

Interactions Among Invasive Plants: Lessons from Hawai'i

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Abstract

Most ecosystems have multiple-plant invaders rather than single-plant invaders, yet ecological studies and management actions focus largely on single invader species. There is a need for general principles regarding invader interactions across varying environmental conditions, so that secondary invasions can be anticipated and managers can allocate resources toward pretreatment or postremoval actions. By reviewing removal experiments conducted in three Hawaiian ecosystems (a dry tropical forest, a seasonally dry mesic forest, and a lowland wet forest), we evaluate the roles environmental harshness, priority effects, productivity potential, and species interactions have in influencing secondary invasions, defined here as invasions that are influenced either positively (facilitation) or negatively (inhibition/priority effects) by existing invaders. We generate a conceptual model with a surprise index to describe whether long-term plant invader composition and dominance is predictable or stochastic after a system perturbation such as a removal experiment. Under extremely low resource availability, the surprise index is low, whereas under intermediate-level resource environments, invader dominance is more stochastic and the surprise index is high. At high resource levels, the surprise index is intermediate: Invaders are likely abundant in the



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environment but their response to a perturbation is more predictable than at intermediate resource levels. We suggest further testing across environmental gradients to determine key variables that dictate the predictability of postremoval invader composition.

1. INTRODUCTION

Over the past 30 years, recognition of the widespread nature of invasive species has made the study of biological invasions an integral part of ecological research. The study of invasive plants has provided a plethora of insights into the factors controlling community structure, local population dynamics, and the role individual species have in controlling the properties of entire ecosystems (D'Antonio & Vitousek 1992, Sax et al. 2007, Vitousek 1990). Yet even though plant invaders are accepted as a part of most ecosystems (Hobbs et al. 2006), individual species are often managed or studied in isolation of other invaders within those same systems, with potentially detrimental consequences (Pearson et al. 2016). For example, weed biological control studies are highly target specific and have demonstrated that single-species control and management can lead to other invasions, often with dire outcomes (e.g., Campbell & McCaffrey 1991, Chikwenhere 1994). In ecological studies, the focus on a single invader has been prevalent despite recognition that initial invaders can facilitate later invaders (Richardson et al. 2000) and might lead to invasional meltdown—i.e., the co-opting of community succession toward complete invader dominance (Simberloff & Von Holle 1999). Together, these observations suggest that interactions among invasive plant species need to be better understood.

In this age of biotic homogenization, almost every ecosystem has multiple invaders within and across trophic levels (Kuebbing et al. 2013, Olden 2006). For plants, the extent to which early arrivers facilitate, outcompete, or inhibit later arrivers has been a fundamental question in ecological succession (Connell & Slatyer 1977), but one that has not been widely applied to multiply invaded ecosystems. The diversity of nonnative plants in most ecosystems and the many conditions that can promote plant invasion suggest that the influence of early-establishing nonnative species on later species or on future ecosystem states will depend strongly on context. Although examples of proposed facilitative interactions and invasional meltdown garner significant attention (Green et al. 2011, Jeschke et al. 2012), other mechanisms are also likely to influence subsequent invasions and invasive plant interactions. For example, several studies demonstrate that initial plant invaders exert priority effects, suppressing later invaders such that their removal allows these later invaders to become abundant (e.g., Cabin et al. 2002, D'Antonio & Mack 2001, D'Antonio et al. 2001a). In contrast, a recent meta-analysis showed that weak competitive interactions between invasive plant species in the face of strong competitive effects on native species leads to apparent facilitation between invasive plant species (Kuebbing & Nuñez 2016). Here, secondary invasions occur when an established invader influences the abundance of other invaders through either facilitative or priority effects. In the latter instance, removal of the primary invader should lead to an increase in the abundance and dominance of the later (secondary) invaders.

The experimental removal of invaders thus allows researchers to dissect the influence of a species in terms of its competitiveness and potential for facilitation, and provides insights into recovery or secondary invasions that may occur after the abundance of initial invaders changes (Diaz et al. 2003, Guido & Pillar 2015, Zavaleta et al. 2001). Yet Pearson et al. (2016) found that only 29% of invasive plant management studies provided data on secondary invasions; i.e., most removal studies did not consider the greater community context in which manipulations were conducted. Likewise, Kuebbing et al. (2013) found that of 153 studies on plant invader

Invasive species:

nonnative species that colonize ecosystems with native species, form persistent populations, and have a significant ecological impact on community structure or ecosystem functioning

Priority effect:

a species that colonizes before other species and prevents subsequently arriving species from establishing

Facilitation:

the process by which one species alters environmental conditions so that they are more favorable for other species

Secondary invasion:

when one ecologically important, well-established (primary) invader influences the abundance of a second or third potentially important invader via either facilitation or priority competition

impacts, only 31% considered more than one invasive species despite widespread acceptance of multiple invasions in single systems. The result of studying or managing invaders in isolation of one another is therefore a lack of predictability of the direction of community development over time, particularly in response to natural perturbations such as hurricanes and droughts or human-driven perturbations such as targeted species removal.

Understanding the general principles of species interactions and factors controlling the structure of invaded plant assemblages through careful evaluation of case studies, particularly those that have involved experimental manipulations of invasive species, is one way to help build a predictive framework for the management of multiply invaded ecosystems. This in turn may help allocate conservation funds in a more targeted fashion: Some ecosystems may need more pretreatment prior to invader removal because of anticipated secondary invasions, whereas others may need more postremoval follow-up.

In this review, we synthesize invasive plant removal studies and long-term observations in three Hawaiian ecosystems to build a general framework for the management of multiply invaded systems. We focus on whether the removal of initial invaders (sometimes one species, sometimes multiple species) from three forest ecosystems that vary in rainfall (mean annual precipitation 625, 1,500, and 3,300 mm; **Figure 1**) led to further invasion or native recovery, and discuss whether the responses could have been anticipated. Hawaiian ecosystems are ideal for this synthetic exercise because they have been reasonably well studied and occur over relatively sharp climatic gradients that represent a variety of resource conditions (Vitousek 2004). In addition, the pool of potential invaders is large (Van Kleunen et al. 2015). These systems are also relatively tractable in terms of native species composition, in contrast to many tropical mainland systems (Ostertag et al. 2014).

