Received: 30 April 2021 | Revised: 17 September 2021 | Accepted: 24 September 2021

DOI: 10.1002/ecs2.3926

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Hypotheses and lessons from a native moth outbreak in a low-diversity, tropical rainforest

Paul C. Banko[1] | **Robert W. Peck**[2] | **Stephanie G. Yelenik**[1,3] | **Eben H. Paxton**[1] | **Frank Bonaccorso**[1] | **Kristina Montoya-Aiona**[1] | **R. Flint Hughes**[4] | **Steven Perakis**[5]

[1]Pacific Island Ecosystems Research Center, U.S. Geological Survey, Hawai'i National Park, Hawai'i, USA

[2]Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo, Hawai'i National Park, Hawai'i, USA

[3]Rocky Mountain Research Center, U.S. Forest Service, Reno, Nevada, USA

[4]Institute for Pacific Island Forestry, U.S. Forest Service, Hilo, Hawai'i, USA

[5]Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, Corvallis, Oregon, USA

Correspondence
Paul C. Banko
Email: pbanko@usgs.gov

Funding information
U.S. Geological Survey

Handling Editor: Uffe Nielsen

Abstract

Outbreaks of defoliating insects in low-diversity tropical forests occur infrequently but provide valuable insights about outbreak ecology in temperate environments and in general. We investigated an extensive outbreak of the endemic koa moth (*Scotorythra paludicola*), which defoliated endemic koa trees (*Acacia koa*) over a third of their range on Hawai'i Island during 2013 and 2014. At Hakalau Forest National Wildlife Refuge, we observed the dynamics of the outbreak and its effects on host trees, nutrient cycling, and insectivorous consumers in reforestation stands of densely planted koa and in natural forest stands of mixed koa and 'ōhi'a (*Metrosideros polymorpha*). Contrary to predictions of the resource concentration hypothesis, caterpillar biomass and defoliation severity were greater in the natural forest sites, where koa density was relatively low. Caterpillars preferentially consumed the most palatable koa foliage type (phyllodes), and koa initially refoliated with the least palatable foliage type (true leaves). Lightly defoliated small trees refoliated more quickly than did heavily defoliated ones but the opposite was true for large trees, which also produced a greater proportion of phyllodes. Mortality was greatest for heavily defoliated small koa. Caterpillar frass caused larger increases in soil nitrogen (N) than phosphorus (P) availability, with the greatest N increases in fine-textured soils. Foliar N increased in alien grasses under koa canopies compared to grasses away from koa and to native woody understory species. Bird activity was influenced by 'ōhi'a flower abundance and the severity of koa defoliation; birds switched to outbreaking caterpillar prey, and they gained weight during the outbreak. Bat foraging times decreased during the outbreak, apparently because they became satiated quickly each night. Parasitoid wasps increased with caterpillar abundance but had little influence on outbreak dynamics. Reducing alien grass cover and increasing tree diversity would likely reduce the impacts of insect outbreaks and similar perturbations to native forests.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of Ecological Society of America. This article has been contributed to by US Government employees and their work is in the public domain in the USA.

KEYWORDS
bat feeding ecology, bird feeding ecology, defoliation, dominant host species, Hawaiian Islands, insect outbreak ecology, low-diversity tropical forest, nutrient cycling, parasitoid wasps, refoliation, resilience to disturbance, resource pulse dynamics

INTRODUCTION

Large-scale outbreaks of defoliating insects in natural systems can be viewed as both a consequence and a cause of ecological perturbation, which makes them important for understanding population, community, and ecosystem dynamics. Extensive and often unpredictable outbreaks can be triggered or facilitated by major deviations in a variety of environmental and biotic conditions and processes (Berryman, 1987), but long-term studies demonstrate the difficulty of identifying key drivers and the complexity of their interactions (Royama et al., 2017). Defoliator outbreaks themselves may produce strong, if sometimes transient, effects on ecosystem processes and consumers across trophic levels, but these events tend to be highly variable and difficult to predict (Yang, 2012). For example, defoliation may significantly reduce primary productivity in some plant communities (Coupe & Cahill, 2003; Esper et al., 2007), whereas these effects may be insignificant or transitory in other communities (Harrison & Maron, 1995; Piene, 1989). Reduced canopy cover due to defoliation can lead to successional states of greater species diversity (Carson & Root, 2000), but defoliation may also facilitate plant invasions (Balzotti & Asner, 2017; Maron & Jefferies, 1999). Additionally, the effects of pulses of insect biomass or frass (their excrement) can cascade within and between trophic levels, affecting competitor, predator–prey, and plant–herbivore interactions. Insects and frass can increase soil nutrients and subsequent plant growth (Yang, 2004) and create short-term food bonanzas for a wide range of species (Haney, 1999; Jennings et al., 1991; Wilson & Barclay, 2006; Yang et al., 2008). Integrative studies, although rare, can reveal how species, communities, and ecosystems respond to perturbations by exploring the dynamics of outbreaks and their direct and indirect impacts on host plants, vegetation dynamics, consumer populations and behavior, and ecosystem processes.

Information about forest defoliator outbreaks comes mostly from strongly seasonal areas. Insect populations are not inherently less variable in the tropics than in temperate areas (Redfern & Pimm, 1987; Wolda, 1978, 1980, 1992), but little is known about outbreak dynamics and consequences in tropical forests with relatively weak or ambiguous seasonality (Dyer et al., 2012; Myers, 1988; Yang, 2012). Where seasonal changes in climate and irradiance are comparatively small, patterns of leaf flush phenology are often indistinct, inconsistent, and weakly synchronized across the landscape (Lamoureux et al., 1981; Reich, 1995), which may affect the variability of leaf-chewing insect populations and their propensity to irrupt. Partly for this reason, Dyer et al. (2012) have encouraged more studies of defoliator outbreaks in relatively aseasonal tropical forests.

We investigated the dynamics of an insect outbreak and the ensuing response of a weakly seasonal Hawaiian forest community to the widespread defoliation of a dominant tree species, the pulse of nutrients into the ecosystem, and the superabundance of prey available to insectivores. At landscape scale, this tropical forest community is dominated by only two canopy tree species, the ubiquitous ʻōhiʻa (*Metrosideros polymorpha*) and the abundant but more narrowly distributed koa (*Acacia koa*). Complementing studies of outbreaks in familiar temperate ecosystems, our broad-spectrum observational study allows for more tractability in disentangling species interactions due to the low-diversity, tropical environment in which it occurred. Moreover, this outbreak system represents a coevolved association between an endemic insect and an endemic host tree rather than a novel interaction between native and non-native species.

In Hawaiian forests, the most familiar irruptive insect is the koa moth (*Scotorythra paludicola*; Geometridae), which is found on the islands of Oʻahu, Maui, and Hawaiʻi, and is an obligate feeder (but see Haines et al., 2013) on the phyllodes of koa. Koa hosts at least 15 species of Lepidoptera (Swezey, 1954), including the koa moth and two non-irruptive species of *Scotorythra*, an endemic genus represented by a radiation of at least 43 species (Heddle, 2003). The koa moth has sporadically irrupted at least 14 times in native forests since 1892 (Haines et al., 2009; Henshaw, 1902). Although the species seems to be distributed throughout the range of its host, it is relatively uncommon when not irrupting, despite systematic sampling (Howarth et al., 2003, Giffin, 2007; R. W. Peck, personal observation; but see Haines et al., 2009). Outbreaks of uncommon insects are generally not expected on abundant host plant species (Dyer et al., 2012) because wide fluctuations in population abundance are more likely to lead to population extinction (Root & Cappuccino, 1992).

As a symbiotic nitrogen-fixing tree that is widespread and abundant in mesic to wet montane forests (Gagné &

Cuddihy, 1999), koa strongly influences soil processes as well as the structure and dynamics of plant, arthropod, and vertebrate communities (Banko & Banko, 2009; Cooray & Mueller-Dombois, 1981; Gagné & Howarth, 1981; Pejchar et al., 2005; Perkins, 1903, 1913; Scowcroft et al., 2004; Swezey, 1954; Tomich, 1986). Koa also is important for reforesting degraded pasture lands due to its high survivorship and rapid growth (McDaniel & Ostertag, 2010) and its ability to support native bird communities (Paxton et al., 2017). For these reasons, koa moth outbreaks can provide important opportunities to understand the dynamics of forest communities and their response to large-scale perturbations and resource pulses.

In January 2013, the koa moth was observed defoliating a large area of remote forest on Hawai‘i Island (Figure 1). In the following months, the outbreak spread to at least five other sites around the island, including the Hakalau Forest Unit of Hakalau Forest National Wildlife Refuge (Hakalau). A variety of ecological studies had been under way at Hakalau for decades, and the resulting knowledge of the forest community led us to focus our study there. Moreover, the forest structure at Hakalau allowed us to consider whether defoliation severity at the stand level would increase with koa density, as would be predicted by the resource concentration hypothesis (Long et al., 2003; Root, 1973). Koa occurs with ‘ōhi‘a in forest recovering naturally from cattle grazing (forest stands) as well as in dense, nearly pure stands that were planted to reforest former pastures (reforestation stands). We therefore expected that dense koa stands would attract koa moths sooner and in greater numbers than would mixed-species stands, resulting in more severe defoliation and tree mortality.

In tropical forests where host plant diversity is high and species distributions are scattered, insect outbreaks tend to occur at small spatial scales, sometimes involving only single host plants (Dyer et al., 2012; Janzen, 1981; Sutton et al., 2021). The ecological consequences of such outbreaks are likely to have limited, local impacts even though the vigor and reproduction of individual trees and their associated plant and animal communities might be affected. Nevertheless, where host tree species are more concentrated, irruptions of tropical insects sometimes result in major defoliation and mortality, even in relatively diverse natural forests (Nair, 2007). In contrast, the scale and consequences of outbreaks in low-diversity forests, such as those typical of Hawai‘i and other remote islands (MacArthur & Wilson, 1967; Price, 2004), can be profound when dominant species are affected (Carson & Root, 2000; McBrien et al., 1983). When dominant species are defoliated or killed over large areas, forest structure and ecosystem function can be altered and disrupted (Ellison et al., 2005). Furthermore, outbreaking insects may act as keystone species by reducing the biomass of dominant hosts, allowing subordinate species to increase in diversity and fecundity (Long et al., 2003).

