

Spatiotemporal Patterns of Alien Plant Invasions in One of the Last Pristine Wet Forests of Hawai‘i¹

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Abstract: Invasion of native communities by alien species is one of the main threats to biodiversity. This threat is particularly high on isolated tropical islands, with the Hawaiian Islands being one of the foremost examples of this phenomenon. The Kīpahulu Biological Reserve on the island of Maui provides a unique opportunity to study how alien plant species establish and spread into native communities. The reserve covers a wide altitudinal range and has been surveyed multiple times. We analyzed the spatiotemporal dynamics of alien plant species invasion in the forest of the valley between 1945 and 2018. At the time the reserve was created, most of the valley was relatively free of alien plant species. Extensive management, including fencing to exclude ungulates, was conducted during the 1980–1990s to stop the invasion by alien plant species occurring since the 1970s. Today, only the forest located in the upper part of the valley (>1400 m) is nearly free of alien plant species. Despite management efforts, the middle portion of the valley (between 960 and 1400 m) is in the process of being invaded by *Clidemia birta* (Melastomaceae), *Hedychium gardnerianum* (Zingiberaceae), and other invasive plants. Although *C. birta* and *H. gardnerianum* were detected at an incipient stage in the 1980s, those species invaded a large part of the Kīpahulu valley. This highlights the importance of control of alien plants following early detection, especially in areas where initial numbers and densities are low. Additional management efforts are urgently needed to limit alien species invasions into one of the last relatively pristine wet forests of Hawai‘i.

Keywords: biodiversity hotspot, Haleakalā National Park, invasive plants, island, Kīpahulu valley, ungulates

THE INVASION OF NATIVE communities by alien species is one of the main threats to biodiversity, and tropical islands are hotspots

for biological invasions (Simberloff 1995, Denslow 2003, Caujape-Castells et al. 2010, Dawson et al. 2017). Isolated tropical islands are particularly affected by alien plant invasions with the Hawaiian Islands being a foremost example of this phenomenon (Denslow et al. 2009, Moser et al. 2018, Ibanez et al. 2019). Today, naturalized alien vascular plant species outnumber Hawaiian native species (Imada 2012, 2019), and vegetation dominated by native species only covers about 30% of the Hawaiian archipelago (Jacobi et al. 2017). Monitoring and understanding how alien species establish and spread in native communities is critical to managing this threat.

The Hawaiian archipelago was first colonized by Polynesians less than 1,000 years ago (Wilmschurst et al. 2011), and later by

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Europeans, after Captain J. Cook reached the archipelago in 1778. As with other Polynesian islands, the settlers intentionally introduced alien plants for food and cultural purposes. Those early Polynesian introductions together with the many other alien plants intentionally or accidentally introduced since European colonization often dominate lowland areas resulting in a mix of alien and native plant species (Mueller-Dombois and Fosberg 1998, Jacobi et al. 2017). Alien plant species are usually more numerous at lower elevation and tend to spread upward in the context of global changes (Pauchard et al. 2009, Guo et al. 2018, Ibanez et al. 2019).

Along with plants, Polynesians and Europeans introduced ungulates, including feral pigs (*Sus scrofa*), which emerged as a major threat to Hawaiian forest biodiversity during the last half of the twentieth century (Stone and Loope 1987, Vitousek et al. 1987). Indeed, the native vegetation of isolated islands is particularly vulnerable to the introduction of ungulates, as these plants generally evolved in their absence (Bowen and van Vuren 1997, Courchamp et al. 2003). Feral pigs favor the establishment and spread of alien plant species in different ways. They consume and damage (girdling, digging up) native plant communities, which open niches for alien plants, and actively or passively disperse their seeds (Yoshinaga 1980, Diong 1982, Weller et al. 2011, Murphy et al. 2014, Wehr et al. 2018, Weller et al. 2018).

The isolated Kīpahulu valley on the island of Maui has long been recognized as sheltering some of the most well-preserved forests in Hawai'i. The first extensive survey of the valley, the Kīpahulu Valley Expedition, was conducted in 1967 (Warner 1968). The members of the expedition found that many ecosystems of the valley were exceptionally undisturbed. Although the lower part of the valley was already highly disturbed and invaded by alien plants, notably by *Psidium cattleianum* (Myrtaceae) and *Rubus rosifolius* (Rosaceae), the wet forest located above 600 m was still considered relatively free of alien species. Indeed, only one dozen alien species were found and those species were restricted to openings disturbed by pigs in the middle

part of the valley (<1200 m). In 1969, following the recommendations of the Kīpahulu Valley Expedition, the Kīpahulu Biological Reserve was added to Haleakalā National Park to protect the unique biodiversity of the valley. In 1986–1987, fences were installed to prevent the movement of feral pigs and delineate invasive species management units in the Kīpahulu Biological Reserve (Anderson and Stone 1993).

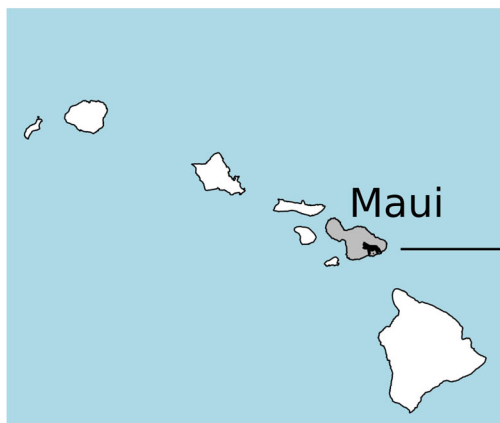
The Kīpahulu Biological Reserve provides critical habitat for numerous threatened and endangered plants and birds (Krushelnicky et al. 2019) as well as a rare opportunity to study spatiotemporal patterns of establishment and spread of alien plant species. The reserve covers a wide altitudinal range (300–2,300 m) and has been surveyed multiple times during the past 75 years. We analyzed the spatiotemporal dynamics of alien plant species invasion between 1945 and 2018 using historical and recent plant surveys. Our aims were (i) to report on the current distribution and abundance of alien plant species in Kīpahulu valley as well as identify which of these species are more likely to constitute a risk for native communities, (ii) to document when the different alien species established and how they spread into the valley, and (iii) to determine if alien plant species have spread upward in the different Kīpahulu management units (lower, middle, and upper Kīpahulu).

MATERIALS AND METHODS

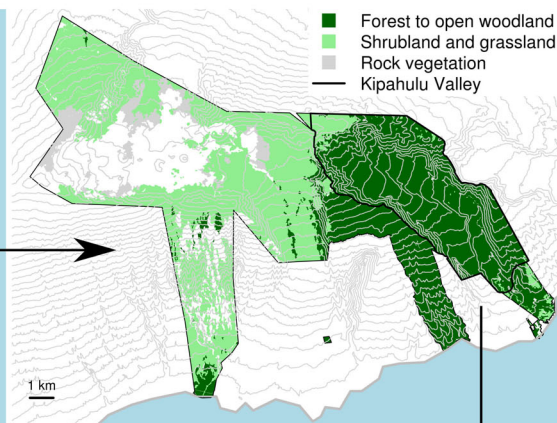
Study Area

The study area consists of the 3,350-ha Kīpahulu Biological Reserve on the eastern slope of Haleakalā Volcano on the island of Maui (Figure 1). Located on the windward coast of the island, it receives high precipitation (from about 2,500 mm/yr in the lower part of the valley to more than 7,000 mm/yr), and mean annual temperatures range from more than 20 °C in the lower part, to less than 10 °C in the higher part of the valley. We focused on forests located above 600 m and extending up to 2,300 m. Native species dominated this area at the time of the first survey and the forests can be divided into

Hawai'i



Haleakalā National Park



Kīpahulu Valley reserve

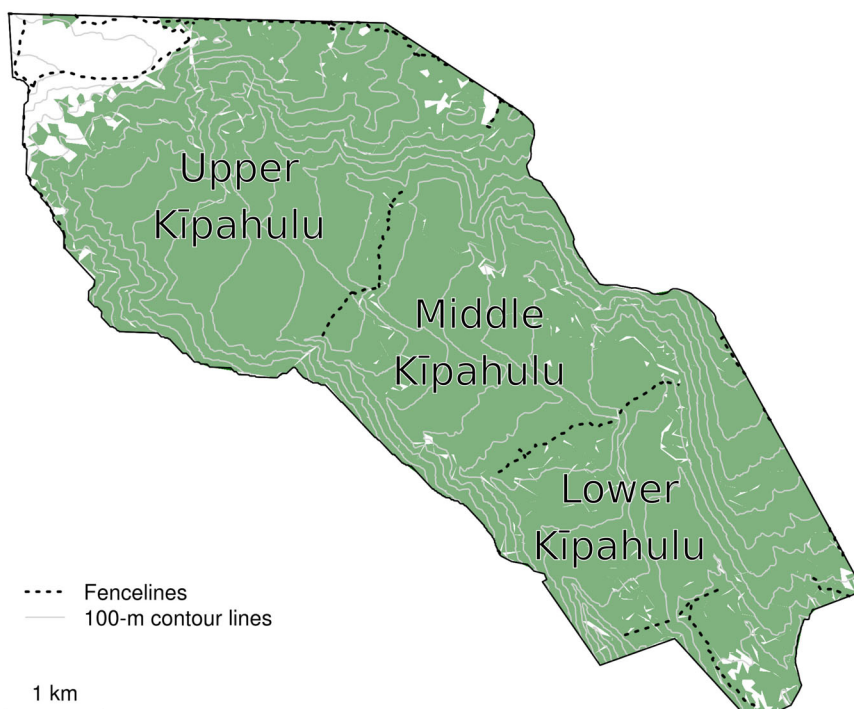


FIGURE 1. Location of the Kīpahulu valley reserve (Haleakalā National Park) on the island of Maui (Hawai'i). Grey lines highlight 100-m elevation interval.