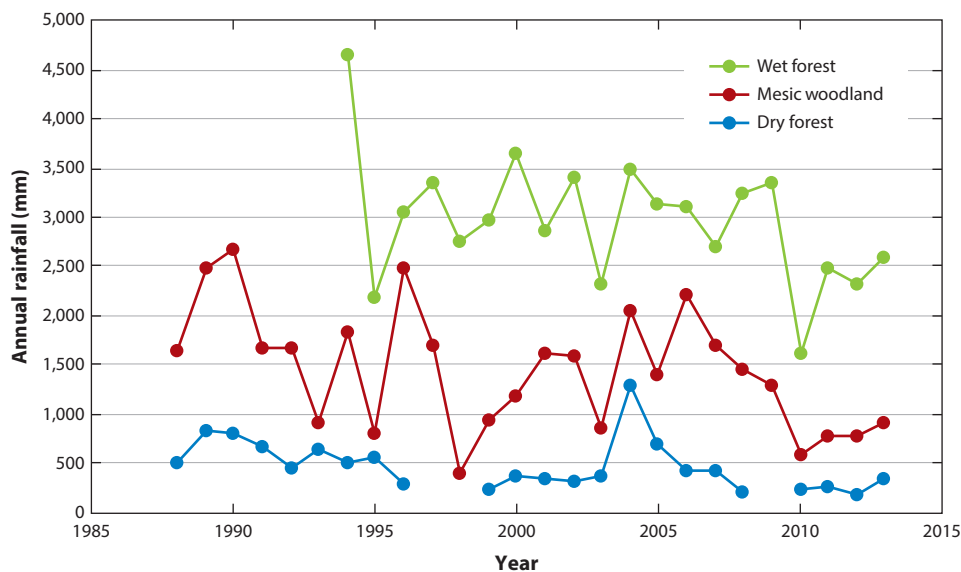


Figure 1

Annual rainfall at three sites on the island of Hawai'i. Note the interannual variability at all sites. Coefficients of variation were 21.9, 42.5, and 53.8 for the wet, mesic, and dry forests, respectively. Raw data were provided by the Hawai'i Department of Fish and Wildlife, US Forest Service (USFS), US National Park Service, Western Regional Climate Center, and National Oceanic and Atmospheric Administration. A gap in dry forest rainfall data between 1999 and 2003 was filled by data from a nearby USFS weather station at Kaupulehu ($R^2 = 0.935$ for correlation of years both stations were available).

Surprise index:

a general index indicating whether a secondary invasion will occur after the decline or removal of a primary invader or group of invaders

Although soil age can vary greatly across Hawaiian ecosystems (Vitousek 2004), our three study areas are on relatively young lava flows (<3,000 years) and thus should be similar in terms of nutrient limitation. Overall, these sites represent a straightforward setting in which to evaluate when invaders and their management are expected to interact and influence the outcome of species removal or ecosystem perturbation (e.g., drought). In some sense, they represent an extreme in how multiply invaded systems may behave across different climatic conditions.

2. CONCEPTUAL BACKGROUND

2.1. Defining the Group of Invaders

Of the sometimes dozens of nonnative species present in a particular ecosystem, few of them have the potential to substantially alter community and ecosystem processes (Jeschke et al. 2012). In this synthesis, we focus on nonnative plant species that enter native-dominated systems and have the potential to transform (Richardson et al. 2000) those ecosystems through competitive or ecosystem-process impacts. These species are likely to become dominant or codominant and to persist long enough to be of management concern. We refer to these species as invasive species. We recognize that there is no consistent or quantitative metric for what a significant ecological impact is, but we focus on the circumstances in which early invaders of significance to management are likely to interact with other invaders of management importance.

2.2. Framework and Hypotheses

That the removal of one invader can lead to the emergence of other invaders with strong ecological impacts has been discussed in the invasive animal literature (e.g., Caut et al. 2009, Zavaleta et al. 2001). Caut et al. (2009) used the term surprise effect to describe instances in which the removal of an invasive animal led to an unexpected (and unwanted) ecosystem-scale response. Here, we use a similar term, surprise index, to describe the extent to which a system's response to a perturbation, with regard to newly appearing invasive plants that are also of management concern, is predictable versus stochastic, the latter being equivalent to a surprise (**Figure 2**). We discuss below reasons why systems may be more or less predictable depending on whether persistent secondary invasions emerge after the decline of initial invaders via environmental change, or from management actions.

We propose that environmental harshness, defined here as extreme resource limitations, particularly during the time available for plant establishment, in combination with the regional species pool, is critical for predicting invader persistence or compositional change (Didham et al. 2005). Harsh environments are those where the occurrence of abiotic conditions that create rapid plant mortality (e.g., frost, extreme heat, and drought) is common. Evaluations of factors influencing ecosystem susceptibility to plant invasion support the idea that abiotic conditions influence susceptibility to invasion, with more environmentally harsh sites having lower numbers of invaders (D'Antonio et al. 2001b, Funk 2013, Stohlgren et al. 2003, Stohlgren et al. 2008, Zefferman et al. 2015). Similarly, in a meta-analysis of invader versus native species' responses to global change factors, Sorte et al. (2013) found that drought tended to favor native over nonnative species in terrestrial experimental studies. Invaders that can become abundant in abiotically severe sites must be stress-tolerant (Funk 2013) and may occupy portions of the habitat not accessible to other species in the system (e.g., Shafroth et al. 2008). When this is true, their removal, from at least those portions of sites, may not result in further invasion (or native recovery) because the likelihood of other strongly stress-tolerant nonnative species being present and able to respond rapidly is low owing to poor growing conditions (e.g., Harms & Hiebert 2006). Under extreme resource

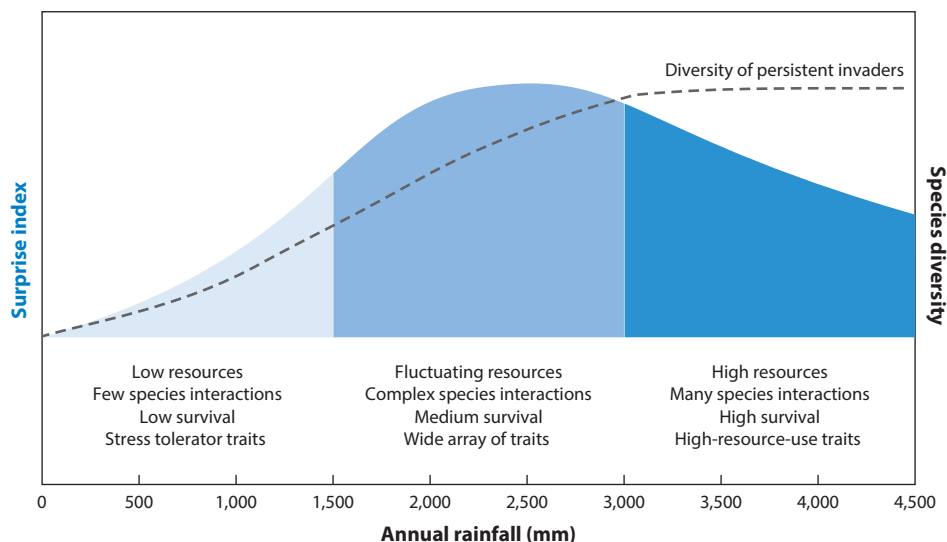


Figure 2

Conceptual model of how plant community composition responds to perturbation. Under low-resource conditions (mean annual rainfall in the Hawaiian case studies described in the text), few invaders persist because the environment favors only species with stress-tolerant attributes, but the surprise index is low because this suite of species was anticipated. Under high-resource conditions, the surprise index is a bit higher, given the high diversity of potentially persistent invaders (*dashed line*). However, intense interspecific competition among many colonizing species with traits favoring fast growth is expected, leading to no single species strongly dominating. In contrast, under intermediate and fluctuating resources, the outcomes of competition in terms of species and functional trait diversity of invaders are more difficult to predict; thus, the postperturbation community composition can be surprising. Consideration of the surprise index before invasive species biomass is manipulated can lead to a more targeted management approach.

