Plant invasions at different scales - two representative case studies

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"An island, on the other hand, is small. There are fewer species, and the competition for survival has never reached anything like the pitch that it does on the mainland. Species are only as tough as they need to be, life is much quieter and more settled [..] So you can imagine what happens when a mainland species gets introduced to an island. It would be like introducing Al Capone, Genghis Khan and Rupert Murdoch into the Isle of Wight - the locals wouldn't stand a chance."
— Douglas Adams, Last Chance to See

for an ever-changing world.

Table of content

Summary

The in-hand document is the result of my work at the Spatial Interaction Working group at iDiv. It deals with non-native plant species in different contexts and aims to engage this extensive topic from many different angles, including different temporal and spatial scales, analysis methods, and questions asked. It illustrates this in three chapters, all published in peer reviewed journals. This document aims for three things: 1) to increase the scientific understanding of how non-native plant species are distributed and which factors influence their dispersal and establishment and 2) to provide practical information to land managers facing an increasing number of non-native species and 3) to illustrate that problem-based approaches and synthesis can work hand in hand.

Das vorliegende Dokument ist das Resultat meiner Arbeit in der Arbeitsgruppe Räumliche Interaktions Ökologie am iDiv in Leipzig. Sie beschäftigt sich mit nicht-heimischen Pflanzen in unterschiedlichen Gegebenheiten und versucht, dieses komplexe Themengebiet von verschiedenen Blickwinkeln aus zu beleuchten. Dies beinhaltet unterschiedliche räumliche und zeitliche Skalen, Analysemethoden, und verschieden Herangehensweisen. Dies wird in drei in wissenschaftlichen Magazinen veröffentlichten Artikeln veranschaulicht. Ziel dieser Arbeit sind drei Punkte: 1) unser Verständnis wie nicht-heimische Arten sich ausbreiten, etablieren, welche Muster daraus resultieren und welche Faktoren diese beeinflussen 2) Umweltschützern und Entscheidungsträgern praxisnahe Informationen zu einer stetig wachsenden Zahl nicht heimischer Arten zukommen zu lassen und 3) um zu zeigen, dass eine problemorientierte und eine theoretische Herangehensweise Hand in Hand einhergehen können. Übersetzungen der Kapitel oder einzelner Passagen sind auf Anfrage verfügbar.

In **Chapter 1** I will give a short introduction to the field of invasion biology and elaborates on why there are so many different perspectives on the matter. This links to why and how this research is important for applied conservation and restoration as well as for the science of ecology. This chapter also gives definitions for the different terms used in this dissertation such as *naturalized* and *invasive*.

Chapter 2 shows my published manuscript in *Restoration Ecology*, which finds that restoration successes can be achieved using priority effects and fertilization treatments to curtail a non-native legume that is aggressively spreading on the North American Prairie and is especially problematic on restoration sites. This chapter assesses the effects of different experimental manipulations on the target species, as well as their effects on of the whole plant community and gives recommendations for practice. Co-authors of this chapter are Tiffany Knight and Michele Schutzenhofer.

Chapter 3 introduces *PacIFlora* (**Pac**ific **I**ntroduced **Flora**), my manuscript published in the *Biodiversity Data Journal*. This manuscript introduces a database I compiled for the naturalized species of the Pacific. In this chapter, I describe how I harmonized datasets, species names, island names and different status values. The database contains 33397 unique records of 3965 species distributed across 481 islands. Co-authors on this manuscript are core members of the two harmonized databases, GloNAF and PIER, as well as Dylan Craven and Tiffany Knight.

Chapter 4 shows my published manuscript in *Diversity and Distributions*, which shows what can be achieved using the PacIFlora database. It presents patterns of naturalized plant species in island groups of the Pacific. In this chapter, I assess which plant families are over-represented, which other regions naturalized species in the Pacific are also recorded as naturalized to, and to what extent naturalized species in the Pacific are shared between island groups. This chapter outlines the drivers responsible for the observed patterns of naturalized species richness and beta-diversity, and how practitioners may profit from this information. Co-authors on this manuscript are the GloNAF core team as well as workshop participants of the Pacific Invaders workshop at iDiv.

Chapter 5 reconciles the differences and similarities across these projects and gives possible explanations for why this may be the case. This chapter focuses on the underlying questions and their limitations and the main take-aways for science and practice. I provide an outlook on promising practical applications and scientific follow-up studies. The chapter closes with my final, personal remarks.

This document avoids assigning any moral connotations to plant species such as "good" or "bad" and tries to engage non-native species from a neutral standpoint, which reflects the standpoint of the author. Collaboratively achieved projects and results are referred to in the first person.

Chapter 1: Introduction

1.1.   Definitions

In the field of invasion biology, it is important to define terms and classifications as this field of science covers many of species that would not necessarily be classified as invasive.

These terms are summarized here in a hierarchical way, starting at the lowest.

- "Non-native", sometimes also referred to as "alien" or "exotic" in the literature, in this study describes a plant species which is not native to a specific region or parts of this region.
- "Naturalized" must fulfil the same criteria, and in addition the plant species must have formed self-sustaining populations which require no human interference to persist. Species exclusively growing in agricultural or horticultural context are therefore not included.
- "Invasive" follows the definition sensu Richardson *et al.* (2000) in which a species must fulfil the above criteria and in addition must cause harm to species, ecosystems, human health or livelihood. In this study, only non-native species can be invasive even though cases of native species displaying invasive behaviour are known.

Borders between these categories are not always clear and are sometimes fluent, but this framework is appropriate for all projects presented in this document. Here, mention of "plant invasion" or "invasion biology" refers to all steps in this process, from introduction over establishment to actual invasion, although many species covered may never reach invasive status.

1.2.   Invasion Biology: Origins

Elton, generally accepted as the "father" of invasion biology (Davis *et al.* 2001), developed his book "The Ecology of Invasions by Animals and Plants" (1958) from his studies on succession of species in ecosystems (Southwood & Clarke 1999). He was strongly influenced by the observations of species becoming more dominant in a community that it was previously not a resident in. His studies pre-date broad notions of a potential negative effects of these species on environment and economy (e.g. Wilcove *et al.* 1998; Pimentel *et al.* 2000) and many species were still introduced all over the globe as resources or for ornamental purposes, as the mindset that they might cause problems in the future was barely present. Appreciation for the environmental harm associated with biological invasions and scientifically guided removal experiments started around the 1980s (Reichard & White 2003). Systematic approaches to studying the impact of invasive species on biodiversity began even later (e.g. Perelman *et al.* 2007; Symstad 2008). It was just a few decades ago that systematic studies began pursuing the question why some "Darwinian Demons" (Silvertown 2005) were so successful in systems they did not evolve in. Case studies revealed that some hypotheses were very well supported to explain the behaviour or patterns of particular species or ecosystems. Well studied

hypotheses included the novel weapons (Callaway & Ridenour 2004), enemy release (Williamson 1996; Crawley 1997) and Darwin's naturalization hypothesis (Darwin 1859; Daehler 2001). Modern studies focus on a wide variety of topics. For example, biological invasions are recognized as a unique opportunity to study the behaviour of species in novel ecosystems (e.g. Godoy 2019), to gain insights into dispersal and establishment processes (e.g. Frischbier *et al.* 2020), to better understand plant community structure (e.g. Santoro *et al.* 2012), to compare differences and similarities of processes for native and non-native species (e.g. Steinbauer *et al.* 2017), and even to utilize non-native species for understanding species responses to global change (e.g. Finch *et al.* 2021). Science based techniques are implemented into active management (e.g. Knight *et al.* 2011) and new computational methods and global databases allow us to ask questions and provide insights in a quality unimaginable before (e.g. van Kleunen *et al.* 2019).

In natural sciences, the search for universally applicable "laws" is common, but generalization across all of studies and hypothesis on invasive species proves to be difficult to achieve (Jeschke & Heger 2018). Although today the search for simple answers in invasion biology continues, most scientists recognize that explanations for the causes and consequences of biological invasions are complex and context dependent. For example, multiple hypotheses can simultaneously or interactively explain invasion patterns, and support for particular hypotheses depends on the context. It is now clear that the particular questions asked and the scale and perspective at which the patterns are observed (Chase & Knight 2013; Chase *et al.* 2018) define the outcome of the study.

1.3.   Invasion Biology: Perspectives

One of the reasons that synthesis is difficult in the field of invasion biology is that the specific questions, objectives, spatial and temporal scales, and methods can vary dramatically between studies. Invasion biology is a theoretical and an applied science, and scientists trying to identify underlying mechanisms of plant invasions will ask different questions and use different spatial grains compared to a practitioner trying to manage a species or prevent future invasions.

The difference in spatial scale can influence the magnitude and direction of response variables (e.g. Gooriah *et al.* 2020), even when similar questions are asked and similar methods are used. However, methods often also vary with spatial scale. For example, non-native species are frequently recorded as present or absent at larger spatial scales, but recorded with count or cover data at smaller spatial scales. Further, the sample size is usually very different on different scales, simply because the larger a study area gets, the more difficult it is to obtain detailed information. The temporal scale of the study can also influence the conclusions. For example, data from a single sampling date provide different insights compared long-term sampling or continuously updated databases.

This is relevant for this document, as in this study, I dealt with two case studies that are set at the opposite points of this metrical scale: One based on 99 10 x 10 meter plots, looking at cover of plant species at one to three points in time, and the other looking at a region covering almost half of the surface of the globe, observing presence/absence patterns of naturalized species collected over many years. Together, these provide a more holistic view of the factors that shape biological invasions.

In the literature, studies vary in the metrics used to illustrate information on non-native species. This can challenge a general understanding and synthesis across these studies, since even seemingly small differences in metric calculations can tell a very different story. A good example for this is describing the effect of non-native plant species on plant diversity. This can be differentiated into several sections (e.g. non-native diversity, native diversity, total diversity, target species diversity) and depicted in several ways (species richness, α- β- γ- diversity, evenness, rarity, phylogenetic diversity, functional diversity) which again can be calculated in using different metrics (β-Simpson, Jaccard,

Sørensen, proportional or absolute richness, different estimates of functional richness). Deciding which variables and metrics to choose can be difficult, but this decision is very important in order to identify the specific questions and hypotheses that the study will address (see Baselga (2010)). The perception of the results can vary drastically across different metrics. For example, a cover increase of 100% can be a cover increased from 1 to 2% or from 30 to 60%, but this would have different ecological implications. Likewise, the plant community of two islands can be virtually identical when using pariwise beta-Simpson diversity while they are vastly different when using pairwise beta-Sørensen diversity if one is a nested subset of the other (Traveset *et al.* 2014). In this example, one metric might support a hypothesis and the other would not, unless the questions and hypotheses are carefully shaped by the author. Likewise, in studies investigating dispersal routes, the relative similarity of the islands may be shown better by beta-Simpson while beta-Sørensen may be better suited to identify islands with similar target scenarios for management, as the total number of non-native species on each island is a relevant factor here. In chapter 2-4, a lot of thought went into the specific questions addressed and the metrics or statistical analyses used, which were always based on the motivation of the study but never followed an agenda. It is important to keep many angles in mind, and different metrics can each give a different piece of information, leading to a more complete understanding of the pattern or process. Thus, looking at many metrics may provide the best total picture. However, displaying every possible way of analysis is often more confusing than beneficial.

Commonly, non-native species are studied either through experiments manipulating environmental factors or by analysing observational data. In an experimental manipulation like the one in the second chapter of this dissertation, precise questions can be asked to examine the effects of particular factors on plant communities in general and non-native species in particular. Experiments allow researchers to isolate the role of specific drivers from the many ecological drivers shaping a plant community. The disadvantages are that these studies can only cover rather small temporal and spatial grains, and it can therefore be difficult to generalize the results to other systems and contexts (Thrush *et al.* 2000). Experiments are therefore very good for precise ecological questions and for specific management applications (e.g., how to manage one invasive species or how to restore one type of ecosystem). Observational databases on species distributions on the other hand might have trouble separating different factors, as entangled factors can be confounded with each other and defining factors are not experimentally manipulated. However, these studies help us to visualize and elaborate broad-scale patterns, which can be linked to their likely drivers (e.g., the third and fourth chapters of this dissertation).

The methods used to categorize the species in the community (i.e., as native - non-native – naturalized – invasive) can also influence the conclusions. Analyses focused on these smaller subsets of species can often contribute to understand the whole community. In chapter 2, I treated seeded native species as an extra category and asked whether any of the treatment combinations could best promote this subset of the native plant community. Further, the removal of an invasive species might not lead to a desirable conservation outcome if this species is replaced by different non-native or invasive species, i.e. secondary invasion takes place (Pearson *et al.* 2016). Finally, communities that are dominated by ruderal native species may be of low value, if one of the conservation purposes is to re-establish rare native species (Matlack 2013). Categorization is not trivial, as show in chapter 3, because there is not always consensus on the status of certain non-native species. For example, the same species can be considered cultivated, naturalized or native in different locations and by different experts. It is also important to consider the temporal aspect of invasions and that categories can change through time (e.g., a species can become invasive or extirpated). If two localities share a species, but it is described as cultivated in one location and as naturalized in

another, possible implications are that a) a species might have the potential escape cultivation and naturalize, b) the species is of horticultural origin, which has implications for introduction pathways and c) certain environmental conditions might prevent some species from escaping cultivation in some locations.

In summary, there are many different aspects to and perspectives on theoretical and applied invasion biology. This remains a challenge and an opportunity at the same time. In this document, I take two very different approaches to understanding the factors that allow non-native species to be successful. In the end, I synthesize some, but not all of the aspects that unite these studies and discuss how some generality in biological invasions might be achieved in this larger field of study.

1.4.   Invasion Biology: implications for practice

Invasion biology has large implications for practice. The removal of naturalized or invasive plant species in conservation is often optimized by trial and error in specific locations, in many cases through huge effort and manual labour. Results are not shared in a standardized manner, leading to land managers to follow only their own personal experiences (Matzek *et al.* 2014). Newly colonializing species are frequently ignored until they are observed to be a threat. Many species are only detected and reported in an area once they are already well established, and therefore very difficult to contain. Studies have shown that the sooner in the process of invasion (introduction – establishment – naturalization – invasion) counter methods are applied, the more cost effective species removal is (Wittenberg & Cock 2001). Thus, it is important that information is shared, so that managers can identify the species to watch out for and the methods have been successfully applied in a different context (Matzek *et al.* 2014). However, local managers might be more limited by resources for conservation than by scientific insights on how to manage their land. Over 80000 plant species have naturalized somewhere on the globe (van Kleunen *et al.* 2019), and it can be overwhelming for managers to identify the current species in their area of responsibility, watch out for new arrivals, and manage existing invasions.

The first problem, limited resources, cannot directly be tackled by science, but science can information on optimization, so that managers can be make more efficient use of their current resources. In addition, a never-ending battle of chemical and manual removal of a plant species for years is not sustainable as a long-term goal, and scientists and managers must work together to develop long-term solutions (Matzek *et al.* 2014). The science of invasion biology can identify critical characteristics of the species that is to be removed, and also of the ecosystem that is to be conserved/restored. This can help develop efficient methods to ideally reach a state in which little or no human management is required to maintain the desired state of the ecosystem. Of course, this is more often feasible in systems for which human interference, e.g. through disturbance, is contributing to the invasion of a plant species. Plant invasions into natural or semi-natural areas are often irreversible, and such areas are likely to require regular intensive management and manual removal once infested (Wittenberg & Cock 2001; e.g. Kıbış & Büyüktahtakın 2017). The second point, identifying species which are likely to be introduced in the future, is engaged by science in a variety of methods and has gained a lot of attention in the recent years (Bradley *et al.* 2010; Ibanez *et al.* 2017). While stochasticity in species introduction and establishment create large uncertainty, much progress has still been made in prediction. In particular, the field of species distribution modelling has made great advances (Beaumont *et al.* 2007; Guillera-Arroita 2017; Liu *et al.* 2019). However, this research requires detailed information of the range of the species, both in its native and introduced range, to adequately model its ecological niche (see e.g. Barbet-Massin *et al.* 2018). Chapter 3 of this document facilitates this line of research in the Pacific region by creating PacIFlora, the most complete database for the **Pac**ific **I**ntroduced **Flora**. Here, I combine the most recent data, and standardizing different parameters, such as species names, island names, and species status (native,

cultivated, naturalized, invasive). In Chapter 4, I combine the species distribution information from chapter 3 with environmental factors to draw conclusion on patterns and processes of naturalized species in the Pacific.

Scientific insights being implemented into practice are often barely visible to the scientific community, as successful applications are often not reported in the peer reviewed literature that scientists read and cite. For example, research conducted by Knight *et al.* (2011) in the USA demonstrated that cultivars of the invasive Japanese Barberry (*Berberis thunbergii*) still have high invasive potential. Their research directly resulted in policy that banned the sales of all cultivars of this plant species in several federal states, even though these plants were economically very important at the time to the horticultural industry. Making meaningful connections to policy can be difficult for scientists, and such connections are seldomly visible in the scientific literature. Global databases such as GloNAF can also be implemented into practice. For example, core-member Franz Essl used GloNAF to create or contribute to several invasive plant watchlists for European countries (e.g. Essl *et al.* 2020). These have not yet led to some of intended reactions (e.g., bans on certain species), but these efforts are nevertheless of immense value for local land managers and require effort from scientists to communicate their scientific products to diverse stakeholders.

This manuscript also strives to provide research that can directly benefit land managers. In Chapter 2, I research how to improve workflow in prairie restoration to make the establishing community more resistant towards plant invasion. Chapter 3 provides land managers in the Pacific with a dataset that can help them to target species most likely to be introduced to their island or island group. The goal is to be able to also identify Pacific and non-Pacific nations that share many species, so that these countries can exchange information on managing existing invasions and minimizing further species exchange.