Dominant host species are particularly vulnerable to insect outbreaks because, according to the resource concentration hypothesis (Long et al., 2003; Root, 1973), specialist herbivores are more likely to find and remain in dense, low-diversity stands of host plants and consume a greater proportion of foliage than in higher diversity stands with lower host plant density. Similarly, in agricultural systems, plant community diversity rather than predator–prey interactions is generally associated with reduced populations of insect herbivores (Redfern & Pimm, 1987; Risch et al., 1983). Beyond local spatial scales, habitat diversity at the landscape scale may also affect herbivore loads on host plants by increasing the mortality and decreasing the fitness of insects having to disperse farther to reach patches of suitable hosts (O‘Rourke & Petersen, 2017).

Studies of gypsy moth (*Lymantria dispar* L.) outbreaks in continental forests have shown that tree mortality increases with the severity of defoliation, and mortality is greater for smaller trees in the subcanopy (Davidson et al., 1999). Within our study stands, we therefore predicted that severely defoliated trees of similar size would suffer greater mortality or require more time to regrow their foliage. All else being equal, we expected large trees to regrow their foliage sooner than small trees and seedlings due to their greater concentrations of carbohydrates (Nykänen & Koricheva, 2004; Stevens et al., 2008).

Koa foliage shifts from a juvenile stage with bipinnately compound “true leaves,” which are associated with maximizing growth, to a mature stage with sickle-shaped phyllodes that develop from the petioles of the true leaves and are associated with greater drought resistance (Pasquet-Kok et al., 2010). Barton and Haines (2013) demonstrated that koa moth larvae grew faster and survived longer on a no-choice diet of young phyllodes, followed by mature phyllodes and finally true leaves, which we also had anecdotally observed before the outbreak. Because true leaves are generally produced first on recently defoliated koa (Haines et al., 2009; Stein & Scowcroft, 1984), true leaves may represent an induced defense against herbivory (Barton & Haines, 2013). Therefore, we predicted that koa moth larvae would eat phyllodes before eating true leaves during the outbreak, if they ate true leaves at all. Because true leaves compose much of the foliage of koa seedlings, in contrast to mature trees, we also expected seedlings to suffer less defoliation than mature trees. Additionally, we anticipated that defoliated trees would first refoliate with true leaves before transitioning to phyllodes.



FIGURE 1 The extent of koa defoliation by koa moth (*Scotorythra paludicola*) caterpillars was apparent at the landscape (a) and individual tree (b) levels. (a) Shows extensive defoliation in the lower koa belt ~3 months before the outbreak began at Hakalau sites (Mauna Kea Volcano is in the background). At the infestation's peak, individual koa phyllodes often contained numerous caterpillars (c). Koa moths are found in two color morphs, with the dark phase much more prevalent than the light phase. Caterpillar frass accumulated on the forest floor and on understory vegetation (d)

Insect outbreaks can also affect biogeochemical cycling and other ecosystem processes by changing nutrient and water uptake by vegetation, increasing nutrient fluxes from vegetation to soil via throughfall leachates and litterfall enriched with frass and dead insect tissue (Schowalter, 2012). Many insect outbreaks result in the heavy deposition of insect frass, insect biomass, and greenfall (young leaves or phyllodes), all of which contain nitrogen (N) and phosphorus (P) that are more labile than senescent litterfall (Christenson et al., 2002; Lovett et al., 2002). Defoliation of symbiotic N-fixing trees in relatively N-rich tropical forests also is expected to increase the availability of soil N more than P when compared to the defoliation of non-N-fixing trees in N-limited temperate forests. Although the litter of N-fixing koa trees has higher N concentrations than do other native forest species and is known to increase soil N over time, it is slow to decompose due to the sclerophyllous nature of its phyllodes (Scowcroft, 1997). However, conversion of koa foliage to highly labile frass by koa moths is expected to increase N and P levels in soils under koa canopies, which could result in changes to the structure of the forest understory (Yang, 2004; Yang et al., 2008) and recovery of defoliated trees (Russell et al., 2004). The relatively high N:P ratio of koa also is expected to increase levels of N more than P in soils and understory vegetation where koa moth abundance and defoliation were greatest. Although N pulses have been measured during insect outbreaks, P dynamics have not been documented frequently (Hollinger, 1986; Lovett et al., 2002; Yang, 2004), even though P is likely to limit the growth of N-fixing koa, especially in young volcanic soils (Pearson & Vitousek, 2001; Vitousek & Farrington, 1997). A potential impediment to this process, especially in our reforestation sites, is the thick layers of alien pasture grasses that

are retained under koa canopies (McDaniel & Ostertag, 2010) and that may be better able to take up nutrients than slower growing native shrubs. We predicted, therefore, that alien grasses would reduce the availability of N and P to the native understory and to koa recovering from defoliation. If so, we did not expect to observe evidence of koa moths acting as keystone species in the transformation of forest structure.

Large-scale outbreaks may trigger trophic cascades when mobile insectivores are attracted to the bonanza of prey, and resident species switch to the newly abundant prey (Eveleigh et al., 2007; Yang et al., 2008). Optimal foraging theory posits that consumers are expected to feed on high-value prey and ignore less valuable prey when search and handling effort can be more profitably spent searching for the high-value prey (Stephens & Krebs, 1986). Larvae of various *Scotorythra* species are high-value foods of adult and nestling Hawaiian forest birds, including nectarivorous and frugivorous species (Banko & Banko, 2009), and koa moth outbreaks historically attracted large numbers of birds, including frugivorous species (Perkins, 1903). Therefore, we anticipated that birds would increase their time spent in koa, consumption of koa moth caterpillars, and fitness (e.g., gain weight). The endemic Hawaiian hoary bat (*Lasiurus cinereus semotus*) is a widespread habitat generalist that undertakes long-range movements and preys nocturnally on moths and other flying insects (Gorresen et al., 2013; Jacobs, 1999; Tomich, 1986). We expected bat numbers and feeding activity to increase during the peak of moth activity. At least 10 species of native and alien insect predators and parasitoids have been associated with koa moth caterpillars, and a parasitism rate of 20% was reported during an outbreak on Maui (Haines et al., 2009). Elsewhere, high rates of caterpillar parasitism have been associated with declines in moth numbers (Klemola et al., 2010) and it is thought that top-down factors could be important in limiting the frequency and scope of outbreaks (Dwyer et al., 2004; Letourneau, 2012; Ostfeld & Keesing, 2000; Symondson et al., 2002), even if they are not critical in stopping them. Therefore, we monitored the abundance and level of attack by parasitoid wasps (Ichneumonoidea) to assess how they might respond to the superabundance of caterpillar prey and whether they might contribute to the termination of the outbreak.

Our goals here are to increase knowledge about the dynamics and consequences of insect outbreaks in low-diversity, tropical forests, which are underrepresented in the literature, and to evaluate hypotheses relevant to outbreaks generally. These hypotheses are (1) herbivore abundance and defoliation severity increase with the density and dominance of host trees, (2) caterpillars discriminate in their consumption of foliage types based on palatability, (3) defoliated trees initially refoliate with the least palatable foliage, (4) mortality is higher and refoliation is slower with the increased severity of defoliation and among smaller host trees, (5) greater herbivore abundance and defoliation severity of symbiotic N-fixing host trees increase the availability of soil N more than P in soils and understory vegetation, (6) N and P inputs from caterpillar frass are reduced due to interception by dense alien grasses underneath host trees, (7) during the buildup of caterpillars, birds increasingly forage in host trees, switch to the irrupting prey species, and gain in fitness, (8) bat feeding efficiency increases with moth abundance, and (9) abundance and attack rates of parasitoid wasps increase with caterpillar abundance.

METHODS

Study areas

The koa moth outbreak originated in the native rainforest of windward Hawai‘i Island on the eastern slope of Mauna Kea Volcano above the town of Hilo. The outbreak was large (11,000 ha) and already spreading rapidly at lower elevations when it was discovered in January 2013. The outbreak defoliated about 28,328 ha of forest by October 2013, becoming the largest ever recorded (Haines et al., 2013). Defoliation occurred in widely scattered windward and leeward tracts around the island to nearly 2000-m elevation, but not all koa forests were affected similarly (Banko et al., 2014).

Our studies focused in the upper koa forest belt in the Hakalau Forest Unit of Hakalau Forest National Wildlife Refuge (Hakalau study site; 1600–1920-m elevation; 19°47′N, 155°18′W; 13,247 ha). There we established sites in two different habitat types that were recovering from heavy, long-term cattle grazing (Figure 2). We also conducted some studies in the lower koa belt near the northern extremity of the outbreak along Blair Road within Laupāhoehoe Natural Area Reserve (Laupāhoehoe study site; 830–1280-m elevation). Additionally, limited sampling was conducted at the southern edge of the outbreak near Saddle Road (Kīpuka study site; 10-mile marker along the former alignment of Highway 200; 800-m elevation).