limitation, functional trait diversity among both persistent invaders and native species may be low, as stress tolerance is a key feature of persistence in these systems (Didham et al. 2005). Funk (2013), however, cites examples of high functional diversity in some low-resource environments. Nonetheless, we argue that low-average site productivity, where extremely harsh establishment conditions are the norm, results in an overarching importance of stress tolerance. In these stressful environments, perturbations of invaders result in a low surprise index when an abundant invader is removed (**Figure 2**). In addition, low productivity or capacity to accumulate biomass in these dry systems reduces the likelihood that successful invaders will be from more energy-requiring functional groups (i.e., that trees will be able to invade). Barbosa et al. (2017) termed this concept the gross primary productivity (or GPP) index, in which the growth of invasive species is related to the productivity of the host plant community. If secondary invaders respond positively to the removal of a primary invader in harsh habitats, managers may have ample time to manage or control the secondary invaders because they should have low population (and individual) growth rates (Funk & Vitousek 2007). We summarize research in an extremely hot, water-limited, dry tropical forest environment as an example of this setting.

Environments with resource pulsing within years and high variability in resource delivery among years (**Figure 1**) may select for higher-than-expected functional trait diversity and lead to initial invasion via coexistence mechanisms (Chesson et al. 2004, Funk 2013, MacDougall et al. 2009). Fast-growing invasive species in pulse-driven desert sites, for example, may take

advantage of resource pulses to germinate and grow, and many are annuals [e.g., *Bromus tectorum* (cheatgrass) and *Bromus rubens* (red brome), two Mediterranean grasses that have invaded western North America deserts]. The dominance of annual or short-lived nonnative plant species across years likely depends on the temporal sequence of high rainfall years (Levine & Rees 2004) and the existence of mechanisms such as positive litter feedbacks that allow for dominance over time (D'Antonio et al. 2001b). The extent to which plant invaders interact with each other in systems that are strongly driven by resource pulses and where invaders are largely annuals or short lived is poorly studied. Such short-lived invaders are largely lacking in Hawaiian ecosystems (discussed below). Yet resource pulses are common in dry and mesic environments, and managers should be alert to secondary invaders that may exploit these short-lived resource bursts by being faster-germinating and quicker-growing species, or by being stress-tolerant perennials that establish during high-resource years and then persist through harsh years. Such invaders may be more likely as they move from an extreme low-resource environment to a more moderate one (**Figure 2**). We use a seasonally dry mesic woodland in Hawai'i to demonstrate the complexity of interactions that can occur under moderate yet variable environmental conditions.

In contrast to strongly abiotically controlled environments, environments with high water and nutrient resource availability should support a broad group of nonnative and native species, and the removal of initial invaders should result in scramble competition among a wide array of native or nonnative species for open resources, particularly light. Weither & Keddy (1995) refer to these settings as ones in which competitive adversity controls who wins in competition. Priority effects are also important in these settings. Traits that lead to invader success are typically those associated with rapid colonization, height growth, and light acquisition (Funk 2013, Van Kleunen et al. 2010). In such settings, multiple nonnative species may co-dominate and many invasive species will likely increase in response to the removal of one or more invaders. Managers should anticipate the ready arrival and rapid increase of a broad taxonomic array of invaders, particularly if the composition of the surrounding vegetation is well known. Several studies also suggest that new species buried in the seed bank but not in the adult vegetation may occur under these types of environmental conditions (Cordell et al. 2009, Drake 1998). Given the rapid response of the plant community, we propose a surprise index lower than that in mesic environments, even if the exact species to become dominant is unpredictable (**Figure 2**). The predictability/surprise is in the likelihood of invasion, dominance, and persistence, not in the exact species composition. In addition to expecting many species of invaders, managers should anticipate that the time period for easy control will be short because of good growing conditions, assuming the landscape is full of propagule sources. Pretreatment reduction of propagule sources may be an important management strategy. We use a lowland wet forest in Hawai'i to demonstrate how strong competitive effects lead to no single dominant invader.

The conceptual model we present in **Figure 2** is rooted in the fluctuating resources hypothesis (Davis et al. 2000), which predicts that ecosystems with strong resource availability pulses that create opportunities for establishment will be more susceptible to invasions than ecosystems that are more stable (Parepa et al. 2013, Rejmánek 1989). All ecosystems experience resource pulses (Yang et al. 2008), and our model stresses their frequency as well as the background (average) rainfall and potential productivity. For example, although resource pulses play a strong role in influencing the dynamics of plant invasions in very dry environments, these invasions are on a short timescale (Hobbs & Mooney 1991). One or two years of high rainfall can enhance the annual grass *Bromus hordeaceus* on harsh serpentine soils in California, but its dominance is lost in drought years (Hobbs & Mooney 1991). Many researchers have argued that the diversity and stability of invasive plants in dry systems depend on whether limiting resources are fixed or variable and on the frequency of catastrophic events for seedling survival, which may be annual during

typical years in a harsh setting (Johnstone 1986). Thus, where an ecosystem falls in terms of its surprise index is rooted in the quantity and predictability of resource pulses and in how these pulses relate to the background potential for productivity (Figure 2).

3. CASE STUDIES OF HAWAIIAN SYSTEMS

3.1. The Need for Invader Removal in Hawai'i

With approximately 90% of the terrestrial biota and 25% of the marine biota endemic (Ziegler 2002), Hawai'i is a global biodiversity hot spot (Myers et al. 2000). Yet over half of the flora is considered nonnative (Wagner et al. 1999), and costs associated with invasive species within Hawai'i are extreme (Pimentel 2011). Many of Hawai'i's ecosystems have been affected by invasive ungulates, including cattle, sheep, goats, deer, and pigs. The impacts of these animals on plant communities have been reviewed elsewhere (Leopold & Hess 2017), but ungulates have generally had negative effects on native biota in Hawai'i and often help facilitate invasion by exotic grasses (Leopold & Hess 2017, Loope & Scowcroft 1985). The degree to which native species recover after grazer removal seems to be driven by the duration of ungulate presence (Hess et al. 1999, Leopold & Hess 2017, Loope & Scowcroft 1985). Climate change also threatens Hawai'i's terrestrial ecosystems, with projected declines in rainfall (Chu et al. 2010, Timm & Diaz 2009) and increases in temperature (Giambelluca et al. 2008). These disruptions to Hawaiian ecosystems are linked to losses of native biological diversity and to social and cultural losses, owing to the highly coupled nature of Hawai'i's human-environmental systems. As a result, Hawai'i's conservation community is focused on controlling invasive species and preventing species extinctions. Thus, the way in which invasive species interact with one another is important for predicting whether management actions will be successful and for metering how much effort to expend in invasive species management.

3.2. Case Study I: Tropical Dry Forest

Tropical dry forest is an example of a strongly abiotically controlled environment in which persistent invaders are few in number.

