding was provided by the National Science Foundation (Awards: 0613701, 0614333, 0613975, 1912729, and 1913501) and by the US Department of Energy to the US Department of Agriculture-Forest Service-Savannah River under Interagency Agreement DE-AI09-00SR22188.

LITERATURE CITED

LITERATURE CITED

- Bohrer, G., G. G. Katul, R. Nathan, R. L. Walko, and R. Avissar. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology* 96: 569–580.
- Caughlin, T. T., J. M. Ferguson, J. W. Lichstein, A. Zuidema, S. Bunyavejchewin, D. J. Levey, and T. T. Caughlin. 2014. Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B* 282: 20142095.
- Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102: 845–856.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer, and G. R. Gradwell [eds.], *Dynamics of Populations*, 298–312. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Damschen, E. I., D. V Baker, G. Bohrer, R. Nathan, J. L. Orrock, J. R. Turner, L. A. Brudvig, et al. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences of the United States of America* 111: 3484–3489.
- Detto, M., G. G. Katul, M. Siqueira, J.-Y. Juang, and P. Stoy. 2008. The structure of turbulence near a tall forest edge: the backward-facing step flow analogy revisited. *Ecological Applications* 18: 1420–1435.
- Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121: 161–170.
- Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, et al. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation* 226: 9–15.
- Goodrich, B., J. Gabry, I. Ali, and S. Brilleman. 2020. rstanarm: Bayesian applied regression modeling via Stan.
- Greene, D. F., M. Quesada, and C. Calogeropoulos. 2008. Dispersal of seeds by the tropical sea breeze. *Ecology* 89: 118–125.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1: 1–9.

- Herrmann, J. D., T. A. Carlo, L. A. Brudvig, E. I. Damschen, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2016. Connectivity from a different perspective: comparing seed dispersal kernels in connected vs. unfragmented landscapes. *Ecology* 97: 1274–1282.
- Hiers, J. K., J. J. O’Brien, R. E. Will, and R. J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. *Ecological Applications* 17: 806–814.
- Horvitz, N., R. Wang, M. Zhu, F.-H. Wan, and R. Nathan. 2014. A simple modeling approach to elucidate the main transport process and predict invasive spread: River-mediated invasion of *Ageratina adenophora* in China. *Water Resources Research* 50: 9738–9747.
- Hovanes, K. A., K. E. Harms, P. R. Gagnon, J. A. Myers, and B. D. Elder. 2018. Overdispersed spatial patterning of dominant bunchgrasses in southeastern pine savannas. *The American Naturalist* 191: 658–667.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.
- Jose, S., E. J. Jokela, and D. Miller eds. . 2006. The longleaf pine ecosystem: Ecology, silviculture, and restoration. Springer, New York City, New York.
- Law, R., D. J. Murrell, and U. Dieckmann. 2003. Population growth in space and time: Spatial logistic equations. *Ecology* 84: 252–262.
- Lemke, A., M. Von Der Lippe, and I. Kowarik. 2009. New opportunities for an old method: using fluorescent colours to measure seed dispersal. *Journal of Applied Ecology* 46: 1122–1128.
- Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309: 146–148.
- Levey, D. J., T. T. Caughlin, L. A. Brudvig, N. M. Haddad, E. I. Damschen, J. J. Tewksbury, and D. M. Evans. 2016. Disentangling fragmentation effects on herbivory in understory plants of longleaf pine savanna. *Ecology* 97: 2248–2258.
- Levine, J. M. 2003. A patch modeling approach to the community-level consequences of directional dispersal. *Ecology* 84: 1215–1224.
- Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics* 34: 549–574.
- Magnusson, M., M. R. Andersen, J. Jonasson, and A. Vehtari. 2020. Leave-One-Out Cross-Validation for Bayesian Model Comparison in Large Data. *Arxiv: arXiv:2001.00980 [stat.ME]*.
- Muller-Landau, H. C., S. A. Levin, and J. E. Keymer. 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pests. *Ecology* 84: 1957–1967.

- Murrell, D. J., J. M. J. Travis, and C. Dytham. 2002. The evolution of dispersal distance in spatially structured populations. *Oikos* 92: 229–236.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement ecology research. *Proceedings of the National Academy of Sciences* 105: 19052–19059.
- Nathan, R., and G. G. Katul. 2005. Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. 102: 8251–8256.
- Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S. A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418: 409–413.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.
- Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520: 45–50.
- van Putten, B., M. D. Visser, H. C. Muller-Landau, and P. A. Jansen. 2012. Distorted-distance models for directional dispersal: A general framework with application to a wind-dispersed tree. *Methods in Ecology and Evolution* 3: 642–652.
- R Core Team. 2020. R: a language and environment for statistical computing.
- Rand, T. A. 2000. Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology* 88: 608–621.
- Riba, M., M. Mayol, B. E. Giles, O. Ronce, E. Imbert, M. Van Der Velde, S. Chauvet, et al. 2009. Darwin's wind hypothesis: Does it work for plant dispersal in fragmented habitats? *New Phytologist* 183: 667–677.
- Rodríguez-Cabala, M. A., M. A. Aizen, and A. Novaro. 2007. Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. *Biological Conservation* 139: 195–202.
- Rogers, H. S., N. G. Beckman, F. Hartig, J. S. Johnson, G. Pufal, K. Shea, D. Zurell, et al. 2019. The total dispersal kernel: A review and future directions. *AoB PLANTS* 11: 1–13.
- Soons, M. B., J. H. Messelink, E. Jongejans, and G. W. Heil. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology* 93: 1214–1225.
- Templeton, A. R., R. J. Robertson, J. Brisson, and J. Strasburg. 2001. Disrupting evolutionary processes: The effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Sciences* 98: 5426–5432.

- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, et al. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 99: 12923–12926.
- Thomson, F. J., A. T. Moles, T. D. Auld, and R. T. Kingsford. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* 99: 1299–1307.
- Uriarte, M., M. Anciaes, M. T. B. Da Silva, P. Rubim, E. Johnson, and E. M. Bruna. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecology* 92: 924–937.
- Vehtari, A., J. Gabry, M. Magnusson, Y. Yao, and A. Gelman. 2019. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.
- Veldman, J. W., W. B. Mattingly, and L. A. Brudvig. 2013. Understory plant communities and the functional distinction between savanna trees, forest trees, and pines. *Ecology* 94: 424–434.
- Wright, S. J., A. Trakhtenbrot, G. Bohrer, M. Detto, G. G. Katul, N. Horvitz, H. C. Muller-Landau, et al. 2008. Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. *Proceedings of the National Academy of Sciences of the United States of America* 105: 19084–19089.