We recorded defoliation first at Laupāhoehoe, about 25 km north of early observations of the outbreak in the forests above Hilo. There, koa trees were defoliated three times at about 18-week intervals during mid-late March, early-mid August, and January 2014 (Table 1). On each occasion, defoliation occurred between 800 and 1180-m elevations. At the Kīpuka study site, also in the lower koa belt, trees were defoliated during mid-late March and 26 weeks later during early-mid October. Although the

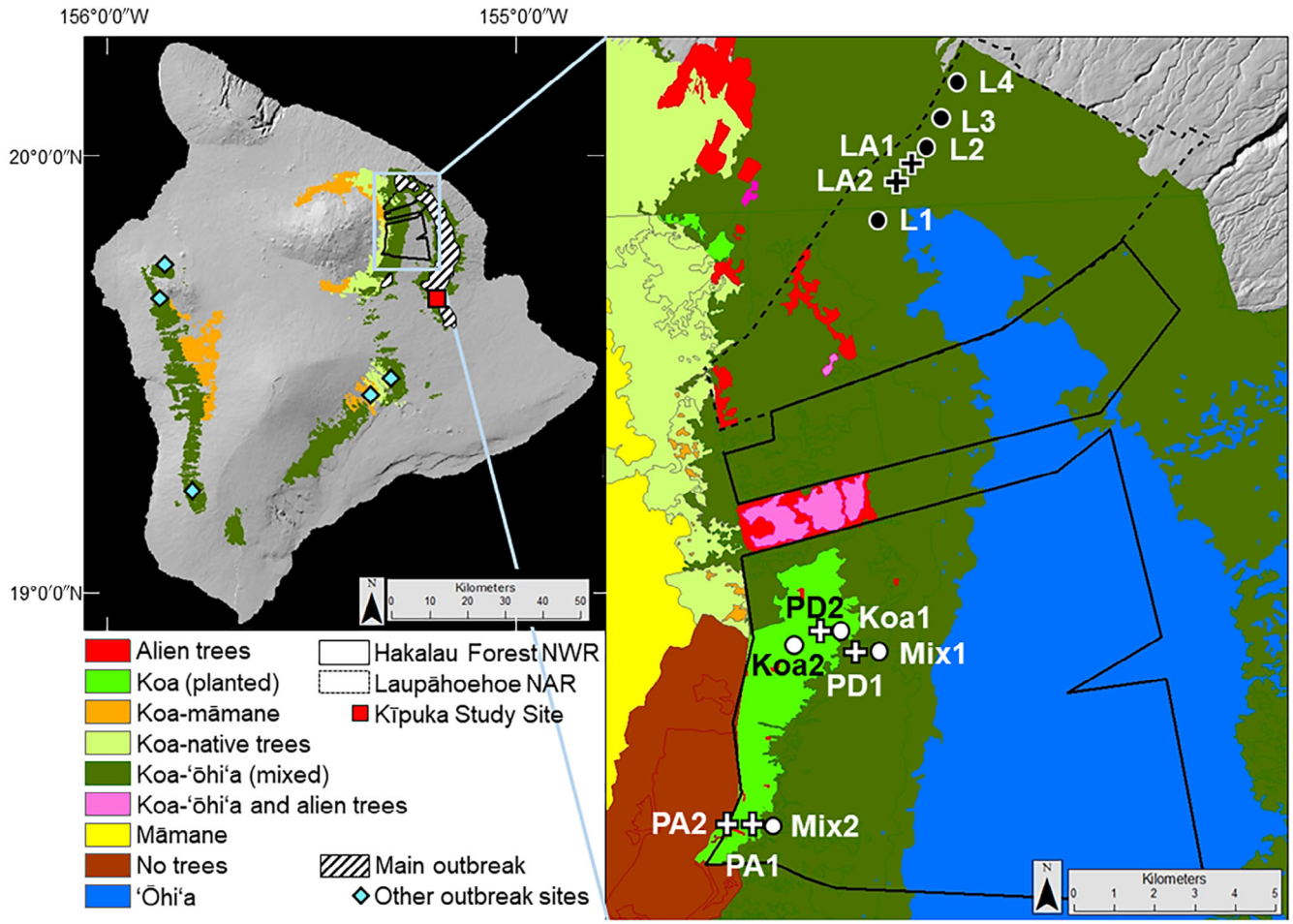


FIGURE 2 Left: Distribution of koa-associated forest types (Jacobi, 1989) and koa moth outbreaks on Hawai'i Island during 2013 and 2014. The polygon with diagonal lines represents the main outbreak in the lower koa belt in May 2013, just before its spread to the upper koa belt and HFNWR (outbreak in the upper koa belt is not shown). The Kīpuka study site is represented by the red square near the southern end of the outbreak polygon. Smaller koa moth outbreaks around the island during May 2013 are denoted by blue diamonds. Right: Distribution of dominant forest trees and study sites in the Hakalau Forest Unit of Hakalau Forest National Wildlife Refuge (black border) and Laupāhoehoe Natural Area Reserve (dashed black border). Study sites at Hakalau included koa-ʻōhiʻa forest naturally recovering from cattle grazing (Mix1 and Mix2) and former cattle pasture planted with koa (Koa1 and Koa2). White dots represent data sites at Hakalau for insects, birds, vegetation, and nutrient cycling; white crosses represent bat acoustic monitoring sites. Laupāhoehoe study sites consisted of natural koa stands; sampling sites are shown with black dots for insects (malaise traps only) and black crosses for bat monitoring

outbreak spread relatively quickly within the lower koa belt, it did not reach the upper koa belt, including the Hakalau study sites (3–8 km upslope), until 6 months after the initial discovery. Trees were not defoliated at Hakalau until 8 or 9 weeks after caterpillars had irrupted there.

Bat studies were conducted at the Laupāhoehoe site from 2007 through 2011, before the outbreak, and then again in 2013, during the outbreak. We began monitoring moth and parasitoid abundance in March 2013 at the Laupāhoehoe and Kīpuka sites, where the outbreak was already underway, and the full complement of studies in April 2013 at Hakalau, before the outbreak arrived there or elsewhere in the upper koa belt (Table 1). Most studies were completed in September 2013, although some continued into May 2014. Ideally, we would have established many study sites across the region, including areas outside as well as inside the outbreak. However, such large tracts of forest were being defoliated that we could not predict where the outbreak would not occur. Neither could we afford to randomly establish many sites to increase the statistical power of analyses.

All study sites were in tropical montane rainforest (Gagné & Cuddihy, 1999), which occurs along windward Hawai'i Island to about 1900-m elevation. The canopy is dominated by ʻōhiʻa and koa, both reaching 30 m in height in some areas. Native forest cover has been removed below about 500-m elevation by settlements, agriculture, and agroforestry; the forest has been removed or substantially reduced by cattle grazing above

TABLE 1 Timeline of outbreak events and schedule of sampling at Hakalau (H), Laupāhoehoe (L), and Kīpuka (K) study sites in 2013 and 2014.

	2013											2014				
Category	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**
Event																
Caterpillar peak—H				✓												
Moth peak—H						✓	✓									
Defoliation peak—H					✓											
>30% Refoliation—H											✓					
>60% Refoliation—H													✓			
Defoliation peak—L,K		✓					✓					✓				
Moth peak—L,K			✓					✓					✓			
Sampling																
Caterpillar density—H			✓	✓	✓											
Malaise trapping—H			✓	✓	✓	✓	✓	✓								
Caterpillar rearing—H			✓	✓	✓											
Extent of defoliation—H								✓	✓							
Extent of refoliation—H								✓			✓		✓			
Extent of koa mortality—H													✓			
Litter traps—H					✓											
N/P dynamics—H				✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Understory uptake—H				✓				✓				✓				
Bird tree use—H				✓	✓	✓	✓									
Bird diet and mass—H	✓	✓	✓	✓	✓											
Bat monitoring—H				✓	✓	✓	✓									
Malaise trapping—L,K		✓	✓	✓	✓	✓	✓	✓								
Caterpillar rearing—L,K							✓									
Bat monitoring—L						✓	✓	✓								

1900-m elevation. Rainfall and temperature are strongly influenced by the elevation gradient extending from the coast to the summit of Mauna Kea at 4205 m. Average annual rainfall exceeds 7850 mm in portions of the lower koa belt (Laupāhoehoe and Kīpuka study sites) but declines to about 2000 mm (with supplementation from cloud water interception) in the upper koa belt, where the Hakalau study site is located (Giambelluca et al., 2013). Mean annual temperatures are up to 6°C warmer at lower elevations (800 m; 16.7°C) than at the higher sites (1900 m; 10.7°C; Giambelluca et al., 2014), and monthly maxima and minima vary by about 9°C annually within this range of elevation (Giambelluca & Schroeder, 1998).

The Hakalau Forest Unit was established in 1985 primarily for the protection of endangered Hawaiian forest birds. It is managed by removing introduced ungulates and weeds (Hess et al., 2010; Jeffrey & Horiuchi, 2003) and restoring forest habitat on former cattle pastures. We established two study sites (reforestation sites) within former pasture (1650–1900-m elevation) with planted stands mostly consisting of koa (about 25 years old at the time of the study) and a few other native tree and shrub species. Two more study sites (natural forest sites) were established in mixed ʻōhiʻa–koa forest with a well-developed understory that was naturally recovering from heavy cattle grazing (1400–1900-m elevation). The two reforestation sites were located along Pedro Road at 1670-m elevation (Koa1) and 1800-m elevation (Koa2). One of the two forest sites was also located along Pedro Road at 1600-m elevation (Mix1) adjacent to closed-canopy forest. The other forest site extended along Pua Akala Road between 1830 and 1920-m elevations (Mix2). Note that these sites are designated differently in Banko and Peck (2021), Banko et al. (2021), Peck and Banko (2021), and Yelenik et al. (2021), as follows:

Koa1 = Pedro Mid, Koa2 = Pedro High, Mix1 = Pedro Low, Mix2 = Pua Akala. The age of the substrates across our study area exceeded 10,000 years (Wolfe & Morris, 1996). Unless otherwise noted, the methods described below pertain to studies at the Hakalau sites.