3.2.1. The habitat. Dry tropical and subtropical forests occur in areas where annual rainfall ranges from 500 to 2,000 mm (Figure 1), the mean annual temperature is higher than 17°C, and the ratio of potential evapotranspiration to precipitation is greater than 1 (Murphy & Lugo 1986). Although dry forests compose a relatively large fraction of tropical forests, they have received limited attention in terms of conservation and protection. For instance, only 5.7% of the remaining dry forests in North and Central America have some conservation status (Miles et al. 2006). Currently, dry tropical forests are among the most endangered of all tropical forest ecosystems (Janzen 1988, Miles et al. 2006), owing largely to the enormous pressure of human activities and grazing by ungulates during the past 100–400 years. Some 97% of the remaining area of tropical dry forest is currently exposed to a high level of one or more threats. As a consequence of this long-term degradation, most of the remaining tropical dry forests are isolated patches immersed in a matrix of pastureland or secondary forest. Hawai'i is not an exception to this pattern. Mehrhoff (1996) estimated that the Hawaiian Islands have lost 90% of their dry forest since the arrival of humans.

Our present research efforts currently occur in Kaupulehu in the North Kona region of the leeward side of the island of Hawai'i (N 19°46'05", W 155°56'19"). Vegetation in the approximately 28-ha preserve ranges from diverse native forests dominated by the tree *Diospyros sandwicensis* to treeless areas completely covered by the introduced C₄ grass *Cenchrus setaceus* (fountain grass,

formerly *Pennisetum setaceum*). The preserve has been protected from ungulates and fire for more than 10 years (Cabin et al. 2000). The substrate is 1,500–3,000-year-old ‘a‘ā lava (Moore & Clague 1987). Long-term average annual rainfall is 500–750 mm (Giambelluca et al. 2013) with high annual variation; thus, each month receives on average less than 100 mm, an important distinction of dry forest. Since 1999, a maximum annual total of 1,249 mm (in 2004) and a minimum of 225 mm (in 1999) have been recorded (Thaxton et al. 2010). Rainfall is not distinctly seasonal, although May to August tends to be drier than November to February (Cordell & Sandquist 2008). Cattle and feral goats continue to browse and trample the few remaining fragments of dry forests in the region, and introduced rodents consume the seeds and seedlings of many native dry forest species (Cabin et al. 2000). In addition, drought and fire (primarily resulting from fountain grass) have been prevalent in the area for the past five years (Trauernicht et al. 2015).

3.2.2. Prediction. Tropical dry forests should have a lower diversity of persistent or high-impact invaders and a low surprise index because abiotic limitation is overarching and consistent, and invading species must have access to available resources to establish and survive. These dry systems fit the framework for environmentally harsh habitats where abiotic resistance should be the strongest mechanism causing invasions to fail (Blackburn & Duncan 2001, D’Antonio et al. 2001b). Whereas others (Burgess et al. 1991, Hobbs & Mooney 1991) have shown that invasions can increase in wet years within otherwise dry systems, we believe the long-term nature of the harshness at these sites and the temporal unpredictability of these rainfall pulses will limit the potential for surprises, specifically the response of secondary invaders to a manipulation of primary invaders.

3.2.3. Experimental and long-term observations. State foresters realized the conservation value of Kaupulehu in the 1950s and sought protection status for a small area of 2.3 ha, which was fenced from nonnative ungulates in 1956. In 1997, 25 additional hectares were fenced. A study by Cabin et al. (2000) revealed that despite the exclusion of ungulates for almost 50 years, native species had not successfully regenerated and the understory was completely dominated by the invasive C_4 grass *C. setaceus*. In the same study, *C. setaceus* was removed from the entire 2.3-ha parcel and biodiversity was compared inside and outside the enclosure. Both native and nonnative species regeneration occurred, and the authors argued that opening up the understory would likely facilitate invasion by potentially new and harmful invaders (Cabin et al. 2000). However, in 2004 this site and two other units in the 1997 enclosure were revisited in a study by Thaxton et al. (2010), who monitored for three years (2004–2007) natural regeneration, seed rain, and dynamics of seedlings and juveniles. All units had been protected from fire for many decades but differed in time since ungulate exclusion and grass removal. The units were (a) long-term restoration (fenced in 1956 with grass removal in 1995), (b) short-term restoration (fenced and grass removal in 1997), and (c) unmanaged (fenced in 1997 but no grass removal). Whereas juvenile plant abundance was highest in the short-term unit, native abundance was highest in the long-term unit. Native woody seedlings established in all units, but recruitment into larger size classes was restricted to units with grass removal, primarily the long-term unit. The study serendipitously spanned a very wet year followed by a dry year and then a normal year (Thaxton et al. 2010), providing the opportunity to follow the effects of a resource pulse from inception to exhaustion—something rarely offered without the context of long-term data sets (Figure 3). Importantly, during a period of high rainfall nonnative biodiversity exploded across all plots but especially so in the short-term restoration unit, where availability of open space was the highest (Figure 3). As resource availability declined, new native and nonnative recruits declined in both short- and long-term plots, but both the relative and the absolute abundance of native species were much higher in the long-term site. In the unmanaged