While direct implications for practice are desirable and a large motivation for this document, I also aim to provide science with theoretical or mechanistic insights that contribute to developing the field of invasion biology. In chapter 2, priority effects that are known from studies on population dynamics (Fukami 2015), but rarely studied in the context of restoration and invasion (Weidlich *et al.* 2021) are put in the focus and secondary effects, such as invasional meltdown and community shift under the presence of dominant invasive species are visualized. In chapter 3, a dataset is provided that can be utilized for taxonomic studies or to study dispersal and establishing processes, which is also picked up in chapter 4. Also in chapter 4, indices usually used in the context of conservation of rare species (Usher 1986; Williams 1993) are applied to naturalized species, and novel analysis tools are used to disentangle the effects of drivers on naturalized richness and beta-diversity (Traveset *et al.* 2014).

In the following chapter 2, which is published in *Restoration Ecology*, I present the most important findings from my experimental work in a North American prairie aimed at preventing the dominance of the non-native legume *Lespedeza cuneata* in restored sites.

Chapter 2: Long term experiment manipulating community assembly results in favourable restoration outcomes for invaded prairies

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RESEARCH ARTICLE

Long-term experiment manipulating community assembly results in favorable restoration outcomes for invaded prairies

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Invasive species are a common problem in restoration projects. Manipulating soil fertility and species arrival order has the potential to lower their abundance and achieve higher abundances of seeded native species. In a 7-year experiment in Missouri, United States, we tested how nutrient addition and the timing of arrival of the invasive legume *Lespedeza cuneata* and seeded native prairie grass and forb species influenced overall community composition. Treatments that involved early arrival of seeded forb and grass species and late arrival of *L. cuneata* were most successful at creating community structure that fulfilled our restoration goals, displaying high abundance of seeded native forb species, low abundances of *L. cuneata*, and non-native species. There were few treatment interactions, with the exception that timing seeded native forbs and timing of *L. cuneata* arrival interactively influenced the abundance of seeded native forbs. This suggests that the individual treatments are supporting the restoration goals, such as creating a community with low abundance of *L. cuneate* or high abundance of native seeded species, without restricting each other. This study demonstrates the importance of priority effects in disturbed habitats prone to invasion, the lasting effects of initial seeding on long-term community composition, and the potential for fertilization to positively benefit restoration of degraded grasslands.

Key words: invasion, *Lespedeza cuneata*, nutrient addition, prairie restoration, priority effects

Implications for Practice

- The invasive *Lespedeza cuneata* can be kept at low abundance in long-term prairie restoration projects if a degraded site is fertilized, if strong competitors are present, or if it is managed early on.
- Different manipulations work independently in decreasing the cover of *L. cuneata*.
- Seeded native forb species have best establishment success when seeded early in the restoration process.
- Early management of *L. cuneata* will result in higher cover of seeded forbs and lower cover of non-native species.

Introduction

Restoration of degraded ecosystems is important to provide valuable ecosystem and cultural services and to contribute to regional efforts to preserve global biodiversity (Losvik & Austad 2002; Wong 2003; Millenium Ecosytem Assessment 2005). The goals of restoration projects are often to have low abundances of invasive non-native species, which cause harm to the environment, economy, and/or human health (hereafter invasive, ISAC 2006), and to have high abundances of target native species, which are often historically connected to the site. Restoration ecologists use a variety of management methods to achieve these goals, such as altering the abiotic or biotic environment in a way that increases fitness of target native species

relative to invasive species. For example, removal of target invasive species, soil alteration, and seeding target native species are common (e.g. Christiansen 1994; Wilson & Gerry 1995; Gucker & Munger 2010).

Both scientists and land managers are interested in understanding how different restoration treatments influence community composition. In many restoration experiments, a single treatment is applied and results are measured in the short term (Suding 2011). However, when possible, restoration experiments include multiple treatments to compare different approaches and to examine possible interactive effects on the desired outcome (Standish et al. 2012; Kuttner & Thomas 2016). In community ecology, similar lines of research address

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the factors that determine community composition. Priority effects, in which the orders of species arrival influence their competitive abilities, are known to interact with environmental conditions to influence community composition (Fukami et al. 2005; Goodale & Wisley 2018). Invasive species that are capable of modifying the environment (e.g. nitrogen-fixing legumes) create internal feedbacks in the system that cause the species to be particularly difficult to eradicate later in the community assembly process (Biggs et al. 2009; Vilà et al. 2011; Powell et al. 2013; Crandall & Knight 2015). Likewise, seeded target species and non-native but not invasive species (hereafter "non-native species") are expected to achieve higher establishment success if introduced early in the process (Young et al. 2017). Restoration projects provide good testing grounds for these concepts.

North American prairie ecosystems (i.e. tall grass, short grass, mixed grass prairies) have been the target of numerous restoration projects. As in many grasslands, prairies support high native species richness (Howe 1994; Sampson & Knopf 1996; Polley et al. 2005) and provide numerous ecosystem services (Millenium Ecosytem Assessment 2005; Maczko & Hidinger 2008). However, land use change has resulted in the loss of 82.6–99.9% of prairie ecosystems (Sampson & Knopf 1994; Polley et al. 2005), and many former prairies have degraded soils from years of tilling and agriculture (Gregorich & Anderson 1985). These diverse and heterogeneous ecosystems face many challenges, including fire suppression (Ratajczak et al. 2016) and the absence of large migratory herbivores (Fuhlendorf & Engle 2001; Allred et al. 2011). Prairie restorations are also particularly plagued by plant invaders. For example, invasive grasses (e.g. *Arrhenatherum elatius*, *Bromus tectorum*, *Bromus inermis*; Wilson & Gerry 1995; Wilson & Clark 2001; Brooks et al. 2004, Ortega & Pearson 2005), and legumes (e.g. *Lespedeza cuneata*) invade degraded tall grass prairies. *Lespedeza cuneata* can become dominant (Eddy & Moore 1998) and can be difficult to eradicate with traditional methods (mowing, burning, grazing, herbicide; Jordan et al. 2002; Farris 2006; Cummings et al. 2007; Gucker & Munger 2010). It is generally associated with a negative effect on the local biodiversity, with some studies indicating a reduction in native species biomass by up to 92% and species richness by approximately 70% (Eddy & Moore 1998). Further, *L. cuneata*-dominated areas have reduced value for cattle grazing (Schmidt et al. 1987) and nature tourism (Secretariat of the Convention on Biological Diversity 2015).

We evaluated how three approaches influence the abundances of invasive *L. cuneata* (our focal non-native species), seeded native species, and naturally colonizing non-native species (not including *L. cuneata*) using a 7-year prairie restoration experiment. First, we experimentally added fertilizer to enhance soil fertility and nitrogen availability. We hypothesized that nutrient addition would result in lower abundance of the nitrogen-fixing *L. cuneata,* and higher abundances of seeded native species and non-native species compared to the control treatment at the end of the 7-year experiment. Sites targeted for restoration often have a long agricultural history, and are often degraded and less fertile than historic prairies (Gregorich & Anderson 1985).

Studies have shown positive effects of nitrogen addition on nonlegume native species cover in tallgrass prairie restoration (McPhee et al. 2015) and on invasion resistance (Tilman 1997). Adding nitrogen could indirectly limit *L. cuneata* through increased competitiveness of native species. However, nutrient enrichment is known to result in in higher establishment success of other non-native and invasive species (Cleland et al. 2013), which may in turn result in lower establishment success of seeded native forbs.

Second, we manipulated the order of arrival of native forbs and grasses (grasses first, forbs first, both added together), with an offset of 1 year. We hypothesized that adding grasses first would result in lower abundance of *L. cuneata*, as well as seeded native forbs and non-native species, since grasses are known to be strong competitors in prairies (Shirley 1994; Fill et al. 2019). Allowing forbs to establish first will likely result in higher establishment rates of seeded native forbs, but it might also result in higher abundances of *L. cuneata* and non-native species due to the lack of strong competitors.

Third, we manipulated the timing of *L. cuneata* arrival. We hypothesized that when *L. cuneata* arrives late, it will have lower abundance after an establishment phase compared to when it arrives at the start of the restoration experiment. Likewise, we expect that native seeded forbs and non-natives will have higher abundances when *L. cuneata* arrives late. Native plant species can often compete better with invasive species if they receive priority in establishment (Mattingly & Orrock 2013). However, it is also possible that non-native species may enter the community and take the space usually filled with *L. cuneata*, which is a frequent problem in invasive species removal projects (Brooks & Pyke 2001; Dickens et al. 2015). A long-term experiment allows for meaningful comparisons between treatments in which *L. cuneata* arrives at the start of the experiment or later, as abundance of *L. cuneata* can be compared across a similar time frame.

We expected treatment interactions, and this experiment can thus identify the combinations of treatments that result in a community closer to the restoration goals (high cover of seeded native forbs, low cover of *L. cuneata* and non-native species). For example, it could be that early seeding of forbs is only effective at increasing the abundance of seeded forbs if other treatments are in place (e.g. nutrients added, late arrival of *L. cuneata*). In addition, we would expect an interaction between the timing of grass arrival and the timing of *L. cuneata* arrival; *L. cuneata* arrival time might have less of an influence on *L. cuneata* abundance in the presence of early-arriving, highly competitive grass species. Identifying synergistic treatment combinations would allow for more efficient prairie restorations in the future.

Methods

Focal Invasive Species

Lespedeza cuneata (common name: Sericea lespedeza) is a legume native to Asia and parts of Australia, and is currently listed as a noxious weed in several states in the United States,

including Colorado, Kansas, Nebraska, and Oklahoma (Colorado Department off Agriculture 2019; Kansas Department of Agriculture 2019; Missouri Department of Agriculture 2019; Nebraska Department of Agriculture 2019; Oklahoma Department of Agriculture 2019; USDA 2016, 2019). This perennial herb produces new sprouts arising from root nodes, and the numerous seeds are small, vivid, and can last in the seed bank for several years (Stevens 2002; Woods et al. 2012).

Study Site

We established our experiment within a 0.5 ha field at Washington University's Tyson Research Center, Missouri, United States, located southwest of St. Louis. The climate of this area is warm and temperate, with 897 mm annual precipitation and 13.7°C annual temperature. Soils are limestone derived and clay rich. The history of our field site represents a good match for sites targeted for prairie restoration. Prior to 1984, the study area was used as an agricultural or hay field. From 1984 to 1989, the study area was an experimental corn field. Prior to our experiment, *L. cuneata* was present on the field and parts of the surrounding area. The initial chemical characteristics of the soil on site are shown in Table S8.

To initially remove *L. cuneata* from the site and prepare the site for seeding, the field was sprayed twice between July 2007 and June 2008 with a 40% glyphosate herbicide. The field was then mowed (July 2008), disced (August 2008), and tilled (February 2009) to deplete the seed bank.

Throughout the course of the experiment (2009–2016), the field was managed with practices generally used in prairie restoration. The entire field was mowed in June and August 2009. Late winter or early spring burns were performed in 2011, 2013, and 2016. Three non-native species that display invasive behavior (*Carduus nutans*, *Vicia villosa*, and *Sorghum halepense*) were removed manually or with a targeted herbicide (40% glyphosate). *Carduus nutans* and *V. villosa* were recorded at low abundance in 2016 (0.26% average cover for *C. nutans*, 0.15% for the *V. villosa*), and were therefore pooled with the non-native species for analysis even though *C. nutans* is listed as a noxious weed in Missouri (USDA 2019).

Treatment Design

In 2009, we established 102 10-m^2 plots, each surrounded by a 2 m buffer and arranged in a 7×15 cell design (see aerial view of experimental design, Fig. S4). The field was split into four blocks that ran from east to west and represented a slight moisture gradient. Treatments included nutrients ("Nutrients," two levels), order of forb and grass arrival ("Assembly," three levels) and timing of *L. cuneata* arrival ("Invasion," two levels). Treatments were assigned to plots semi-randomly, first by randomly assigning treatments to all plots and then making modifications to ensure that each of the unique treatment combinations (12 in total) was represented at least twice per block.

For the first treatment, "Nutrients," plots were divided into two groups: control (not fertilized) and nutrients added. The later plots were fertilized annually in June (2009–2015) with a slow-release fertilizer containing 6 gN m^{-2} year^{-1}: 2.7 g ammoniacal nitrogen and 3.2 g nitrate nitrogen as well as 2 g phosphorus (as P_2O_4), and 4 g potassium (as K_2O) (Scotts Osmocote Classic).

In the second treatment, "Assembly" plots were divided into three groups: forbs seeded first, grasses seeded first, or both seeded simultaneously. One-year priority was found to have significant effects on community composition in other studies (e.g. Young et al. 2017), and our seeding design gave a 1-year seeding head start. In the forbs-first treatment group, forbs were seeded in 2009 and grass species were seeded in 2010 and vice versa in the grasses-first treatment group. In the both treatment group, both groups were seeded in 2009. A total of 25 Missouri ecotype native forb and five grass species that are typical prairie restorations in this region were hand-broadcasted into the plots (seeding densities and common names in Table S6). The rate of seeding of *L. cuneata* in all plots was equal to that of a congener, *L. capitata,* which was reseeded in all plots in 2010 due to very low initial establishment and a research plan to compare the two congeners.

In the third treatment, "Invasion timing," plots were divided into two groups: early and late. *Lespedeza cuneata* was seeded into the plots in 2009 and 2012 in the early and late treatments, respectively. In the late treatment, emerging *L. cuneata* was spot sprayed with "Roundup" (Monsanto Company Inc., main active ingredient glyphosate) to maintain integrity of the treatment until 2012. These methods were adequately successful in all but three plots (#81, #93, #101) on the edge of the experiment; these plots were removed from all analyses.

Each of the 12 ($2 \times 3 \times 2$) unique treatment combinations was replicated at least seven times, with five additional replications for one treatment group to allow for future research projects. These additional replicated plots received the same treatment as the other plots in this treatment combination, were not used for any other purposes, and thus were included in the analysis (see Table S7, Fig. S4).

Sampling Design and Evaluation of Treatment Effects

A single researcher (TM Knight) visually estimated the plot-level cover of *L. cuneata* in 2010 and 2016. In 2013 and 2016, *L. cuneata* cover was visually estimated in subplots and then averaged to estimate the plot-level coverage. Resulting cover values for *L. cuneata* on subplot and plot level in 2016 were very similar and are therefore comparable.

In 2016, we sampled all plots for community composition, documenting the identity and percent cover of each plant species. We sampled 0.5 by 0.5 m subplots within each of the nine grid cells (3.33 × 3.33 m) of each plot. Each plot was searched for rare species that were not observed in the nine subplots. These rare plants were not assigned a cover value, but were recorded as present. Assigning a very small cover value to them did not change the message of the analysis. Most plants could be identified at the species level, and all could be classified based on whether or not they were non-native, native, or seeded native species. Cover of plot/subplot was in every case greater than 100%, as plants overlapped. First, to determine how the
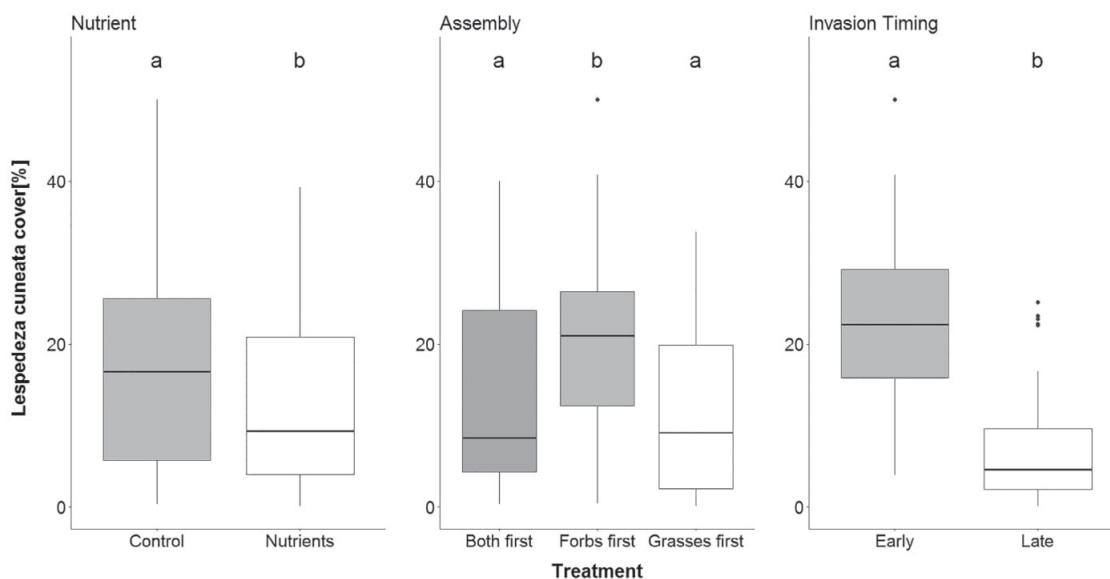
Figure 1. Effect of treatments on *Lespedeza cuneata* abundance (% cover) in the final year of the experiment (2016). The results of a TukeyHSD test are displayed above the boxplots in letters, indicating significant differences (different letters signify $p < 0.05$). Replication is listed in Table S7.

treatments and their interactions influenced *L. cuneata* cover in the final year of the experiment (2016), we performed an analysis of variance (ANOVA). We additionally performed Tukey's honestly significant difference tests (TukeyHSD) to examine pairwise differences between all treatment combinations. Second, we asked if the invasion timing treatment was effective at reducing *L. cuneata* cover across a 3-year time horizon by comparing its cover in the early invasion treatment in 2013 to that observed in the late treatment in 2016 using a Welch two-sample *t* test. Third, we tested whether *L. cuneata* cover was decreasing or increasing in cover through time by comparing *L. cuneata* cover in 2010, 2013, and 2016 for both groups of the invasion timing treatment in Welch two-sample *t* tests. Finally, we asked how the treatments and their interactions affected the cover of (1) seeded forb species and (2) non-native species using an ANOVA and TukeyHSD test, similar to the methods used for *L. cuneata* abundance. The seeded native forb species are of particular interest for prairie restoration, as these are known to be difficult to establish compared to native grasses, are expensive, and are desirable for restoration (Wagner et al. 2018). Non-native species have generally low value for conservation. We used an analysis of similarities (ANOSIM, 10,000 free permutations) and nonmetric multidimensional scaling (based on Bray–Curtis similarity, try = 10,000) to statistically evaluate and visualize the main effects of treatments on community composition. We displayed the cover of the 15 most common species across the entire experiment to give further insight into the composition differences.