Forest structure

Tree density

Comparing outbreak dynamics and outcomes on reforestation and natural forest sites provided a framework for evaluating many of our hypotheses but representing the two habitat types with only two sites each (due to logistical constraints) limited our ability to statistically test our results. Nevertheless, large differences in tree species dominance between the habitat types allowed us to qualitatively evaluate the resource concentration hypothesis and our predictions that in the dense reforestation stands koa moths would build up numbers earlier and to higher levels, defoliation would be more severe and refoliation would be slower, and deposits of caterpillar frass and its resulting nutrients would be greater.

To quantify structural differences between reforestation and natural forest stands, we established 55 survey plots, 85% of which were in natural forest habitat. The total area surveyed was 17,279 m^2 (1.73 ha) of which forest habitat comprised 14,765 m^2 (Mix2 6911 m^2, Mix1 7854 m^2) and reforestation habitat comprised 2513 m^2 (Koa1 1571 m^2, Koa2 942 m^2). More area was surveyed in natural forest habitat due to its lower koa density and greater habitat heterogeneity. In each habitat, plots were placed at 50-m intervals that were offset at random distances and directions perpendicular to our line of travel along unimproved roads and fence lines. We marked each plot location using Global Positioning System (GPS) and counted all koa and ʻōhiʻa within a 10-m radius (314 m^2) of the plot center. Densities of koa and ʻōhiʻa were estimated from the count data pooled from all plots at each site.

Tree size

Expecting to find greater mortality and slower refoliation in smaller trees, we measured individual koa according to the following size classes, as determined by stem diameter at breast height (dbh, 1.4 m; USFS, 2007):

- Seedling <1 m; no dbh; individuals counted but not marked and defoliation not assessed.
- Class 0: seedling ≥1 m but <1.4 m; no dbh; individuals marked and defoliation assessed.
- Class 1: seedling ≥1.4 m, dbh <1 cm, individuals marked and defoliation assessed.
- Class 2: small tree, dbh 1–8 cm, individuals marked and defoliation assessed.
- Class 3: large tree, dbh >8 cm, individuals marked and defoliation assessed.

Koa trees usually (54%) consisted of one main stem at 1.4 m height, but dbh for trees with two (29% of trees) or more (17%) major stems was measured at 1.4 m height at each stem (a, b, c, ...) and the total was calculated with the formula ($\sqrt{[a^2 + b^2 + c^2 + \cdots]}$; USFS, 2007). We placed ʻōhiʻa into size classes 1–3 (as above), but we did not measure dbh except when we could not determine size class by visual inspection.

Koa moth abundance and impacts

To determine whether koa moth abundance and impacts would be greater and appear sooner in the dense koa reforestation stands, we evaluated (1) moth abundance, (2) caterpillar abundance, biomass, and age structure, and (3) patterns and dynamics of defoliation and refoliation. We periodically collected moths in traps and sampled caterpillars on koa branches to determine whether the outbreak occurred earlier and more intensely in the denser reforestation stands. We also assessed the developmental stage (instar) of caterpillars to reaffirm the timing and dynamics of the outbreak and the peak of defoliation in each stand. For example, a stand with a greater proportion of early instars would indicate a later buildup of caterpillars relative to a stand with a greater proportion of later instars.

Moth abundance

At Hakalau, we sampled the dynamics of moth abundance with Townes-style ground and canopy malaise traps (BioQuip Products, Rancho Dominguez, California, and Sante Traps, Lexington, Kentucky, respectively) at each site except at Koa1, where only a ground trap was installed due to logistical constraints. We deployed ground and canopy traps at both lower- and higher-elevation trap locations at Mix2. Ground traps were deployed on 11 April 2013 and canopy traps deployed on 16 May 2013 and were operated continuously until 26 September 2013. Contents of traps were collected every 2 or 3 weeks, and moths were counted according to species using reference specimens.

At Laupāhoehoe study sites, we installed Townes-style ground malaise traps but not canopy traps.

Caterpillar abundance, biomass, and age structure

We counted caterpillars on 4–10 branches removed from up to 10 koa trees at each site at 1 to 3-week intervals from 18 April to 26 July 2013 (11 sampling events). Samples from the two natural forest trapping locations at Mix2 were composited for caterpillar assessment. Branches were randomly sampled before and during the early stages of the outbreak, but as foliage became patchy and sparse, we targeted branches containing sufficient foliage to support caterpillars. We used one extendable pole to clip a branch while a second pole with a nylon bag was held beneath to catch it. Each branch sample was approximately 50 cm in length. Caterpillars were separated from samples by shaking the branches inside the bag, after which the head width of each caterpillar was measured to determine its instar category (1–5). Foliage was separated from stems and dried to a constant mass at 50°C. One subset of caterpillars was maintained on young koa phyllodes to measure rates of parasitism (see below) and to confirm species identification. Another subset of caterpillars was dried to a constant mass at 50°C to determine the average mass for each of the five instars, which was then used to calculate the biomass of all caterpillars within the sample.

Patterns of defoliation and refoliation

We predicted that the high-density reforestation stands would be defoliated earlier and more heavily and that refoliation would be slower in the more heavily defoliated trees. At each marked koa, therefore, we visually estimated the amount of foliage that had been eaten by caterpillars from 0% to 100% in 5% increments (also see Nakajima, 2018). Any uneaten foliage was quantified to the nearest 5% according to the proportion of leaves or phyllodes. The amount of new foliage produced after defoliation was assessed from September through December, when most trees were recovering vigorously. New foliage was quantified to the nearest 5% according to the proportion of leaves or phyllodes.

We used a generalized linear modeling approach with Akaike information criterion with correction for small sample size (AIC_c) model selection to assess the effects of the severity of defoliation, tree size (dbh), habitat type (natural forest, restoration stand), and site on the degree of new foliage production 34 weeks after the peak of defoliation.

Nutrient pulse dynamics

We expected that a large pulse of N and P derived from caterpillar frass, dead caterpillars, and greenfall would be deposited in the soil and taken up by understory vegetation, especially in stands with higher koa density, foliage biomass, caterpillar abundance, and frass production. Because fast-growing alien grasses were prevalent in all sites, we sampled grasses and understory shrubs to determine whether grasses diverted much of the N and P and whether the amounts captured were greater in the reforestation sites, where grass cover was especially dense.

Litter traps

We deployed eight litter traps under koa canopies at each of two natural forest sites (Mix1 and Mix2) and one reforestation site (Koa2) to measure litterfall rates during and after defoliation. Traps were made from plastic lattice seedling flats (41 × 41 cm) with mesh screen glued to the bottom and sides. Sampling started in May 2013, and we collected litter monthly until August 2014. Litter types were not separated by species, although most litter was from koa. Large branches, twigs, and loose lichen material that had presumably fallen from the canopy were discarded because phyllodes were most likely to contribute to a nutrient pulse, given the N-fixing ability of koa, and other material would not contribute to nutrient cycling during the time frame of our study. Litter was dried to a constant mass at 70°C.

Nitrogen redistribution

We estimated N redistribution rates to evaluate variation in N pulse data derived from estimates of caterpillars (see above), frass production, and foliage consumption. For each sample date, we multiplied the number of caterpillars of each instar (individual/g foliage) by frass production of each instar (mean dry mg frass/caterpillar) to estimate frass production (dry mg frass/g foliage). We used foliage biomass (g/m) to predict frass deposition per unit area and sample date. Lastly, we linearly interpolated between caterpillar sample dates to estimate frass production over time.

Koa foliar biomass under non-outbreak conditions was calculated by allometric equations (Pearson & Vitousek, 2001) for dbh 1–8 cm ($y = 0.0268 \times \text{dbh}^{2.168}$) and for dbh 8–30 cm ($y = 0.034 \times \text{dbh}^{1.746}$). The equation for small koa was developed for dbh 1.5–8 cm. The equation for large koa was developed for dbh 8–30 cm, but we also used it for dbh >30 cm (10% of trees had dbh 30.1–60.0 cm; 3% of trees had dbh 60.1–300 cm). Improved methods for estimating the foliar biomass of koa

(Ostertag et al., 2014) require measurements of tree height, which we did not record. Nevertheless, the relatively similar ratios of small to large trees at natural (47:53) and reforestation (58:42) stands indicate that estimates of foliar biomass are comparable.

Caterpillar frass production was estimated by rearing caterpillars in growth chambers maintained at 15°C, which approximated the daily average (12.2–13.8°C) and hourly maximum (14.9–16.4°C) temperatures expected at our Hakalau study sites during June (Giambelluca et al., 2014). Caterpillars representing instars 3, 4, and 5 were weighed at the beginning of the experiment after having been fasted for 24 h and then fed fresh, young koa phyllodes over a 48-h period. Frass produced by these caterpillars was collected at 24-h intervals and subsequently dried to a constant mass at 50°C. Caterpillars were reared to moths after the experiment to confirm their identities. Mean dry mass of each of the five instars was calculated for caterpillars collected during the outbreak (i.e., $n = 30$ randomly selected individuals per instar). A best-fit regression equation based on the amount of frass produced by instars 3–5 was used to estimate frass production for instars 1 and 2, where instar mass was used to predict frass mass.

We pooled samples of frass from caterpillars in the laboratory (see above) into a single aggregate that was dried (70°C) to a constant mass, ground, subsampled in triplicate, and analyzed for total %N by the University of Hawai'i, Hilo Analytical Lab. To determine whether there was a distinct peak in frass production over time, we used the fit curve platform in program JMP (version 10.0.2; 2012; SAS Institute, Cary, North Carolina), using a Gaussian Peak function and site as the level of replication. Frass collected from randomly selected caterpillars reared in the laboratory on young koa phyllodes was composited into a single sample for determination of total N by the University of Hawai'i, Hilo Analytical Laboratory to be used in N deposition estimates.