CHAPTER FIVE

EXPERIMENTAL HABITAT FRAGMENTATION REVEALS THE ROLE OF EDGES FOR PLANT RECRUITMENT

Abstract

Despite decades of research, debate remains about how — and even whether — habitat fragmentation impacts biodiversity. This debate is due, in part, to the complex ways that landscapes change when habitat is destroyed and fragmented; these changes operate both within and among habitat patches (e.g., edge effects and isolation effects, respectively). Adding to confusion and controversy is a typically narrow focus on simple response metrics, such as species richness. A focus on richness can obscure changes to the abundance and demography of component populations. We test the effects of habitat fragmentation on recruitment of four experimentally established plant species. In doing so, we disentangle three effects of habitat fragmentation on recruitment through a large-scale fragmentation experiment: patch connectivity, patch edge-to-area ratio, and distance from the edge of the patch. There was no effect of connectivity or patch edge-to-area ratio on the recruitment patterns of any species. However, distance from the patch edge influenced recruitment of two species. For one of these species, there were more recruits at patch edges. For the other species, the effect of edge was modulated by patch type, with greatest recruitment in the centers of isolated patches with high edge-to-area ratio. These edge effects were driven by how edge proximity and structure (e.g., canopy cover) influenced adult plant reproductive output, which in turn structured plant recruitment. Our findings demonstrate that habitat fragmentation can lead to changes in recruitment, an important population-level process. Distance to edge, not connectivity or patch edge-to-area ratio, was primarily responsible for these changes.

Introduction

Habitat fragmentation is a major cause of biodiversity decline (Pereira et al., 2010; Haddad et al., 2015). There has been much effort by conservationists to reduce the effects of fragmentation on natural communities (Diamond, 1975; Wilcox and Murphy, 1985; Lindenmayer and Fischer, 2006). Conservation strategies, including corridors that connect otherwise isolated patches of habitat, seek to ameliorate the effects of fragmentation on species that are found in those patches (Crooks and Sanjayan, 2006; Haddad and Tewksbury, 2006). However, despite decades of work, debate continues about how exactly — even whether — habitat fragmentation leads to biodiversity declines (Didham et al., 2012; Fahrig, 2013; Fletcher et al., 2018; Fahrig et al., 2019). Disentangling the effects of fragmentation on biodiversity may be clarified through examination of the underlying population processes, including recruitment, which is the subject of our study.

Much of the debate about the link between habitat fragmentation and biodiversity may be due to the focus on simple metrics like species richness in fragmentation research (Fischer and Lindenmayer, 2007; Vellend et al., 2013; Haddad et al., 2015). This focus can obscure important changes to biodiversity because richness is a scale-dependent metric (Chase et al. 2020), which ignores the abundance of species. For example, species richness may remain the same following fragmentation, in spite of substantial declines in populations of some species or local extinctions followed by novel colonization events by other species (Schoereder et al., 2004; Jackson and Sax, 2010; Banks-Leite et al., 2012; Damschen et al., 2019). Therefore, to understand the consequences of fragmentation for biodiversity, it is critical to move beyond a focus on species richness to consider the effects of fragmentation on population dynamics and the processes that drive them. Studies of population responses to fragmentation can illustrate effects on individual

species and predict future local extinctions resulting from fragmentation (Banks-Leite et al., 2012). Unfortunately, the majority of plant demographic studies occur only within one or two patches and do not account for the context of the broader landscape around and between patches that may influence these processes (Salguero-Gómez et al., 2015; Gurevitch et al., 2016). This is of pragmatic concern, as species likely respond differently to fragmentation, and their responses can shape biodiversity management decisions (Gurevitch et al., 2016).

Further clouding fragmentation effects is the fact that they can manifest through multiple mechanisms that operate at different spatial scales and are difficult to disentangle (Lindenmayer and Fischer, 2006; Didham et al., 2012; Haddad et al., 2015). Habitat loss typically results in landscapes with patches that are smaller, less connected to each other (i.e., more isolated), have higher edge-to-area ratio, and increased prevalence of edge effects (Didham et al., 2012); each of these fragmentation effects may affect populations differently (Bruna, 2002; Caughlin et al., 2019). For example, distance from the edge of a fragment might affect populations of plants by altering microclimate (Tuff et al., 2016) and influencing populations of interacting species, such as insects and pathogens (Bruna, 2002; Sullivan et al., 2011; Evans et al., 2012; Brudvig et al., 2015). At larger spatial scales, fragmentation effects like connectivity and edge-to-area ratio might influence plant populations by altering among-patch dispersal and because effects of edge proximity may scale up by altering patch geometry, by, for instance, changing the number of herbivores present in a given habitat patch (Uriarte et al., 2010; Haddad et al., 2014; Damschen et al., 2019). Experiments can disentangle the mechanisms contributing to fragmentation effects (Haddad et al., 2015; Fletcher et al., 2018). Coupling experiments with the study of population responses can resolve both how and why species respond to habitat fragmentation.

Here, we employ a landscape-scale experiment to evaluate how fragmentation influences recruitment for four plant species. Our experimental design enables us to disentangle effects of patch connectivity, patch edge-to-area ratio, and distance from patch edge, which are common consequences of habitat destruction (Didham et al., 2012). Previous work in this system has focused on seed production (Brudvig et al., 2015) or on the ability of short-term models to capture long-term population trends (Caughlin et al., 2019). Here, focus on how recruitment patterns are shaped on local scales. We measure recruitment patterns of four plant species that we introduced into our experimental landscapes 7-8 years prior to our study, affording a highly controlled assessment of recruitment patterns. We ask the following questions: (1) In what ways does fragmentation (through connectivity, edge-to-area ratio, and edge proximity) affect plant recruitment? and (2) How do biotic and abiotic factors mediate fragmentation effects on recruitment patterns.

For Question (1), we focused on three fragmentation effects: (a) Connectivity, for which we expected positive effects on recruitment for all species. We expected this effect because connectivity has been shown to promote population persistence in fragmented landscapes, which may be due to higher rates of recruitment, as a result of, for instance, higher rates of pollination as corridors may allow for movement of insects, leading to more pollination, and, thus, higher seed production (Townsend and Levey, 2005; Damschen et al., 2019; Griffin and Haddad, 2021). (b) Altered patch edge-to-area ratio, for which we expected more recruitment in high edge-to-area patches. We expected this effect based off past work in our system which noted higher herbivory rates for two of our study species in low edge-to-area patches (Levey et al., 2016), and high herbivory may depress recruitment. (c) Distance from patch edge, for which we expected species to respond positively to the distance from the edges of our patches (Brudvig

et al., 2015). This is because our study species are species of open habitat and close to edges, these species encounter increased shading and litter fall.

For Question (2), we examined those same three fragmentation effects as well as both biotic (e.g., seed predation, germination rates) and abiotic factors (e.g., amount of bare ground, a proxy for microsite availability) that may be important in determining plant recruitment patterns. Given the complexity of how these factors may influence each other, examining them together may be more enlightening than examining them separately (Brudvig et al., 2015).