three broad types: (1) between 600 and 1,000 m, the forest is dominated by the native koa tree (*Acacia koa*, Fabaceae), (2) between 1,000 and 1,200 m, the forest is co-dominated

by the native ōhi'a (*Metrosideros polymorpha*, Myrtaceae) and koa trees, and (3) between 1,200 and 2,300 m, the forest is dominated by the native ōhi'a tree (see [Anderson et al. 1992](#)

and Medeiros et al. 1998 for a more detailed description of the different vegetation types found in the valley). This area has been closed to public access (e.g., no recreational trails) since the creation of the reserve. In 1986–1987 fences were installed, delineating the valley into three management units, lower, middle, and upper Kīpahulu, corresponding roughly to the koa, koa-ōhi'a, and ōhi'a dominated forests (Figure 1).

Alien Plant Surveys

We analyzed the invasion of Kīpahulu valley by alien plant species over the last 73 years using historical plant surveys conducted in 1945 (Fagerlund 1945), 1967 (Lamoureux 1968), 1976 (Lamoureux and Stemmermann 1976), 1979 (Yoshinaga 1980), 1983–1988 (Anderson et al. 1992), and recent plant surveys conducted between 2012 and 2018 (Ainsworth et al. 2011, 2012).

Most of the historical surveys (those conducted between 1945 and 1979) consisted of qualitative surveys using trails around which the presence of alien plant species were reported. The itineraries, the number of days spent in the valley, and the number of people involved varied between plant surveys. In 1945, two rangers surveyed the valley from top to bottom during a five-day trip. They did not report their precise itinerary but they likely went through the Southeast side of the upper plateau (Yoshinaga 1980). In 1967, the Kīpahulu Valley Expedition (Warner 1968) involved approximately 28 people, including three botanists, all of whom stayed 29 days in the valley. They explored the valley upward following the central ridge and used lateral trails around three basecamps located at 950, 1,270, and 2,000 m elevation (Figure S1 in supplementary material). In 1976, four people, including a botanist from the former Kīpahulu Valley Expedition, re-surveyed the trails and basecamps of the expedition during three days (Lamoureux and Stemmermann 1976). Yoshinaga (1980) did not provide details about its 1979 survey.

Anderson et al. (1992) used a more quantitative approach in which fourteen

500-m long transects were established with 20 m × 20 m plots placed every 100 m (Figure S1 in supplementary material). In each plot, the presence and the coverage of alien plant species were notated using modified Braun-Blanquet cover classes (Mueller-Dombois and Ellenberg 1974). The last survey was conducted between 2012 and 2018 within the framework of the Pacific Island Inventory and Monitoring Network (see <https://www.nps.gov/im/pacn/index.htm>). Sampling within Kīpahulu valley consisted of thirty 20 m × 50 m plots and fourteen 1,000-m long transects (see Ainsworth et al. 2011, 2012, Fig. S1). In each plot, all alien plant species were listed and all large trees with a diameter at breast height (dbh) ≥ 10 cm were recorded. All small trees (1 cm ≤ dbh < 10 cm) and large tree ferns (dbh ≥ 10 cm) were recorded in 10 m × 25 m sub-plots, and all seedlings (dbh < 1 cm and height ≥ 50 cm) and small tree ferns (dbh < 10 cm), and shrubs (height ≥ 50 cm), were recorded in 2 m × 50 m sub-plots. The coverage of species in the undergrowth was also measured along three 50 m transects located along the two long edges and middle of the plot. Along these transects, the presence of species was recorded every 0.5 m if one or more species intercepted a 2-m height pole. The fourteen 1,000-m long transects consisted of continuous 5 m × 20 m plots in which the coverage of all alien species was estimated using modified Braun-Blanquet cover classes (Mueller-Dombois and Ellenberg 1974).

Analyses

For each survey, we gathered all available information about the occurrence, abundance, location, and elevational boundaries of alien plant species (Table S2). We also noted whether a species was considered a threat to the native diversity as stated by the reporting authors and when available, the Weed Risk Assessment (WRA) score from the Hawaiian Pacific Weed Risk Assessment database (www.hpwwra.org, Daehler et al. 2004). The WRA score facilitates an evaluation of the likelihood that an alien plant

species may become invasive and negatively impact natural ecosystems given a series of traits (invasion history, biology, and ecology). Species with scores higher than six are designated high risk, predicted to become invasive in tropical island ecosystems, and may negatively impact natural ecosystems. We also noted if the alien species is listed as one of the “100 of the world’s worst invasive alien species” (Global Invasive Species Database 2018, http://www.iucngisd.org/gisd/100_worst.php).

Given that alien plant surveys between 1945 and 2018 differed in their protocols, changes in alien species invasion through time were analyzed using species presence records and, when available, elevation ranges. None of the surveys fully covered the valley and the areas surveyed differed among them. As a result, the absence of a species in a survey does not necessarily mean that the species was not present in another area of the valley. We used the 2012–2018 surveys to analyze the current spatial variation in alien species invasions. For each plot, we computed the number of alien plant species, the coverage of alien species in the undergrowth (the ratio between the number of measurement points where at least one alien species was intercepted and the total number of measurement points), and the relative density of alien plant species in different size or life form classes (large trees, small trees, seedlings, large tree ferns, small tree ferns). These different features were modeled as a function of elevation using generalized linear models (GLMs) with a Poisson distribution for species number and a binomial distribution for relative density and coverage. The elevation of each plot was extracted from the USGS 10-m digital elevation model. All analyses were performed using R statistical software (R Core Team 2018).

RESULTS

A total of 75 naturalized alien species have been observed at least once in the Kīpahulu valley throughout the different plant surveys (see Table S2 in supplementary material). Among those species, 33 have been evaluated as representing a high invasion risk in the Hawaiian Islands (WRA score > 6), and four have been listed as one of the 100 of the

world’s worst invasive alien species (Table 1). Most of the other species have yet to receive WRA scores (Table S2). The number of alien plant species observed in the valley sharply increased in the 1970–1980s (Figure 2). This increase was larger in management units located at lower elevation compared to those located at higher elevation.

In comparison to the preceding surveys, 11 new alien species were recorded between 2012 and 2018 among which six received WRA scores and three have been evaluated with a WRA score > 6: *Blechnum appendiculatum* (Blechnaceae, WRA score = 17), *Centella asiatica* (Apiaceae, WRA score = 7), and *Tibouchina herbacea* (Melastomaceae, WRA score = 24). The number of alien plant species found per plot between 2012 and 2018 decreased with increasing elevation (Figure 3A). Plots located in the lower and middle Kīpahulu exhibited relatively high alien species richness compared to those located in the upper Kīpahulu. When we combined observations in plots and transects between 2012 and 2018, 13 alien species were observed in the upper Kīpahulu while 18 and 24 species were observed in middle and lower part of the valley, respectively (Figure 3B).

The coverage of alien plant species in the undergrowth and their relative density in the different plant size classes sharply decreased between lower and middle Kīpahulu (Figure 4). *Clidemia birta* (Melastomataceae) and *P. cattleianum* had the highest coverage in the undergrowth; they were inventoried in 8 and 9 plots with average coverage of 17.3% and 13.5%, respectively (see Figure S3 in supplementary material). *Psidium cattleianum* was the only species recorded as a seedling, small tree, or large tree within plots. In the lowest plot, *P. cattleianum* largely dominated the large-tree and seedling size-classes and formed dense thickets. Two alien species, *C. birta* and *R. rosifolius* dominated the shrub layer in lower Kīpahulu. The alien tree fern *Sphaeropteris cooperi* (Cyatheaceae) was observed in locations below 1,000 m elevation.

Psidium cattleianum, established in the lower Kīpahulu prior to 1967, was one of the first alien plant species considered a threat to native plant diversity in the valley (Table 1).