Resin bags

Variation in available soil N and P over time was measured with ion-exchange resin bags. Resin bags capture ions present in soil solution and are well correlated with other measures of inorganic nitrogen (Binkley & Matson, 1983) and effectively capture increased P flux to soil (Shaw & DeForest, 2013). Resin bags sorb nutrients throughout their time of burial in soil and thus can provide a more integrated measure of overall nutrient flux than static soil nutrient tests (Binkley & Matson, 1983). We refer to the inorganic nitrogen captured by resin bags over the time of burial as "resin available N."

We made resin bags by sewing 8 g of wet Mixed Bed Anion Exchange IONAC Resin (J. T. Baker, Center Valley, Pennsylvania) in silkscreen pouches. These were buried at an angle at a depth between 5 and 10 cm, using a soil knife to lift soil, creating as little soil disturbance as possible. We used a shallow depth to quickly capture the N signal from the caterpillar frass as it moved down the soil profile. Resin bags were buried under the koa canopy and in adjacent open-canopy grassland plots. The understory of koa also tended to be occupied by exotic grasses, although understories of certain intact forest sites were also occupied by native shrubs. We placed resin bags within eight paired plots at the two natural forest sites and one reforestation site, for a total of 48 resin bags per time point.

Resin bags were buried between 15 and 47 days spanning May 2013 to May 2014. Caterpillars were already present during the first resin bag deployment, and, due to observations of heavy frass deposition, we collected the bags only 15 days later. We accounted for varying burial times by calculating resin available N as a rate per day. We continued collecting and replacing resin bags every month for 240 days, after which we skipped every third month. Between time points, we changed resin bag placement slightly to avoid disturbed soil. Resin bags were returned to the laboratory, rinsed with deionized water to remove roots and soil, and extracted by shaking with 100 mL 2 M KCl for 6 h. Samples were analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) at the University of Hawai'i, Hilo Analytical Lab on a Lachat Qui Chem 8500 (Hach, Loveland, Colorado) and for soluble reactive P on a Lachat QC8000 at the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center (FRESC) laboratory in Corvallis, Oregon. We used repeated-measures analysis with site and habitat (koa vs. grass) as fixed effects. We log-transformed data to account for non-normality.

Understory species foliar nitrogen

To evaluate patterns of N uptake by understory vegetation, we first measured the percent cover of understory species in natural forest plots to characterize understory community composition. At one reforestation site, Koa2, we added five transects spaced at 50-m intervals. Few plots were established at this site due to the high density of koa and homogeneity of the canopy, but additional replication was needed to characterize the understory. We used plot centers as the midpoint of a 20-m transect that followed a north–south bearing and used a point-intercept method by holding a 2-m pole upright every 0.5 m. We noted all species touching the pole below 1 m, and we included litter or moss at the bottom point of the pole. Percent cover was calculated

as the number of contact points divided by the total number of sample points (40). Because all plant species touching the pole at each point were recorded, percent cover values often summed to >100%, reflecting the multi-layered nature of the understory. We used linear discriminant analysis to cluster sites, given the percent cover of understory species.

We tracked the foliar N of species in open areas and under the koa canopy to determine whether understory plants displayed increased N uptake due to frass deposition. We sampled four of the eight plots that contained resin bags in each site by taking new, fully expanded leaves from exotic pasture grasses and from the native woody species ʻōhiʻa, ʻōhelo (*Vaccinium calycinum*), and pūkiawe (*Leptocophylla tameiameiae*). We pooled two to three leaves, including petioles, from three separate individuals (or bunches in the case of grasses) per replicate plot. Grasses were a mixed-species assemblage dominated by *Cenchrus clandestinus*, but also including *Anthoxanthum odoratum*, *Ehrharta stipoides*, *Holcus lanatus*, *Paspalum dilatatum*, *Agrostis stolonifera*, and *Axonopus fissifolius*. We took care not to include any inflorescences in the grass foliage samples. Foliage was sampled in May and September 2013 and January 2014. We added one extra sample date for grasses (August 2013) as grasses tend to grow and assimilate resources more quickly than woody species. Foliage was dried to a constant mass at 70°C, ground with a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey), and analyzed for total carbon (C) and N by the University of Hawaiʻi, Hilo Analytical Lab (Costech 4010 Elemental Analyzer, Valencia, California). Foliar samples were not analyzed for P.

Response of birds

Use of tree species

Anticipating that birds, regardless of their foraging guild, would be attracted to a pulse of high-quality insect prey, we monitored the relative frequency of birds in koa and ʻōhiʻa trees during the outbreak. In the reforestation plots, we expected little change in behavior because birds were expected to continue to forage predominantly in koa, due to its dominance there. In the natural forest plots, however, we expected to see birds spending more time in koa and less time in ʻōhiʻa, although we anticipated that ʻōhiʻa flowers would continue to attract nectarivores, possibly diminishing their attraction to koa compared to insectivores.

To evaluate the effects of forest structure on foraging behavior, we conducted 1017 focal surveys of koa and ʻōhiʻa trees in each of the four study sites during 12 surveys at approximately weekly intervals between 22 May and 15 August 2013. We estimated the date of peak defoliation as 20 June for the two reforestation sites and the Mix1 natural forest site and 27 June for the Mix2 natural forest site. We estimated heights of trees to the nearest meter. Mean heights of koa and ʻōhiʻa were similar within the natural forest sites (14.7–14.9-m koa; 14.8–16.0-m ʻōhiʻa) and within the reforestation sites (10.7–11.4-m koa; 11.8–11.9-m ʻōhiʻa), but both species were 3–4 m shorter in reforestation sites compared to natural sites. We estimated flower production of ʻōhiʻa as: none (0); light (≤5% of tree canopy with flowers); medium (≤20%); heavy (>20%). We classified the extent of defoliation of koa as: none, light (1%–25% of foliage missing), or heavy (>25% of foliage missing). We counted the number of birds that visited koa and ʻōhiʻa trees during a 2-min period. The presence of a bird in a tree was recorded regardless of its activity there; for example, a bird was counted if it perched even briefly in the tree. We attempted, but often failed, to identify the species of birds occupying the tree. As an index of bird activity, we calculated the number of birds per min; this calculation included instances when we observed no birds in a tree. Focal trees (usually >5 m in height) were selected without regard to phenology as we walked along or near roads or fence lines.

We used logistic regression to identify factors explaining observed differences in the proportion of birds observed in koa and ʻōhiʻa before and after peak defoliation in both the natural forest and reforestation habitats. Predictor variables were tree species (koa, ʻōhiʻa), habitat type (natural forest, restoration), date, severity of koa crown defoliation (as above), ʻōhiʻa flowering intensity (as above), and observer. The analysis categorized the proportion of birds in either koa (with or without defoliation) or ʻōhiʻa (with or without flowers). To simplify the interpretation of coefficients, some variables were combined. *Flowdefol* represented a combination (factor plus interaction) of the three categories of ʻōhiʻa flowering plus the three categories of koa defoliation. *Sppflow* represented a combination of koa (regardless of defoliation status) plus the three categories of ʻōhiʻa flowering. *Sppdefol* represented a combination of ʻōhiʻa (regardless of flowering status) plus the three categories of koa defoliation. We analyzed data in this way for all species combined and for the four most frequently observed species: ʻapapane (APAP, *Himatione sanguinea*), Hawaiʻi ʻamakihi (HAAM, *Chlorodrepanis virens*), ʻiʻiwi (IIWI, *Drepanis coccinea*), and warbling [Japanese] white-eye (WAWE, *Zosterops japonicus*).

Changes in diet

To investigate whether birds shifted their diets to include more koa moth larvae in response to the outbreak, we

identified arthropod prey fragments within fecal samples. Birds were captured and banded in 2013 at Koa1 (reforestation) and Mix1 (natural forest) as part of a multi-year demographic study of forest birds begun in 2012. Work began 26 February as part of the pre-planned banding season, which was scheduled to run for 3 months during the core breeding season. However, in response to the koa moth outbreak, we extended the banding season until 27 June. From February through April, each site was visited three times during every 2-week period. During May and June, we visited the two Pedro sites once each week. Mist nets (2.6 m × 12 m) at established locations (typically 10–12 nets/day at each site) were used to capture birds across the study period. Captured birds were removed from the nets, placed in light-weight cotton bags to keep them calm and safe, and taken back to a central banding location and held until ready for processing, weighing, and releasing. At the time of release, the bird bags were carefully searched for fecal samples deposited by the birds (bags were used only once per bird, then were cleaned). If a fecal sample was found, the sample was carefully scraped into a plastic microcentrifuge tube and immersed in 95% ethanol for storage.

Diet analysis focused on fecal samples collected opportunistically from Hawai'i 'amakihi and warbling white-eye, both of which feed on arthropods and 'ōhi'a nectar. Although these two species provided the most fecal samples for comparing pre-outbreak and outbreak diets, we also combined samples from forest and reforestation sites to increase our power to detect changes. Pre-outbreak samples were collected from 26 February to 25 April, before we observed the rapid increase in caterpillar numbers, and outbreak samples were collected from 22 May to 27 June, when caterpillars were abundant. Overall, 34 Hawai'i 'amakihi and 63 warbling white-eye samples were processed, resulting in 19 pre-outbreak and 15 outbreak samples for Hawai'i 'amakihi and 24 pre-outbreak and 35 outbreak samples for warbling white-eye.

In the laboratory, fecal samples were teased apart, and individual arthropod fragments were photographed and compared to a reference collection of known arthropods collected primarily at Hakalau. Estimates of numbers of individual arthropods within a sample were conservative, so for example, if three spider fangs similar in size and structure were found in a sample, it was assumed that there were two individuals in the sample, rather than three, because each spider has two fangs. The shape of caterpillar mandibles can indicate taxonomic affinity, although many mandibles were not identified to species, genus, or family level. However, the unique shapes of koa moth caterpillar mandibles are known and thus were quantified separately from all other taxa.