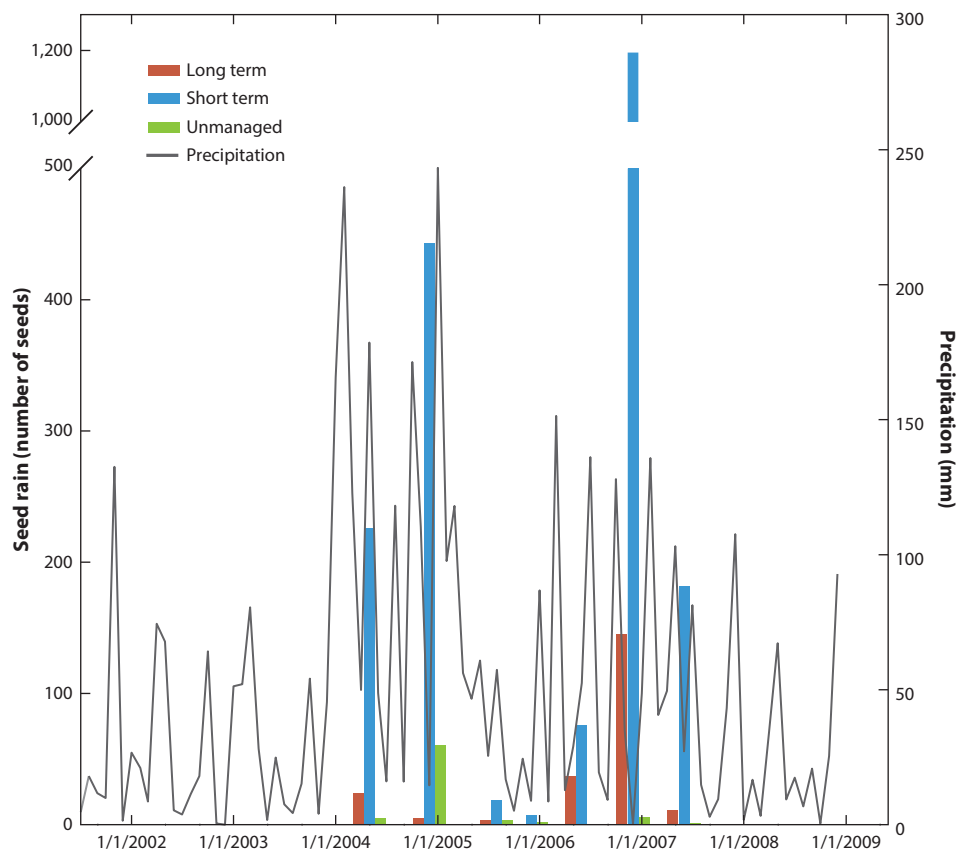


Figure 3

The episodic nature of seedling regeneration in the Hawaiian dry forest system demonstrates that surprises in community composition after invasive grass removal are few. Precipitation (*solid line*) is highly variable annually but not temporally predictable. During wet periods, there are short-term increases in seedlings of nonnative species, but these individuals do not persist in the long-term restoration plots—where stress-tolerant species dominate—or during periods of drought (2006). The experimental design compared long-term restoration (fenced in 1956 with grass removal in 1995), short-term restoration (fenced and grass removal in 1997), and unmanaged (fenced in 1997 but no grass removal). **Figure 3** is based on data reported in Thaxton et al. (2010).

control plots (fenced but fountain grass intact), biodiversity was reduced to near dominance by *C. setaceus* (Thaxton et al. 2010).

3.2.4. Conclusions. Overall, we conclude that infrequent and unpredictable pulses in critically important resources affect the invasion potential of the tropical dry forest and that the surprise index is low because species that invade with a pulse quickly disappear and nothing invades between pulses. Propagule pressure of invasive species is high in this dry forest but germination and survival requirements are infrequently met. Successful invaders of these systems must therefore match or surpass the evolved resource conservation/acquisition strategies of the existing native communities. This hypothesis supports other studies showing that the environmental suitability of the introduction site is critical for success and that abiotic factors are potentially the most

important cause of invasion failure in many areas and are more important than dispersal limitation for predicting future species distributions (Blackburn & Duncan 2001, Menke & Holway 2006, Moyle & Light 1996).

3.3. Case Study II: Seasonal Submontane Mesic Woodland

Seasonal mesic woodlands experience a strong drought during the summer but have a higher net primary productivity (NPP) than dry forest and a wider array of persistent invaders.

3.3.1. The habitat. The seasonal submontane shrublands and woodlands of Hawai'i Volcanoes National Park on the island of Hawai'i receive between 1,400 and 2,100 mm of rainfall annually (**Figure 1**) that is delivered seasonally, with more than 70% of the rainfall occurring in a discrete wet season (October through April). These systems occur at elevations between 500 and 1,200 m. Below 500 m the habitats are too hot to be submontane, and above 1,200 m they can experience cool nighttime temperatures between November and February. Because the mean annual precipitation (MAP) is roughly twice the dry forest average and evapotranspiration is lower (Giambelluca et al. 2013), these seasonal habitats support greater cover and NPP than the dry forest systems, and lower cover and NPP than tropical lowland systems (submontane cover: D'Antonio et al. 2011; productivity in submontane woodlands: Mack et al. 2001; productivity in dry forest: Litton et al. 2006; productivity in wet forest: Ostertag et al. 2009). They characteristically have high interannual variability in the timing and amount of rainfall, with a wider range of MAP, compared with the dry forest (Giambelluca et al. 2013).

Since 1990, we have been working at sites between 800 and 920 m within Hawai'i Volcanoes National Park. The area receives approximately 1,500 mm of precipitation annually (D'Antonio et al. 2011, D'Antonio et al. 2017) (**Figure 1**). Between 1990 and 2014, the annual maximum was 2,668 mm (in 1990) and the minimum was 403 mm (in 1998) (D'Antonio et al. 2011). Also, in both 2011 and 2012, the average amount of rainfall between May 1 and October 1 was only 1.5 cm/month, whereas during that same period in 2014 the amount was 16.8 cm/month. Another example of high variability occurred in the 1990s; the very dry years of 1998 and 1999 (average of 1.49 cm/month from May through September 1) followed the much wetter year of 1997 (average of 13.5 cm/month during the same period). Because the soils of this area are typically less than 50 cm deep, low rainfall during the warm summer months can exert drought stress on the plants, and successive years of low rainfall can lead to plant mortality and compositional change (D'Antonio et al. 2011). The soils are derived from volcanic ash less than 1,000 years old; hence, nitrogen is limiting to plant growth (D'Antonio & Mack 2006).

Prior to the 1960s, these habitats were primary forests consisting of an open canopy dominated by the native tree *Metrosideros polymorpha* with a high density of native understory shrubs and scattered sedges. Native grasses were and are rare. Diversity and richness are low compared with that of subtropical woodlands in mainland settings. Sites were invaded by two New World C₄ bunchgrasses, primarily *Schizachyrium condensatum* (Kunth) from tropical America, in the 1960s during a time of feral ungulate grazing. The first recorded wildfire carried by these grasses burned the area in 1970. By 1988, more than 70% of the submontane woodlands with enough soil to support grasses had burned in grass-fueled fires (Tunison et al. 2001). After these fires, the sites were invaded by an African C₄ grass, *Melinis minutiflora* P. Beauv., a species that suppresses native species recovery through competition for light (Hughes & Vitousek 1993, Hughes et al. 1991, Yelenik & D'Antonio 2013). Throughout this habitat several other invasive C₄ perennial grasses are present, most of which have wide environmental tolerances (Xavier & D'Antonio 2017) and all have the potential for persistence because they are long-lived and self-replacing (e.g., D'Antonio et al. 2001a).

3.3.2. Prediction. As a result of the greater MAP, lower evapotranspiration (Giambelluca et al. 2013), and higher productivity compared with that of the dry forest at Kaupulehu, we predict that longer-lived, perennial species and self-replacing invasive species are able to survive in these sites. In addition, we predict that species interactions are of high importance despite nitrogen limitation and seasonal drought. However, this system should have a high surprise index because of the importance of priority effects; the potential for fluctuating plant-soil feedbacks, as described below; and the interactions of invasive species with fire, a novel disturbance in these systems. With regards to the last factor, the native species within Hawaiian mesic forests are not adapted to fire disturbance, which has increased over the past 80 years (Tunison et al. 2001). And native species have consistently declined with fire disturbance even after long fire-free periods (Ainsworth & Kauffman 2009, D'Antonio et al. 2011, Wasser 2015). Here, fire reduces the priority effects of invaders and changes nutrient and light availability. We predict that several long-lived invasive species have the ability and opportunity to invade and persist at these sites and that their dominance can be rearranged by climate and fire. Thus, mesic woodlands have a higher surprise index than either dry tropical or wet lowland tropical forests because they are near a threshold in which wetter years promote invaders that thrive in higher rainfall and drier years promote more drought-tolerant invaders. In addition, the system is dry enough for fire to be a regular occurrence but wet enough to allow invaders that have a wider range of functional traits than those observed in the dry forests.