TABLE 1

Alien Species List Found in the Kīpahulu Valley During the Different Surveys in 1945 (Fagerlund 1945), 1967 (Lamoureux 1968), 1976 (Lamoureux and Stemmermann 1976), 1979 (Yoshinaga 1980), 1983–1988 (Anderson et al. 1992), and 2012–2018 (This Study)

Family	Taxa	WRA Score	Life Form	1945	1967	1976	1979	1983– 1988	2012– 2018
Melastoma- taceae	<i>Clidemia birta</i> (L.) D. Don	28	Shrub					X⁺⁺	X
Poaceae	<i>Paspalum conjugatum</i> P. J. Bergius	28	Herb		X	X	X [†]	X [†]	X
Asteraceae	<i>Ageratum conyzoides</i> (L.) L.	26	Herb				X	X	X
Melastoma- taceae	<i>Tibouchina herbacea</i> (DC.) Cogn.	24	Herb- subshrub						X
Commelin- aceae	<i>Commelina diffusa</i> Burm. f.	23	Herb				X	X	
Poaceae	<i>Andropogon virginicus</i> L.	22	Herb					X [†]	
Poaceae	<i>Setaria palmifolia</i> (J. Koenig) Stapf	22	Herb	X					X
Myrtaceae	<i>Psidium guajava</i> L.	21	Shrub- small tree	X	X		X	X [†]	?
Poaceae	<i>Holcus lanatus</i> L.	20	Herb		X	X	X	X [†]	X
Myrtaceae	<i>Syzygium jambos</i> (L.) Alston	20	Tree				X		
Poaceae	<i>Ebrharta stipoides</i> Labill.	19	Herb					X ⁺⁺	
Poaceae	<i>Melinis minutiflora</i> P. Beauv.	18	Herb				X [†]	X [†]	
Poaceae	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	18	Herb					X [*]	
Myrtaceae	<i>Psidium cattleianum</i> Afzel. ex Sabine	18	Shrub- small tree		X	X[†]	X[†]	X[†]	X
Polygonaceae	<i>Rumex acetosella</i> L.	18	Herb		X		X	X	
Blechnaceae	<i>Blechnum appendiculatum</i> Willd.	17	Fern						X
Poaceae	<i>Axonopus fissifolius</i> (Raddi) Kuhlm.	16	Herb					X [†]	
Zingiber- aceae	<i>Hedychium</i> <i>gardnerianum</i> Sheppard ex Ker Gawl.	16	Herb				?	X⁺⁺	X
Asteraceae	<i>Hypochoeris radicata</i> L.	16	Herb		X	X	X	X [†]	X
Orchidaceae	<i>Spathoglottis plicata</i> Blume	16	Herb				X		
Cyatheaceae	<i>Sphaeropteris cooperi</i> (F. Muell.) R. M. Tryon	16	Tree fern					X [†]	X
Pteridaceae	<i>Adiantum raddianum</i> C. Presl	15	Fern		X		X		
Poaceae	<i>Axonopus compressus</i> (Sw.) P. Beauv.	15	Herb				X [†]		
Poaceae	<i>Anthoxanthum odoratum</i> L.	14	Herb					X [†]	
Asteraceae	<i>Senecio vulgaris</i> L.	14	Herb				X		
Bignoniaceae	<i>Spathodea</i> <i>campanulata</i> P. Beauv.	14	Tree				X[†]	X⁺⁺	
Asteraceae	<i>Youngia japonica</i> (L.) DC.	14	Herb		X		X	X	X
Euphorbi- aceae	<i>Aleurites moluccana</i> [‡] (L.) Willd.	12	Tree		X				
Poaceae	<i>Paspalum dilatatum</i> Poir.	12	Herb				X	X [*]	
Cyperaceae	<i>Rhynchospora caduca</i> Elliott	11	Herb					X	X
Rosaceae	<i>Rubus rosifolius</i> Sm.	10	Subshrub- shrub	X	X	X	X	X	X
Apiaceae	<i>Centella asiatica</i> (L.) Urb.	7	Herb						X
Onagraceae	<i>Epilobium billardierianum</i> Ser.	7	Herb					X	

Only species with a weed risk assessment (WRA) scores ≥ 6 (high) are shown here (see Table S2 for full table). Species highlighted in bold font belong to the “100 of the World’s worst invasive alien species.” “X” represents species found by the valley and “?” represent species for which the identification was uncertain.

[†] Observed in the Kīpahulu valley but not in the plots.

[‡] Reported by the authors as a threat.

^{*} Polynesian introduction.

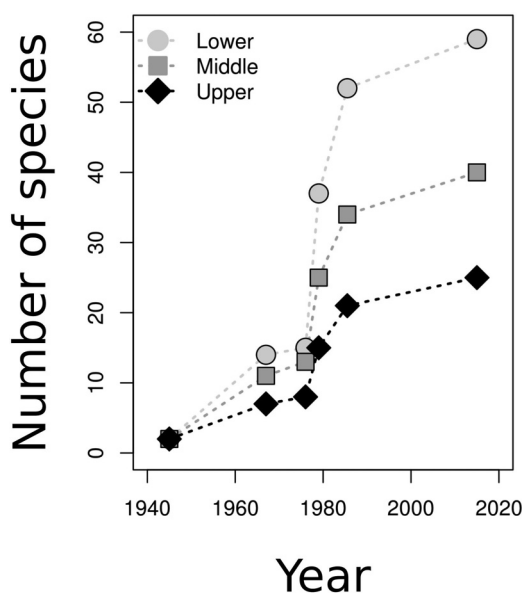


FIGURE 2. Cumulative number of alien plant species observed in the different management units of the valley (lower, middle, and upper Kīpahulu) across the different surveys (see Table S2).

It has greatly spread upward nearly doubling the upper elevation boundary. It was observed up to 670 m in 1967, up to 1,000 m in 1976, and up to 1,200 m in 1983–1988. Although the upper elevation limit did not change during the last 30 years, *P. cattleianum* is now widely distributed in the lower Kīpahulu and in the lower two-thirds of the middle Kīpahulu (Figure 5).

Our 2012–2018 surveys highlighted that some alien species have dramatically expanded during the past two decades. The most notable ones are *C. birta* and *H. gardnerianum* (Zingiberaceae). *Clidemia birta* was first observed in the Kīpahulu valley in 1988 at 850 m where one plant was found and removed. In our 2012–2018 surveys, this species was widely recorded in the lower Kīpahulu and in the lower part of the middle Kīpahulu (between 740 and 1,150 m, Figure 4). In some places it even dominated the undergrowth (Figure 5).

A clump of gingers (likely *H. gardnerianum*) was first reported by Yoshinaga (1980) and more than 10 years later Anderson et al. (1992) reported that the invasion by

H. gardnerianum was still at an incipient stage with an individual recorded between 880 and 1,100 m. During our recent surveys, *H. gardnerianum* was widely recorded in both the lower and middle Kīpahulu (between 775 and 1,535 m, Figure 3). Its coverage remained relatively low however as it never exceeded more than 25% of the undergrowth in any plot (Figure 5). *Rubus rosifolius* which was already present in the valley <610 m in 1945 has spread upward and was found up to 1,570 m during our last survey. Another potentially highly invasive Melastomataceae, *T. herbacea*, was newly observed in the valley between 2012 and 2018 and has already colonized all three parts of the valley between 770 and 1,490 m.

DISCUSSION

The elevational boundary separating the relatively alien-free wet forest of Kīpahulu valley from the invaded areas has been pushed upward by persistent alien plant invasions over the last few decades. While the first surveys of the valley in 1945 suggested that pristine forest could still be found in lower Kīpahulu (down to 600 m), our recent surveys indicate that only the forest located in upper Kīpahulu (>1,400 m) remains relatively free of invasive alien plant species.

The relative density and coverage of alien species in plant communities exhibited a strong elevational pattern with dramatic decreases from lower to upper elevation. This pattern is very common worldwide and can be explained by multiple factors including higher human disturbance levels and propagule pressure associated with lower biotic resistance and climatic constraints at lower elevations compared to upper elevations (Pauchard et al. 2009, Guo et al. 2018). Invasion by alien plant species (notably *Holcus lanatus*, *Hypochaeris radicata*, *P. cattleianum*, *Paspalum conjugatum*, and *R. rosifolius*), likely promoted by feral pigs occurred in the late 1970s (Yoshinaga 1980, Diong 1982). A vast program of conservation was put in place in the 1980–1990s to tackle this invasion and keep the middle and upper part of the valley free of ungulates and alien plant species