We analyzed our data using R v.3.4.2 (R Core Team 2016, www.cran-r.org). For the non-metric multidimensional

scaling analysis (NMDS) and the ANOSIM, we used the "vegan" package in R (Oksanen et al. 2017). Other graphs were created using the "ggplot2" (Wickham 2009) and the "gridExtra" (Auguie 2017) packages. Residuals were normally distributed for all analyses. Accounting for block effects or scaling to relative cover did not change the message of analyses.

Results

Lespedeza cuneata Cover

Across all plots the average cover of *Lespedeza cuneata* was 15% (maximum 50%, minimum 0.06%) in 2016. Each of the treatments significantly influenced *L. cuneata* cover in 2016 ($p = 0.03$ for the nutrient treatment, and $p < 0.01$ for the other two treatments), but none of the interactions were significant (Table S3, Figs. 1 & S3). All main effects supported our hypotheses: plots in the "Nutrients" treatment had lower *L. cuneata* cover than those in the "Control," plots the "Late" invasion timing treatment group had lower cover than those in the "Early" treatment group, plots in the grasses seeded first ("Grass") and both groups seeded in the beginning ("Both") treatment groups had lower *L. cuneata* cover than those in the forbs seeded first ("Forbs") treatment group.

Lespedeza cuneata cover was higher in the late invasion group in 2016 than in 2013, the year of introduction to the late invasion treatment (*t* test, $p < 0.01$). When compared to *L. cuneata* cover in the early invasion treatment group over a similar time horizon, plots in the early invasion treatment group

contained higher cover (*t* test, $p < 0.01$) (Fig. 2). For comparisons of *L. cuneata* cover in each timing and year combination, see Table S5. All cover values within unique treatments can be extracted from Figure S3.

Seeded Native Species

Of the 25 native forb species contained in the original seed mix, 7 were not present in any plot in 2016 and only 10 species occurred in more than eight plots (Table S1). Assembly order and invasion timing (ANOVA, $p < 0.01$), but not nutrient treatment (ANOVA, $p = 0.57$), significantly affected the cover of seeded forb species in 2016 (Table S4, Fig. 3). There was a significant interaction between the invasion timing and assembly treatment ($p < 0.01$) but no other significant interactions. Seeded forbs achieved higher abundances in plots that they were introduced to early in the assembly process and in plots in which *L. cuneata* was introduced late (Fig. 3).

Seeded native grass cover was significantly affected by the invasion timing and assembly treatments (ANOVA, $p < 0.01$), but not by the nutrient addition treatment (ANOVA, $p = 0.26$), and none of the interactions were significant. There was lower grass cover in the "forbs first" treatment group (Fig. S2). Thus, the "both" treatment group had highest total seeded native species cover.

Non-native Species

In 2016, 142 plant species were recorded. Of those, 93 were native forb species, 11 woody native species, and 37 were non-native forbs, 1 our focal invasive plant *L. cuneata* (note, *L. cuneata* was analyzed separately and was not included in the non-native forb category). Only the invasion timing treatment significantly affected the cover of non-native species in 2016 (ANOVA, $p < 0.01$, Fig. S1); non-native species cover was lower in the late invasion treatment group. None of the other treatments or their interactions influenced non-native species cover in 2016 (all $p > 0.05$). None of these non-native species achieved cover values across the experiment that were comparable to that of *L. cuneata*, and thus we did not classify them as invasive species. However, some non-native species reached considerable covers in some plots (e.g. *Persicaria maculosa* and *Chenopodium* sp. in plot #25, Fig. 4).

Changes in the Community Composition

All of the treatments created significantly different plant communities (All $p < 0.02$, Table S2, Fig. 4). Plots in which grasses were established first had, in general, higher abundances of graminoids (plot #48, Fig. 4, Photo S3), whereas those with early forb establishment contained high abundances of forb species (plot #62, Fig. 4, Photo S4). Species composition in the early invasion treatment was dominated by *L. cuneata* (plot #25, Fig. 4, Photo S2). *Lespedeza cuneata* was also more dominant in the control compared to the nutrients-added treatment, but to a far lesser extent than that seen in the timing treatment (plot #10, Fig. 4, Photo S1).

Discussion

Establishing a community that has high abundances of seeded species and low abundances of non-native, and especially invasive, species are often key goals of restoration ecology. Manipulating the abiotic environment, targeted removal of invasive species, and manipulating the community assembly process all hold promise for reaching these goals, and we expected that combinations of approaches might be necessary to achieve the best restoration results. In our 7-year study, we found strong effects of our treatments on *Lespedeza cuneata* abundance, seeded native species, as well as non-native species abundance, and overall community composition after 7 years. However, we found few interactive effects of our treatments on these response variables.

We hypothesized that nutrient addition would result in a lower competitive advantage of *L. cuneata,* and thus it would have lower abundance, resulting in communities with higher abundances of seeded native species or non-native species. Indeed, we found that nutrient addition led to significantly lower cover of *L. cuneata* and shifted community composition, although these main effects were modest compared to other treatments. However, we did not find that nutrient additions resulted in higher seeded native forb or non-native species cover. Instead, native ruderal species that were not planted, such as *Teucrium canadense*, became more abundant. Nutrient additions might have larger effects in other restoration projects than we see here. The effects of nutrient additions on community structure are known to be variable across studies, due to a variety of mechanisms such as the degree of initial nutrient limitation, the magnitude, ratios, and type of nutrients that are manipulated, and the feedback effects of the nutrients with other biological processes (Harpole et al. 2017). In some cases, nutrient additions might have no effect or may result in higher cover of non-native species (Hobbs & Huenneke 1992), and the results might depend on how the nutrient-enriched environment compares to a historic state and whether or not the focal invasive species are N-fixers (Daehler 2003).

We hypothesized that early seeding of native grass species would reduce the cover of *L. cuneata*, and possibility also reduce the cover of seeded native species or non-native species, thus altering community composition. When grasses are added first, the cover of both *L. cuneata* and native forb species were reduced. When grasses and forbs were added together, *L. cuneata* had similarly low cover, but seeded native forbs species had a higher cover than in the grass first treatment. When forbs were added first, *L. cuneata* reached high cover. Thus, adding both grasses and forbs early in the experiment was the best treatment to achieve multiple restoration goals. Our results suggest that *L. cuneata* is restricted by the presence of strong grass competitors, but that it is not necessary to give these grasses a head start over seeded forb species in order to reach a maximized reduction in *L. cuneata* cover. Other studies have found that functionally diverse communities resist invasions better (Foster et al. 2015). Our "both" treatment offered the highest initial functional diversity, and it is unclear if the presence of diverse competitors played a role. Plots in
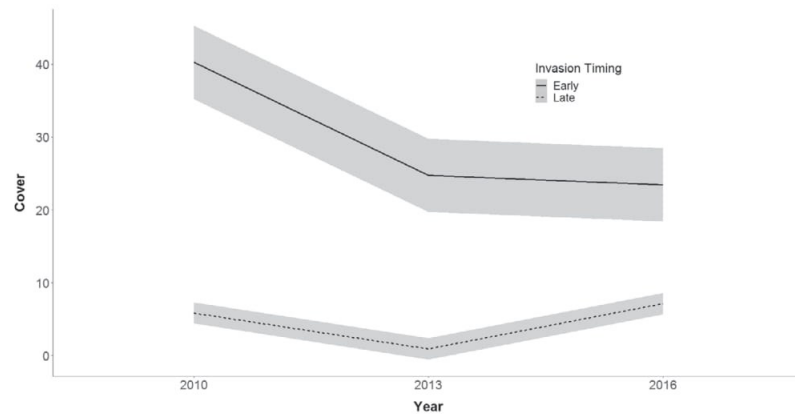
16

Figure 2. *Lespedeza cuneata* abundance for early and late invasion timing treatment in three different years. Lines represent a loess type line function; ±95% CI are displayed in dark gray.
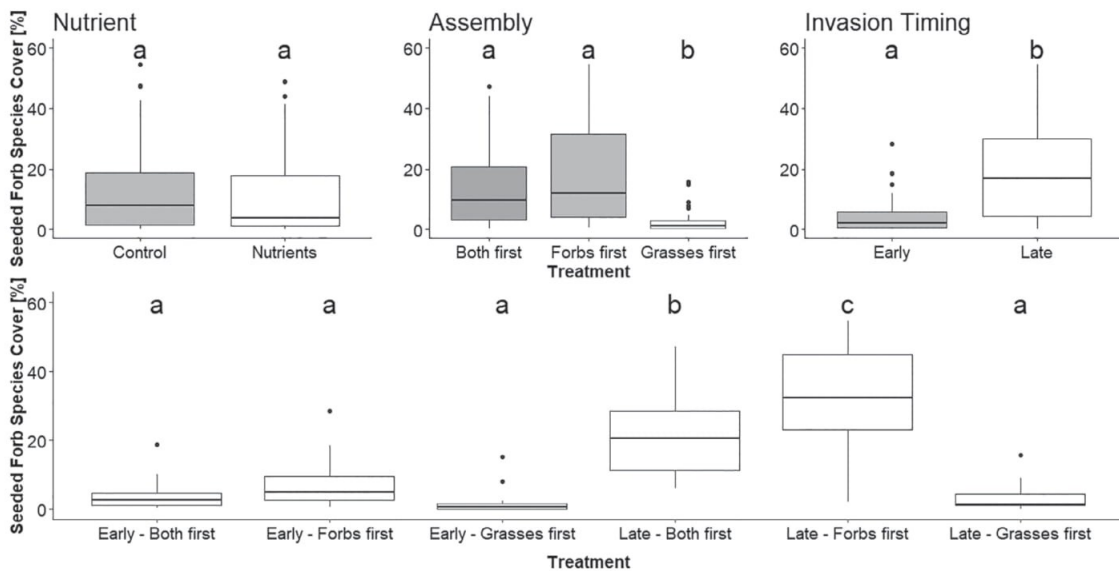

Figure 3. Seeded forb abundance in the final year of the experiment (2016) within the different treatment groups and the significant interaction between the assembly and the invasion timing treatment. The results of a TukeyHSD test are displayed in letters, as a visualization of significant differences (different letters signify $p < 0.05$). Replication is listed in Table S7.

the "grasses first" treatment were more homogeneous in their community composition, with plots consistently dominated by grasses and a few nonseeded native forb species and non-native species, such as *Barbarea vulgaris* and *Verbena hastata*.

As expected, we found that *L. cuneata* cover was lower and seeded native species cover was higher in this late invasion treatment group. This indicates that priority effects can increase *L. cuneata* abundance. The importance of priority effects for early colonizing species establishment was also found in other studies (Fry et al. 2017). "Seasonal" priority (Seabloom et al. 2003; Wolkovich & Cleland 2011) may also be important for

L. cuneata establishment, as the species may be able to start growing in earlier month compared to native species. In contrast to our expectation, non-native species cover was also lower in the late invasion treatment group. The resulting community composition was very different between the invasion timing treatment groups, leading to almost separate polygons in the NMDS visualization. The lower cover of *L. cuneata* in the early relative to the late treatment group remains true if we standardize the time of establishment, that is, the *L. cuneata* cover in the "early" invasion treatment group in 2013 and "late" invasion treatment group in 2016 (3 years after seeding for each
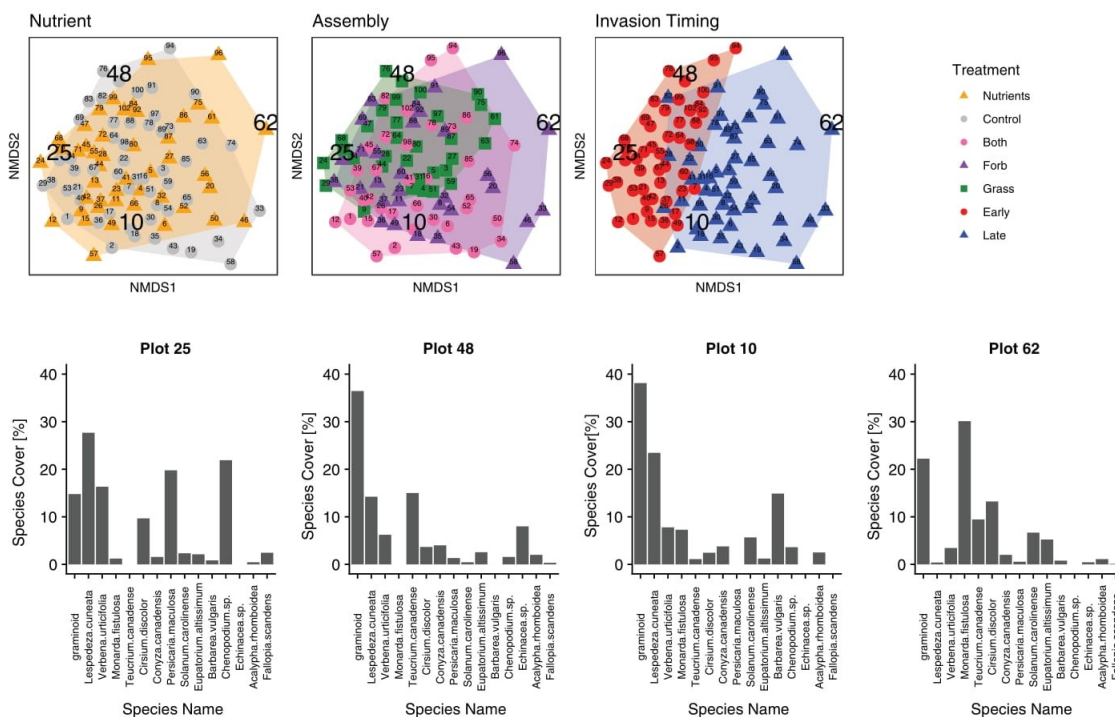
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Figure 4. Top: NMDS plots to visualize species composition for each treatment (plots in each treatment are seen in different symbols and colors, see legend). Bottom: histograms of selected plots show the cover of the 15 most common species (ordered from most to least cover across all plots in the experiment).

treatment type). Thus, the late treatment group would likely not reach the high cover observed in the early treatment group if given more time, suggesting that early efforts to prevent *L. cuneata* invasion will yield long-term benefits. In our system, as in many prairie restorations, *L. cuneata* is present in all plots, and has propagule sources in close proximity. Therefore, despite these promising results, we agree with other studies that recommend continued, intense management every 3 years to keep the cover of the invader permanently low (Souza et al. 2011; Bütüktahtakin et al. 2015; Foster et al. 2015). The lower non-native cover in the late treatment suggests an invasional meltdown scenario, where the presence of one non-native species favors the establishment of another (Simberloff & Von Holle 1999), contrary to the suspected secondary invasion scenario (Pearson et al. 2016). Management of *L. cuneata* therefore could fulfill multiple purposes—reducing cover of this focal invasive, other non-natives, and increasing cover of seeded native species. The underlying mechanism for this is in our case is unclear. Few studies have examined the timing of invasions, but those that do tend to confirm our results (Dickson et al. 2012; Goodale & Wisley 2018).

We expected to find treatment interactions; however, we found no evidence for interactive effects of our treatments on *L. cuneata* cover and on non-native cover. This is a positive

sign for managers, as it means that utilizing each of treatments individually can significantly reduce invader cover. We find that the assembly treatment and timing treatment interactively influenced the abundance of seeded native species. This is likely because late-arriving seeded native species are outcompeted by either grasses or *L. cuneata*. This is in line with other experimental results demonstrating that native species are at a competitive disadvantage when arriving late (Körner et al. 2008; Stuble & Souza 2016). In general, many of our seeded species, including iconic prairie species such as *Liatris pycnostachya*, did not establish or had low cover (e.g. we found one individual of *L. pycnostachya* in 2016). Other restoration ecologists describe difficulties with prairie species establishment (e.g. Hillhouse & Zedler 2011; Trowbridge et al. 2017), and have speculated about the causes. Species may be historically not suited for a site, due to the abiotic and biotic site conditions. In addition, seedlings are more vulnerable to mortality compared to established plants, especially in years with low precipitation (Ratzlaff & Anderson 1995; Goodale & Wisley 2018), freezing conditions, and in the presence of pathogens (James et al. 2011). Further, newly restored habitats often lack a protective litter layer to shield seedlings from environmental stressors. Despite the difficulties of seedling establishment in early restoration due to these stresses, our findings emphasize the importance of

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adding seeded species early in the process before competitively dominant species reach high cover. For the integration of target species which, as in our case, do not establish when seeded early nor are likely to establish when seeded in later, other approaches might be necessary, such as creating microhabitats, creating weeded monospecific patches, or selectively transplanting adult specimens (Drayton & Primack 2000; Seahra et al. 2019).