Methods

Study Site and Focal Species

We conducted our work at the Savannah River Site (SRS), a National Environmental Research Park located near Aiken, SC. Our work takes place in a replicated landscape experiment that is designed to test effects of connectivity, patch edge-to-area ratio, and distance from the nearest edge of a patch. Each replicate landscape ($n=7$; hereafter, “block”) contains a central patch (1 ha), which is connected to a second patch (“connected patch”) via a corridor that is 150m long and 25m wide (Figure 5.1). The area of the connected patch (including the corridor) and of the individual unconnected patches is 1.38ha each. The unconnected patches are “winged,” with two dead-end corridors (the “wings”) that, together, equal the dimensions of the main corridor, and “rectangular” with dimensions of 100m x 137.5m (Figure 5.1). All blocks contain one of each patch type (central, connected, winged, rectangular) plus either an additional winged or rectangular patch, chosen at random.

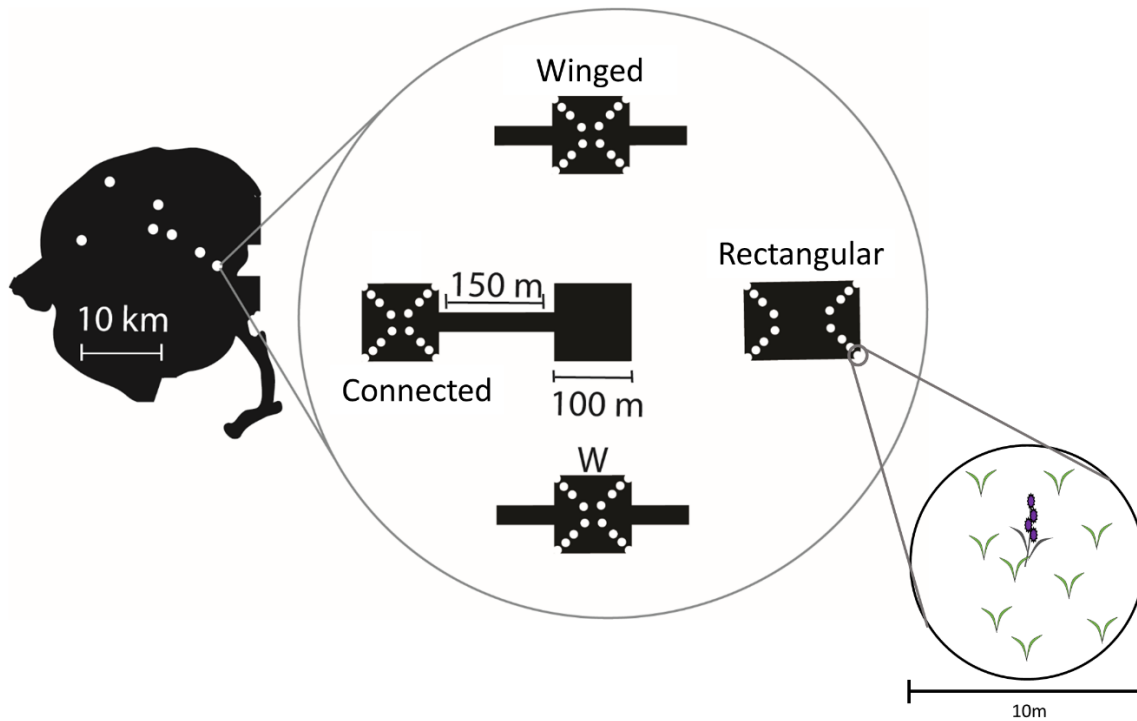


Figure 5.1. Experimental design. Winged patches are isolated and have a high edge-to-area ratio, differing from the connected patches only in connectivity. Rectangular patches are isolated and have a low edge-to-area ratio, differing from winged patches only in edge-to-area ratio.

To test for effects of connectivity, we compare winged and connected patches, as winged patches are unconnected and have approximately the same edge-to-area ratio as connected patches; they differ in connectivity. To test for effects of edge-to-area ratio, we compare winged and rectangular patches, as rectangular patches are isolated and low-edge, differing from winged patches only by having a lower edge-to-area ratio. Patches were open habitat with very little canopy cover, surrounded by a matrix of pine plantation forest. Following the initial clearing of habitat patches from the pine plantation matrix, we have managed the patches with prescribed

fire and brush clearing to facilitate the recovery of the longleaf pine savanna that would have been the historic vegetation type in this region (Damschen et al., 2019).

In 2007 and 2008, we established (by planting) populations of four species equally into all habitat patches ($N = 7 \text{ blocks} \times 4 \text{ patches/block} = 28 \text{ patches}$; Figure 5.1). To test edge proximity effects, we planted one individual of each species into plots at 1, 10.5, 20, and 37m from the nearest edge, (Figure 5.1). Two of our species were forbs in the aster family (Asteraceae): *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray and *Liatris squarrulosa* Michx. (synonym: *Liatris earlei* (Greene) K. Schum., following Radford et al. [1968]), while the remaining two are grasses (Poaceae): *Sorghastrum secundum* (Elliott) Nash, and *Anthenantia villosa* (Michx.) P. Beauv. Hereafter, we refer to these species by their genus names. All four are relatively long-lived perennials and can flower within two years of planting (Brudvig et al., 2015). All populations are derived from seed collected at SRS. We deposited a voucher specimen of a mature plant from one seed source for each population at the Michigan State University Herbarium (herbarium code: MSC). Additionally, these four focal species did not previously occur in our experimental landscape patches, but they would have been present historically and are currently regionally uncommon to rare. Thus, we assumed that recruits we encountered within our habitat patches were from our original transplanted individuals.

Recruitment Counts

We used a combination of datasets to answer our questions. In all cases, we counted individuals that recruited (hereafter “recruits”) following planting of the original transplanted individuals, which were tagged. Because some recruits have flowered and dispersed seed since the initial establishment of these populations, it is likely that some of the recruits that we found

were not offspring of the original transplanted plant. The recruitment that we measured is the result of seven years of population dynamics.

To explore the effects of edges on recruitment patterns, we counted the number of recruits of each species during the summer of 2015 at the edges (1m from edge) and the centers of patches (37m from edge), within a 5m radius around each transplanted conspecific individual. We chose the 5m distance both to minimize any ambiguity of the plot of origin, as well as because most recruits were located within that 5m zone. Within this 5m zone, the percentage of recruits within 3m of the parent plant was 95%–100%, depending on species.

To explore the effects of connectivity and edge-to-area ratio, we combined the above-mentioned data with two other datasets, in order to cover nearly the whole of each patch. The first of these was a survey from fall of 2015 of plots located at 10.5m and 20m from patch edges, with all recruits to a distance of 1.5m from each transplanted conspecific. The second of these was a survey from fall of 2016 of reproductive recruits anywhere in our patches at distances >5m from the transplanted individuals.

Additional Biotic and Abiotic Factors

To address Question 2, we collected additional data on a suite of biotic and abiotic factors that may influence recruitment patterns. Methods for each of these is described below and a summary of each variable can be found in Table 5.1. We have previously examined some of these data in a mechanistic population model (Caughlin et al., 2019), but are using those and additional data here to explore the covariates that influence our population outcomes. The Caughlin et al. (2019) paper focused on whether demographic models parameterized from short-term data could predict long-term population trends, while the present work focuses on how these covariates actually influence local recruitment outcomes.