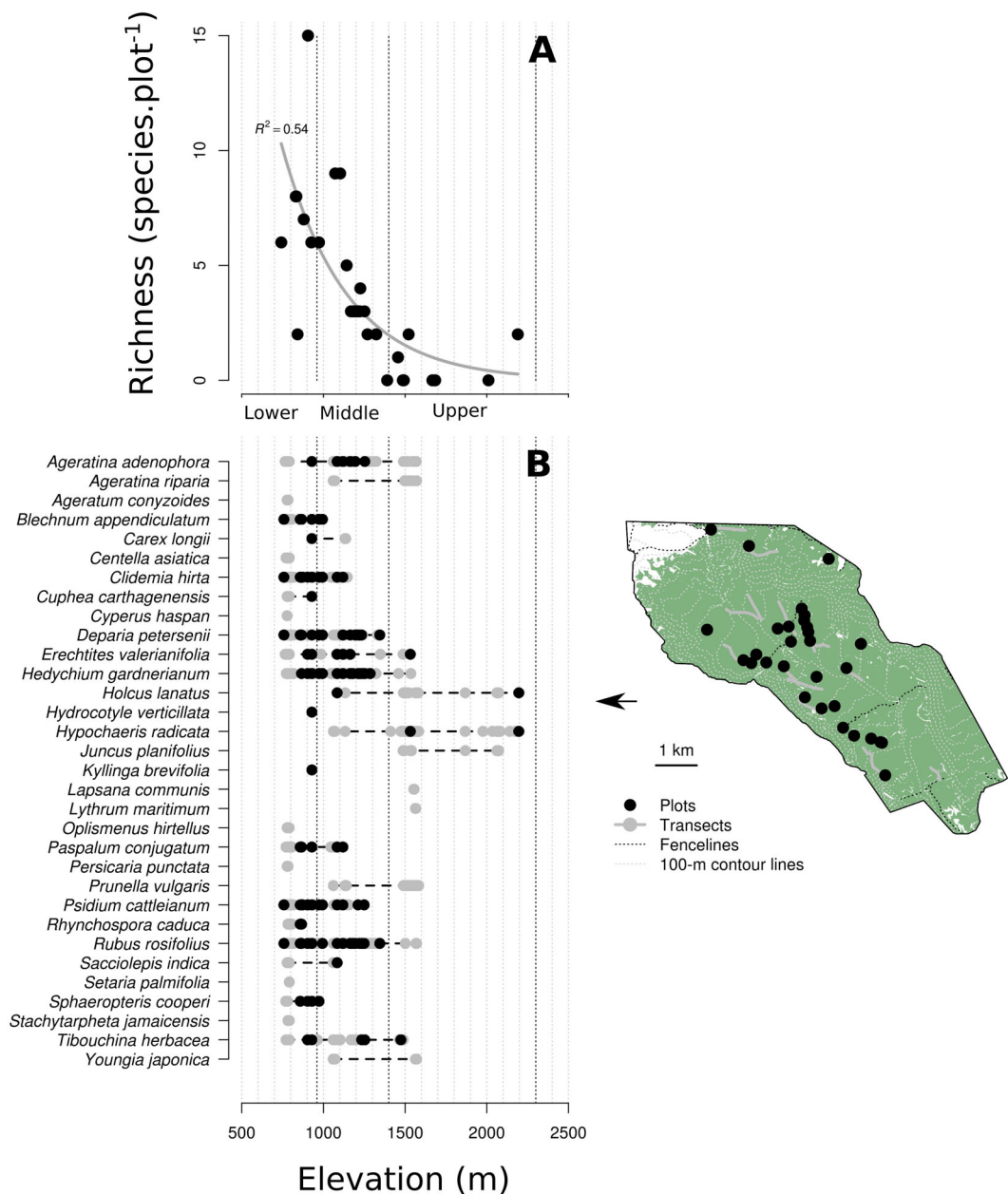


FIGURE 3. Elevational patterns of alien species richness and composition from National Park surveys in 2012–2018. (A) Number of alien species per plot ($N = 30$) as a function of elevation; gray line represent generalized linear model (GLM) fit with a Poisson distribution (P values < 0.001). (B) Occurrences of alien species in plots (black points) and along transects (grey points) located at different elevations (only species identified at the species level are shown). The vertical dotted black lines represent the fence lines delineating the lower, middle, and upper Kīpahulu management areas.

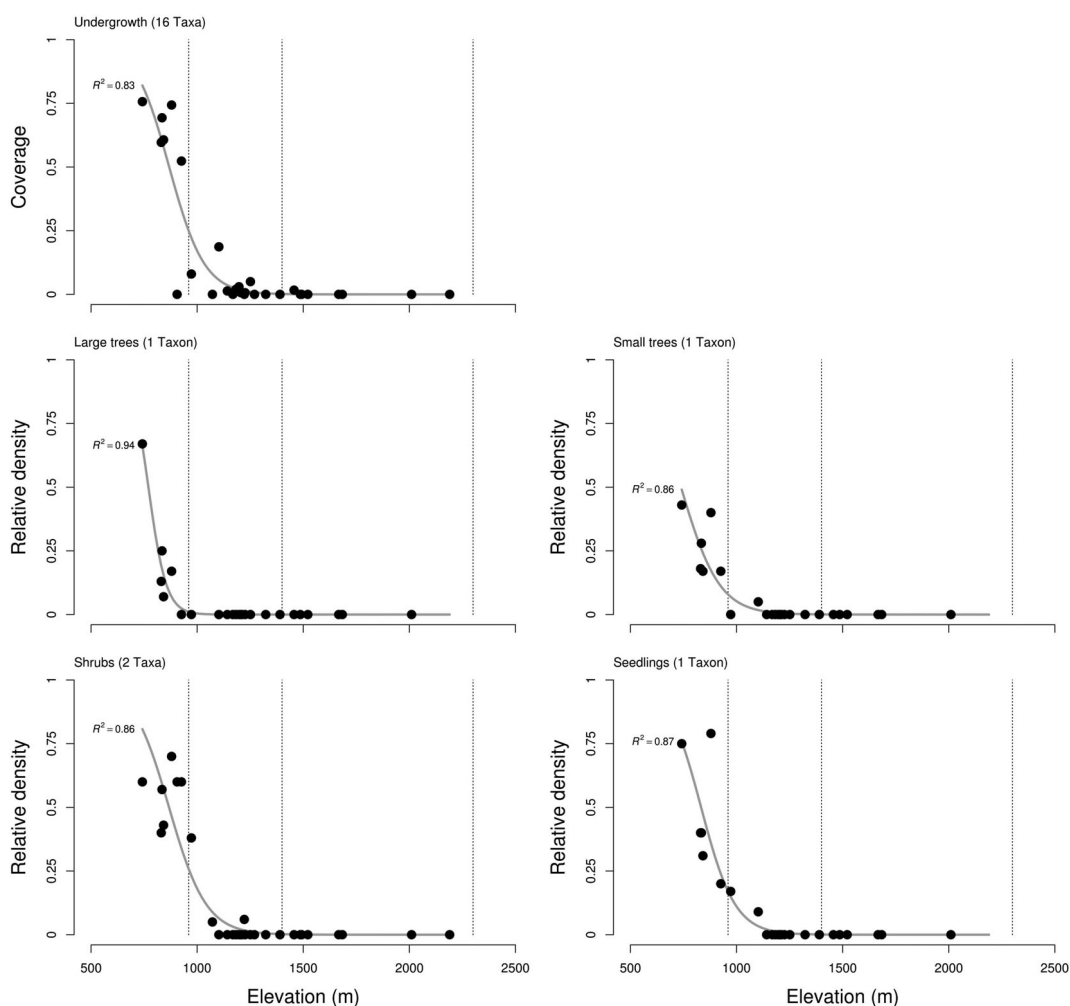


FIGURE 4. Elevational patterns of alien species coverage and relative density from National Park plots surveys in 2012–2018 ($N=30$). Gray lines represent generalized linear model (GLM) fit with binomial distribution (P values < 0.001). The vertical dotted black lines represent the fence lines delineating the lower, middle, and upper Kīpahulu management areas.

(Anderson et al. 1992, Loope et al. 1992, Anderson and Stone 1993, Loope et al. 2013). Those conservation efforts may have slowed down the invasion but failed to stop the establishment and spread of alien plant species upward.

Since the last extensive survey by Anderson et al. (1992), 11 new alien plant species, among which three exhibit high WRA scores, have been observed (*B. appendiculatum*, *C. asiatica*, and *T. herbacea*). Invasion by

T. herbacea, which is able to invade undisturbed forests is of particular concern (see Almasi 2000). This tall, shrub-like herb has been first recorded in the valley in 1998 (National Park Service unpublished data) and has quickly spread in all three management units of the valley. Two previously observed species with high WRA scores, *C. birta* and *H. gardnerianum*, have spread and expanded within the valley. *Clidemia birta*, which was first observed in the valley in 1988 at 850 m,