3.3.3. Experimental and long-term observations. During the 1990s, investigators studied the community- and ecosystem-level impacts of invasive species in these woodland environments. Within the unburned woodland, D'Antonio et al. (1998) removed invasive C₄ grasses from large (20 × 20 m) plots and maintained them as grass-free for approximately four years. With the primary grass removed, *S. condensatum* composed more than 70% of the cover and 35% of understory biomass (Mack et al. 2001). Native woody species recruited at a higher density when these grasses were removed, and existing native species increased in stem growth and leaf tissue nitrogen (D'Antonio et al. 1998). Initially, other nonnative species did not invade, but the invasive grass *M. minutiflora* could easily recruit when seeded (D'Antonio et al. 2001a), and by four years, the invasive tree *Morella faya* (formerly *Myrica faya* Aiton) was recruiting rapidly into cleared, but not nearby, control plots (D'Antonio & Mack 2001). These responses to manipulation demonstrate that the initial invader, *S. condensatum*, was reducing invasion by *M. faya* (as well as native species) (D'Antonio et al. 1998) through priority competition. D'Antonio et al. (2001b) further showed experimentally that fire disrupted the priority effect of *S. condensatum*, allowing rapid invasion of the fast-growing, highly nitrogen-responsive *M. minutiflora*. A census of permanent transects in 2007 and 2013 showed that, after several years of severe drought, *S. condensatum* had declined substantially (D'Antonio et al. 2011) and that both *M. minutiflora* and *M. faya* had simultaneously increased across the unburned woodland, consistent with the declining priority effect of *S. condensatum* (Figure 4).

The rise to dominance of two later invaders highlights the importance of variability in environmental tolerance (i.e., trait variation) among ecologically important invaders in response to environmental fluctuation. In support of *M. minutiflora* being more drought tolerant than *S. condensatum*, Xavier & D'Antonio (2017) found that the former occurs from hot, dry coastal lowlands (after fire) to wet forest edges in Hawai'i, whereas the latter is limited to more mesic higher-elevation sites with or without fire. The ability of both of these species to densely occupy the seasonally submontane zone, depending on who gets there first, allows this system to favor either more native species (the *S. condensatum* woodland) or greater invasive species dominance (under *M. minutiflora* domination). *M. faya* also inhabits a wide temperature and precipitation range, yet it has traits different from those of grasses (e.g., C₃, life form, and nitrogen fixation) that may allow

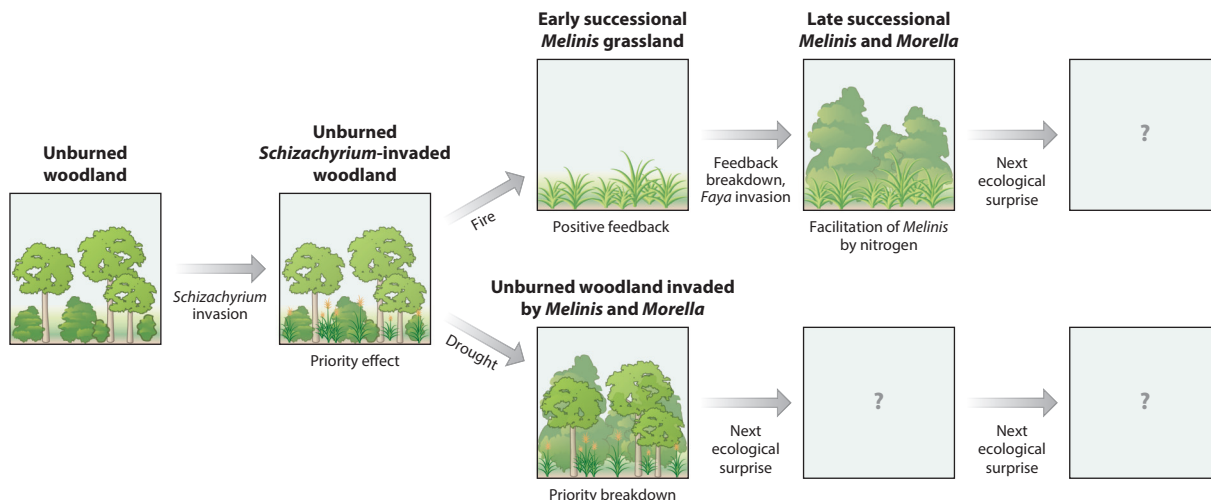


Figure 4

Schematic representation of changes that have occurred in submontane mesic woodlands in response to invasion, fire, and species interactions. Initial *Schizachyrium* invasion occurred in the 1960s. Fires occurred between 1970 and 1987. Drought occurred in the 1990s until 2011. Transitions such as feedback breakdown, *Morella faya* invasion, and rapid facilitation of *Melinis* sp. were fast. Future transitions will depend on climate and species arrival.

it to occupy a separate niche within the unburned and burned woodlands. Xavier & D'Antonio's (2017) survey further suggests that other invaders, such as the large C_4 grass *Hyparrhenia rufa*, another species with wide temperature and moisture tolerances, could expand in these environments if something causes the decline of *M. minutiflora*. *H. rufa* has increased dramatically along trails and in small patches away from trails during the recent drought.

Burned woodland sites present additional lessons regarding invasive plant interactions and the challenge of managing multiply invaded habitats (Figure 4). As mentioned above, sites that had burned in two fires were heavily invaded by *M. minutiflora* in the 1990s. D'Antonio et al. (2001b) demonstrated that this species responds rapidly to high-nitrogen soil and can quickly displace *S. condensatum* after fire. Mack et al. (2001) and D'Antonio & Mack (2006) documented that *M. minutiflora*-dominated sites had higher rates of nitrogen mineralization than woodland sites did. Similarly, Asner & Beatty (1996) demonstrated high mineral nitrogen availability under patches of *M. minutiflora* in a shrubland on the island of Moloka'i. Because *M. minutiflora* is nitrogen limited (D'Antonio & Mack 2006), these studies together suggest that *M. minutiflora*'s dominance sets up a positive plant-soil feedback via promotion of high nitrogen availability, which helped sustain its dominance in the first decade after fire. The exact mechanism of this feedback through nitrogen mineralization is not known. By 2011, however, rates of nitrogen availability and net mineralization along *M. minutiflora* transects in burned areas were indistinguishable from rates in woodland sites lacking this grass (Yelenik & D'Antonio 2013), suggesting a general decline in the importance of the positive feedback. This finding is consistent with reviews of plant-soil feedbacks showing that feedbacks tend to be weak or negative (Kulmatiski et al. 2008), although temporal dynamics of feedbacks are unstudied. Simultaneous with this decline, *M. faya*, a nitrogen-fixing invasive tree that is strongly negatively affected by competition with *M. minutiflora*, had begun to increase (D'Antonio et al. 2011, Yelenik & D'Antonio 2013). Hence, instead of these sites returning to native species dominance with a decline in grass vigor, a secondary invader rose to codominance. Thus, *M. minutiflora* dominance and decline indirectly facilitated *M. faya* invasion.

This role of changing feedbacks was not anticipated and could be an interesting area for further research in other systems.