Table 5.1. Explanation of factors used in constructing the SEMs

Variable	Units	Method	Methods Citation (if applicable)
bare ground	percent (range: 0-74)	visual estimation	described in present study
canopy cover	counts (range: 0-56)	densiometer	described in present study
connectivity	binary (connected or not)	experimental design	see Figure 1
edge distance	continuous (range: 1-37)	experimental design	see Figure 1
edge-to-area ratio	binary (high edge or low edge)	experimental design	see Figure 1
germination	counts (range: 0-26)	number of seeds that germinated, out of 40	Caughlin et al. 2019
herbivory	proportion (range: 0-1)	number of leaves with herbivory, divided by the total number of leaves	Brudvig et al. 2015
number of recruits	counts (range: 0-137)	counted number of individuals	Caughlin et al. 2019
reproductive output	counts (range: 0-1113)	total number of flower structures from each of 2009, 2012, and 2015	Caughlin et al. 2019
seed predation	counts (range: 0-20)	number of seeds that were removed from seed predation trays, out of 20	described in present study

Bare Ground

We collected data on bare ground in 2017 using a visual estimation approach in which we recorded the amount of bare ground within a meter-squared quadrat at the location of each of the original transplant plants. We recorded cover on a continuous basis, using whole integers for cover values greater than 1% of a square meter, and for cover values less than 1%, we recorded values to the nearest tenth of a percent, and for cover values less than a tenth of a percent, we recorded values to the nearest hundredth of a percent.

Canopy Cover

Canopy cover data were collected in 2017, using convex Model A densiometers (Robert E. Lemmon Forest Densiometers, Rapid City, South Dakota). We counted the number of vertices of the densiometer that were covered by the canopy, following the subsetting methods of Strickler (1959).

Connectivity, Edge-to-Area Ratio, Edge Distance

These are structural to our experiment and are described in the second and third paragraphs of the Methods of this chapter.

Germination

In February 2010, at half of all plots that contained our transplanted species, we planted 40 seeds of each of our study species in a separate plot to ensure that germinants would be from

these added seeds, rather than from our study populations. Over the course of that growing season, from March 31-September 8, we checked these plots weekly and tagged germinants with sewing pins to ensure no duplication of counts between checks. At the conclusion of the growing season we assumed all remaining seeds had died and summed the total number of germinants from that season, including those that had died. We realize that this assumption may not reflect any additional germination from subsequent years; however, we are interested in the relative difference in germination between the different plot locations, rather than the absolute number of germinants across all years. For the data associated with this, please see Caughlin et al. (2019).

Number of Recruits

In fall of 2015, we counted all recruits within 1.5m of each of our transplanted individuals at each of the four distances from the edge of the patch. For the data associated with this, please see Caughlin et al. (2019).

Reproductive Output

In each fall of 2009, 2012, and 2015, we counted the total number of flowering structures on each transplanted individual. We then summed them to obtain a total number of flowering structures per transplanted individual. A subset of these data are present in Caughlin et al. (2019).

Herbivory Data

In September of 2009, we counted the number of leaves with visual signs of herbivory as well as the total number of leaves on each of our transplanted individuals. For individuals with >100 leaves, we did this with a haphazard sample of 100 leaves. For additional details, please see Brudvig et al. (2015).

Seed Predation

We collected these data on post-dispersal seed predation in 2009. we placed 20 seeds on top of 0.5 cm of sand within a 19 x 14 x 10 cm plastic container fitted with a tight cover. Two holes, 2.5 cm diameter each, were cut on adjacent sides of the container to allow insect and mammalian seed predators to enter freely. Seeds for this experiment were collected from other populations of plants located outside our experiment. For each individual plant in the experiment, seeds of the same species were placed in containers adjacent to, but 1m away from the plant. We placed these seeds during the time of natural seed dispersal for each species and then left the seeds in the field for 20 days. After 20 days, any remaining seeds and sand were collected in plastic bags. Seeds were later separated from sand and counted. For each of our species, the mean $\pm$ standard deviation of the number of seeds removed during the 20-day period is as follows:

Anthenantia: 4.7 ± 4.9 ; *Carphephorus*: 7.1 ± 7.6 ; *Liatris*: 5.2 ± 6.0 ; *Sorghastrum*: 7.5 ± 6.0 .

Analysis

To answer Question 1, about fragmentation effects on recruitment, we ran two generalized linear mixed effects models (GLMM) for each species. For both models, our response variable was the count of the number of individuals of each species. One model tested edge effects on recruitment for each species, using the count data at patch edges and centers. Our predictor variables were distance from the edge of the patch, patch type (included to allow for the interaction term), and the interaction term between distance from the edge and patch type. Our second model used the combination of the three types of data (as described in the section titled “*Recruitment Counts*,” above) and examined the patch-level factors of connectivity and patch edge-to-area ratio for each species and had a single predictor variable of patch type. For

both models, we used a nested random effect of patch within block to account for the nested nature of our experimental design. For all models, we used a negative binomial distribution (typical for over-dispersed count data), as implemented through the `glmer.nb` function of the `lme4` package within R (Bates et al., 2015). However, the *Anthenantia* edge model did not converge using this function, so we instead used the same model structure, through the `glmmTMB` function (with the “`nbinom1`” parameterization) within the `glmmTMB` package within R (Brooks et al., 2017). All analyses were run using R, version 3.6.3 in RStudio, version 1.2.5033 (RStudio, 2019; R Core Team, 2020).

To answer Question 2, about factors mediating fragmentation effects on recruitment, we ran a set of structural equation models (SEMs). SEMs allow for testing whether fragmentation effects influence recruitment by altering various abiotic and biotic factors. To do this, we constructed a single SEM for each study species using the `piecewiseSEM` package, version 2.1.1 (Lefcheck, 2016). To examine potential mechanisms as well as our fragmentation effects, we constructed SEMs containing our three fragmentation effects (distance from the edge, edge-to-area ratio, connectivity), two demographic factors (rates of germination and reproductive output of transplanted individuals), two factors of habitat structure (canopy cover and the amount of bare ground), and two biotic interactions (rates of seed predation and levels of herbivory). For a brief methodological explanation of each of these factors, please see Table 5.1. Of these, we expected that the two demographic factors would positively correlate with recruitment. Of the aspects of habitat structure that we examined, we predicted a negative relationship between canopy cover and recruitment (as higher canopy cover results in more shade), but a positive relationship with bare ground (i.e., available microsites for new recruits). We predicted negative correlations for both of our biotic interactions of seed predation and levels of herbivory on

recruitment, as seed predation leads to fewer potential recruitment opportunities and herbivory can decrease seedling survival. We standardized all path coefficients, enabling comparison of their relative effects. We constructed SEM paths based on our initial hypotheses and expected relationships based on our understanding of the ecology of our study system and left all nonsignificant paths in the final models. We also determined goodness-of-fit tests for each SEM (using the function `summary.psem`) and the goodness-of-fit test statistic was $p > 0.05$ for all SEMs.