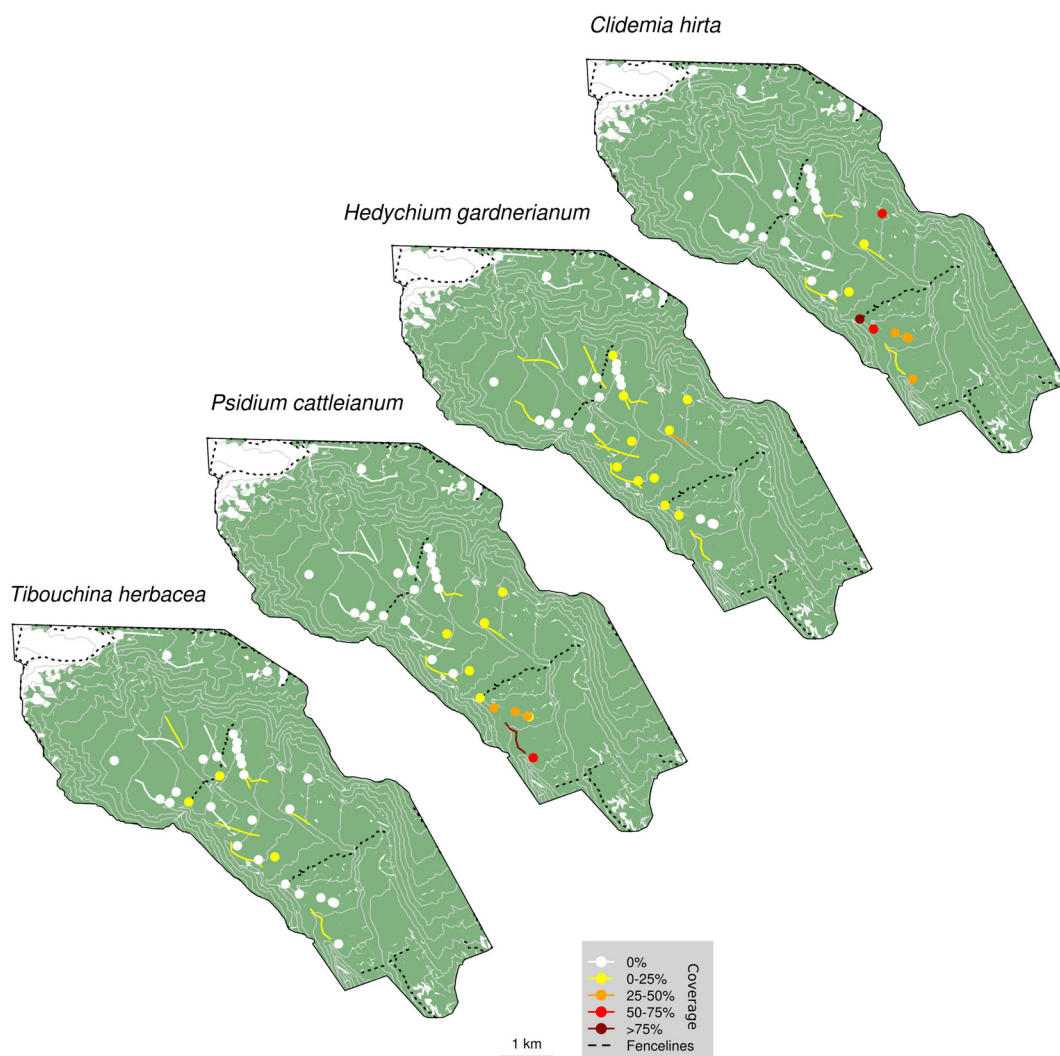


FIGURE 5. Distribution and coverage of some of the worst invasive alien plant species from National Park surveys in 2012–2018.

was already well-established by 2004 between 825 and 1,040 m (Medeiros 2004). It continued to spread and is currently well-established between 740 and 1,150 m. According to Loope et al. (1992), *C. hirta* could continue to expand up to 1,500 m and higher due to global warming.

Invasion by *H. gardnerianum* is particularly threatening. This tall herb (up to 2–3 m high) can establish a monospecific understory and decrease the recruitment of native trees

without affecting the recruitment of *P. cattleianum* (Minden et al. 2010). In the long-term this can lead to the replacement of the native canopy species by *P. cattleianum* along its elevational range (currently up to 1200 m) with lasting effects on biodiversity (Boehmer 2011). Furthermore, although *H. gardnerianum* currently occurs up to 1,535 m this species is native to the Himalayas, is cold tolerant and capable of establishing in native forest understory, even in the

absence of pig disturbance, and therefore constitutes a major threat to the upper Kīpahulu forest (Medeiros 2004).

Our results support that ungulate removal and fencing did not stop the spread of alien plant species. This is in agreement with other studies in Hawai‘i showing that fencing alone, without active alien plant species removal and restoration efforts, can still benefit alien plants (Weller et al. 2011, 2018). The spread of alien plant species in upper Kīpahulu may have been limited by an higher biotic resistance of the ōhi‘a dominated forest. Indeed, compared to areas dominated by koa trees at lower elevations, areas dominated by ōhi‘a trees exhibit lower invasibility because of lower light and nutrient availability in the undergrowth (Denslow et al. 2006, McDaniel and Ostertag 2010, Yelenik 2017).

Although some species such as *C. birta*, *H. gardnerianum*, and *T. herbacea* are able to grow in the shade of undisturbed native canopies, most alien plant species grow better with higher light availability (e.g., Pattison et al. 1998, Almasi 2000, Baruch et al. 2000, McDaniel and Ostertag 2010). Massive defoliation of koa trees due to an outbreak of the Hawaiian koa moth (*Scotorythra paludicola*, Geometridae) in 2003–2004 may have favored the establishment and spread of alien plants in the valley (Haines et al. 2009). This defoliation event may partly explain the observed spread of alien plants species into the koa and ōhi‘a-koa forests in lower and middle Kīpahulu compared to the survey by Anderson et al. (1992).

The ōhi‘a dominated forest in upper Kīpahulu has remained relatively undisturbed and free of alien species. As in the other Hawaiian Islands, this ōhi‘a forest is threatened by two non-native fungi, *Ceratocystis lukuohia* and *Ceratocystis buliobia* (Ceratocystidaceae), known to cause rapid and widespread death of ōhi‘a (known as Rapid Ōhi‘a Death, ROD) that appeared in a variety of locations on the neighboring island of Hawai‘i in 2010 (Asner et al. 2018, Vaughn et al. 2018). So far those fungi have not spread on Maui but environmental conditions in Kīpahulu valley are suitable for their development (Fortini et al. 2019). *Ceratocystis*

buliobia has been detected in 2019 on one tree near Kīpahulu valley. The establishment and spread of those fungi in the Kīpahulu valley would promote accelerated spread of alien plant species through the relatively well preserved ōhi‘a forest. Spread of alien plant species toward higher elevation is also supported by ongoing climate changes (Vorsino et al. 2014, Koide et al. 2017).

Unfortunately, fencing may do nothing to prevent the movement of non-native frugivorous bird species such as Japanese white-eye (*Zosterops japonicus*, Zosteropidae) and red-billed leiothrix (*Leiothrix lutea*, Timaliidae), both common in Kīpahulu valley. These bird species play a significant role in the dispersal of *C. birta*, *H. gardnerianum*, *P. cattleianum*, as well as other highly invasive weeds like *Miconia calvescens* (Melastomataceae) also recently been detected in the lower valley and outside the area of this study (Medeiros et al. 1998, Medeiros 2004, Leary et al. 2014).

CONCLUSION

Given the limited resources to combat invasive alien plant species, a priority management area has recently been set up with alien plant species management focusing above 1,067 m to try to prevent continued upward spread. Currently, upper Kīpahulu is still considered pig-free; however, within the last five years, lower and middle Kīpahulu have increased pig populations (National Park Service unpublished data). Although *C. birta* and *H. gardnerianum*—two of the world’s worst invasive alien species—were detected at an incipient stage in the 1980s, these species are now pervasive in Kīpahulu valley. Today, it seems unrealistic to eradicate these species from the valley. However, the development of new and effective biocontrol strategies for well-established invasive plants could help to prevent their spread into or reduce their impacts on one of the last relatively pristine wet forests of Hawai‘i. Conservation efforts should focus on controlling alien plant species in middle Kīpahulu and preventing the spread of those species into the upper part of the valley. The quick expansion of *C. birta* and

H. gardnerianum highlights the importance of early detection and control of invasive alien plant species particularly in areas where initial numbers and densities are low.

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Literature Cited

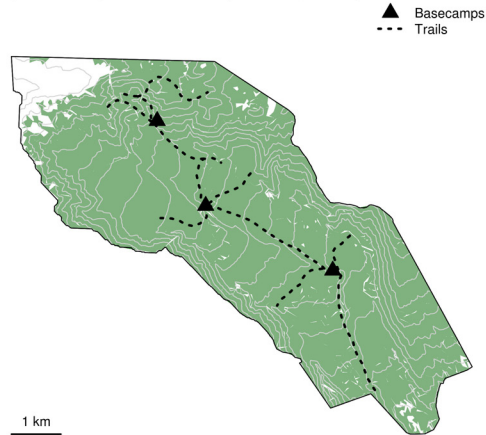
- Ainsworth, A., P. Berkowitz, J. D. Jacobi, R. K. Loh, and K. Kozar. 2011. Focal terrestrial plant communities monitoring protocol: Pacific island network. Natural Resource Report NPS/PACN/NRR-2011/410. National Park Service, Fort Collins, Colorado.
- Ainsworth, A., J. D. Jacobi, R. K. Loh, J. A. Christian, C. Yanger, and P. Berkowitz. 2012. Established invasive plant species monitoring protocol: Pacific island network. Natural Resource Report NPS/PACN/NRR-2012/514. National Park Service, Fort Collins, Colorado.
- Almasi, K. N. 2000. A non-native perennial invades a native forest. *Biol. Invasions* 2 (3):219–230. <https://doi.org/10.1023/A:1010009123469>.
- Anderson, S. J., and C. P. Stone. 1993. Snaring to control feral pigs *Sus scrofa* in a remote Hawaiian rain forest. *Biol. Conserv.* 63: 195–201. [https://doi.org/10.1016/0006-3207\(93\)90712-A](https://doi.org/10.1016/0006-3207(93)90712-A).
- Anderson, S. J., C. P. Stone, and P. K. Higashino. 1992. Distribution and spread of alien plants in Kīpahulu Valley, Haleakala National Park, above 2,300 ft elevation. In: *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawaii Press, Honolulu, Hawai'i.
- Asner, G. P., R. E. Martin, L. M. Keith, W. P. Heller, M. A. Hughes, N. R. Vaughn, R. F. Hughes, and C. Balzotti. 2018. A spectral mapping signature for the Rapid Ohia Death (ROD) pathogen in Hawaiian forests. *Remote Sensing* 10(3):404. <https://doi.org/10.3390/rs10030404>.
- Baruch, Z., R. R. Pattison, and G. Goldstein. 2000. Responses to light and water availability of four invasive Melastomataceae in the Hawaiian Islands. *Int. J. Plant Sci.* 161(1):107–118. <https://doi.org/10.1086/314233>.
- Boehmer, H. J. 2011. Vulnerability of tropical montane rain forest ecosystems due to climate change. Pages 789–802 in H. G. Brauch, Ü. Oswald Spring, C. Mesjasz, et al., eds. *Coping with global environmental change, disasters and security: Threats, challenges, vulnerabilities and risks*. Springer, Berlin Heidelberg.
- Bowen, L., and D. van Vuren. 1997. Insular endemic plants lack defenses against herbivores. *Conserv. Biol.* 11(5):1249–1254.
- Caujape-Castells, J., A. Tye, D. J. Crawford, A. Santos-Guerra, A. Sakai, K. Beaver, W. Lobin, V. F. B. Florens, M. Maura, R. Jardim, I. Gomes, and C. Kueffer. 2010. Conservation of oceanic island floras: present and future global challenges. *Perspect. Plant Ecol.* 12(2):107–129. <https://doi.org/10.1016/j.ppees.2009.10.001>.
- Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* 78 (3), 347–383.
- Daehler, C. C., J. S. Denslow, S. Ansari, and H.-C. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from