Our unique long-term experiment highlights the importance of the order of species' arrivals on long-term community composition. We demonstrate that treatments can be used separately to reach restoration goals, and that restoration of barren fields is an ideal testing-ground for ecological theory. A prairie restoration similar to ours that receives early management of *L. cuneata* ("late" invasion), early seeding of all target species ("both" assembly), and an addition of nutrients is likely to have reduced *L. cuneata* abundance, higher abundance of focal native species, and a reduced abundance of non-native species. These treatments can guide community assembly toward favorable outcomes for restoration.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Figure S1: Effect of the invasion treatment on secondary exotic weed abundance (% cover) in the final year of the experiment (2016).

Figure S2: Effect of treatments on seeded grass abundance (% cover) in the final year of the experiment (2016).

Figure S3: (Top left to bottom): Effect of treatments on *Lespedeza cuneata* abundance (% cover) in the final year of the experiment (2016).

Figure S4: Aerial view and design.

Table S1: Number of plots each seeded species was present in and average percent cover across all plots (rounded to two digits) for each seeded species, in descending order of number of plots they were recorded in (2016).

Table S2: Results of an analysis of similarities (ANOSIM) to test for treatment effects on community composition in 2016.

Table S3: Results of an analysis of variance (ANOVA) testing the effects of treatments and their interactions on *Lespedeza cuneata* cover in 2016.

Table S4: Results of an analysis of variance (ANOVA) testing the effects of treatments and their interactions on seeded forb species cover in 2016.

Table S5: Significant differences (Welch two-sample *t* tests) between years and invasion timing treatment groups on *Lespedeza cuneata* abundance.

Table S6: Species in the original seed mix.

Table S7: Replication.

Table S8: Soil chemical characteristics.

Photo S1: Plot 10, West-South-West facing.

Photo S2: Plot 25, West-South-West facing.

Photo S3: Plot 48, West-South-West facing.

Photo S4: Plot 62, West-South-West Facing.

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Suppl. material 3: Reference Table doi

    Authors: Michael Wohlwend
    Data type: Sources and Source IDs
    Brief description: Allows for linking additional source ids to the actual source
    Download file (232.95 kb)

Chapter 3, which is published in the *Biodiversity Data Journal*, introduces PacIFlora, a database for the introduced flora of the Pacific.

Chapter 3: Data Descriptor: Pacific Introduced Flora (PaciFlora)

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Data Paper

Data Descriptor: Pacific Introduced Flora (PaciFLora)

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Abstract

Background

The Pacific Region has the highest density of naturalised plant species worldwide, which makes it an important area for research on the ecology, evolution and biogeography of biological invasions. While different data sources on naturalised plant species exist for the Pacific, there is no taxonomically and spatially harmonised database available for different

subsets of species and islands. A comprehensive, accessible database containing the distribution of naturalised vascular plant species in the Pacific will enable new basic and applied research for researchers and will be an important information source for practitioners working in the Region.

New information

Here, we present PacIFlora, an updated and taxonomically standardised list of naturalised species, their unified nativeness, cultivation and invasive status and their distribution across the Pacific Ocean, including harmonised location denoination. This list is based on the two largest databases on naturalised plants for the Region, specifically the Pacific Island Ecosystems at Risk (PIER) and the Global Naturalised Alien Flora (GloNAF) databases. We provide an outlook for how this database can contribute to numerous research questions and conservation efforts.

Keywords

Island Biogeography, naturalised species, Pacific Ocean, plant invasion, species database

Introduction

The Pacific Ocean covers a large area and contains over 25,000 islands (National Oceanic and Atmospheric Administration & Western Pacific Regional Fishery Management Council 2009). A rich endemic flora has evolved in the Pacific, which is now threatened by, amongst other drivers, an increasing number of naturalised plant species (Seebens et al. 2017, van Kleunen et al. 2019). The Pacific Ocean is unique, with vast areas of ocean stretching between thousands of islands that create substantial barriers to the natural dispersal of plant species. It is also unique in its relatively recent colonialisation history through Polynesian and later, European settlers (Matisoo-Smith and Robinson 2004) and the large socio-economic differences that exist between island groups of different geological origin (*Seidel and Lal 2010*). However, human-mediated dispersal has resulted in many islands being inhabited by naturalised plant species, defined as alien plant species that maintain self-sustaining populations without human intervention (Richardson et al. 2000). Understanding naturalisation is facilitated by detailed information about introduction and establishment processes. Although some alien plants are introduced accidentally (e.g. stowaways, contaminated seeds), most of them are deliberately introduced for cultivation (e.g. for ornamental or other economic uses; Hulme et al. 2008, van Kleunen et al. 2020). The extent to which plant species escape cultivation and become naturalised will vary in space and time, so that a single species can be considered cultivated in one location and naturalised in another location, even in close proximity. Likewise, the shift of a plant species from naturalised to invasive, that is when species harm the environment or humans (sensu Richardson et al. 2000, Blackburn et al. 2011), will also vary in space and time. Information on a species' invasion status in one location may be useful for the

development and implementation of measures designed to mitigate its impacts or prevent invasions in other locations across the region. Finally, because of the vastness of the Pacific, intra-Pacific naturalisations occur, i.e. some species are categorised as naturalised on some islands, but native on others.

To address research questions in an objective and accessible way, databases are required that contain occurrences (presences) of naturalised plant species and harmonised region information that span the whole Pacific Region, while also being interoperable with other databases (e.g. origin, BIEN, TRY and GIFT; Kattge et al. 2011, Weigelt et al. 2019, Chamberlain and Bartomeus 2020, Maitner 2020). Additional features, such as cultivation and invasive status, can extend the range of applicability. The Global Naturalised Alien Flora (GloNAF) and the Pacific Island Ecosystems at Risk (PIER) databases meet these criteria. While these databases provide unique information on species' characteristics (e.g. cultivation, invasive status), they also overlap in information for many naturalised species and locations. However, even when the information overlaps between the databases, there are sometimes different names or spellings for the same islands or species and there is also variation between the databases in the quality and method of evaluating species invasion status. In addition, information is available inconsistently at different spatial scales, namely at island group and individual island level. These sources of data variation in the databases present a challenge to the direct combination and use of the databases in a single study.

Figure 1. doi

Map showing the boundaries of island groups in the Pacific used in this database. Underlying map: World Coastline for R, based on data from Natural Earth. Polygons surrounding island groups are designed to include all islands in the group using straight lines and, thus, these lines do not correspond to any political border.

Here, we present PaciFlora, a consolidated database on naturalised plant species on Pacific islands which overcomes the challenges posed by combining two large databases. By merging, harmonising and standardising information on naturalised species on Pacific islands from GloNAF and PIER, we created this new database reporting the presence of

naturalised plant species on each island or island group. We also categorised the islands with available data into sociogeographic groups, as this is useful for many invasion science research questions (Fig. 1, see also Wohlwend et al. 2021). GloNAF was initiated in 2011 and launched in 2015 as a worldwide database of naturalised plant occurrences in mostly geopolitical regions (Pyek et al. 2017, van Kleunen et al. 2015, van Kleunen et al. 2019). PIER is a project of the Institute of Pacific Islands Forestry (USDA Forest Service) initiated in 1997 to compile and disseminate reference information on alien plant species of known or potential threat to Pacific island ecosystems (http://www.hear.org/pier/). These two databases are, to our knowledge, the only ones covering the entire Pacific, which was important for us to not further artificially increase sampling effort differences amongst regions.

We structured our data and R code in a way that makes PacIFlora easy to combine with other databases. We also provide our R code to facilitate the integration of additional data, in case, for example, a user of our database wants to focus on a smaller part of the Pacific Region or integrate additional data.
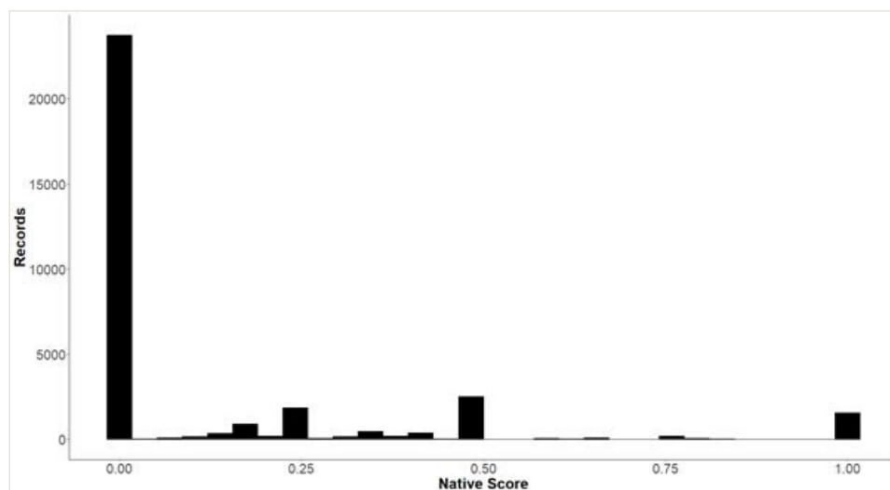
Figure 2. doi

Total number of records in categories of native status. Nativeness Score indicates naturalisation certainty, i.e. 0 indicates records that are certainly naturalised and 1 indicates records that are certainly native, respectively. Intermediate values indicate uncertainty in the native status. See main text for detailed clarification.

Accepted plant species scientific names were identified using the recently-published Leipzig Catalogue of Vascular Plants using the original names (LCVP, Freiberg et al. 2020). In total, this resulted in 33301 unique records, including 3963 species distributed over 482 islands aggregated in 50 island groups. A total of 125 records from 34 unique original species names could not be assigned to an accepted species name by the algorithm and were included as "NA". Manual matching is possible for some of them, but we abstained from this as we wanted to exclude all subjectivity from our side. A total of 847

records lack island level information and, as a result, the species x island matrix has fewer species then the species x island group matrix. The output table of PaclFlora includes plant family, plant order invasion status (if a species is currently evaluated as harmful on a certain island), native status (how likely a species is to be considered native on an island), cultivation status (how likely a species only exists as a cultivar on an island) and the name and coordinates of each island. We show the relative frequency of different categories of native status in Fig. 2.

In addition, we provide a phylogeny of the naturalised plant species in PaclFlora by pruning the comprehensive supertree by Smith and Brown 2018) to all species it has in common with Paclflora (3150) and adding the remaining (813) via a congeneric merge resulting in some polytomies. All genera where found in the supertree. Fifty-four orders of naturalised plants are present in the Pacific. Most naturalised plant species in PaclFlora belong to the orders Poales, Fabales, Lamiales, Asterales, Caryophyllales, Myrtales and Malpighiales (in descending order), but the relative representation of these orders varies across island groups (Fig. 3).
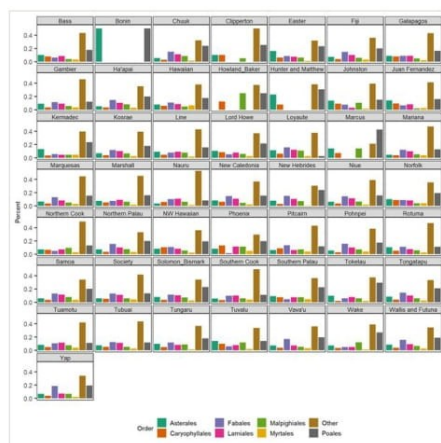
Figure 3. doi

Proportional representation of naturalised plant species in the seven most common orders for each island group.

This database can be used to address a wide variety of research questions and for management applications, for example, by combining it with different datasources on environmental drivers (Wohlwend et al. 2021), taxonomic or trait information, native flora information or data on dispersal pathways. There is also potential to use PaclFlora for invasion forecasting and species distribution modelling.

General description

Purpose: This dataset can be used for research on a wide variety of questions, including: (1) the study of patterns of richness and composition of naturalised plants in the Pacific

and the roles of anthropogenic and biogeographic drivers (Wohlwend et al. 2021); (2) the study of patterns of taxonomic and phylogenetic composition of naturalised plants in the Pacific compared to other regions of the world; (3) the development of forecasting tools to identify naturalised species that are present in the Pacific and are likely to expand their ranges to new island groups; (4) for comparing patterns of native and naturalised species richness and composition to test whether islands poor in native species are more vulnerable to invasion and (5) for identifying mechanisms that determine the range of naturalised species by combining this dataset with information about functional traits (e.g. Kattge et al. 2011:TRY www.try-db.org) and common introduction pathways.

This dataset represents a second step (after PIER and GloNAF) towards the development of a comprehensive list of the presence and status of naturalised plant species in the Pacific Region. Important next steps involve validating and updating these data in strong collaboration with local experts from each island group. For example, naturalised data exist for 488 of the > 25000 islands in the Pacific. It remains to be validated whether the remaining islands in the Pacific really do not have established naturalised plant species (e.g. the numerous tiny atolls) or whether local information about naturalised plant presence was not included in the two region-spanning sources and, thus, in PacIFlora. We hope that PacIFlora can serve as a foundation for local organisations in the Pacific that can be updated and extended in the future. The authors provide their full support for the application, validation and extension of PacIFlora. Main contact persons for this are Michael Wohlwend (application), Mark van Kleunen (validation and extension, GloNAF) and Philip Thomas (validation and extension, PIER).

We note that the results in Wohlwend et al. (2021) used a subset of the records in PacIFlora (e.g. excluding all cultivated records for most analyses) and considered data aggregated by island group. PacIFlora aims to provide more comprehensive resources that can be used for other purposes than those that were the focus of Wohlwend et al. (2021), but information presented in this publication can give insights into the data.

Project description

Design description: To create a matrix of species presences on islands and island groups, we used raw data from GloNAF version 1.1 and raw data from PIER (updated 2 June 2018). Both PIER and GloNAF list their sources for all records of a naturalised species on an island.

We harmonised species names using the LCVP (Freiberg et al. 2020) and the associated R-package 'lcvplants' (https://github.com/idiv-biodiversity/LCVP). Subspecies and varieties were aggregated to the binomial level, which we refer to as "species" level for simplicity. If hybrid taxa were not recorded in the LCVP database, it was pooled with the first parent species, affecting 20 species. Forty species names were identified by the LCVP as synonyms for more than one possible species. In these cases, we chose the first species name provided by the LCVP as the assigned name to ensure reproducibility. Twenty species could not be linked to an accepted name by the LCVP with certainty and were

assigned 'NA' values for species name, family and order. We kept these unassignable species in the list format of PacIFlora to allow for future name resolution.

All calculations were performed and graphs were created using R (version 4.0.3, R Core Team 2020). Maps were created using R and the packages 'ggplot2' (Wickham 2016), 'ggtree' (Yu 2020) and 'rnaturalearth' (South 2017) for visualisation. We created background polygons for island group association using QGis 3.12.3 (QGIS Development Team 2021). Matrix aggregation was performed using the fuzzySim package in R (Barbosa 2015).

PacIFlora includes the following columns: ID, Species, Island, Island group, Family, Order, Native, Cultivated, Source, Original_Name, Invasion. **ID** provides a unique number. **Species** is the accepted name of the species based on the LCVP. A total of 3963 species were recorded. **Island** is the location where the species is present. Islands often have many names or different spellings. We used web research and other information in our sources to identify synonyms and chose one name from the sources (usually the most commonly used name). Island refers to the smallest available unit of reference and is, therefore, sometimes used for several unnamed islets of an atoll in close proximity which are not or only sometimes (tidally) connected by land. A total of 488 islands where recorded. **IslandGroup** is a group name assigned by us. The inclusion of island groupings is useful for many types of research questions, as a complete species list at a broader spatial scale decreases problems of data deficiency for individual islands in an archipelago. Our groups are largely based on political borders, such as municipalities or states. If political borders did not reflect geographic borders, we used distance between islands and ocean trenches to assign each island to one of 50 island groups. Island group aggregation is visualised in Fig. 1. We excluded 146 records that could not be linked to any island group. This particular grouping is useful for questions related to the influence of dispersal barriers on biological invasions, as distance creates a natural barrier and political borders are known to influence dispersal via human imports (either intentional or accidental). However, islands also vary in age, size and geomorphology and, thus, we make it possible to regroup the islands in our database into formats that might be better suited for other research questions (e.g. on establishment barriers). **Family** is the plant family and **Order** is the plant order. **Native** status indicates the certainty if the species is native at the given location. While all of the species in PacIFlora are naturalised in at least one location in the Pacific, some species might be native in other locations of the Pacific. We assigned numerical values, indicating certainty of native status on each specific island between 0 (unanimously described as naturalised on the specific island) and 1 (unanimously described as native on the specific island) to the categorical classes defined in GloNAF and PIER, which were averaged if there was no agreement amongst the sources. There were 36 species with only "native" records, which were excluded. The vast majority of records (94%) are not described as likely native. A total of 255 species were described at least once as likely native (Fig. 2). **Cultivated** provides information on whether the species is classified as being only cultivated on the island or island group. Cultivated values of 1 define species that are only known to exist in horticultural plantings at the location, whereas those clearly described as naturalised by any source at the location are given a

value of zero. A value of 0.5 indicates that there is no information available documenting whether the species is either cultivated or naturalised at the location. There were 40 species with only "cultivated" records, which were excluded. A total of 19,944 records were described as not cultivated, 9150 had no information on cultivation status and 4207 were described as cultivated. A total of 630 (16%) species were described as cultivated at least once, which also means that those species escaped cultivation at least once. Cultivated and native scores were determined differently since a species can be both cultivated and naturalised on an island, but not native and alien. **Database** indicates if the record was present in GloNAF (glon), PIER (pier) or both (glon_pier). **Orignal_Name** shows the species name prior to standardisation. **Invasive** status is a column indicating invasive status of the species on a given island, with "1" meaning unanimously described as invasive in this location, "0" meaning unanimously described as not invasive. The value in this column was achieved by forming a mean of the evaluation of all records for a particular species island combination, why this column should be handled with care, as there was no information if one occurrence was evaluated differently by different authors or if two different occurrences on one island were evaluated differently. In total, 15,713 records where described as likely invasive, including 1550 species. **Source** provides the original reference as listed in GloNAF and PIER. Only one reference is provided for each record and additional references can be accessed via the **Source_ID** column, which lists the IDs of all references listing this record. References for the IDs can be found in Suppl. material 3. Most records have only one record, but a record can have as many as eighteen references (e.g. due to voucher specimens). An overview of the 22 most frequently used sources can be seen in Table 1. **Latitude** and **Longitude** give the geographical coordinates of the island centroid in decimal degrees, which were taken from the Global Inventory of Floras and Traits (GIFT) database (Weigelt et al. 2013, Weigelt et al. 2019). In total, 84 islands could not be connected to a unique ID in GIFT; coordinates for these were taken from Google Maps (Google 2020). All coordinates are provided in WGS84.