M. faya is a vigorous nitrogen fixer (Vitousek & Walker 1989), and new evidence indicates that its invasion into burned sites is reinvigorating *M. minutiflora* because it provides nitrogen well beyond (4–5 m) its canopy edges (C.M. D'Antonio & S. Yelenik, manuscript in review). This alleviates nitrogen limitation (C. D'Antonio, S. Yelenik, unpublished data) and perpetuates *M. minutiflora*'s dominance. In addition, native seedlings have a similarly low recruitment rate under *M. faya* as within the *M. minutiflora* (Yelenik et al. 2015). This system should thus reach a new alternative state of codominance: *M. faya* trees interspersed with patches of *M. minutiflora* (Figure 4), with little opportunity for invasion by either native or nonnative species. It is not clear what could disrupt this dominance, but *M. faya* is susceptible to extreme drought (C.M. D'Antonio, personal observation) and to death by an introduced insect, the two-spotted leaf hopper, *Sophonia rufofascia* (Kuoh and Kuoh) (Alyokhin et al. 2004). Other potentially ecologically significant invaders are present at the edges of these sites and over time could increase. These include *Schinus terebinthifolius*, *Psidium guajava* (already present on two transects), *Psidium cattleianum*, *Lantana camara* (invading nitrogen-rich sites; see August-Schmidt et al. 2015), *Olea europaea* (bird-dispersed and already found on one transect), and *H. rufa* (already on two burned transects). Their ability to invade likely depends on climatic influences on dominance and priority effects or the occurrence of further fires. Depending on the type of resources that become available and over what timescales (e.g., many years versus a single year of drought), the varied traits of the potential invaders will help drive which ecological surprise emerges next.

3.3.4. Conclusions. We conclude that seasonal submontane mesic woodlands have a stronger potential for surprises because the climate is favorable enough to support a range of long-lived invaders that can exist in sites that are either wetter or drier than sites found in this system. Priority effects both before and after fire are extremely important, and indirect facilitation can occur via changes in plant-soil dynamics. The shifting importance of plant-soil feedbacks was unanticipated. Together, these processes result in a high potential for stochastic factors, which are inherently likely in this particular system due to fire and rainfall variability, to influence the outcome of disturbance or species management. Subtle differences in the ability of the two most common C_4 grasses to tolerate drought and respond to fire and rainfall allow for either grass to be dominant depending on the circumstance. Likewise, the invasion of this system by *M. faya*, a species whose range spans from very wet to mesic and seasonally dry habitats and that can capitalize on declining nitrogen-cycling feedbacks, emphasizes the surprises that can occur through multiple mechanisms in a system of intermediate productivity and high interannual variability.

3.4. Case Study III: Wet Forest

Lowland wet forests are not constrained by water availability and have a high diversity of persistent invaders.

3.4.1. The habitat. Lowland wet forests are widely distributed across tropical zones, but in Hawai'i these forests are often somewhat distinct from other tropical areas. In Hawai'i and other tropical islands, lowland wet forests are today a remnant habitat, owing to extensive clearing for agriculture and development (Ostertag et al. 2009). These remnants are often heavily invaded by nonnative trees (Green et al. 2004, Hughes & Denslow 2005, Lorence & Sussman 1986). Lowland wet forests in Hawai'i are defined to have a MAP rate greater than 2,500 mm at 1,000 m.a.s.l.

(meters above sea level) and greater than 3,000 mm at sea level (**Figure 1**) (Price et al. 2007) and to be light limited (Cordell et al. 2009, Ostertag et al. 2009, Schulten et al. 2014).

A comparison of the degree of invasion in Hawaiian lowland wet forest remnants found that sites on lava flows older than 300 years crossed a threshold and had much greater nonnative stem density and basal area than did sites on younger lava flows, which may also be more abiotically constrained (Zimmerman et al. 2008). Native seedling recruitment is limited in all lowland wet forest sites (Schulten et al. 2014, Zimmerman et al. 2008). Furthermore, Hawaiian lowland wet forests tend to have higher understory light levels than their mainland counterparts (Schulten et al. 2014), which explains the high rates of invasion.

We have worked most extensively at the Keaukaha Military Reservation (N 19°42'15", W -155°2'40", 30 m.a.s.l.) in Hilo, Hawai'i. Rainfall averages 3,347 mm/year and the mean annual temperature is 22.7°C (Giambelluca et al. 2013). We conducted two different invasive plant removal experiments. In the first experiment, we created four 10 × 10-m² removal plots with paired controls, for which management consisted of continued removal of all recruiting nonnative species over several years, and a small-scale outplanting. After we recognized that the weeding required to keep out woody invasive species was unsustainable (Cordell et al. 2016), we developed a second experiment in which we removed all nonnative species from 400-m² plots but kept the native species. Then we planted four different hybrid communities that varied in their functional trait diversity (Ostertag et al. 2015). These planted hybrid communities had mixtures of native and nonnative (but noninvasive) species, after we determined that all native communities are constrained in their functional trait expression (L. Warman, R. Ostertag, S. Cordell, N. Zimmerman & J. Mascaro, manuscript submitted) and that more functionally diverse hybrid mixtures will likely enhance invasion resistance (Funk et al. 2008).

3.4.2. Prediction. Tropical lowland wet forests should have a high species diversity of persistent invaders because of favorable climate conditions and the potential for high sustained productivity. Most lowland wet forest sites are limited by light rather than water or nutrients (Denslow 1980, Nicotra et al. 1999); therefore, removal will favor colonizing species with trait values that typically engender fast rates of growth and plasticity under gap-like conditions. If, for the sake of argument, species distributions in wet tropical forests are driven by competition and niche processes rather than neutral processes (e.g., Kraft et al. 2008), then in mature tropical forests a high number of species typically develop over time, with enough functional diversity in trait profiles to allow coexistence. With such high species and functional diversity, few invaders will be able to invade by using resources in a manner different from that of key species established in the habitat; therefore, these systems are unlikely to be susceptible to invasion (Denslow & DeWalt 2008, Fine 2002). However, tropical forests on islands are exceptions because they generally contain a low number of species and, owing to biogeographic filtering, may be missing functional groups (Simberloff 1995) and have lower functional diversity than mainland tropical forests.

Despite the high number of invaders, lowland wet forests have a low to moderate value of invasion stochasticity or surprise effect. Owing to the intense competition among species, and a generally large propagule pool from surrounding invaded areas (or the seed bank), no species is likely to dominate across the landscape. The invaders, although taxonomically diverse, have a response to perturbation that is functionally similar. Removal areas will quickly fill up with biomass, monopolizing light resources, but this rapid colonization by disturbance-adapted species is expected. Priority effects may be important in the short term because of the importance of rapid colonization. However, as gaps do not persist for long, most canopy openings will fill in quickly with vegetation, and because most invaders are short-lived pioneers, initial species composition may not persist in the long term. However, new successful invaders from all possible functional