Results

Overall, we did not see major effects of connectivity and patch edge-to-area ratio on recruitment patterns for our species. Distance from the edge, especially as mediated through effects on canopy cover and reproductive output on parent plants was important for recruitment patterns in several of our species.

Question 1: Effects of Fragmentation on Recruitment

There was no effect of connectivity or patch edge-to-area ratio on recruitment patterns for any species ($p > 0.05$ in all cases; Table 5.2) (Figure 5.2).

Table 5.2. Statistics table for the effect of patch type, as obtained from the patch-level GLMM.

Species	Chi.Sq Value	p-value
<i>Carphephorus</i>	0.133	0.94
<i>Liatris</i>	1.6	0.45
<i>Sorghastrum</i>	3.13	0.21
<i>Anthenantia</i>	3.93	0.14

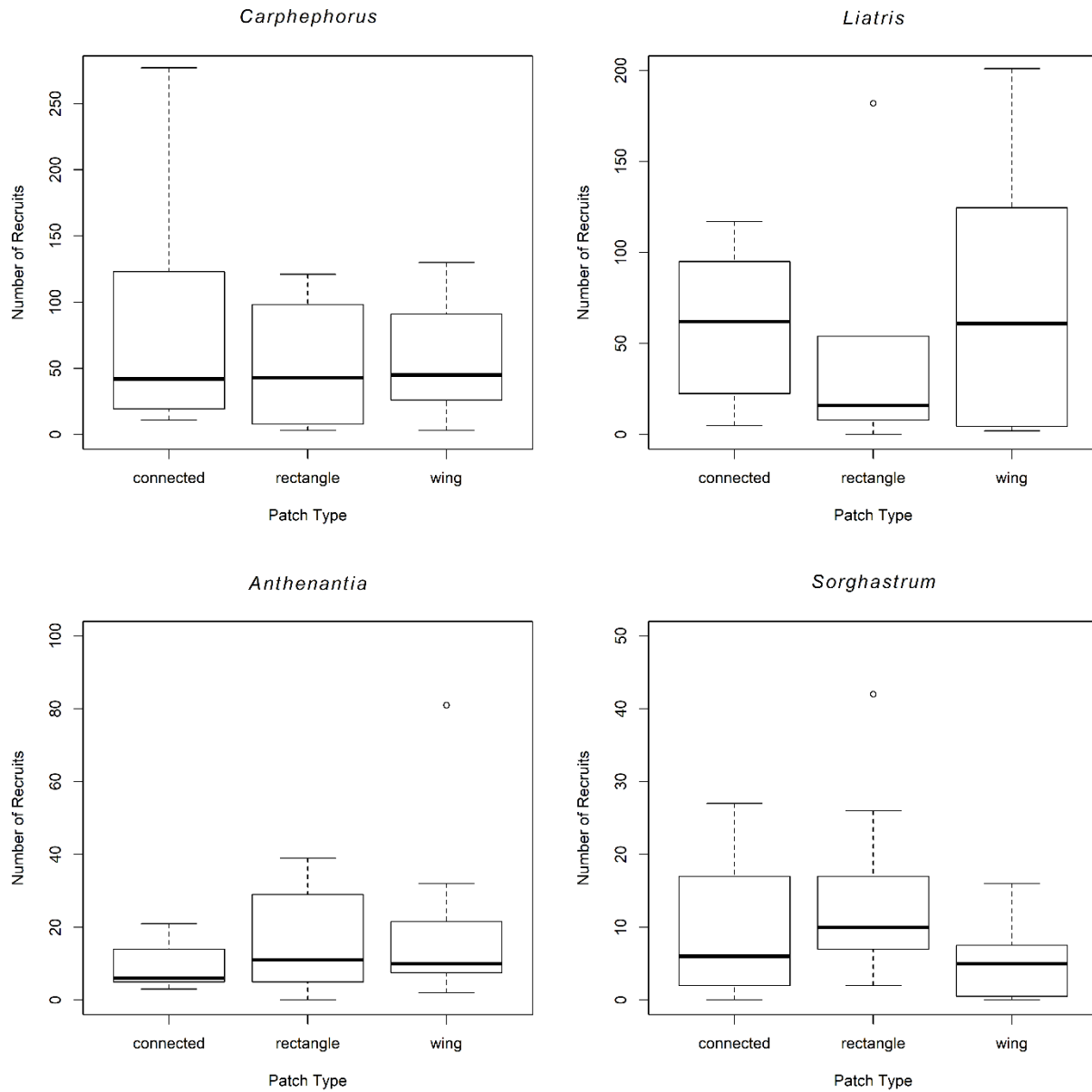


Figure 5.2. Effects of isolation and shape on recruitment patterns of our four study species.

Note that the y-axis is scaled differently for each species.

Distance from the edge affected recruitment patterns for the two members of the Asteraceae. For *Liatris*, plants at edges had 3.49 times more recruits than plants at centers, on average ($p=0.002$; Table 5.3) (Figure 5.3).

For *Carphephorus*, the effect of edge differed by patch type, with a higher number of recruits at patch centers, but only in isolated, high-edge patches (2.5-12.7 times higher, on average, than other patch $\times$ edge distance combinations [derived from estimated marginal means from the model], $p=0.009$; Table 5.3) (Figure 5.3).

For both grass species, there was no effect of distance from the edge on recruitment patterns (Figure 5.3; Table 5.3).

Table 5.3. Statistics table for edge models. See main text for effect size of significant factors.

Species	Predictor	Chi.Sq Value	p-value
<i>Carphephorus</i>	Distance from Edge	0.27	0.61
	Patch Type	1.22	0.54
	Edge:Patch Type Interaction	9.49	0.0087
<i>Liatris</i>	Distance from Edge	9.38	0.0022
	Patch Type	0.76	0.68
	Edge:Patch Type Interaction	0.48	0.78
<i>Sorghastrum</i>	Distance from Edge	1.38	0.24
	Patch Type	4.65	0.098
	Edge:Patch Type Interaction	3.42	0.18
<i>Anthenantia</i> [†]	Distance from Edge	1.4	0.24
	Patch Type	3.9	0.14
	Edge:Patch Type Interaction	2.85	0.24

[†]Values for *Anthenantia* were obtained using the identical model structure as the other species, but with the glmmTMB package, as described in the Methods