Changes in mass

We used mass as a measure of the change in fitness of birds in response to the caterpillar outbreak. Mass can reflect either the accumulation of fat (e.g., resulting in mass gain due to birds consuming more energy than they are burning) or the loss of muscle (and mass) that can be associated with insufficient food intake. We set 26 February to 21 May as the pre-outbreak period (25 banding-days) and 22 May to 30 June as the outbreak period (10 banding-days). A total of 656 birds were captured and processed at the two sites during this 4-month period.

We used an analysis of variance model with an adjustment for multiple comparisons (Holm, 1979) to test for significant differences ($\alpha = 0.05$) in species mass pre-outbreak versus outbreak. Data were tested for normality, and only species with five or more captures in each of the two periods were included. Program JMP (version 10.0.2; 2012; SAS Institute, Cary, North Carolina) was used for statistical analysis.

Response of bats

We expected that bats would respond to the pulse of prey through increased foraging efficiency during peak koa moth abundance, so we conducted acoustic surveys to compare echolocation data recorded at the same locations before (2007–2011) and during (2013) the outbreak. Echolocation pulses were recorded using Anabat SD1 Bat Detectors (hereafter, SD1; Titley Electronics, Brendale, Australia) from 5:00 PM until 5:00 AM each night at four stations in Hakalau from May through August and at two stations in Laupāhoehoe from July through September.

Weather-proofed, battery-powered SD1 detectors logged bat calls on compact flash-memory cards. An ultrasonic Hi-Mic microphone was mounted inside a PVC pipe oriented with the microphone toward the ground to prevent rain damage. A 15 × 15 cm plexiglass plate was attached 12 cm below the microphone at a 45° angle to reflect and enhance calls from bats flying above the microphone. The PVC pipe and microphone were affixed to the top of a 7-m steel pole anchored to the ground, surrounding trees, or fence posts. Anabat Hi-Mic (Titley Electronics, Brendale, Australia) microphones in this configuration have an omnidirectional maximum effective range of 30 m. Microphones were inspected periodically for operational efficiency.

SD1 recordings were downloaded from compact flash cards using the program CFCread (version 4.2.1; Titley

Scientific, Brendale, Australia). Recordings were organized in folders of call events by night. AnalookW software (version 3.3.6; Titley Scientific, Brendale, Australia) enabled collected call events to be downloaded, displayed, and managed for computer analysis. "Zero-crossings analysis" created frequency/time graphs of detected signals from which echolocation pulses were identified and counted. We categorized pulses as: call events (number of times a microphone recorded a calling bat), echolocation pulses (number of discrete sound pulses in a call event), and feeding buzzes (rapid increases in rate and number of echolocation pulses, indicating attacks on prey).

An index of bat detectability was calculated with the program PRESENCE (version 4.2, Hines, 2006) for each sampling location (Hakalau, Laupāhoehoe). Maximum detectability of 1.0 was equivalent to every recording station detecting a minimum threshold of three confirmed echolocation pulses within at least one call event every night within a monthly sampling period. Zero detectability represented no call event identification exceeding the threshold value at any station during a monthly sampling period. All call events were verified by audio and visual inspection of sonograms. We conservatively discarded any recorded events of sound that did not conform to standard hoary bat vocalization parameters. Call events, echolocation pulses, and feeding buzzes were calculated and standardized per recording night at each station.

Response of parasitoid wasps

We monitored changes in parasitoid abundance at the Hakalau and Laupāhoehoe study sites using the same malaise traps used to assess koa moth abundance. Caterpillar attack rates at Hakalau and Laupāhoehoe study sites were measured before (18–25 April) and during (16 May−20 June) the outbreak by collecting caterpillars from koa foliage and rearing them in the laboratory. Caterpillar head widths were measured to determine instar category before being placed individually in plastic vials and maintained on fresh young koa foliage until they pupated and emerged as a moth or until a parasitoid emerged from their body. Vials were cleaned of frass and searched for head capsules indicative of molt into the next instar about three times a week. The parasitism rate was calculated as the percentage of caterpillars from which a parasitoid emerged. Haines et al. (2009) found that parasitoids emerged from early instars during the 2003 koa moth outbreak on Maui, and we observed anecdotally that parasitoids emerged almost exclusively from third and fourth instars of various species of *Scotorythra* at Hakalau study sites several years before the 2013–2014 outbreak. Shortly before and during the outbreak, we observed only two parasitoids emerging from fifth (final)-instar caterpillars; therefore, we excluded them from our estimate of the parasitism rate. We did not collect eggs or pupae, so we had no way to determine parasitism rates for those stages. Therefore, the overall rates of parasitism that we report are underestimates.

All data used in the analyses that follow are available at ScienceBase (www.sciencebase.gov; Banko et al., 2021; Banko & Peck, 2021; Montoya-Aiona et al., 2020; Peck & Banko, 2021; Yelenik et al., 2021).

RESULTS

Except where noted, the following sections pertain to our results at Hakalau study sites.

Vegetation structure in natural forest and restoration habitats

Tree density

Our survey of 55 plots (1.73 ha total) confirmed that koa dominated in all size classes at reforestation sites (Table 2). Compared to koa in natural forest sites, reforestation sites supported about 2.5 times greater basal area (m^2/ha), 8.6 times greater density of small trees (dbh 1–8 cm), and 4.8 times greater density of large trees (dbh >8 cm). Koa densities were highest at Koa2 in all size classes. ʻŌhiʻa dominated the natural forest sites with a density of large trees (dbh >8 cm) twice that of large koa and 43.7 times that of ʻōhiʻa in reforestation sites. Although large ʻōhiʻa were nearly absent from the reforestation stands, they were scattered immediately outside of the planted areas and were frequently visited by birds from the koa stands. Additionally, the density of small ʻōhiʻa (dbh 1–8 cm) was slightly greater in the reforestation sites. The Koa2 reforestation site was exceptional in terms of its high densities of both small koa and ʻōhiʻa.

Understory community

Understory communities differed in species composition between sites. Koa1 and Koa2, the two reforestation sites, were dominated by exotic species more than were Mix1 or Mix2, largely due to the prevalence of exotic grasses (Appendix S1: Tables S1 and S2). In contrast, vegetative cover of native shrubs, ferns, and trees was higher at Mix1 and Mix2. Discriminant analysis indicated that

TABLE 2 Koa basal area (m^2/ha) and koa and ʻōhiʻa tree density (trees/ha) in reforestation (Koa1, Koa2) and natural forest (Mix1, Mix2) sites at Hakalau.

Basal area/density	Size class (dbh)	Koa1 (5 plots)	Koa2 (3 plots)	Mix1 (25 plots)	Mix2 (22 plots)
Koa basal area (m^2/ha)	<1 cm	0.004	0.015	<0.001	<0.001
	1–8 cm	0.169	0.649	0.065	0.096
	>8 cm	25.002	39.630	6.611	19.828
	Total	25.175	40.294	6.677	19.924
Koa density (trees/ha)	0	114.6	456.2	24.2	7.2
	<1 cm	95.5	307.7	12.7	4.3
	1–8 cm	197.4	806.4	49.7	66.6
	>8 cm	261.0	382.0	67.5	66.6
ʻŌhiʻa density (trees/ha)	<1 cm	133.7	21.1	53.5	21.7
	1–8 cm	0	350.1	121.0	198.2
	>8 cm	6.4	0	155.3	124.4

Note: Size classes indicate dbh in cm with 0 = seedling height ≥1 m but <1.4 m.

Koa1 and Koa2 were more like one another than they were to Mix1 or Mix2 (Appendix S1: Figure S1). Although the latter two sites had relatively high percentages of native species cover in the understory, they separated in multivariate space due to different native species being present or dominant.

Koa moth abundance patterns

We predicted that caterpillars would begin to build up first in the reforestation sites, where koa was dominant. In the initial stage of the outbreak (18–25 April), small numbers of caterpillars varying in age (instar class) were found at all sites (Figure 3). Second- and third-instar caterpillars were most abundant everywhere during mid- and late April, but first-, fourth-, and fifth-instar caterpillars also were present. By 16 May, age-structured cohorts dominated at each site, with first-instar caterpillars composing 73.9% (Mix1) and 85.9% (Mix2) of the samples at the natural forest sites. The cohort at the Koa2 reforestation site was slightly more advanced, with only 27.9% first instars and 52.3% second instars. The pulse of first-instar caterpillars was missed at the Koa1 reforestation site, but the relative proportion of instars on 30 May was equivalent to that at Koa2, indicating a similar onset of egg-laying. Instars 1–3 were present for less time compared to instars 4–5. The first three instars composed <20% of the total by 6 June at both reforestation sites and the Mix1 natural forest site and by 13 June at Mix2. Over the remaining 4–5 weeks of the outbreak, caterpillars were almost exclusively fourth and fifth instars (Figure 3). At peak levels, the density of caterpillars across the study sites ranged between about 4.4×10^6/ha at Koa1 and 18.9×10^6/ha at Mix2 and consisted mainly of fifth-instar larvae (Table 3). Numbers of caterpillars per branch sample rose dramatically at the natural forest sites starting the week of 16 May and peaking by the week of 30 May, but numbers had already peaked at the Koa2 reforestation site by the week of 16 May (Figure 4). The timing of peak abundance at the Koa1 reforestation site was unclear because that site was not sampled before 30 May. Following peak abundance, caterpillar numbers declined at all sites until 6–8 weeks later during the week of 13 July, when they dropped to near zero due to the depletion of koa foliage.