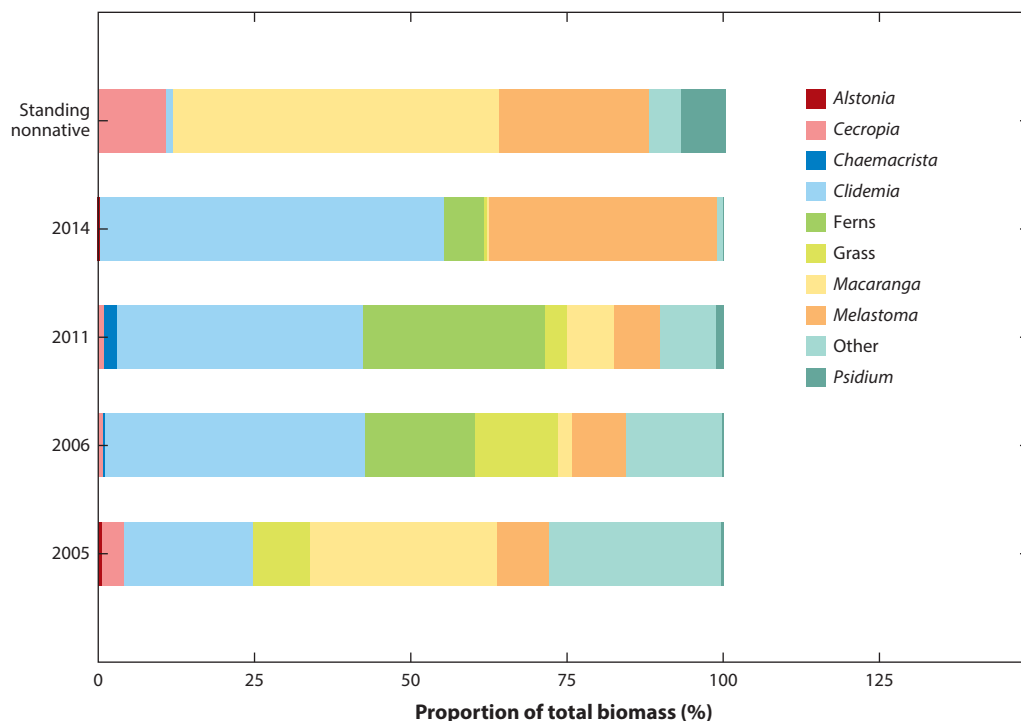


Figure 5

Makeup of invader biomass removed over time in Hawaiian lowland tropical wet forests. The top bar represents the proportion of total standing adult nonnative vegetation in each species category taken from before the initial removal of all nonnative species from four 100-m² plots in 2004. The other four bars represent the proportion of species' biomass of invasive seedlings removed from the plots according to year. The category Other is a mixture of as many as 32 species with low individual biomass.

groups (e.g., vines, herbs, shrubs, and trees) that can persist and grow in low-light environments are also common in this system because their productivity is not limited by climatic factors.

3.4.3. Experimental and long-term observations. In the first removal experiment, as predicted, the surprise index was low and the species diversity of invaders was high (Figure 5). For example, only 9–10 tree or tree fern species were abundant as adults at the site (Ostertag et al. 2009), yet 26 species (only one native) germinated from the seed bank and 17 species (only two native) were captured in the seed rain (Cordell et al. 2009). However, years of weeding data demonstrate that none of these invaders became dominant and transformative (Figure 5). The most abundant species, *Clidemia hirta*, is an understory subshrub rather than a fast-growing tree (DeWalt et al. 2004), but it is unclear whether it will persist in the long term. Managers need to expect that for wet forest sites constant invasive species control will be necessary after removal if the goal is to allow native species to recruit. Similarly, in the second removal experiment, the number of species regenerating after removal was high (29–41 species) relative to adult species, but many are herbaceous and unlikely to persist (see Cordell et al. 2009). Of those species likely to persist without future management, there are few surprises: Most are the same primary invaders returning to the sites post initial removal. There is a large variation in species composition among plots, but no clear or unexpected dominants, again supporting the hypothesis that the surprise index is lower in lowland wet forests than in forests closer to a climatic threshold.

3.4.4. Conclusions. As predicted, species invasion was high after the creation of removal areas in the lowland wet forest, and species composition varied in space and time. No single invader became dominant and scramble competition appears to be ongoing. Managers need to understand that working in this kind of habitat is challenging, given that invaders are abundant and constantly recruiting, unlike in the tropical dry forest habitat, where it is possible to allow climate filtering to remove most invaders. However, work in lowland wet forests in Hawai'i has shown that invasive species removal without outplanting is not sustainable (Cordell et al. 2016). Thus, managers should keep in mind a desired alternative community composition before investing in invader removal.

4. SUMMARY: LESSONS LEARNED FROM THESE HAWAIIAN SYSTEMS

Our case studies demonstrate that removal experiments can guide managers about how systems might respond to invasive plant control while informing ecological theory on mechanisms of species interactions and succession. In warm tropical climates, mean annual rainfall and plant productivity potential are key variables that can dictate the predictability of species composition postremoval. Future studies need to examine species composition after invasive species removal across environmental gradients or at different points along the rainfall and productivity axes. Additionally, the importance of interannual variability in climate and the location of thresholds of invader change should be investigated.

Comparing the three different ecosystems that varied in rainfall yielded several insights:

1. Not all systems will benefit in terms of native recovery or invasive plant control. Sometimes no other persistent invaders successfully come in (lowland dry forest), suggesting species interactions among invaders and priority effects of the initial invader are not important. Transitions to functional groups with greater energetic requirements are unlikely. These are situations in which managers have more time to control invaders or can invest substantially less time in postremoval monitoring.
2. Other times, new invaders arrive (mesic forest) after initial invader control (or decline), supporting the concept that early invaders keep out later invaders through priority effects. In the case of the mesic/submontane forest, the invaders that come in after the removal or decline of the grass *S. condensatum* are ecologically more challenging for managers if the goal is a native-dominated ecosystem. New transformative invasive functional groups, such as a transition from grasses to trees, are much more likely in this system than in the dry or wet systems. The lesson for managers is that secondary invaders could be worse than what is currently at a site and that removals must be conducted with careful consideration of propagule sources and the identity of invaders that could emerge next.
3. In habitats where light is the primary limiting resource, such as the lowland wet forest, invaders scramble for light in gaps created by invasive plant removal (or natural canopy disturbance). The diversity of invaders is typically high, yet no single invader dominates postremoval. Further, owing to a lack of climatic constraints, the potential for biomass accumulation is high, thereby allowing invaders from a range of functional groups to coexist. Thus, management should aim to control a broad suite of fast-growing invaders by outplanting either native species or a suite of species that may include nonnative (noninvasive) species that will eventually resist the undesirable invaders.
4. Observations suggest that invasive plants rarely appear to directly facilitate one another in the systems studied here, but this assumption requires testing. Yet invasive species may indirectly facilitate one another as in the submontane zone (where the decline of *M. minutiflora* in burned areas facilitated the invasion by *M. faya*, which in turn facilitated growth of surrounding patches of *M. minutiflora*).

5. Priority effects are most important in medium- to high-resource environments when the competition and the potential for persistence is high. In fluctuating-resource environments near climate thresholds, priority effects can be overridden by disturbances or climate variability that changes resource limitation, producing a high potential for species composition to be determined by stochastic factors. Although priority effects can also be important in the higher-NPP wet forest environment, these environments also likely have lower persistence of invader individuals and greater turnover among species.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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