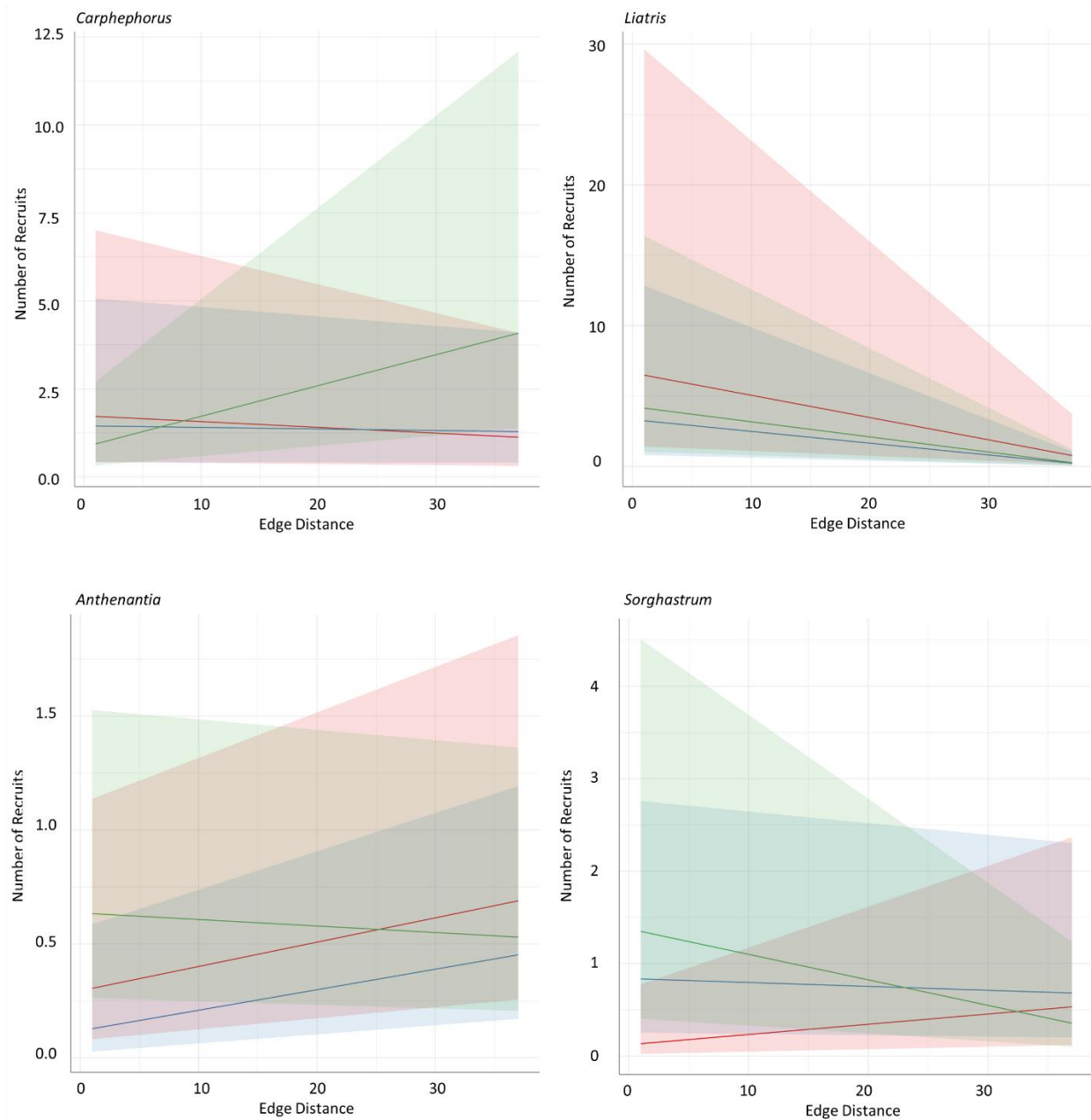


Figure 5.3. Interaction plots for the interaction on the number of recruits between distance from the edge of the patch and the patch type. The red line is for connected patches, the blue line is for rectangular (low edge-to-area, isolated) patches, and the green line is for winged (high edge-to-area, isolated) patches. Shaded regions indicate 95% confidence intervals.

Question 2: Factors Mediating Fragmentation Effects

The relationship between canopy cover and distance from the edge was identical for all species, as the underlying canopy cover data was applied to all species. These data showed that canopy cover was negatively related to the distance from the edge of the patch, as expected ($r=-0.39$, $p<0.0001$). The SEMs all fit the data well (Fisher's C of 10.27–18.70 and p-values from 0.85–0.997, with p-values >0.05 indicating a good fit; Figure 5.4).

Carphephorus

Carphephorus recruitment was positively related to reproductive output ($r=1.00$, $p<0.0001$) and negatively related to herbivory ($r=-0.34$, $p=0.034$) and canopy cover ($r=-0.45$, $p=0.048$). Reproductive output itself, for *Carphephorus*, was negatively related to canopy cover ($r=-0.098$, $p=0.044$) and patch edge-to-area ratio ($r=-0.16$, $p=0.047$).

Liatris

Recruitment of *Liatris* was positively related to reproductive output ($r=1.07$, $p=0.0014$). However, reproductive output was not significantly predicted by any other model component ($p>0.05$ in all cases).

Anthenantia

Recruitment of *Anthenantia* was positively related to reproductive output ($r=0.78$, $p<0.0001$). Reproductive output was negatively related to canopy cover ($r=-0.13$, $p=0.034$). Herbivory of *Anthenantia* was positively related to distance from the edge of the patch ($r=0.12$, $p=0.0002$).

Sorghastrum

Sorghastrum recruitment was positively related to reproductive output ($r=1.11$, $p<0.0001$) and germination ($r=0.68$, $p=0.0040$). However, neither reproductive output nor germination were significantly predicted by any other model component ($p>0.05$ in all cases).