- Hawaii and other Pacific Islands. *Conserv. Biol.* 18:360–368. <https://doi.org/10.1111/j.1523-1739.2004.00066.x>.
- Dawson, W., D. Moser, M. van Kleunen, H. Kreft, J. Pergl, P. Pyšek, P. Weigelt, et al., 2017. Global hotspots and correlates of alien species richness across taxonomic groups. *Nat. Ecol. Evol.* 1:0186. <https://doi.org/10.1038/s41559-017-0186>.
- Denslow, J. S. 2003. Weeds in paradise: thoughts on the invasibility of tropical islands. *Ann. Mo. Bot. Gard.* 90(1):119–127. <https://doi.org/10.2307/3298531>.
- Denslow, J. S., A. L. Uowolo, and R. F. Hughes. 2006. Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* 148(1):118–128. <https://doi.org/10.1007/s00442-005-0342-7>.
- Denslow, J. S., J. C. Space, and P. A. Thomas. 2009. Invasive exotic plants in the tropical Pacific Islands: patterns of diversity. *Biotropica* 41(2):162–170. <https://doi.org/10.1111/j.1744-7429.2008.00469.x>.
- Diong, C. H. 1982. Population biology and management of the feral pig (*Sus scrofa* L.) in Kīpahulu Valley, Maui. Ph.D. Dissertation, Department of Zoology, University of Hawaii, Honolulu. <http://www.hear.org/articles/diong1982/>.
- Fagerlund, G. O. 1945. Report on Kīpahulu Valley.
- Fortini, L. B., L. R. Kaiser, L. M. Keith, J. Price, R. F. Hughes, J. D. Jacobi, and J. B. Friday. 2019. The evolving threat of Rapid ‘Ōhi‘a Death (ROD) to Hawai‘i’s native ecosystems and rare plant species. *For. Ecol. Manag.* 448:376–385. <https://doi.org/10.1016/j.foreco.2019.06.025>.
- Guo, Q., S. Fei, Z. Shen, B. V. Iannone, J. Knott, and S. L. Chown. 2018. A global analysis of elevational distribution of non-native versus native plants. *J. Biogeogr.* 45(4):793–803. <https://doi.org/10.1111/jbi.13145>.
- Haines, W. P., M. L. Heddle, P. Welton, and D. Rubinoff. 2009. A recent outbreak of the Hawaiian Koa moth, *Scotorythra paludicola* (Lepidoptera: Geometridae), and a review of outbreaks between 1892 and 2003. *Pac. Sci.* 63(3):349–369. <https://doi.org/10.2984/049.063.0305>.
- Ibanez, T., P. Hart, A. Ainsworth, J. Gross, and R. Monello. 2019. Factors associated with alien plant richness, cover and composition differ in tropical island forests. *Divers. Distrib.* 25(12):1910–1923. <https://doi.org/10.1111/ddi.12989>.
- Imada, C. T. 2012. Hawaiian native and naturalized vascular plants checklist. Bishop Museum, Honolulu, Hawai‘i.
- Imada, C. T. 2019. Hawaiian naturalized vascular plants checklist (February 2019 update). Bishop Museum Technical Report 69, Honolulu, Hawai‘i.
- Jacobi, J. D., J. P. Price, L. B. Fortini, S. M. Gon, and P. Berkowitz. 2017. Baseline land cover. Pages 9–20 in P. C. Selman, C. P. Giardina, J. D. Jacobi, and Z. Zhu, eds. Baseline and projected future carbon storage and carbon fluxes in ecosystems of Hawai‘i. U.S. Geological Survey Professional Paper 1834. <https://doi.org/10.3133/pp1834>.
- Koide, D., K. Yoshida, C. C. Daehler, and D. Mueller-Dombois. 2017. An upward elevation shift of native and non-native vascular plants over 40 years on the island of Hawai‘i. *J. Veg. Sci.* 28(5):939–950. <https://doi.org/10.1111/jvs.12549>.
- Krushelnicky, P. D., C. G. Chimera, and E. A. VanderWerf. 2019. Natural resource condition assessment: Haleakalā National Park. Natural Resource Report NPS/HALE/NRR-2019/1977. National Park Service, Fort Collins, Colorado.
- Lamoureux, C. 1968. The vascular plants of Kīpahulu valley, Maui. In: Scientific report of the Kīpahulu valley expedition, Warner RE, The Nature Conservancy, pp. 23–54.
- Lamoureux, C., and L. Stemmermann. 1976. Kīpahulu expedition 1976. University of Hawaii at Manoa.
- Loope, L. L., R. F. Hughes, and J.-Y. Meyer. 2013. Plant invasions in protected areas of tropical Pacific Islands, with special reference to Hawaii. Pages 313–348 in L. C. Foxcroft, P. Pyšek, D. M. Richardson, and P. Genovesi, eds. Plant invasions in protected areas: Patterns, problems and challenges, invading nature – Springer series in invasion ecology. Springer Netherlands, Dordrecht.

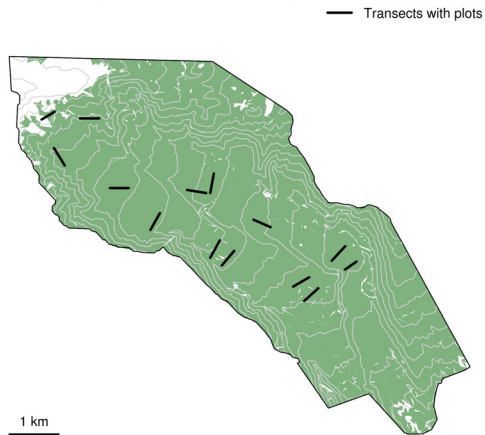
- Leary, J., B. V. Mahnken, L. J. Cox, A. Radford, J. Yanagida, T. Penniman, D. C. Duffy, and J. Gooding. 2014. Reducing nascent miconia (*Miconia calvescens*) patches with an accelerated intervention strategy utilizing herbicide ballistic technology. *Invas. Plant Sci. Mana.* 7(1):164–175. <https://doi.org/10.1614/IPSM-D-13-00059.1>.
- Loope, L. L., R. J. Nagata, and A. C. Medeiros. 1992. Alien plants in Haleakala National Park. Pages 551–576 in *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawaii Press, Honolulu, Hawai'i.
- McDaniel, S., and R. Ostertag. 2010. Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests. *Appl. Veg. Sci.* 13(3):280–290. <https://doi.org/10.1111/j.1654-109X.2009.01074.x>.
- Medeiros, A. C. 2004. Phenology, reproductive potential, seed dispersal and predation, and seedling establishment of three invasive plant species in a Hawaiian rain forest. Ph.D. Dissertation, Department of Botany, University of Hawaii, Honolulu. <http://www.hear.org/articles/medeiros2004dissertation>.
- Medeiros, A. C., L. L. Loope, and C. G. Chimera. 1998. Flowering plants and gymnosperms of Haleakala National Park. Pacific Cooperative Studies Unit, University of Hawaii at Manoa, Department of Botany, Technical report no. 120, 181.
- Minden, V., J. D. Jacobi, S. Porembski, and H. J. Boehmer. 2010. Effects of invasive alien kahili ginger (*Hedychium gardnerianum*) on native plant species regeneration in a Hawaiian rainforest. *Appl. Veg. Sci.* 13:5–14. <https://doi.org/10.1111/j.1654-109X.2009.01056.x>.
- Moser, D., B. Lenzner, P. Weigelt, W. Dawson, H. Kreft, J. Pergl, P. Pyšek, et al. 2018. Remoteness promotes biological invasions on islands worldwide. *PNAS* 115:9270–9275. <https://doi.org/10.1073/pnas.1804179115>.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, New York, NY, 547 pp.
- Mueller-Dombois, D., and F. R. Fosberg. 1998. *Vegetation of the tropical Pacific islands*. Springer, New York, 733 pp.
- Murphy, M. J., F. Inman-Narahari, R. Ostertag, and C. M. Litton. 2014. Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. *Biol. Invasions* 16(1):63–71. <https://doi.org/10.1007/s10530-013-0503-2>.
- Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117(4):449–459. <https://doi.org/10.1007/s004420050680>.
- Pauchard, A., C. Kueffer, H. Dietz, C. C. Daehler, J. Alexander, P. J. Edwards, J. R. Arévalo, et al. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. *Front. Ecol. Environ.* 7(9):479–486. <https://doi.org/10.1890/080072>.
- R Core Team. 2018. R: A language and environment for statistical computing (Version 3.4.4). Retrieved from <https://www.R-project.org/>
- Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pac. Sci.* 49:87–97.
- Stone, C. P., and L. L. Loope. 1987. Reducing negative effects of introduced animals on native biotas in Hawaii: what is being done, what needs doing, and the role of National Parks. *Environ. Conserv.* 14:245–258. <https://doi.org/10.1017/S0376892900016453>.
- Vaughn, N. R., G. P. Asner, P. G. Brodrick, R. E. Martin, J. W. Heckler, D. E. Knapp, and R. F. Hughes. 2018. An approach for high-resolution mapping of Hawaiian *Metrosideros* forest mortality using laser-guided imaging spectroscopy. *Remote Sensing* 10(4):502. <https://doi.org/10.3390/rs10040502>.
- Vitousek, P. M., L. L. Loope, and C. P. Stone. 1987. Introduced species in Hawaii. Biological effects and opportunities for ecological research. *Trends Ecol. Evol.* 2:224–227. [https://doi.org/10.1016/0169-5347\(87\)90026-7](https://doi.org/10.1016/0169-5347(87)90026-7).
- Vorsino, A. E., L. B. Fortini, F. A. Amidon, S. E. Miller, J. D. Jacobi, J. P. Price, S. 'Ohukani'ohi'a Gon III, and G. A. Koob.