Table 1.

Table 1: Most frequent sources used in PacIFlora. We note that some of the sources might provide overlapping information on naturalised plant occurrences. Records refers to species × island occurrences. Sources are sorted in decreasing order, based on the number of records each source provide. The names of the three island groups with the most records from each source are displayed.

Source	Records	Most recorded island groups
Gargominy et al. 2018	9126	New Caledonia, Clipperton
Imada 2019	5104	Hawaiian, NW Hawaiian
Florence et al. 2013	4119	Society, Marquesas, Tubuai
Fosberg et al. 1979	2780	Mariana, Northern Palau, Yap
Wagner et al. 1999	2600	Hawaiian, NW Hawaiian, Solomon_Bismark
Raulerson 2006	1982	Mariana
Charles Darwin Foundation 2008	1601	Galapagos, Solomon_Bismark

Source	Records	Most recorded island groups
Florence et al. 2007	1600	Society, Marquesas, Tubuai
Fosberg et al. 1987	1467	Mariana, Northern Palau, Chuuk
McCormack 2007 McCormack 2013	1170	Southern Cook, Northern Cook, Chuuk
McCormack 2007	1076	Southern Cook, Northern Cook
MacKee 1994	1054	New Caledonia, Loyaute, Hunter and Matthew
Lorence and Wagner 2013	1042	Marquesas
Wagner and Lorence 2002	1020	Marquesas
Space et al. 2003	881	Northern Palau, Southern Palau
Welsh 1998	781	Society, Bass, Tuamotu
Guézou et al. 2014	775	Galapagos
Invasive Species Specialist Group ISSG. 2019	635	Tongatapu, Nauru, Easter
Whistler 1998	614	Samoa, Tokelau
Florence 2004	599	Society Marquesas, Tuamotu
Swarbrick 1997	574	Solomon_Bismark, New Caledonia, New Hebrides
Yuncker 1959	519	Tongatapu, Vava'u, Ha'apai

We present our database in three formats:

(1) PacIFlora - Full list format of all records (species x island, including records with no information on island, but just island group level and records that could not be identified by the LCVP), Suppl. material 2.

Additionally, you can find the following files:

(2) An island × species matrix, excluding records that were missing information. Specifically, this list does not include data that have no island information or species that could not be identified by the LCVP (Dryad only).

(3) An aggregated island group × species matrix (Dryad only).

(4) A table to access reference IDs, Suppl. material 3.

(5) List format of PaciFLora on island level, excluding all records with no information on island, but just island group level and records that could not be identified by the LCVP (Dryad only).

(6) List format of PaciFLora on island group level, excluding all records that could not be identified by the LCVP and providing aggregated values for naturalisation, cultivation and invasion status (Dryad only).

Both data matrices (2 and 3) are included to provide an easy-to-use format for research and conservation applications. When using these matrices, be aware that they include all records (e.g. including cultivated species for some records). We provide our full R code used for aggregation, starting from GloNAF and PIER raw data, which allows, for example, for the generation of personalised subsets.

To create a phylogeny for the naturalised plant species in the Pacific, we pruned the supertree by Smith and Brown (2018). Species names in PacIFlora and in this supertree were first harmonised using the LCVP (Suppl. material 1). Focal species which were missing from this supertree were grafted onto it at the genus level using the function congeneric.merge in the "pez" package of R (Pearse et al. 2015). We summarise the spatial variation of plant order composition on island groups in a bar chart, showing the proportional representation of species in the seven overall most common (measured in species/family) plant orders (Figs 1, 3).

Our R code allows a complete workflow from the publicly available PIER and GloNAF data to the final species x island matrix. All codes used to unify and aggregate the data are provided in the R programming language and is open access via github (https://github.com/MichaelWohlwend42/PacIFlora.git). We provide code to merge new data with PacIFlora in a standardised manner, using universally applicable harmonisation functions for species and islands. The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at https://datadryad.org/stash/dataset/doi: 10.5061/dryad.qfttdz0hd, as well as partly in the supplementary material and on the abovementioned GitHub Page.

Geographic coverage

Description: PaciFlora covers all islands with available data in the Pacific Ocean. Only oceanic islands between 40°N and 40°S are included as our focus was on (sub-)tropical islands. Larger landmasses, such as Japan, New Zealand the Philippines and Papua New-Guinea, as well as all islands on the Japanese, Pacific American or Australian coasts, were excluded. So, this database focuses on (sub-)tropical islands that are isolated from larger landmasses.

Usage licence

Usage licence: Creative Commons Public Domain Waiver (CC-Zero)

Data resources

Data package title: Pacific Introduced Flora (PaciFLora)

Number of data sets: 1

   Data set name: PaciFlora

Column label	Column description
Species	Simple species name.
Island	island name.
IslandGroup	assigned island group name.
Native	Standardised native score ranging from 0 (unanimously described as not native) to 1 (unanimously described as native) in given location.
Cultivated	Standardised cultivation score ranging from 0 (unanimously described as not cultivated) to 1 (unanimously described as cultivated) in given location.
Family	plant family.
Order	plant order.
Database	Origin GloNAF, PIER or both (glonpier).
Invasive	Standardised invasive score ranging from 0 (unanimously described as not invasive) to 1 (unanimously described as invasive) in given location.
Orginal_name	pre-harmonisation species name.
Latitude	latitude of island (mercator).
Longitude	longitude of island (mercator).
Source	Literature cited for this entry in the raw data.
Source_ID	Full list of references provided for this occurrence, which can be referenced using the attached list.

Acknowledgements

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Supplementary materials

Suppl. material 1: PacIFlora Phylogeny doi

    Authors: Smith & Brown, harmonised, pruned and extended by Michael R Wohlwend
    Data type: Phylogeny
    Download file (117.78 kb)

Suppl. material 2: PacIFlora doi

    Authors: Us
    Data type: List, Species, Location, Additonal Information
    Brief description: Complete Datasbase in list form, as it will be uploaded to zenodo and GitHub.
    Download file (11.12 MB)

Chapter 4, which is published in *Diversity and Distributions*, utilizes a predecessor of PacIFlora to analyse patterns and drivers of naturalized plant species in the Pacific.

Chapter 4: Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific

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Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific

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Abstract

Aim: The Pacific exhibits an exceptional number of naturalized plant species, but the drivers of this high diversity and the associated compositional patterns remain largely unknown. Here, we aim to (a) improve our understanding of introduction and establishment processes and (b) evaluate whether this information is sufficient to create scientific conservation tools, such as watchlists.

Location: Islands in the Pacific Ocean, excluding larger islands such as New Zealand, Japan, the Philippines and Indonesia.

Methods: We combined information from the most up-to-date data sources to quantify naturalized plant species richness and turnover across island groups and investigate the effects of anthropogenic, biogeographic and climate drivers on these patterns. In total, we found 2,672 naturalized plant species across 481 islands and 50 island groups, with a total of 11,074 records.

Results: Most naturalized species were restricted to few island groups, and most island groups have a low number of naturalized species. Island groups with few naturalized species were characterized by a set of widespread naturalized species. Several

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plant families that contributed many naturalized species globally also did so in the Pacific, particularly *Fabaceae* and *Poaceae*. However, many families were significantly over- or under-represented in the Pacific naturalized flora compared to other regions of the world. Naturalized species richness increased primarily with increased human activity and island altitude/area, whereas similarity between island groups in temperature along with richness differences was most important for beta diversity.

Main conclusions: The distribution and richness of naturalized species can be explained by a small set of drivers. The Pacific region contains many naturalized plant species also naturalized in other regions in the world, but our results highlight key differences such as a stronger role of anthropogenic drivers in shaping diversity patterns. Our results establish a basis for predicting and preventing future naturalizations in a threatened biodiversity hotspot.

KEYWORDS

anthropogenic drivers, beta diversity, island biogeography, naturalized species, Pacific Ocean, plant invasion

1 | INTRODUCTION

The Pacific ocean covers almost half of the earth's surface and contains many isolated islands with a rich and highly endemic flora that has become threatened by non-native plant species introductions (Loope, 1998; SPREP, 2016). Island floras in the Pacific region show a strong turnover in naturalized species among islands leading to the steepest regional species–area relationship in the world (van Kleunen et al. 2015), meaning that the number of naturalized species sharply increases with the number of islands analysed. Unique features of the Pacific, such as its geographic isolation, biogeographic history and spatial variation in natural and anthropogenic factors, could explain the naturalized species distribution patterns for this region. Understanding patterns and drivers that shape naturalized plant richness and composition in the Pacific is necessary for a better global understanding of naturalization processes. Further, region-specific knowledge is a prerequisite for guiding conservation planning, such as compiling regional watchlists to mitigate future invasions (Sherley et al., 2000).

Previous studies have shown that most naturalized species occur in one or a few Pacific islands and that most islands have low naturalized species richness (Denslow et al., 2009; Meyer, 2004). Species-poor islands tend to have a nested subset of the species present on species-rich islands (Traveset et al., 2014). Rarity indices that quantify the range size of species were developed for conservation research to identify areas with many endemic species (Usher, 1986; Williams, 1993). This same index can be used to quantify whether the naturalized species that are present on an island group are those with small or large ranges. If species-poor island groups have rare naturalized plant species, this could indicate strong environmental filtering for unique local conditions, whereas if they are inhabited by widespread naturalized plant species, this could indicate that dispersal limitation so far limits the arrival of rarer species due to

stochastic factors. Quantifying patterns of rarity in combination with patterns of beta diversity will elucidate the drivers of naturalized species composition, with strong implications for conservation.

The success of naturalized plant species in the Pacific is often attributed to the weak competition ability of native plant species (e.g. Gillespie et al. 2008; MacDougall et al. 2009). The extreme isolation of many island groups in this region has led to phylogenetically clustered compositions of native species, whereby some native plant lineages are absent because of dispersal limitation and other lineages are over-represented due to high rates of in situ diversification and local extinctions (Cabral et al., 2019; Cavender-Bares et al., 2009; Crisp et al., 2009; König et al., 2020; Weigelt et al., 2015). As a result, the Pacific region might have under-exploited resources (i.e. absence of species-trait combinationsDenslow, 2003; Elton, 1958; Gillespie et al., 2008) that could favour the naturalization of plant species from lineages that are under-represented in the native flora of the Pacific, resulting in a disproportionate representation of certain plant families compared to global patterns. For example, the treeline in Hawai'i was low, because the typical cold-adapted functional groups (e.g. *Pinaceae*) did not arrive to these islands through natural dispersal. Analyses of the over- or under-representation of plant families in the Pacific compared to the global naturalized flora can provide a first look at these patterns and serve as an indirect indicator of the representation of certain trait combinations in the naturalized flora of the Pacific.

For native plants, climate is known to strongly influence species richness (Kreft & Jetz, 2007; Wright, 1983), and both geographic distance and climate dissimilarity strongly influence dissimilarity in species composition (often measured as beta diversity) (Keil et al., 2012; König et al., 2017; Soininen et al., 2007). Naturalized plant diversity patterns are shaped disproportionately by other drivers (Denslow et al., 2009; Moser et al., 2018; Qian et al., 2008; Winter et al., 2010), and globally, naturalized plant

richness is strongly linked to human activity (e.g. represented by human population density and economic activity, Essl et al., 2019; Pyšek et al., 2017). Humans import and export species, purposefully and accidentally, through trade activities (Hui et al., 2017; Hulme, 2009; van Kleunen et al., 2018, 2020) and directly or indirectly create disturbances that favour their establishment (Frenot et al., 2001; Hulme, 2009; Marvier et al., 2004; Merlin & Juvik, 1992). The broad range of biogeographic (area and isolation) and anthropogenic (e.g. human density and GDP) factors present in the Pacific is uniquely suited for studying naturalized species distributions, as it includes both highly invaded (Kueffer et al., 2010) and almost untouched islands.

To understand the climatic, biogeographic and anthropogenic factors underlying diversity patterns of naturalized plant species across the Pacific, we quantify (a) naturalized species richness per island group, average distribution ranges of naturalized species per island group and naturalized species sharing between island groups in the Pacific, (b) the rarity of naturalized species present on each island group, (c) the species richness of naturalized plant families in the Pacific in relation to worldwide total and naturalized species richness, and (d) the anthropogenic, environmental and biogeographic drivers of naturalized species richness and beta diversity across Pacific island groups. Combined, these analyses provide a description of current naturalized species richness and composition in the Pacific and give insights into the forces that shape these patterns, serving as guidelines for applied conservation.

2 | METHODS

2.1 | Compilation of naturalized plant species occurrence data

In our study, the Pacific is defined as all islands between 40°N and 40°S, excluding large landmasses such as Japan, New Zealand, Indonesia, the Philippines and Papua New-Guinea as well as small islands on the Pacific-American or Australian coast. Japanese and South East Asian Islands west of Bonin/ Palau are also excluded (Table S1). We used species record data from two databases with comprehensive information on the presence of naturalized plant species, PIER and GloNAF. PIER (Pacific Island Ecosystems at Risk) contains reports of non-native species in the Pacific region at the island level (http://www.hear.org/pier/). GloNAF (Global Naturalized Alien Flora; van Kleunen et al., 2019) contains reports of naturalized non-native plant species across 861 geographic regions worldwide (Dawson et al. 2017; Moser et al. 2018; van Kleunen et al. 2015). The GloNAF database contains information using an island grouping based on political borders rather than the groupings we develop here (see below). We therefore used raw data at the (mostly) island level from GloNAF version 1.1 (van Kleunen et al., 2015) and aggregated them at the level of the island groups defined in this study. Table S1 gives a list of all 481 islands with species records.

Our data mostly contained information at island level, but we aggregated occurrences to island group level to ensure high completeness of the species lists analysed. We acknowledge that this reduces but does not eliminate the issue of data deficiency. To create island groups, we started with (a) political borders, including municipals or states. If political borders poorly reflected geographic borders (e.g. Samoa and American Samoa), we used (b) distance between islands and (c) ocean trenches to assign each island to one of 50 island groups. We excluded species x island records that could not be assigned to any island group with absolute certainty (e.g. when location information was imprecise). Our island groups reflect both geographic and political borders, because both are known to be important for non-native species movement. A list of all islands included in each island group is provided in Table S1.

Naturalized species were assigned accepted binomial species names using the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020) and the associated R package lcvplants (https://github.com/idiv-biodiversity/lcvplants). Different subspecies and varieties of the same species were merged to the species level. Hybrids were treated as separate species, except if no valid entry could be identified in which case they were treated as the first parent species. Species records were removed when they could not be assigned to an accepted plant species (e.g. information only at plant family level). In the rare case of more than one corresponding accepted species for a synonym, we selected the first output of the lcvplant function to ensure reproducibility.

Some species x island records in the databases were listed as cultivated (incl. for ornamental purposes) or native. For some species, naturalization status varies among species x island combinations (i.e. a species can be naturalized in one island group and cultivated or native in another), which we attribute to the large area of the Pacific, and the temporal nature of naturalization (i.e. a species may have escaped cultivation only in some island groups). When aggregating to island group level, we considered a species as naturalized for the island group if it has naturalized on any island within the group. When classifying the native status of species records, we averaged the expert evaluation in the sources for each island. We considered a species to be native if it is listed as native on any island within the group. Species that are not explicitly listed as naturalized in any record on the Pacific but listed as cultivated/ native at least once were excluded from our study. With these criteria, 2,672 naturalized species were included in our analyses which can be found in Table S2.

For most analyses, we evaluated our questions excluding records of species on island groups classified as native and cultivated. We show the results of the full data set (i.e. including those records) in the Figures S1–S3. Results of both approaches were comparable, indicating the robustness of our results. For beta diversity and shared species analyses, excluding records of island groups with species classified as native and cultivated would create false absences (i.e. type I errors) and may generate false negatives (i.e. type II errors). Thus, we present analyses using all data for these analyses. We did not categorize species as "invasive" or

similar (sensu Blackburn et al. 2011; Richardson et al., 2000), because this classification is not available for all species in the study region.

2.2 | Patterns of naturalized species richness, range size, rarity and composition

We first quantify basic patterns of naturalized plant species distributions in the Pacific. Compositional species sharing between each pair of the 50 island groups was quantified in two ways: (a) the total number of shared species, "(b) beta Simpson pairwise dissimilarity calculated as $\frac{\min(b,c)}{a+\min(b,c)}$, with a being the species two island groups have in common and b and c being the richness of the individual island groups; this metric considers species turnover without the influence of species richness differences (monotonic transformation as in Baselga (2010), using the betapart package in R (Baselga et al., 2020).

We used our naturalized species by island group matrix to calculate species richness per island group (n_g), species occupancy (c_i, range size of species i) and compositional species sharing. Average (geographic) rarity per island group is defined as $\frac{\sum\left(\frac{1}{c_i}\right)}{n_g}$, that is the average over all species present in an island group of the inverse of their occupancy (Usher, 1986; Williams, 1993). We assessed whether there is a relationship between the average rarity of the naturalized species and the naturalized species richness of an island group using Pearson's product–moment correlation to assess whether species-poor island groups tend to have more common or more rare species, indicating a strong role of dispersal or environmental filtering.