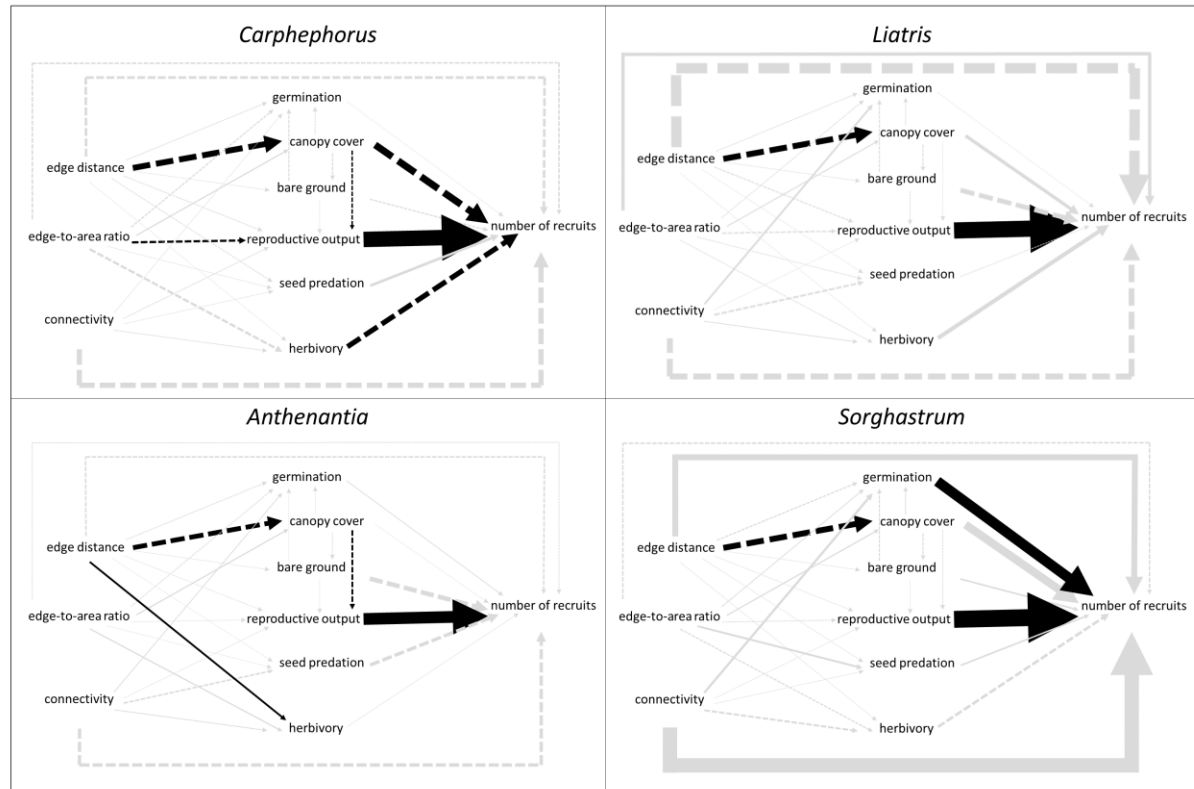


Figure 5.4. SEM diagrams for each species. Black arrows indicate significant relationships ($p<0.05$), while gray arrows indicate nonsignificant relationships ($p>0.05$). Dashed lines indicate negative relationships, while solid lines indicate positive relationships. Line and arrow size is scaled to standardized effect size.

Discussion

We found that habitat fragmentation affects plant recruitment patterns mostly through local edge effects. There was little evidence that the larger-scale factors of patch connectivity and edge-to-area ratio affected recruitment. These results illustrate the need to disentangle the different ways that habitat fragmentation can change populations.

In contrast to the effects of edge proximity, we found little evidence that the larger-scale fragmentation factors of patch connectivity and edge-to-area ratio influenced recruitment. Our structural equation models reveal a likely reason: recruitment is strongly structured by parent plant reproductive output and reproductive output is insensitive to patch connectivity and edge-to-area ratio (see also Brudvig et al. 2015). In spite of having little effect on recruitment in our study, connectivity and edge-to-area ratio do affect plant species diversity in our system and others (Yamaura et al., 2008; Hoofman et al., 2016; Arellano-Rivas et al., 2018; Damschen et al., 2019). Damschen et al. (2019) illustrated how patch connectivity increases plant diversity through elevated colonization and reduced extinction. Our present study suggests that reduced extinction rates may be a consequence of among-patch, dispersal-driven rescue effects, as opposed to elevated plant population growth or performance within connected patches. Although rates of colonization are higher in connected fragments (Damschen et al. 2019), our study suggests that rates of recruitment may be similar across connected and unconnected patches following colonization, but that patterns of recruitment across patches may be modified by edges for at least some species. Together, these studies illustrate the importance of considering biodiversity responses to fragmentation from perspectives of species diversity and component populations.

We do find that edges affect patterns of recruitment, and our findings expand understanding of how edges influence ecological systems (Ries et al., 2004). In our system, edges modified plant reproductive output, which was the strongest predictor of recruitment for most of our study species. Canopy cover, which is highest near patch edges in our study system, had negative effects on reproductive output. In other systems where reproductive output has been examined in a landscape context, proximity to edge is also an important influence (Bruna, 2002; Melo et al., 2007), usually with proximity to edge being negatively correlated with survival and/or reproductive rate. Edges are a ubiquitous consequence of fragmentation, with 70% of the world's forest within 1 km of an edge (Haddad et al., 2015). Fragment edges can also affect open grasslands and savannas, like our study system (Winter et al., 2000; Mendonça et al., 2015; Stevens et al., 2017). Therefore, with edges being so pervasive on the landscape, such negative effects on reproductive rate of species that are not edge-adapted may be a major factor in population declines worldwide.

Conversely, we found little evidence for biotic interactions or the amount of bare ground (i.e., microsite availability) influencing plant recruitment. Although microsite availability is often important in seedling establishment (Eriksson and Ehrlén, 1992), fragment edges can modify a suite of abiotic factors like temperature and moisture availability (Bruna, 2002; Tuff et al., 2016), which may also influence plant recruitment patterns (Bruna, 2002). Thus, our edge proximity and canopy cover findings may relate to additional microenvironment factors that play key roles for recruitment of our species. Seed predation did not affect recruitment. Herbivory significantly influenced recruitment patterns only of *Carphephorus*. This overall lack of support of biotic interactions on recruitment patterns in our system occurs despite the potential of edges to modify these interactions (Melo et al., 2007; Brudvig et al., 2015). Additional unmeasured interactions

(e.g., those with pathogens/soil microbes or plant-plant interactions) are likely to influence recruitment in our system and elsewhere.

Our work suggests several approaches for mitigating fragmentation effects on plant populations in open habitats. Reducing the effects of edges is a primary concern, given that canopy cover and/or edge proximity influenced recruitment for several of our species. We suggest that edge effects might be lessened by softening edges through thinning trees near patch edges, thereby decreasing canopy cover (Templeton et al., 2011). Where possible, enlarging patches would benefit populations by increasing the area of internal habitat, away from edges (Yamaura et al., 2008). Although we did not find effects of patch connectivity on plant recruitment, connectivity is known to mediate the arrival of individuals and persistence of populations (Damschen et al., 2014). Thus, we suggest the coupling of edge effect-mitigation with enhancement of connectivity through strategies like corridors (Damschen et al., 2019) and modification of the matrix between patches, to increase permeability by, for example, the use of prescribed fire (Templeton et al., 2011) or tree thinning in systems like ours. By increasing patch occupancy and the growth and persistence of populations within patches, a multi-pronged management approach can mitigate multiple landscape modifications resulting from habitat fragmentation.

Our work connects landscape changes resulting from habitat fragmentation to specific processes structuring population responses. By experimentally disentangling consequences of fragmentation, we show how edges play particularly important roles for plant recruitment patterns of species of conservation interest. However, even within our study, we see positive, negative, and neutral responses of recruitment to edges. Given the pervasiveness of edges on the world's terrestrial landscapes and their importance to plant recruitment patterns, managing to

reduce the effects of edge should have important benefits for population recovery of species of concern.