2014. Modeling Hawaiian ecosystem degradation due to invasive plants under current and future climates. PLOS ONE 9 (5): e95427. <https://doi.org/10.1371/journal.pone.0095427>.
- Warner, R. E. 1968. Scientific report of the Kīpahulu valley expedition. The Nature Conservancy.
- Wehr, N. H., S. C. Hess, and C. M. Litton. 2018. Biology and impacts of Pacific Islands invasive species. 14. *Sus scrofa*, the feral pig (Artiodactyla: Suidae). Pac. Sci. 72(2):177–198. <https://doi.org/10.2984/72.2.1>.
- Weller, S. G., R. J. Cabin, D. H. Lorence, S. Perlman, K. Wood, T. Flynn, and A. K. Sakai. 2011. Alien plant invasions, introduced ungulates, and alternative states in a mesic forest in Hawaii. Restor. Ecol. 19(5):671–680. <https://doi.org/10.1111/j.1526-100X.2009.00635.x>.
- Weller, S. G., A. K. Sakai, M. Clark, D. H. Lorence, T. Flynn, W. Kishida, N. Tangalin, and K. Wood. 2018. The effects of introduced ungulates on native and alien plant species in an island ecosystem: implications for change in a diverse mesic forest in the Hawaiian Islands. For. Ecol. Manag. 409:518–526. <https://doi.org/10.1016/j.foreco.2017.11.023>.
- Wilmshurst, J. M., T. L. Hunt, C. P. Lipo, and A. J. Anderson. 2011. High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. PNAS 108(5):1815. <https://doi.org/10.1073/pnas.1015876108>.
- Yelenik, S. G. 2017. Linking dominant Hawaiian tree species to understory development in recovering pastures via impacts on soils and litter. Restor. Ecol. 25(1):42–52. <https://doi.org/10.1111/rec.12377>.
- Yoshinaga, A. Y. 1980. Upper Kīpahulu Valley weed survey. University of Hawaii at Manoa, Honolulu, Hawai‘i.

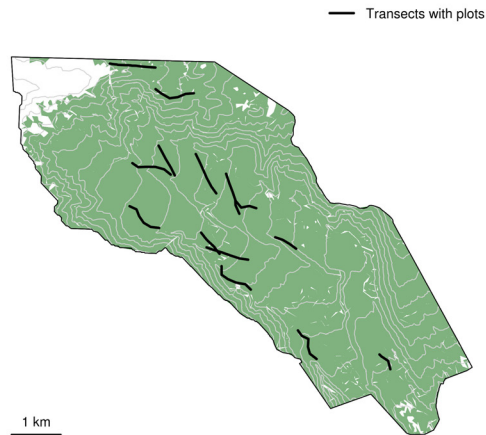
Kipahulu expedition 1967 (Warner, 1968)



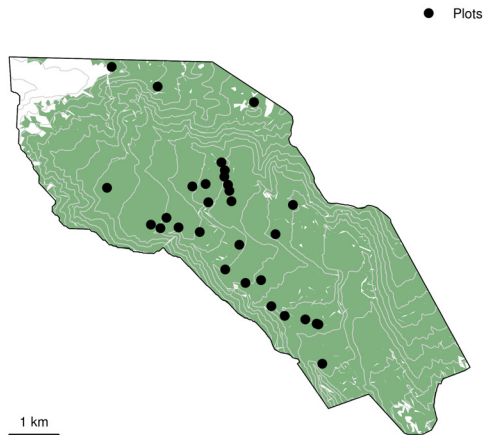
1983-1988 (Anderson et al., 1992)



2012-2017 (this study)



2012-2018 (this study)



SUPPLEMENTARY FIGURE S1. Some of the historical and the recent plant surveys in the Kipahulu valley.

SUPPLEMENTARY TABLE S2

Alien Species List Found in the Kīpahulu Valley During the Different Surveys in 1945 (Fagerlund 1945), 1967 (Lamoureux 1968), 1976 (Lamoureux and Stemmermann 1976), 1979 (Yoshinaga 1980), 1983–1988 (Anderson et al. 1992), and 2012–2018 (National Park Surveys)

Family	Taxa	WRA Score	1945	1967	1976	1979	1983–1988	2012–2018
Peridaceae	<i>Adiantum raddianum</i> C. Presl	15		610 m		<760 m		
Asteraceae	<i>Ageratina adenophora</i> (Spreng.) R. M. King. & H. Rob.						720–2380 m	770–1570 m
Asteraceae	<i>Ageratina riparia</i> (Regel) R. M. King. & H. Rob.					610 m		1060–1570 m
Asteraceae	<i>Ageratum conyzoides</i> (L.) L.	26				<1110 m		780 m
Euphorbiaceae	<i>Aleurites moluccana</i> [†] (L.) Willd.	12		<460 m				
Poaceae	<i>Andropogon virginicus</i> L.	22					1000–1340 m	
Poaceae	<i>Anthoxanthum odoratum</i> L.	14					1070 m	
Asparagaceae	<i>Asparagus</i> sp.	(11–15)						X
Poaceae	<i>Axonopus compressus</i> (Sw.) P. Beauv.	15				960–1400 m		
Poaceae	<i>Axonopus fissifolius</i> (Raddi) Kuhlmann.	16					720–1160 m	
Blechnaceae	<i>Blechnum appendiculatum</i> Willd.	17					720–960 m	740–970 m
Blechnaceae	<i>Blechnum occidentale</i> L.	(4–17)						
Cyperaceae	<i>Carex longii</i> Mack.	(8)						900–1140 m
Orobanchaceae	<i>Castilleja arvensis</i> Schlttdl. & Cham.					920 m		770–790 m
Apiaceae	<i>Centella asiatica</i> (L.) Urb.	7					720–750 m	790 m
Thelypteridaceae	<i>Christella dentata</i> (Forsk.) Brownsey & Jermy							
Thelypteridaceae	<i>Christella parasitica</i> (L.) H. Lévl.						720–960 m	
Melastomataceae	<i>Clidemia birta</i> (L.) D. Don	28					850 m*	740–1150 m
Poaceae	<i>Coix lacryma-jobi</i> L.		1220–1980 m			<610 m		
Commelinaceae	<i>Commelina diffusa</i> Burm. f.	23				<670 m	720 m	
Asteraceae	<i>Conyza canadensis</i> (L.) Cronquist					880–990 m		
Asparagaceae	<i>Cordylone fruticosa</i> [†] (L.) A. Chev.	4		<60 m		<730 m		
Lythraceae	<i>Cuphea carthagenensis</i> (Jacq.) J. F. Macbr.	(1–5)		X	<1300 m	1180–1520 m	720–960 m	780–900 m
Cyperaceae	<i>Cyperus brevifolius</i> (Rottb.) Hassk.	(8–20)		X		<1110 m		
Cyperaceae	<i>Cyperus haspan</i> L.	(8–20)				<1180 m	720–960 m	780 m
Athyriaceae	<i>Deparia japonica</i> (Thunb.) M. Kato						X	
Athyriaceae	<i>Deparia petersenii</i> (Kunze) M. Kato							740–1330 m
Caryophyllaceae	<i>Drymaria cordata</i> (L.) Willd. Ex Schult			760 m		<1110 m	720–960 m	
Poaceae	<i>Eberhartia stipoides</i> Labill.	19					1280 m*	X
Elaeagnaceae	<i>Elaeagnus</i> sp.	(13)						
Onagraceae	<i>Epilobium billardierianum</i> Ser.	7						
Asteraceae	<i>Erechtites valerianifolia</i> (Link ex Wolf) Less. ex DC.			<1220 m	<1300 m	<1450 m	750–2070 m	770–1520 m