2.3 | Naturalized plant family representation in the Pacific

We investigated whether the Pacific has a different naturalized plant family composition compared to other regions of the world. We assessed whether certain plant families have more or fewer naturalized species in the Pacific than expected based on (a) their global species richness and (b) their naturalized species richness in other regions of the world. Data for the number of plant species per family came from the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020). Data for naturalized plant species per family in other regions of the world came from GloNAF (van Kleunen et al., 2019). We tested whether each plant family was over- or under-represented relative to expectations from a null model using a hypergeometric distribution test. For this, we used the phyper function in R, giving the distribution of binomial probabilities comparable to a one-tailed Fisher's exact test (Johnson et al., 1992).

2.4 | Naturalized species occurrences outside the Pacific

Using GloNAF, we quantified the number of alien species in the Pacific that are also naturalized in other continents or countries. For each continent or country, we then computed the proportion of the total number of naturalized species that are shared with the Pacific. As spatial units, we used (biogeographical) continents as defined by the World Geographical Scheme for Recording Plant Distributions developed by the Biodiversity Information Standards (TDWG). We also used countries, as information exchange concerning potential non-native species exchange occurs primarily at the country level (e.g. Global Invasive Species Database; http://issg.org/database/reference/index.asp). Additionally, we quantified the proportion of naturalized plant species in the Pacific that are unique naturalizations to this region and compared this to other continents, to test whether there are proportionally more naturalized species exclusive the Pacific. To complete this picture, we used Pearson's correlation coefficient to test whether species that are widespread in the Pacific (occupy many island groups) are also widespread globally (occupy many countries).

2.5 | Drivers of naturalized species richness and beta diversity

We assessed the relative importance of anthropogenic, biogeographic and climatic drivers in explaining patterns of naturalized species richness and beta diversity across island groups in the Pacific. One of our main goals was to investigate which factors promote naturalized richness and compositional similarity between island groups. We used GIFT (Global Inventory of Floras and Traits, Weigelt et al., 2020), a global archive of regional plant checklists and floras including physical, geographic, bioclimatic and anthropogenic characteristics, which are computed based on the spatial polygons and summary statistics for each island group (islands with naturalized species records not yet included were added to GIFT for this purpose): land area (combined area of all islands belonging to the same island group), distance to mainland (closest distance from coast to coast) and land area in proximity (SLMP: standardized land mass in proximity, averaged among islands, that is partly reflecting the spatial arrangement of a group (Weigelt & Kreft, 2013)). Further, we extracted other variables from additional resources and assigned them to the island groups. These included the following: airport capacity (number of airports x airlines visiting them as a proxy for their size; https://openflights.org/), harbour capacity (number of harbours x their size in three classes (World Port Index, https://msi.nga.mil/Publications/WPI)), mean annual temperature and precipitation (Chelsea (Karger et al., 2017), elevation (maximum) (WorldClim 1.4 digital elevation data (United States Geological Survey, 2011)), human population number and density (Doxsey-Whitfield et al. 2015)

and Human Footprint and Human Influence Index (WCS, 2005). Finally, we extracted a GDP Index which estimates GDP based on night light emission (NOAA et al., 2010). A low proportion of values were missing in our data set (18% for GDP Index and Human Population, 4% for precipitation and temperature), and for these, we imputed missing values using a random forest algorithm that is trained on observed values to predict missing values, using the R package "missForest" (Stekhoven & Buehlmann, 2012). We imputed missing values with 100 trees in each forest and five variables randomly sampled at each split; the estimated out-of-bag error imputation error rate across all variables was low (Out-of-bag (OOB) error = 0.144).

We assessed which variables promote naturalized species richness on Pacific island groups. Because variable importance may be biased towards correlated variables (Strobl et al., 2007), we used a two-step variable selection procedure when fitting random forest models using the R package "VSURF" (Genuer et al., 2015). The first step of this procedure ranks variables by importance and eliminates the redundant ones, where the threshold value is an estimate of the standard deviations of redundant variables. The second step selects variables that are important for interpretation, which retains variables that are strongly associated with the response variable but allows for some degree of redundancy. We used 100 trees in each forest, 10,000 forests in each interpretation step. This selection process is visualized in Figure S6.

To assess which drivers promote beta diversity of Pacific island groups, we calculated the absolute difference of each environmental and anthropogenic variable between each pair of island groups, and the geographic distance of the island groups to each other (instead of distance to continent). We included richness difference between island groups as a predictor in the random forest model to test whether pairwise beta Simpson depends on how similar or different the pairwise island groups are in their species richness. This factor must be interpreted carefully as it does not represent a biogeographical, anthropogenic or strictly environmental driver. Rather, richness difference provides meaningful information on the possible pathways in which species disperse in the Pacific. As beta Simpson examines species turnover without the influence of species richness differences, it is meaningful to examine how species richness differences influence beta Simpson. If species with similar richness have similar beta Simpson values, this could indicate that species-poor island groups all have the same composition of widespread naturalized species. Alternatively, if species with different richness values have high beta Simpson values, this could indicate that species-poor island groups contain a nested subset of the naturalized species found on species-rich island groups. When running the random forest model without the factor richness difference included, results changed only to a minor degree (Figure S7), showing the robustness of our results. To support the interpretation of our results, we included partial dependence plots of a standard random forest model in the Appendix S1, as there is no indicator of direction or shape of the drivers influence in VSURF. This function draws the regression, which represents the effect of our drivers on naturalized species richness (Figure S8-a) or beta Simpson diversity (Figure S8-b, randomForest package in R, Liaw & Wiener, 2002). This allows us to consider trends in these regressions for a better interpretation of our results.

For all analyses and data visualization, we used R (R Core Team, 2020, version 4.0.3) and the packages ggplot2 (Wickham, 2016), raster (Hijmans, 2020), rnaturalearth (South, 2017) and rgeos (Bivand & Rundel, 2020).

3 | RESULTS

3.1 | Patterns of naturalized species richness, range size and composition

On average, there were 258 species per island group (median of 182, Figure 1a). The lowest number of naturalized species was recorded for Howland and Baker (6) and the highest number for the Hawaiian Islands (1,544; Table S3). Most naturalized species were present on one or a few island groups (Figure 1b). Of the 2,672 naturalized species found in the Pacific region, only 1,377 (52%) occurred on more than one island group and only 367 (14%) occurred on more than 10.

Island groups with many naturalized species also tended to share many naturalized species with other species-rich island groups in absolute terms (Figure 2a), but this relationship was not observed for beta Simpson diversity (Figure 2b) likely because naturalized species-rich island groups had proportionally more rare species (Figure 3). Indeed, we found a positive association between the average rarity and the species richness of island groups in the Pacific ($p < .001$; Pearson's correlation estimate = 0.78; Figure 3).

3.2 | Naturalized plant family representation in the Pacific

In total, naturalized species from 228 plant families were recorded in the Pacific. Many plant families ($N = 91$) had more naturalized species in the Pacific than expected based on the global number of species in the family, such as *Poaceae*, *Arecaceae* and *Fabaceae*, whereas others ($N = 30$) had fewer naturalized species than expected, such as *Orchidaceae* and *Rubiaceae* (Figure 4a). When we considered the representation of plant families in the Pacific compared to the global number of naturalized species for the 227 families found both in the Pacific and in other regions (only *Marcgraviaceae* are exclusively naturalized in the Pacific), 94 families were over- and 31 were under-represented in the Pacific compared to other regions. For example, *Brassicaceae* and *Apiaceae* are under-represented in the Pacific, whereas *Poaceae*, *Arecaceae* and *Fabaceae* are still over-represented (Figure 4b). Five families were under-represented when the Pacific naturalized flora was compared to total global family richness, but were over-represented
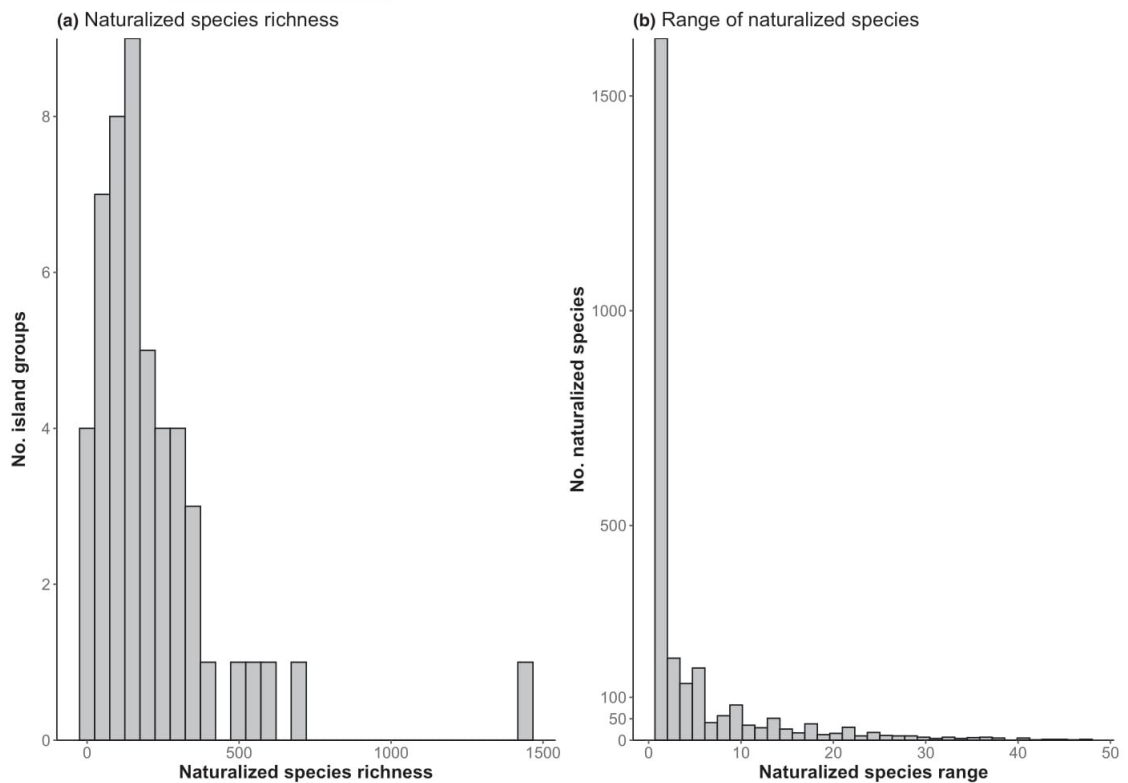
(a) Naturalized species richness

(b) Range of naturalized species

FIGURE 1 Histograms of the frequency of (a) naturalized species richness for all island groups and (b) naturalized species range (number of island groups each naturalized species is present on) for all naturalized species

when the Pacific naturalized flora was compared to the global naturalized family richness. Eight families were over-represented when the Pacific naturalized flora was compared to total global family richness, but were under-represented when the Pacific naturalized flora was compared to the global naturalized family richness. Thus, 13 families were evaluated opposingly depending on the context (Table S4), showing that naturalized families can perform very differently in the Pacific.

3.3 | Naturalized species occurrence outside of the Pacific

Twenty-one per cent of naturalized species found in the Pacific were not recorded as naturalized elsewhere in the world (Figure S4), but this is neither exceptionally high nor low (within the standard deviation). Many naturalized species in the Pacific were also found as naturalized species in South America and Africa, and in the large countries bordering the Pacific including the United States, Australia and Mexico (Table 1). The top eight countries which shared the most naturalized species with the Pacific are shown in Table 1, and these countries serve as indicators for their

larger regions (i.e. Portugal for the Mediterranean, Puerto Rico for the Caribbean). Naturalized species that were present as naturalized species in many countries outside the Pacific were also widespread within the Pacific (Figure S5).

3.4 | Drivers of naturalized species richness and beta diversity

Human footprint and airport capacity were the most important variables explaining naturalized species richness of island groups, closely followed by other drivers that also reflect human influence and economic activity (Figure 5a; $R^2 = .88$). The difference between island groups in naturalized species richness and temperature were the most important variables explaining beta Simpson across island groups (Figure 5b, $R^2 = .95$). The partial dependence plots we included to foster interpretation (Figure S8) do not provide a slope, but we observe clear trends. We can observe a generally positive trend for all drivers influencing richness (e.g. the higher the human footprint index and the land area of an island group, the higher the naturalized species richness). We observe a generally positive trend for differences in temperature and in geographic distance influencing
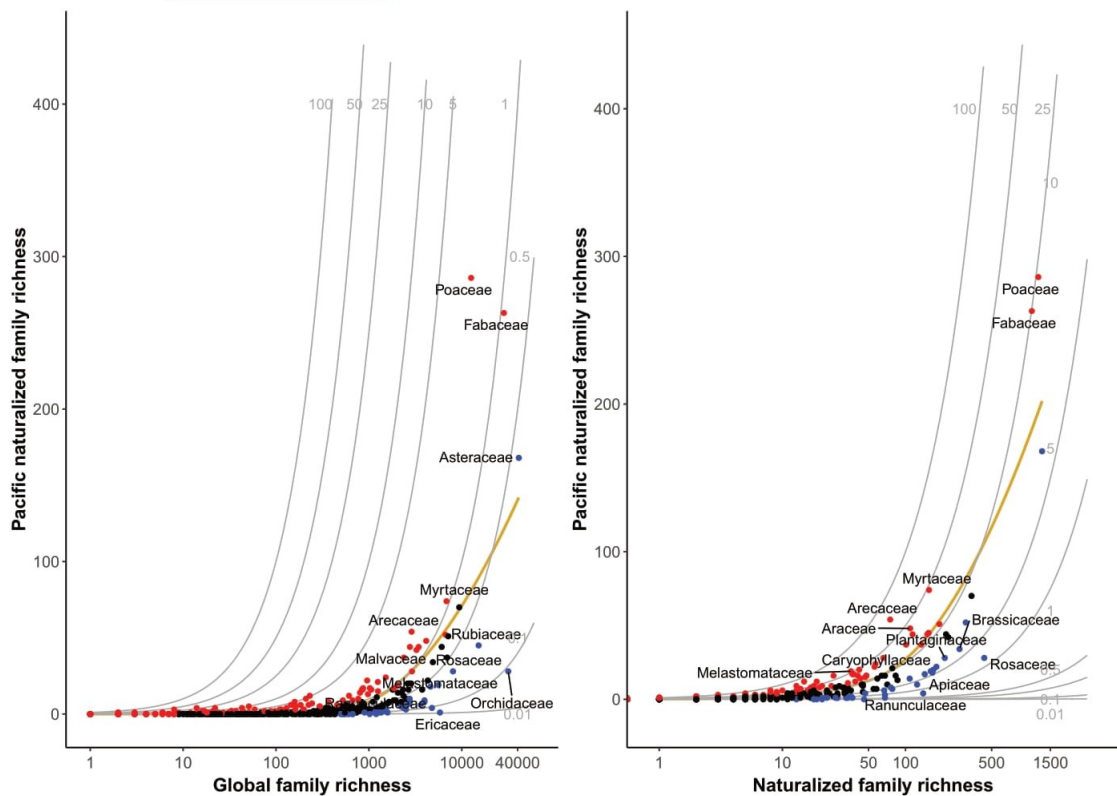
FIGURE 2 Pairwise patterns of shared species between island groups (more yellow colours indicate more shared species). Top (a): Total richness and total species shared between island groups. Bottom (b): Beta Simpson dissimilarity between island groups and average rarity of species on each island group

FIGURE 3 Average rarity of naturalized species on each island group in relation to naturalized species richness for each island group in the Pacific. High average rarity indicates the presence of many naturalized species that are located on few other island groups. A linear model (black line) and its 95% confidence interval are displayed. Names of many island groups with low naturalized richness are not displayed for visibility reasons

beta diversity, while we observe a generally negative trend for differences in naturalized species richness, in GDP, in airport capacity, and in population count, and for differences in the human influence index, we observe a hump-shaped pattern. Our results therefore show that the more different islands are in their naturalized species richness and GDP, the more similar they are in their naturalized species composition.

4 | DISCUSSION

In our comprehensive analysis of the naturalized flora of the Pacific region, we find 2,672 naturalized plant species from 228 different plant families. We show that the richness of naturalized plant species on island groups in the Pacific is strongly linked to anthropogenic factors, reflected in several drivers, while compositional similarity

FIGURE 4 Total global species richness (a) and total naturalized global species richness excluding the Pacific (b) per plant family compared to naturalized richness per plant family in the Pacific. Coloured points indicate significantly over-represented (red) or under-represented (blue) plant families in the Pacific (*p* < .05). The names of the six most over- and under-represented families are displayed. Grey lines are for the relative per cent of species per family. Golden line shows a loess type linear model

TABLE 1 Total numbers of naturalized species recorded in the Pacific that are also naturalized elsewhere (per continent and country)

Continent	Africa	South America	North America	Australasia	Trop. Asia	Temp. Asia	Europe	Antarctic
Shared Naturalized	1,558	1,546	1,470	1,310	1,103	1,055	691	90
Total Naturalized	3,490	3,158	5,803	3,415	1,878	2,880	3,997	153
%	44.6	49	25.3	38.4	58.7	36.6	17.3	58.8
Country	USA	Australia	Mexico	Japan	New Zealand	Portugal	Puerto Rico	South Africa
Shared Naturalized	1,338	1,205	703	690	652	631	629	599
Total Naturalized	5,303	2,805	1,115	1,669	1,710	1,344	806	1,080
%	25.2	43	63	41.3	38.1	46.9	78	55.5

Note: Sorted in descending order, total naturalized richness per continent and country is given. Data for these countries do not include their Pacific territories. This table is based on GloNAF (van Kleunen et al., 2019).

between island groups is linked to richness differences and temperature similarities. The high isolation of many island groups seems to provide no barrier for naturalizations, indicating that dispersal of naturalized plant species is largely human mediated. Our findings have great potential to inform the development of applied conservation tools, such as watchlists.