Acknowledgments

We thank the US Forest Service, and particularly John Blake, Andy Horcher, Ed Olson, Jim Seger, Traci Thomas, Kim Wright, and the fire management team for the creation and most of the management of our experimental blocks. We would also like to thank the people that helped contribute to some part of the fieldwork process, including Sabrie Breland, Lisa Dlugolecki, Sean Griffin, Melissa Habenicht, Brenda Johnson, Lindsey Kemmerling, Elizabeth Long, Stephen McCann, Uma Nagendra, Marilena Nunez, John Orrock, Leslie Peck, Julian Resasco, Lauren Sullivan, and Stephanie Wagner. Funding for this work was provided by the National Science Foundation (Awards 0613701, 0614333, 0613975, 1354085, 1720896, 1912729, and 1913501) as well as by the US Department of Energy to the US Department of Agriculture-Forest Service-Savannah River under Interagency Agreement DE-AI09-00SR22188.

LITERATURE CITED

LITERATURE CITED

- Arellano-Rivas, A., J. A. De-Nova, and M. A. Munguía-Rosas. 2018. Patch isolation and shape predict plant functional diversity in a naturally fragmented forest. *Journal of Plant Ecology* 11: 136–146.
- Banks-Leite, C., R. M. Ewers, and J. P. Metzger. 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology* 93: 2560–2569.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9: 378–400.
- Brudvig, L. A., E. I. Damschen, N. M. Haddad, D. J. Levey, and J. J. Tewksbury. 2015. The influence of habitat fragmentation on multiple plant-animal interactions and plant reproduction. *Ecology* 96: 2669–2678.
- Bruna, E. M. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* 132: 235–243.
- Caughlin, T. T., E. I. Damschen, N. M. Haddad, D. J. Levey, C. Warneke, and L. A. Brudvig. 2019. Landscape heterogeneity is key to forecasting outcomes of plant reintroduction. *Ecological Applications* 29: e01850.
- Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation: maintaining connections for nature. In K. R. Crooks, and M. Sanjayan [eds.], *Connectivity Conservation*, 1–19. Cambridge University Press, Cambridge, UK.
- Damschen, E. I., D. V Baker, G. Bohrer, R. Nathan, J. L. Orrock, J. R. Turner, L. A. Brudvig, et al. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences of the United States of America* 111: 3484–3489.
- Damschen, E. I., L. A. Brudvig, M. A. Burt, R. J. Fletcher, N. M. Haddad, D. J. Levey, J. L. Orrock, et al. 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science* 365: 1478–1480.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7: 129–146.
- Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121: 161–170.

- Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91: 360–364.
- Evans, D. M., N. E. Turley, D. J. Levey, and J. J. Tewksbury. 2012. Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant. *Ecology* 93: 1016–1025.
- Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40: 1649–1663.
- Fahrig, L., V. Arroyo-Rodríguez, J. R. Bennett, V. Boucher-Lalonde, E. Cazetta, D. J. Currie, F. Eigenbrod, et al. 2019. Is habitat fragmentation bad for biodiversity? *Biological Conservation* 230: 179–186.
- Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265–280.
- Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, et al. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation* 226: 9–15.
- Griffin, S. R., and N. M. Haddad. 2021. Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. *Ecography* 44: 1–9.
- Gurevitch, J., G. A. Fox, N. L. Fowler, and C. H. Graham. 2016. Landscape demography: Population change and its drivers across spatial scales. *Quarterly Review of Biology* 91: 459–485.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1: 1–9.
- Haddad, N. M., L. A. Brudvig, E. I. Damschen, D. M. Evans, B. L. Johnson, D. J. Levey, J. L. Orrock, et al. 2014. Potential negative ecological effects of corridors. *Conservation Biology* 28: 1178–1187.
- Haddad, N. M., and J. J. Tewksbury. 2006. Impacts of corridors on populations and communities. In K. R. Crooks, and M. Sanjayan [eds.], *Connectivity Conservation*, 390–415. Cambridge University Press, Cambridge, UK.
- Hooftman, D. A. P., B. Edwards, and J. M. Bullock. 2016. Reductions in connectivity and habitat quality drive local extinctions in a plant diversity hotspot. *Ecography* 39: 583–592.
- Jackson, S. T., and D. F. Sax. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution* 25: 153–160.
- Lefcheck, J. S. 2016. piecewiseSEM : Piecewise structural equation modelling in R for ecology,

- evolution, and systematics. *Methods in Ecology and Evolution* 7: 573–579.
- Levey, D. J., T. T. Caughlin, L. A. Brudvig, N. M. Haddad, E. I. Damschen, J. J. Tewksbury, and D. M. Evans. 2016. Disentangling fragmentation effects on herbivory in understory plants of longleaf pine savanna. *Ecology* 97: 2248–2258.
- Lindenmayer, D. B., and J. Fischer. 2006. *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, DC.
- Melo, F. P. L., D. Lemire, and M. Tabarelli. 2007. Extirpation of large-seeded seedlings from the edge of a large Brazilian Atlantic forest fragment. *Ecoscience* 14: 124–129.
- Mendonça, A. H., C. Russo, A. C. G. Melo, and G. Durigan. 2015. Edge effects in savanna fragments: a case study in the cerrado. *Plant Ecology and Diversity* 8: 493–503.
- Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, et al. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330: 1496–1502.
- R Core Team. 2020. R: a language and environment for statistical computing.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. The University of North Carolina Press, Chapel Hill, North Carolina.
- Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35: 491–522.
- RStudio. 2019. RStudio.
- Salguero-Gómez, R., O. R. Jones, C. R. Archer, Y. M. Buckley, J. Che-Castaldo, H. Caswell, D. Hodgson, et al. 2015. The COMPADRE Plant Matrix Database: An open online repository for plant demography. *Journal of Ecology* 103: 202–218.
- Schoereder, J. H., T. G. Sobrinho, C. R. Ribas, and R. B. F. Campos. 2004. Colonization and extinction of ant communities in a fragmented landscape. *Austral Ecology* 29: 391–398.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy, and G. Durigan. 2017. Savanna woody encroachment is widespread across three continents. *Global Change Biology* 23: 235–244.
- Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. Portland, Oregon.
- Sullivan, L. L., B. L. Johnson, L. A. Brudvig, and N. M. Haddad. 2011. Can dispersal mode predict corridor effects on plant parasites? *Ecology* 92: 1559–1564.
- Templeton, A. R., H. Brazeal, and J. L. Neuwald. 2011. The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92:

1736–1747.

- Townsend, P. A., and D. J. Levey. 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* 86: 466–475.
- Tuff, K. T., T. Tuff, and K. F. Davies. 2016. A framework for integrating thermal biology into fragmentation research. *Ecology Letters* 19: 361–374.
- Uriarte, M., E. M. Bruna, P. Rubim, M. Anciães, and I. Jonckheere. 2010. Effects of forest fragmentation on the seedling recruitment of a tropical herb: Assessing seed vs. safe-site limitation. *Ecology* 91: 1317–1328.
- Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P. De Frenne, et al. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America* 110: 19456–19459.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation Strategy: The Effects of Fragmentation on Extinction. *The American Naturalist* 125: 879–887.
- Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* 102: 256–266.
- Yamaura, Y., T. Kawahara, S. Iida, and K. Ozaki. 2008. Relative importance of the area and shape of patches to the diversity of multiple taxa. *Conservation Biology* 22: 1513–1522.