The temporal trend in caterpillar biomass (mg/g foliage), lagged about 2–4 weeks behind the peak of caterpillar numbers due to the larger size of later instars. Caterpillar mass increased exponentially during development ($y = 0.00002e^{1.1906x}$, $R^2 = 0.9923$), with the mass (pooled average) of fifth-instar larvae (7.673 μg) being ~121 times greater than that of first-instar larvae (0.063 μg) and 2.7 times greater than that of fourth-instar larvae (2.793 μg). Caterpillar biomass peaked at both reforestation sites and the Mix1 natural forest site on 13 June and at Mix2 on 20 June (Figure 3), with the peaks occurring about a week before maximum defoliation. Caterpillar biomass was highest at Mix1 and Mix2, intermediate at Koa2, and as indicated by defoliation levels, lowest at Koa1.

Low numbers of moths were recorded before the buildup of caterpillars and peak of defoliation (Figure 5); thus, we could not confirm that moths began ovipositing earlier at the reforestation stands. Subsequently, however, moth abundance peaked about 9–11 weeks after the peak of caterpillar numbers and 5–8 weeks after the peak of caterpillar biomass. Strong peaks in moth abundance (see

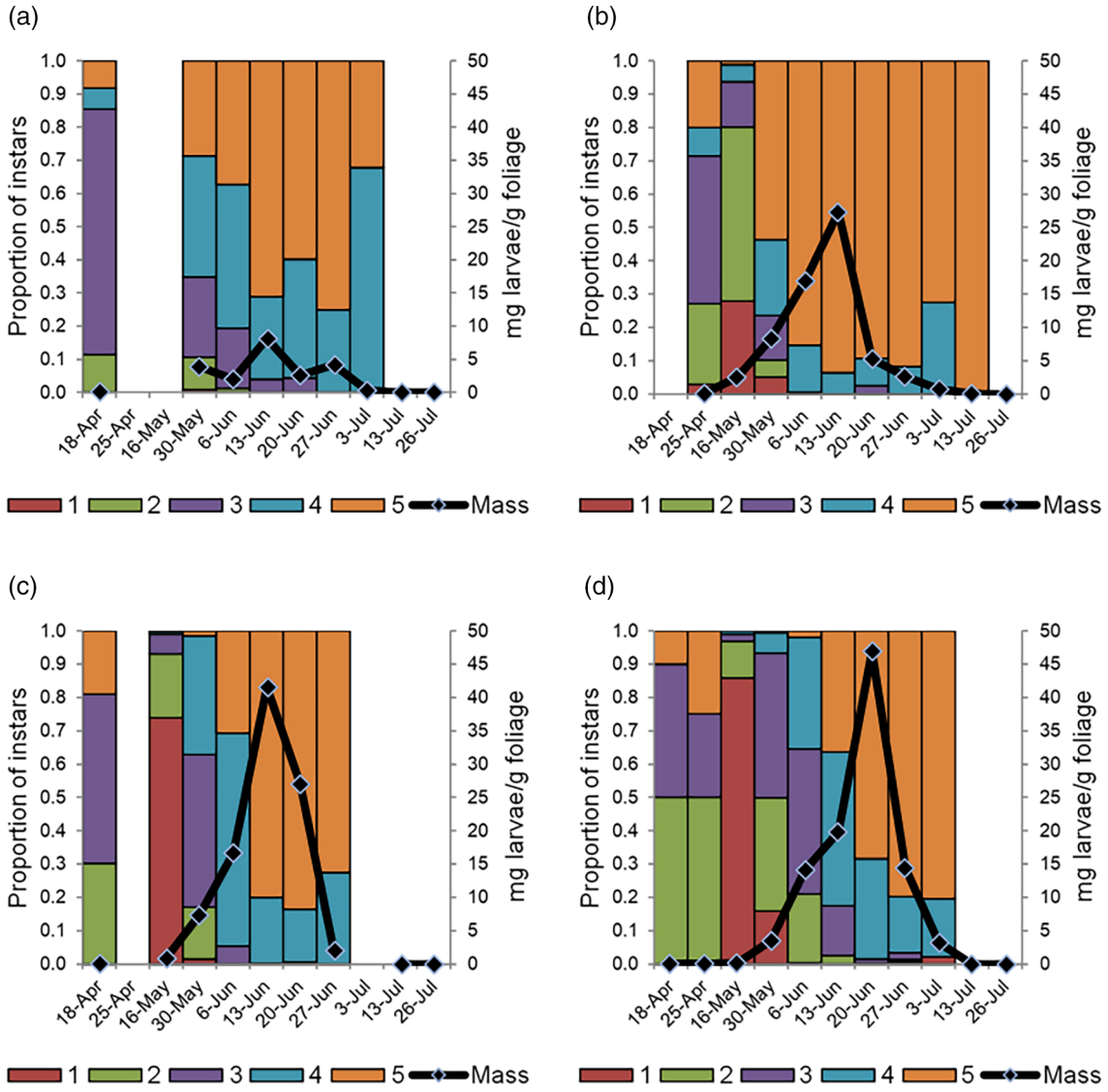


FIGURE 3 Temporal distribution of koa moth larval instars and total biomass of larvae at reforestation sites (a) Koa1 and (b) Koa2 and forest sites (c) Mix1 and (d) Mix2 during 2013. Primary (left) *y*-axes represent proportions of instars 1–5 (bars); secondary (right) *y*-axes represent total larval biomass (mg/g foliage; line)

TABLE 3 Density of koa moth larval instars in reforestation (Koa1, Koa2) and natural forest (Mix1, Mix2) sites at Hakalau during the peak of caterpillar abundance.

Instar	Koa1	Koa2	Mix1	Mix2
Instar 1	0	0	0	0
Instar 2	0	0	0	36
Instar 3	159	0	9	326
Instar 4	1238	1019	1074	6117
Instar 5	3043	13,386	4908	12,378
All instars/ha	4440	14,405	5990	18,856
Koa foliage (t/ha)	4.30	6.67	1.09	2.53

Note: Numbers ($\times 10^3$) of caterpillars/ha are shown for each instar during 13 June (Koa1, Koa2, Mix1) and 20 June (Mix2), 1 week before maximum defoliation. Dry biomass of foliage estimated in the forest canopy is shown in ton/ha (1 ton = 1000 kg).

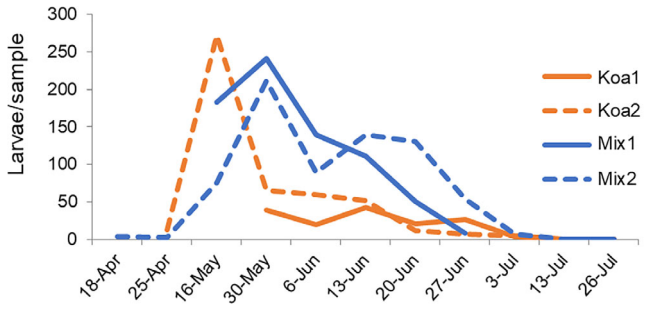


FIGURE 4 Caterpillar abundance on branches (mean number/sample) at reforestation (Koa1 and Koa2) and forest (Mix1 and Mix2) sites during the koa moth outbreak. The abundance of caterpillars on branch samples provides a smaller-scale appreciation of the impact of the outbreak on individual trees. Branch samples consisted of similar amounts of foliage, making numbers of caterpillars per sample roughly comparable. Maximum defoliation occurred on 20 June at Koa1, Koa2, and Mix1 and on 27 June at Mix2

video link within https://doi.org/10.5066/P9HE9WKK) were observed from 19 July to 2 August at the Koa2 reforestation site and the Mix1 natural forest site. In contrast, peaks in the other reforestation and natural forest sites were indistinct.

Defoliation and response of koa

Patterns of defoliation

Defoliation severity was variable at the four sites, and the pattern did not meet our expectation that reforestation sites would be more heavily defoliated than natural forest sites. The amount of foliage collected during branch clipping decreased over time until maximum defoliation on 20 June at the two reforestation sites and the Mix1 natural site and 27 June at the Mix2 natural forest site. Compared to pre-outbreak levels, foliage biomass declined by 69% overall, with natural sites experiencing relatively high levels of defoliation (72% at Mix2, 85% at Mix1). Defoliation was also high at one of the reforestation sites (82% at Koa2) but was relatively low (42%) at Koa1 by 13 June.

At landscape scale, defoliation was heavy and widespread, averaging 55%–93% of crown volume across all size classes of koa in both habitats (Table 4). Severe defoliation (≥90% of crown) was observed among 57% of natural forest seedlings (dbh <1 cm) and 77% of reforestation seedlings as well as 83% of small trees (dbh 1–8 cm) in each habitat.