Our results extend those of previous studies, in which the Pacific region showed the steepest slope for naturalized species accumulating per unit area (van Kleunen et al., 2015). This pattern emerges due to the strongly skewed distributions of richness and range size patterns. For example, 59% of all naturalized plant species found in the Pacific are present on the Hawaiian Islands
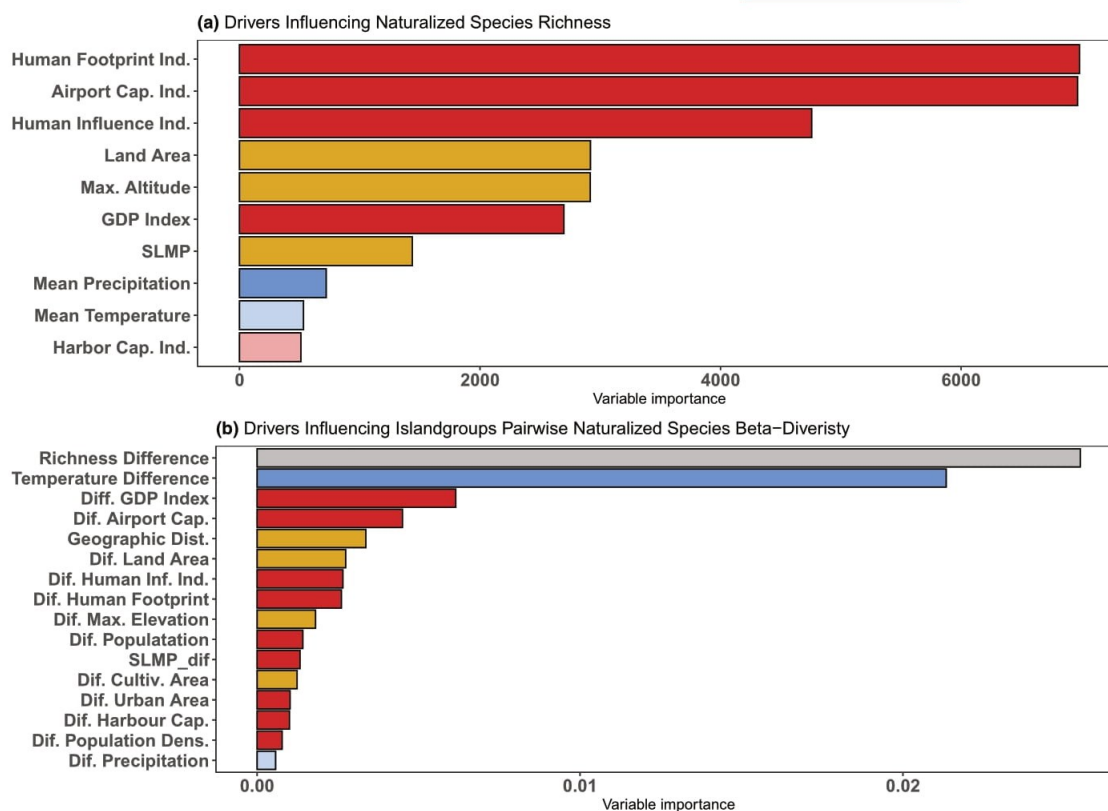
FIGURE 5 Variable importance from VSURF random forest models explaining species richness (a) and beta Simpson (b) of naturalized plant species in the Pacific. Explanatory variables are ranked by relative variable importance. Anthropogenic, biogeographic and climatic drivers are shown in red, gold and blue, respectively. Richness differences are in shown in grey. Only variables retained by the variable selection process are included. Light colours (least important) indicate that these drivers were not selected as suitable, that is not included in the calculation of the R^2, but is included in this figure to put them in a broader context

alone. We found an even more skewed distribution of naturalized plant richness across island groups than reported by Denslow et al. (2009) on 1,332 naturalized plant species. This is likely due our larger data set that includes more rare naturalized species. The four most widespread species in our data set are all associated with anthropogenic factors and disturbed habitats, including the following: *Eleusine indica* (45/50 island groups), an agricultural weed that is resistant to glyphosate (Lee & Ngim, 2000), *Cynodon dactylon* (44/50), a graminoid which is resilient to drought, salt and trampling (Fischer et al., 2008; Kaffka, 2009), *Portulaca oleracea* (44/50), a common agricultural weed, and *Euphorbia hirta* (42/50), a weed with a wide native and naturalized ranges. Other generalist species known to thrive in disturbed ecosystems, such as species of the genus *Chenopodium*, are currently rare in the Pacific, but could spread further in the future.

Pacific island groups with few naturalized plant species are populated by "common" naturalized species (i.e. these island groups have a low average rarity score), indicating a set of notorious species that are able to establish readily and are frequently transported, even to the most poorly connected places. This pattern has been observed for invasive naturalized species on islands globally (Traveset et al., 2014), and for native species (native species-rich islands have more endemic species) on tropical archipelagos (König et al., 2017) and in the Aegean archipelago (Kallimanis et al., 2010). As the processes that result in native species patterns are likely to be very different than those of naturalized species, a direct comparison of patterns of rarity for native and naturalized species in the Pacific and in other regions could provide insights into the underlying processes. Further, our result indicates that it is important and feasible to prioritize the prevention of the (further) spreading of common naturalized species on islands with currently low naturalized species richness and that anthropogenic introduction barriers such as trade by ship and plane, but also the availability of human-altered ecosystems, are very important.

We expected the Pacific region to contain more unique naturalized species compared to other regions due to its unique native floras

and potentially lower resistance to biological invasions (Atkinson & Cameron, 1993; L. Loope & Mueller-Dombois, 1989). In contrast, we found that a high proportion of naturalized plants in the Pacific are also naturalized in other regions. Neighbouring countries and some distant coastal countries (e.g. Portugal) and islands (e.g. Puerto Rico) share a large percentage of their naturalized species pool with the Pacific. Several smaller island regions also share a large percentage of their naturalized species with the Pacific (e.g. the Christmas Islands, which share 97% of their 176 naturalized species with the Pacific). This provides evidence that human activity overcomes geographic barriers (di Castri, 1989, 1990) and that more species in these regions could be exchanged with the Pacific, as saturation in the accumulation of naturalized species has not yet been reached (Seebens et al., 2017).

Global patterns of naturalized family richness are mirrored in the Pacific, with deviations likely resulting from the (sub-)tropical conditions and highly human-altered ecosystems. *Ranunculaceae* and *Rosaceae* are particularly under-represented in the Pacific, potentially because these families are most common in temperate latitudes (Watson & Dallwitz, 1992). *Convolvulaceae*, *Malvaceae* and *Meliaceae* are over-represented both in the Pacific naturalized flora and in the global naturalized flora. *Poaceae*, *Fabaceae* and *Arecaceae* are particularly over-represented in the Pacific, which may indicate either unique niche space or an overabundance of ubiquitous niche space available to those families in the Pacific (see e.g. Vitousek et al. 1987). Many naturalized species may have traits that favour their accidental and purposeful introductions by humans or their abilities to thrive in degraded or anthropogenic ecosystems (Doyle, 2001). There are many ecosystems or whole islands in the Pacific that have been degraded, altered or transformed entirely by human colonialization (Braje et al., 2017), and this may explain the over-representation of these families and highlights the association of naturalized species with human activity.

Variation in naturalized species richness among island groups in the Pacific was explained largely by human activity and to a lesser degree by island group size. Island size was linked to naturalized richness in the Pacific in a previous study (Denslow et al., 2009), but the other variables we consider here were heretofore largely unexplored in the Pacific. In a global analysis of islands, elevation and distance to the mainland were also linked to naturalized plant species richness (Moser et al., 2018). Our results highlight human activity (e.g. human footprint and airport capacity) as the main driver of non-native species richness, while biogeographic variables (e.g. land area and SLMP) play a secondary role. We could not show any influence of distance to mainland on naturalized species richness. This finding suggests that either naturalized species follow the similar pathways and thrive under similar conditions as humans (e.g. island groups with more area are more attractive for human activities and harbour more habitats that may host non-native species), and/or the presence of humans increases the availability and strength of introduction pathways (i.e. harbours, airports and trade volume) and suitable habitats (i.e. urban/agricultural/disturbed areas).

We find that island groups are compositionally similar to other island groups that are different in their species richness, GDP and area, but are similar in their mean annual temperature. Species-poor island groups are inhabited by widespread naturalized species. However, there is high variation in the beta diversity of species-poor islands groups, with some pairs having the exact same widespread species and others having completely different compositions. Species-poor island groups tend to have a nested subset of the species that are present on species-rich island groups (see also Traveset et al. 2014), and thus, pairings of species-poor with species-rich island groups have consistently high values of Simpson pairwise beta diversity. These results suggest that species dispersal likely follows a pathway by which species-poor and monetarily poor islands receive their naturalized species not directly from outside of the Pacific, but rather from dispersal from species- and monetarily rich island groups, which are in turn the initial introduction points of non-native species to the Pacific ("hubs" for invasion, as in Traveset et al., 2014). Naturalized species that arrive will be more likely to establish if they come from an island group of similar temperature, due to the high importance of niche constrains for establishment. In this context, it is interesting that mean annual precipitation was not considered relevant in our model. Temperature and other niche constraints such as maximum elevation are important factors shaping compositional similarity, while factors related to anthropogenic dispersal define richness.

Our analysis identified three island groups that were notable outliers in terms of richness and composition: Juan Fernandez, the Hawaiian Islands and the Solomon and Bismarck islands. Juan Fernandez has many naturalized species that are not found anywhere else in the Pacific. This could be due to the combined effects of its (a) unique colonization history, first being discovered by Spanish seafarers rather than Polynesians and later strengthening ties to Chile (Cuevas & van Leersum, 2001), (b) high isolation from other island groups and therefore poor connection to major trade routes, (c) unique biogeographic factors that shaped its highly endemic flora (Cuevas & van Leersum, 2001) and (d) lower temperatures (lowest in our data set). The Hawaiian Islands are the most invaded island group in the Pacific and contain many species that are not found anywhere else in the Pacific. The Hawaiian Islands are the third-largest island group, are heterogeneous in climate and altitude, are remote and have a unique colonization history shaped by Polynesians, British, Americans and Japanese. In contrast, the Solomon and Bismarck islands have large land area (largest in our data set) but are overall sparsely populated with a relatively low GDP Index. This island group might be understudied (e.g. no records in GloNAF) and/or might truly contain few naturalized species. These outliers help to provide a refined understanding of the patterns and the likely processes that generate them. The list of naturalized species on the Hawaiian naturalized plant species can serve as a preliminary watchlist for other island groups in the Pacific. Species-rich island groups such as Hawai'i might provide sources of naturalized species for other island groups in the Pacific and, together with the

consideration of environmental drivers, can serve as early warning sites. Future research could apply our results to (a) draw conclusions on how many species could naturalize in other island groups and (b) create more specific naturalization–risk assessments for problematic species.

The large number of naturalized plants in the Pacific gives reason to be worried, as some of them are, or will likely become invasive (Jeschke & Pysek, 2018; Traveset et al., 2014, sensu Blackburn et al., 2011; Richardson et al., 2000). Even if they do not become invasive, the presence of naturalized species reduces regional floristic distinctiveness through biotic homogenization (Vitousek et al., 1997). Our results highlight the human-mediated connectivity between the Pacific and other parts of the world (see also Capinha et al., 2015) and highlights potential entry points for non-native species. There are groups of naturalized species that may be particularly suited to establish in the Pacific (e.g. because they are pre-adapted to climatic conditions or have traits associated with human use or disturbed ecosystems) and identifying additional common traits of these species holds much promise for predicting future establishment. Naturalized species patterns in the Pacific are intrinsically bound to human activities, but economic growth and naturalized species richness increase do not have to be coupled in the future, as this is a human-made connection that can be mediated using human-made measures. Management strategies to prevent undesired introduction and establishment of non-native must be put in place or strengthened and the same increased global connectivity that leads to the introduction of naturalized species can also limit it (Essl et al., 2019; Pyšek et al., 2010; Seebens et al., 2015). Cooperative initiatives to prevent and manage non-native species (e.g. "The Cooperative Islands Initiative"; http://www.issg.org/cii/) could be used to create specific watchlists for the Pacific, especially for invasive species, to make screening in trade easier (SPREP, 2016; Sherley et al., 2000). In this study, we provide a comprehensive overview of patterns and drivers of naturalized species establishment in the Pacific, as a foundation for future work on the processes of naturalized species spread and on applied management of naturalized species.

DATA AVAILABILITY STATEMENT

Our data are compiled from GloNAF and PIER which are both open source. Species names and island/island group names can be found in the Table S1 and S2. We plan to publish our aggregated data set in an upcoming data publication.

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BIOSKETCH

Michael R. Wohlwendis interested in the field of plant ecology and biogeography. Changing patterns and dynamics fascinated him the most. He was specialized in non-native species and their dispersal as well as experimental restoration projects, which are often sabotaged by non-native and invasive plant species. It has always been important for him to work on an applied issue on multiple scales. This project is the result of a workshop at iDiv, and his co-authors have many different backgrounds such as demography, macroecology and community ecology, sharing an interest in invasion biology.

Author contributions: T.M.K. organized the initial workshop on this topic with M.R.W., D.C., P.W., M.W., H.S., J.S.C., D.Z. and H.K. as participants. M.R.W. and D.C. compiled the data set. M.R.W., D.C. and P.W. conducted the initial analyses. M.R.W. finalized the analysis. M.R.W. and T.M.K. wrote the manuscript. All authors contributed to the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

In Chapter 5, I will summarize the most relevant results, identify limitations, draw conclusions that transcend the individual studies, and try to find common denominators and significant differences.

Chapter 5: Synthesis

The previous chapters show a different picture of non-native species, their distributions, and reasons for this. They are conducted on hugely different scales, from 99 10 x 10 meter plots on the prairie to the over 100 million km² in the Pacific, and from a single sampling period to the analysis of data collected over decades. I investigated cover data to quantify the influence of experimental treatments on plant species as well as observational presence absence data to assess the effects of different drivers on patterns of naturalized species. I used very different statistical tools to capture the responses in a rigorous manner. And yet, despite all these differences and the widely different outcomes, the underlying questions were rather similar – how do non-native plant species behave, what influences their establishment success and what can we do to prevent unintentional naturalizations and invasions. Generalization remains challenging and is not always productive, but in aiming to reach it we get a better and more holistic picture of invasion biology.

5.1. Summary of the most relevant results

Before going further into the implications of my findings and synthesis across all my results, I will shortly recapitulate on which are, in my opinion, the most important findings of my projects.

In chapter 2, the target invasive species *Lespedeza cuneata* could successfully be managed utilizing priority effects in seeding order of grasses and graminoids as well as intense management in the first three years after seeding and nutrient addition. This is in line with other studies that show that management early in the invasions process is important to prevent establishment and dominance of invasive plants (Wittenberg & Cock 2001; Kıbıs & Büyüktahtakın 2017). However, it is clear that a ceasing of all management after three years is also not possible, and that some low-level management will be required to prevent *Lespedeza cuneata* from becoming dominant (sensu Kıbıs & Büyüktahtakın 2017). However, if the long-term prospect is low-input management, that this still poses a highly efficient management practice. Applying this strategy to a whole area will most likely have an even larger success rate, as in our experiment propagule sources were always in close proximity to experimental plots. *Lespedeza cuneata* seems to facilitate secondary invasions either because it works as an ecosystem engineer promoting the establishment of other non-native species or because the same conditions that favour its dominance also favour secondary naturalized species establishment. Some seeded species had problems establishing, and further use of priority effects or other manipulations, or later inoculated introduction (Middleton & Bever 2012; Weidlich *et al.* 2021) will be required to truly restore native prairies, but this experiment provides evidence of success in the first step towards this goal.

In Chapter 3, I documented the challenging process of harmonizing data to create a new, most complete database for the **Pac**ific **I**ntroduced **Flora**. I suggested ways of standardizing different parameters, such as species name using the LCVP, island name, phylogeny, invasion status, native status, and cultivation status. This database has many possible applications for science and practice.

In Chapter 4, I utilize PacIFlora to ask how many and which naturalized species are present in the Pacific, how these are shared within the Pacific and with non-Pacific nations, why some island groups have more naturalized plant species than others, and why some island groups share more naturalized plant species than others. There is a vast number of naturalized plant species in the Pacific, belonging frequently to plant families known to contain many naturalized species, but also to families common in tropical regions. Species are commonly shared with neighbouring regions, but also other coastal and tropical nations. Island groups with more naturalized species are inhabited by over-proportionately rare naturalized species. Naturalized species poor islands are inhabited by a

nested subset of the species found on naturalized species rich islands that are often larger in size and have higher levels of human influence. Together, these findings lead me to the conclusion that human-mediated dispersal routes in the Pacific cause species to be first moved from outside of the Pacific to more developed island groups. After that, they are moved to less anthropogenically modified and less accessible groups from there. Which species are naturalized is not random but rather is strongly influenced by local temperature. The clear results provided by the random Forest analysis show that forecasting introductions is possible and given the high number of potentially introducible species, this is also very necessary.