SUPPLEMENTARY TABLE S2

Family	Taxa	WRA Score	1945	1967	1976	1979	1983–1988	2012–2018
Asteraceae	<i>Eupatorium adenophorum</i> Spreng.			<1370 m	1280–2150 m	<1580 m		
Geraniaceae	<i>Geranium carolinianum</i> L.	(7)		2130 m		X		
Zingiberaceae	<i>Hedychiium gardnerianum</i> Sheppard ex Ker Gawl.	16				810 m	<1100 m*	770–1540 m
Poaceae	<i>Holcus lanatus</i> L.	20		>910 m	>1280 m	930–1450 m	720–2380 m	1070–2190 m
Araliaceae	<i>Hydrocotyle verticillata</i> Thunb.							
Asteraceae	<i>Hypochaeris radicata</i> L.	16		<1070 m		<1010 m	720–1490 m	910 m
Juncaceae	<i>Juncus planifolius</i> R. Br.	(12–21)		>1980 m	>2150 m	>980 m	750–2380 m	1060–2190 m
Cyperaceae	<i>Kyllinga brevifolia</i> Rorth.							1490–2070 m
Cyperaceae	<i>Kyllinga nemoralis</i> (J. R. Frost. & G. Forst)					<1280 m	720–960 m	900 m
Asteraceae	Dandy ex Hurch. & Dalziel							
Asteraceae	<i>Lapsana communis</i> L.						720–2380 m	1550–1560 m
Onagraceae	<i>Ludwigia octovalvis</i> (Jacq.) P. H. Raven	(13–22)				<1110 m	720–960 m	
Lythraceae	<i>Lythrum maritimum</i> Kunth					<1110 m	2070 m	1560–1570 m
Poaceae	<i>Melinis minutiflora</i> P. Beauv.	18				1040 m	720–960 m	
Musaceae	<i>Musa</i> sp. [†]	(–2 to –11)	<820 m	X		<650 m	720 m	X
Poaceae	<i>Opismenus hirtellus</i> (L.) P. Beauv.					<730 m		780–790 m
Oxalidaceae	<i>Oxalis</i> sp	(9–16.5)						X
Poaceae	<i>Paspalum conjugatum</i> P. J. Bergius	28		<1220 m	<1300 m	<1250 m	720–1280 m	770–1100 m
Poaceae	<i>Paspalum dilatatum</i> Poir.	12				1050–1250 m	<900 m*	
Poaceae	<i>Paspalum urvillei</i> Steud.	(7–28)				<900 m	X*	
Poaceae	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	18					1460 m*	
Polygonaceae	<i>Persicaria glabra</i> (Willd.) M. Gómez	(0–22)				<900 m		
Polygonaceae	<i>Persicaria punctata</i> (Elliott) Small	(0–22)					X	780 m
Lamiaceae	<i>Prunella vulgaris</i> L.			>1220 m	1280–2150 m	800–1450 m	1000–2380 m	1060–1580 m
Myrtaceae	<i>Psidium cattleianum</i> Afzel. ex Sabine	18		<670 m	<1000 m	<1310 m	<1220 m	740–1220 m
Myrtaceae	<i>Psidium guajava</i> L.	21		<610 m		<940 m	<720 m	?
Cyperaceae	<i>Rhynchospora caduca</i> Elliott	11	<550 m				750–960 m	780–830 m
Cyperaceae	<i>Rhynchospora</i> sp.	(11)						X
Rosaceae	<i>Rubus rosfolius</i> Sm.	10	<610 m	460–1220 m	<1300 m	<1520 m	720–1490 m	740–1570 m
Polygonaceae	<i>Rumex acetosella</i> L.	18		1980 m		>2150 m	1600–2380 m	
Poaceae	<i>Sacciolepis indica</i> (L.) Chase			<1220 m	<1300 m	<1430 m	1050–1400 m	780–1070 m
Asteraceae	<i>Senecio vulgaris</i> L.	14				1920 m		
Poaceae	<i>Setaria palmifolia</i> (J. Koenig) Stapf	22	1220–1980 m					790 m
Poaceae	<i>Setaria parviflora</i> (Poir.) M. Kerguelen	(9–22)				<730 m		
Solanaceae	<i>Solanum nigrum</i> L.	(1–24)		<910 m		<910 m		

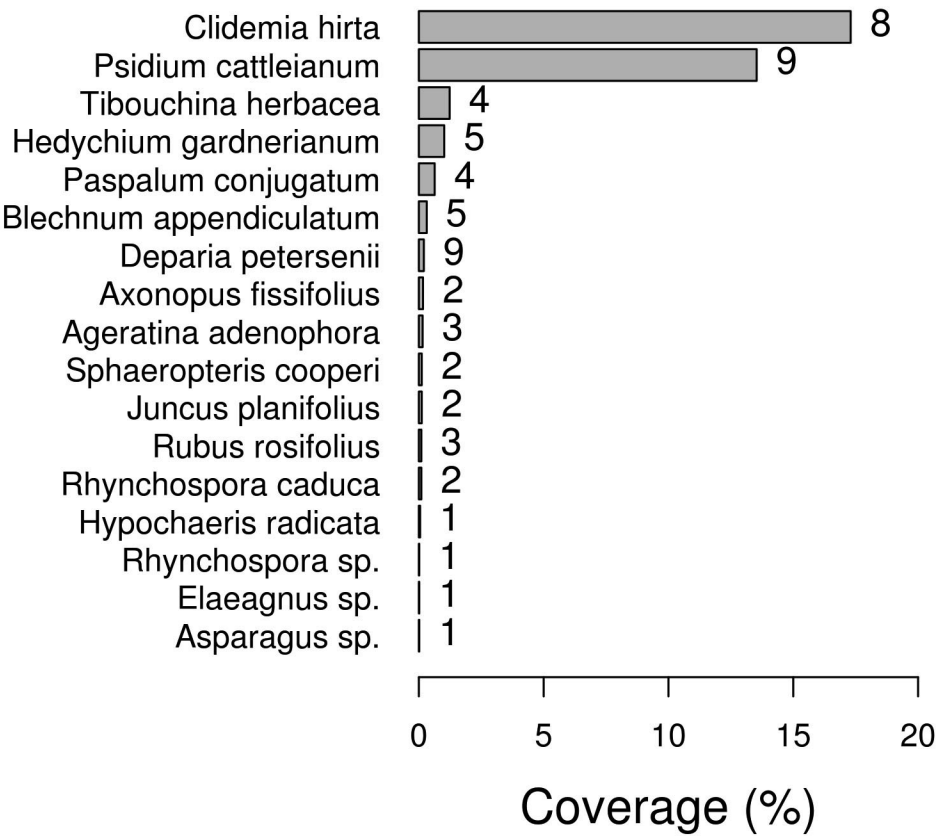
SUPPLEMENTARY TABLE S2

Family	Taxa	WRA Score	1945	1967	1976	1979	1983–1988	2012–2018
Bignoniaceae	<i>Spathodea campanulata</i> P. Beauv.	14				<670 m	<850 m*	
Orchidaceae	<i>Spathoglottis plicata</i> Blume	16				<730 m	730–1010 m	770–925 m
Cyatheaceae	<i>Sphaeropteris cooperi</i> (F. Muell.) R. M. Tryon	16						
Verbenaceae	<i>Stachytarpheta jamaicensis</i> (L.) Vahl	(12)				<730 m	720 m	780–790 m
Verbenaceae	<i>Stachytarpheta urticifolia</i> (Salisb.) Sims	(12)						
Myrtaceae	<i>Syzygium jambos</i> (L.) Alston	20				<640 m		
Melastomataceae	<i>Tibouchina herbacea</i> (DC.) Cogn.	24						770–1490 m
Fabaceae	<i>Trifolium</i> sp.	(4.5–13.5)						X
Asteraceae	<i>Youngia japonica</i> (L.) DC.	14		<1220 m		1080–1450 m	720–2070 m	1060–1570 m

Species highlighted in bold font belong to the “100 of the World’s worst invasive alien species.” “X” represents species found by the valley and “?” represent species for which the identification was uncertain. When available we indicated species’ WRA score (or range of WRA for congeneric species) and at which elevation the species have been observed.

* Species that have been observed outside the plots.

† Polynesian introduction.



SUPPLEMENTARY FIGURE S3. Average coverage of alien species in the undergrowth (in plots where the species occurred, National Park surveys in 2012–2018). Numbers next to the bars indicate the number of plots ($N = 30$) where the species were inventoried in the undergrowth.