5.2. Limitations and recommendations for future research

As all scientific research projects, this study has limitations. But, in this case I think that the limitations are not only interesting in pointing out what cannot be said, but also why this is the case and how this should be engaged in future research projects. In the experimental study on *Lespedeza cuneata* and plant community response (Chapter 2), the main limitations are:

1) Nutrient addition had a negative effect on *Lespedeza cuneata* cover in prairie restoration and no effect on native species cover in general, but that does not imply that there were not any, potentially rare and native species, which did not decrease in cover with nutrient addition. Future research could quantify the detailed demographic responses of native species to gain a mechanistic understanding of the effects of treatments on vital rates and population dynamics of target native species.

2) Communities were different depending on the seeding order, but that does not imply that any community valuable for conservation was created. Moving forward from this point, the created systems could be analysed for their ecosystem services and value for conservation efforts, also with regards to their suitability for the inoculated introduction of additional rare native species.

3) Treatments were successful in limiting *Lespedeza cuneata* cover, but this effect may not last indefinitely, so management may need to be continued. Long-term monitoring combined with new experimental treatments on different management techniques could give a longer-term perspective of prairie restoration.

In macroecological study of naturalized plants in the Pacific, the following limitations (Chapter 4) became obvious:

1) Some island groups (e.g., the Solomon & Bismarck Islands) have low numbers of naturalized species compared to their size, but this does not imply that this will be the case in the future or that these islands are in fact less invaded (i.e., because one single species could cover an entire island). Further, some islands may only appear to have fewer species because that have not been intensively surveyed or due to disagreement among local experts on the naturalization status (McGeoch *et al.* 2012). Future research could improve our understanding through long-term monitoring, monitoring of abundance rather than presence/absence, and targeted surveys in poorly surveyed island groups.

2) Geographic distance to mainland does not matter in general for naturalized species richness in the Pacific, but that does not mean that this can be generalized for non-Pacific regions (see Moser *et al.* 2018) or that distance plays no role for intra island/archipelago dispersal. Future research could differentiate for which species groups or under which circumstances geographic distance is relevant and what the underlying reasons for this are (e.g. method of transport).

Other limitations, such as the uncontrollability of stochastic dispersal processes between plots in the prairie experiment or potential false reports in PacIFlora, exist, but I do not evaluate those shortcomings as deviation from the norm for ecological studies nor can I provide any recommendations for how to avoid them in the future.

Further recommendations for research include an in-depth biodiversity analysis for the prairie experiment. Preliminary analysis suggest either highly complex or no effects of the treatments and *Lespedeza cuneata* on common diversity indicators (results not shown). Pursuing the field of priority effect in restoration and community assembly is very promising (see Weidlich *et al.* 2017; Stuble & Young 2020). For the pacific, I suggest species distribution modelling for common and potentially dangerous species and the implementation and validation of PacIFlora into and through local management. This is made possible by PacIFlora being open source.

5.3. Implications of this study

The prairie experiment (Chapter 2) was designed to understand the importance of priority effects and to inform on specific applications for the restoration of an endangered ecosystem in the context of plant invasion. In a global meta-analysis, Weidlich *et al.* (2021) looked at my study and 42 others and concluded, that priority effects play a generally important role in restoration, and highlighted my study as a model that should be applied for future research in data deficient ecosystems. Stuble & Young (2020) discussed my results in the context of theirs, which demonstrated that some types of priority effect can increase invader presence. Fukami (2015) suggested that priority effect experiments in the context of restoration can teach us about the importance of priority effects in general for community assembly. Further research and synthesis in this field is needed in order to understand which species can profit from priority effects under which circumstances (e.g. density, seasonal differences) and how this knowledge can be used to reach desired restoration outcome in various ecosystems. Using my study in similar frameworks, but with more data collection on particular groups of species, could inform on other important topics, such as invasional meltdown, succession analysis, and establishment of target native species in restoration projects. These would be very promising approaches to improve our understanding of ecological processes.

The macroecological study in the Pacific (chapters 3 and 4) has two important scientific implications: First, the differences and similarities to other studies, and second, the notion of what is possible when harmonizing databases. My research updates research conducted by Denslow and colleagues (2009), confirming their patterns and expanding to show potential causality of patterns. For example, naturalized species rich island groups are not rich because of their large land mass, but because larger island groups have a higher human influence. My results confirm that some plant families are notorious in contributing naturalized species (Pyšek *et al.* 2017), and that this is even more pronounced in the Pacific. I can show that in the Pacific, geographic distance to the mainland becomes irrelevant for naturalized plant species richness, despite the fact that globally, isolated islands have more naturalized species (Moser *et al.* 2018). I demonstrated that over 90 % of the variance in beta-diversity can be explained by a few drivers, which is especially important for species distribution modelling, as it shows that meaningful predictions can be made with this approach. These results, together with an open-source database increase the possibilities to asked more precise questions in the future. In particular, future research on native species, traits, and island group floras utilizing my data has a great potential to improve scientific insight within and beyond the Pacific.

Producing results applicable to applied management was the largest motivation for this study. Indeed, there are many outcomes that can be incorporated into practice. In prairie restoration, the goal of the restoration project matters in how my results can be applied. If an endangered or rare

species should be established, my research clearly shows that this will require additional treatments. Many of my seeded species, especially iconic prairie species like *Liatris pycnostachya* did not establish in any of my treatment combinations. However, I could show that the success of seeded native species as well as their invasive adversaries is often determined by early establishment and priority effect. This is in line with the findings of other researchers (Stuble & Souza 2016; Werner *et al.* 2016; Weidlich *et al.* 2017, 2021; Stuble & Young 2020). As giving only forbs a head start over grasses seems to open windows for invasion of *Lespedeza cuneata*, seeding density, reseeding after fire and seeding in monospecific patches seems promising to establish more forb species (Reinhardt Adams & Galatowitsch 2008; Eiswerth *et al.* 2009; Seahra *et al.* 2019). Given the importance of priority effects found in our study, transplantation of native species early in the restoration seems like a promising approach to be considered in future research and in practice. This could be accomplished by "artificially" establishing rare species by transplanting them, often with inoculated soil, as the soil microbial community may be essential for the establishment of some rare species (Suding *et al.* 2013; Adu-Oppong *et al.* 2020; Humphries *et al.* 2021). Those transplantations do not necessarily need to take place at the beginning of a restoration project, but could also be attempted at a later stage, where parts of an intact, but target species poor prairie stands could be modified (e.g. tilled, fertilized or inoculated etc. before transplantation of adult specimen) to host rare species. The accumulation of naturalized species under the presence of other naturalized species, sometimes referred to invasional meltdown, could be self-reinforcing and must therefore be prevented (Simberloff & Holle 1999). The risk of a "secondary invasion" is always present when removing the main invader (Pearson *et al.* 2016), but I found no naturalized species profiting from the absence or low abundance of *Lespedeza cuneata*. Using priority effects and focusing most available resources on intense management in the early years of a restoration will be more successful in managing *Lespedeza cuneata*, but management should be continued, most cost-efficiently on a three year base as suggested by Bütüktahtakin *et al.* (2015). Maintaining and restoring a prairie ecosystems holds not only ecological but also cultural value. However, prairie management is a challenge even without invasive species to control or vulnerable native species to conserve, as introducing a burning regime that mimics historical conditions and/or the presence of large herbivores are often in conflict with human interests (Dickman 2010). Although my experiment did not result a natural prairie ecosystem, the created system is relatively easy to establish can serve as a first step in restoration to a more natural, native prairie species rich ecosystem.

Lespedeza cuneata is a well-studied species and tests of different control methods are available (Eddy & Moore 1998; Koger *et al.* 2002; Eddy *et al.* 2003; Schutzenhofer & Knight 2007; Schutzenhofer *et al.* 2009; Allred *et al.* 2010; Dudley & Fick 2013). However, in the Pacific there are thousands of plant species capable of establishing (van Kleunen *et al.* 2015), hundreds of which have invasive potential, and many of these are poorly researched. Research is needed on this immediately, before these become widespread and abundant and more difficult and resource demanding to manage. Currently, just monitoring the presence of thousands of species is difficult (Finnoff *et al.* 2007). Mitigating non-native species introduction in general is as important as developing methods to manage one invasive species. A pragmatic approach, which would already be feasible with my database and research results, would be to focus on species that are a) already widespread b) fall into categories identified to indicate spreading likelihood and/or c) are recorded as invasive in some locations. Those species can be put on Pacific-wide watchlists. As a next step, the islands most vulnerable to invasion can be identified, and Pacific or non-Pacific areas/islands with similar climatic conditions can be compared to quantify their naturalized species composition and their potential for species exchange in the future. All species found on one island, but not the other, can be put island or even island pair specific watchlists. Those watchlists can be consulted when trade between two islands occurs.

Nevertheless, methods developed on the prairie are valid strategies for the Pacific and the other way round, depending on the context. Utilizing priority effects is something worth looking into in Pacific restoration projects. Likewise, watchlists based on climatic and compositional similarities can help prevent future invasions in the prairie ecosystems. Desired outcome should guide towards the questions asked and methods implemented. So, if native species presence and abundance is the goal, identification and management of naturalized species that are directly harmful to those native species should be prioritized, and special protected areas can be established.

Paragraph 10: Final remarks

Understanding the patterns and processes involved in non-native species dispersal, establishment, persistence, and effect on the community requires considering multiple spatial scales and metrics. This document unites insights from projects asking similar questions at very different spatial scales. At a small scale, priority effects and abiotic factors (such as nutrients) can dramatically shape the abundance of the invader and the composition of the community. At the regional scale, diversity of naturalized species on island groups is determined by anthropogenic factors, whereas abiotic factors such as temperature play a strong role in explaining beta-diversity. In both studies, I have adequate data to draw applied conclusions that are useful for practice. I hope that my research will stimulate further scientific research and topic-oriented synthesis, help with designing management for the invasive plant *Lespedeza cuneata* using priority effects and fertilization treatments that do not negatively impact the native plant community, and support the design of restoration practice and targeted trade supervision in the Pacific.

Acknowledgements

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Wohlwend, M.R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., *et al.* (2021b). Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. *Divers. Distrib.*, 1–14.

Wohlwend, M.R., Schutzenhofer, M.R. & Knight, T.M. (2019). Long-term experiment manipulating community assembly results in favorable restoration outcomes for invaded prairies. *Restor. Ecol.*, 27, 1307–1316.

Appendix

A) Information on supplementary material

Supplementary material of publications is too large to be printed here (e.g. a 33.000 row table) and therefore can be found on the journal's website or by request from the author. R code and additional, unpublished graphs and material can be requested from the author. Text and figures can be found on the attached CD.

B) Curriculum Vitae

Nationality: German
Date of Birth: 15.07.1990
Place of Birth: Eichstätt (Bavaria)

Education

Since 08/2016: Research Officer Martin-Luther-Universität Halle-Wittenberg/ German Center for integrative Biodiversity Research Halle - Jena - Leipzig (iDiv), Workinggroup Spatial Interaction Ecology (SIE), Prof. Tiffany Knight. Topic: Distribution of non-native species in the context of restoration and management

10/2013 – 05/2016: Master studies at the University of Bayreuth, Global *Change Ecology M.Sc*

Thesis topic: Regeneration of the Northern Hemlock (*Tsuga heterophylla*) in Bavaria

10/2010 – 01/2014: Bachelor studies an der University of Bayreuth, *Geoökologie B.Sc.*

Thesis topic: Drought resilience in *Aeonimum canariense var. palmense*

09/1997 – 07/2010: Willibald-Gymnasiums Eichstätt

Additional Job Experience

Since 2021: Scientific Coordinator RTG 2123 ConFoBi, Chair of Wildlife Ecology and Management, University of Freiburg

06/2016 - 07/2016: Scientific Employee at the Environmental Research Centre (UFZ) Leipzig. Tasks: Ecological fieldwork

04/2015 - 07/2015: Scientific Assistant at the Ecological-Botanical Garden of Bayreuth (ÖBG). Tasks: Fieldwork, Statistical Support

01/2015: International Biogeography Society Conference. Task: Session helper

11/2011 – 01/2015: Tutor at the Chair for Biogeography

09/2011 – 11/2011:   Student Assistant Biogeography: Lab assitant

Conferences, Schools, Workshops (Selection):

Since 2016:   yDiv Graduate school

08/2019:   iDiv Summerparty (Main Organizer, 120 Guests)

09/2018:   sDiv Workshop Invasive Species in the Pacific

06/2018:   PopBio Halle (Poster)

09/2017:   EMAPI Conferenz Portugal (Presentation)

01/2014 – 06/2014:   La Palma Summer School

Internships (Selection):

02/2018-05/2018:   yDiv Stay Abroad. Honolulu, Oʻahu, Hawaiʻi (Greenhouse Experiments)

07/2014 – 08/2014:   Bureau for Nutrition, Agriculture and Forestry Ingolstadt. Tasks: Public relations

03/2012 – 05/2012:   Bureau for Forestry Kipfenberg (Revier Rupertsbuch), Bayerische Staatsforsten. Tasks: Forest inventory analysis, tree planting

Additional Skills:

Languages: Beginner	German: Native Speaker	Spanish: Beginner	Italian:
	English: business fluency	Latin: Latinum	
PC:	R (Expert in Statistical Programming), Microsoft Office, Esri ArcGIS, QGIS		
Trainings:	Intensive coaching for future leaders (ENB), yDiv courses in the field of statistical analysis, communication and presentation as well as biodiversity science		
Mobility:	Car (Offroad experience), experienced in working in rough terrain		

Voluntary work & social projects:

09/2017 – 11/2019:   PhD Representative yDiv Board

09/2016 – 09/2018:   Solidaric Agriculture "Kleine Beete" Leipzig

01/2011 – 03/2016:   Share & Care Bayreuth: Administrative work

01/2014 – 02/2016:   TransitionHaus Bayreuth: Founding Member

07/2015 – 09/2015:   Edible City Bayreuth: Technical Support

Hobbies:

Hiking, (ethno)botany, gardening, woodworking

C) List of publications and conference participations

Publications of this dissertation

(Wohlwend *et al.* 2019, 2021a, b)

Wohlwend, M.R., Schutzenhofer, M.R. & Knight, T.M. (2019). Long-term experiment manipulating community assembly results in favorable restoration outcomes for invaded prairies. *Restor. Ecol.*, 27, 1307–1316.

Wohlwend, M.R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., *et al.* (2021). Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. *Divers. Distrib.*, 1–14.

Wohlwend, M. R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., *et al.* (2021a). Data Descriptor: Pacific Introduced Flora (PaciFLora). *Biodivers. Data J.*, 9.

Conference talks

Wohlwend, M.R., Schutzenhofer, M., Knight, T. 2017: Management of *Lespedeza cuneata* in an experimental prairie restoration. International Conference on Ecology and Management of Alien Plant Invasions (EMAPI) Lisbon, Portugal.

Wohlwend, M.R., Schutzenhofer, M., Knight, T. 2018: Management of *Lespedeza cuneata* in an experimental prairie restoration. 4th iDiv Conference, Leipzig, Germany.

Conference posters

Wohlwend, M.R., Schutzenhofer, M., Knight, T. 2017: Management of *Lespedeza cuneata* in an experimental prairie restoration. Population Biology in a changing World, 30th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GFÖ), Halle / Saale, Germany.

D) Authors' contributions

Chapter 2: Wohlwend, M.R., Schutzenhofer, M.R. & Knight, T.M. (2019). Long-term experiment manipulating community assembly results in favorable restoration outcomes for invaded prairies. *Restor. Ecol.*, 27, 1307–1316. Design: Tiffany Knight (65%), Michelle Schutzenhofer (25%), Michael Wohlwend (10%). Analysis: Michael Wohlwend (70%) Tiffany Knight (20%) Michelle Schutzenhofer (10%). Writing: Michael Wohlwend (76%), Tiffany Knight (19%), Michelle Schutzenhofer (5%).

Chapter 3: Wohlwend, M. R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., Dawson, W., Essl, F., van Kleunen, M., Pergl, J., Pyšek, P., Space, J., Thomas, P., Knight, T. (2021). Data Descriptor: Pacific Introduced Flora (PaciFLora). Biodiversitsy Data Journal, 9.: Design Tiffany Knight (37%), Dylan Craven (10%) (Workshop initiators), Michael Wohlwend (38%), Patrick Weigelt (9%), Hanno Seebens (2%), Marten Winter (1%), Holger Kreft (1%), Damaris Zurell (1%), Juliano Sarmento Cabral (1%) (all

workshop participants). Analysis: Michael Wohlwend (90%), Dylan Craven (5%), Patrick Weigelt (5%). Writing: Michael Wohlwend (70%), Tiffany Knight (19%), all other authors each ~1%.

Chapter 4: Wohlwend, M.R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., Zurell, D., Sarmento Cabral, J., Essl, F., van Kleunen, M., Pergl, J., Pyšek, P., Knight, T.M. (2021). Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. Divers. Distrib., 1–14. Design: Tiffany Knight (35%), Dylan Craven (15%) (Workshop initiators), Michael Wohlwend (35%) (Development and refinement of hypotheses and questions), Patrick Weigelt (9%), Hanno Seebens (2%), Marten Winter (1%), Holger Kreft (1%), Damaris Zurell (1%), Juliano Sarmento Cabral (1%) (all workshop participants). Analysis: Michael Wohlwend (85%), Dylan Craven (8%), Patrick Weigelt (7%). Writing: Michael Wohlwend (75%), Tiffany Knight (14%), all other authors each ~1%.

E) Eigenständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit mit dem Titel " Plant invasions at different scales - two representative case studies" bisher weder an der Naturwissenschaftlichen Fakultät I der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde. Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne unzulässige fremde Hilfe verfasst, sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um die Erlangung eines Doktorgrads beworben habe.

Kirchzarten, den 28.02.2021   Michael Rudolf Wohlwend