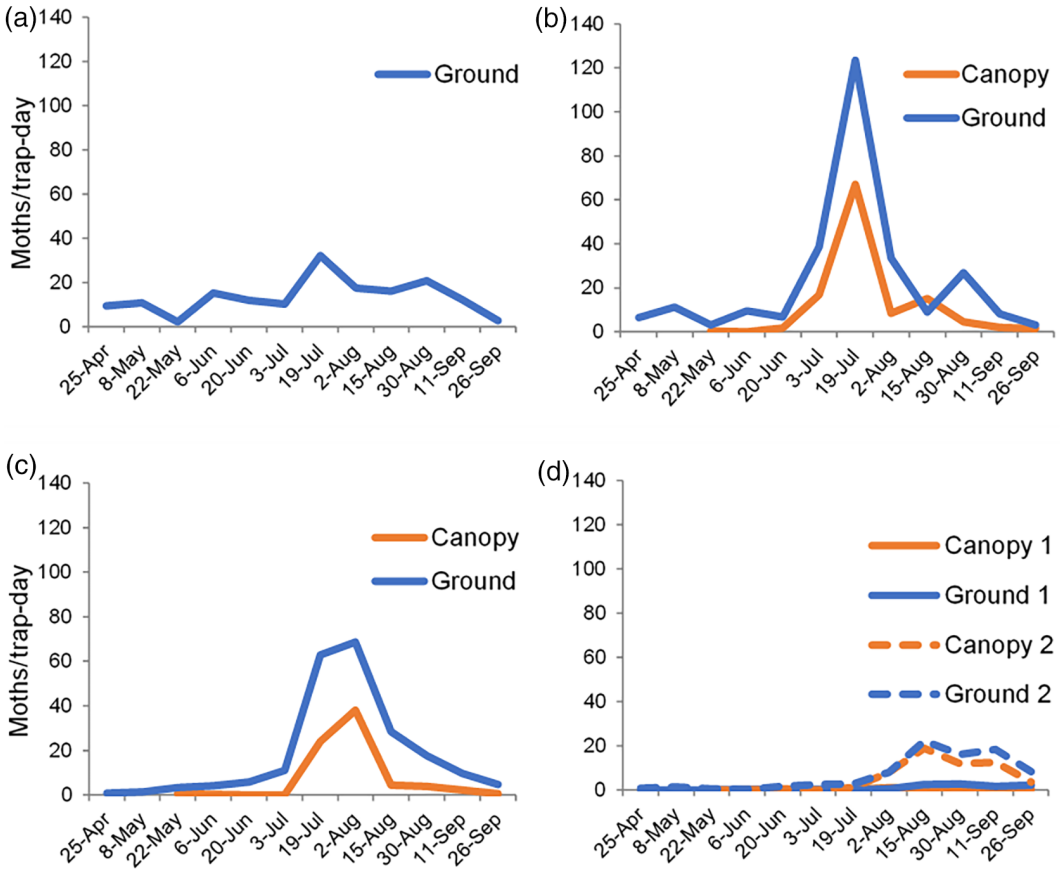


FIGURE 5 Adult koa moth abundance during the 2013 outbreak at reforestation sites (a) Koa1 and (b) Koa2 and forest sites (c) Mix1 and (d) Mix2. The *y*-axes represent numbers of moths/trap-day. A canopy malaise trap was not deployed at Koa1 (b). Ground and canopy (aerial) malaise traps produced similar temporal patterns of abundance, although ground traps averaged about 2.0 times more moths than canopy traps across all dates

TABLE 4 Mean proportion of koa crown defoliated in reforestation (Koa1, Koa2) and natural forest (Mix1, Mix2) sites at Hakalau.

Site (*n*)	0 (85)	<1 cm (57)	1–8 cm (193)	>8 cm (175)
Koa1 (105)	0.84	0.86	0.93	0.68
Koa2 (184)	0.88	0.86	0.89	0.82
Mix1 (121)	0.55	0.91	0.87	0.96
Mix2 (100)	0.73	0.55	0.90	0.80
Koa1 + Koa2 (289)	0.87	0.86	0.90	0.74
Mix1 + Mix2 (221)	0.59	0.83	0.89	0.88

Note: Size classes indicate dbh in cm (measured at 1.4 m height); class 0 = no dbh (height ≥1 m but <1.4 m). Numbers of koa (*n*) are pooled for each size class and site and are shown in parentheses.

TABLE 5 Changes in koa foliar biomass due to defoliation by koa moth caterpillars at reforestation (Koa1, Koa2) and natural forest (Mix1, Mix2) sites at Hakalau.

Site	Pre-defoliation	Post-defoliation	Decline (%)	Total consumed
Koa1	4.30	1.57	63.6	2.73
Koa2	6.67	1.41	78.8	5.26
Mix1	1.09	0.08	93.0	1.01
Mix2	2.53	0.55	78.3	1.98

Note: Foliar biomass is estimated in ton dry foliage/ha; 1 ton = 1000 kg).

More large trees (dbh >8 cm) were severely defoliated in natural forest sites than in reforestation sites (80% vs. 49%; $\chi^2 = 7.01$, df = 1, $p = 0.008$). Among large trees, the extent of extreme defoliation was heaviest at the Mix1 natural forest site (94%), similar at both the Mix2 natural forest site (62%) and Koa2 reforestation site (61%), and least at the Koa1 reforestation site (39%).

Changes in foliar biomass

Foliar biomass, initially consisting almost entirely of phyllodes, was higher per unit of area in reforestation sites before defoliation (Table 5). Nevertheless, due to heavy defoliation at both natural forest sites but only one reforestation site, foliar biomass was reduced by about 78%–93% in natural forest habitat (two-tailed Mann-Whitney *U* compared to about 64%–79% in reforestation habitat test corrected for ties across groups; $t = 4.07$; $p < 0.001$). Phyllodes were nearly always consumed first, but we occasionally observed caterpillars eating true leaves on koa seedlings even when phyllodes were available. We also occasionally observed swarms of caterpillars on other plant species growing underneath koa, including pilo (*Coprosma rhynchocarpa*) and ʻākala (*Rubus hawaiensis*). Although we observed herbivory on the leaves of these species, it was generally not extensive.

Response of koa to defoliation

Following defoliation, production rates of new foliage were variable and were not always consistent with our expectations. Few true leaves and phyllodes were evident 12 weeks after defoliation, but at 24 weeks, 35% of koa crowns (all size classes combined) consisted of new foliage. Small seedlings (height <1.4 m; no dbh) produced new foliage rapidly in both habitat types, but rates were slower for larger seedlings (dbh <1 cm) and small trees (dbh 1–8 cm; Appendix S1: Table S3). Large trees (dbh >8 cm) initially produced foliage more quickly in natural forest habitats, but foliage production in reforestation habitats had caught up by week 34. In both habitats, large trees produced about 1.5 times more new foliage (as a percentage of crown volume) than had small trees by week 34.

The amount of new foliage may also have been influenced by the severity of crown defoliation, although sample sizes for lightly defoliated koa were small. Seedlings and small trees (dbh ≤8 cm) that were relatively lightly defoliated (≤50%) tended to produce more new foliage than did seedlings and small trees that were more heavily defoliated, even after 34 weeks (Appendix S1: Table S3). Contrary to expectations, heavily defoliated large trees (dbh >8 cm) initially produced more new foliage than did lightly defoliated trees, but we recorded more foliage on lightly defoliated large trees than on heavily defoliated large trees after 34 weeks. Subsequently, we could no longer discriminate between new and old foliage, but the canopies even of heavily defoliated trees in both habitats had regrown most of their foliage after 1 year.

The best-fit model of foliage regrowth at 34 weeks included defoliation severity, tree size, and site as contributing factors. Taken individually, the severity of defoliation had a non-significant negative effect on regrowth (odds ratio of 90% reduction in regrowth for 100% defoliation), and dbh had a non-significant positive effect (10% increase in regrowth/10 cm of dbh). Tree mortality by week 34 was nearly entirely explained by tree size and severity of defoliation: 13 of 14 dead trees were small (dbh 1–8 cm), all were severely defoliated (99%–100%), and equal numbers died in each habitat type.

Of 510 seedlings, saplings, and small and large koa in our sample, 93 (18%) produced little or no (0%–5%) new foliage 24–25 weeks after the partial or complete loss of their canopies. Five trees and two seedlings that were moderately defoliated (10%–50%) recovered <5% of their canopies. Of trees that were heavily defoliated (>50%; $n = 452$), 40 (9%) produced 0%–5% new foliage 24–25 weeks after defoliation (Appendix S1: Table S3).

True leaves composed 73% of the new foliage across all koa size classes and habitats 24–25 weeks after defoliation. The new foliage of small trees (dbh ≤8 cm) was predominately true leaves in both natural forest (81%) and reforestation (89%) habitats, but true leaves composed only 55% of the new foliage of large trees in natural forest habitat and 32% in reforestation habitat.

Nutrient pulse dynamics

Frass production

The amount of frass produced by caterpillars reared over 24 h at 15°C in the laboratory showed a strong relationship with caterpillar mass for instars 3, 4, and 5 ($y = 2.2747x - 0.1595$, $R^2 = 0.9985$; Table 6). Based on this equation, we estimated that individual first- and second-instar caterpillars produced <0.01 and 0.4698 mg of frass over 24 h, respectively. Therefore, the maximum daily frass production (kg/ha) of all caterpillars at the reforestation sites ranged from 92.63 (Koa1) to 280.28 (Koa2), and at the natural forest sites, it ranged from 100.80 (Mix1) to 206.63 (Mix2).

Litterfall

Initially, canopy litter fell at the highest rates at the Koa2 reforestation site, although litterfall dropped precipitously at this site after caterpillars reached maximum biomass in June (Figure 6). Litterfall rates at the other sites started to decrease ~1 month later. After defoliation, litterfall rates stabilized at generally lower levels at all sites. A peak in litterfall in late 2014 was due to a large wind event, which resulted in as much litter as during the outbreak.

Nitrogen concentrations were lower in koa phyllodes than in caterpillar frass (%N content: koa phyllodes [mean ± SE] = 2.46 ± 0.10, frass = 3.30 ± 0.02). Phyllodes also contained slightly lower carbon concentrations (%C content: koa phyllodes = 49.16 ± 0.36, frass = 51.30 ± 0.07), leading to lower overall C:N ratios for frass (C:N: koa phyllodes = 19.98 ± 0.77, frass = 15.55 ± 0.14).

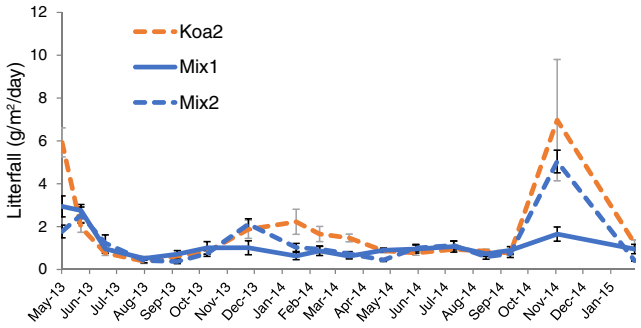


FIGURE 6 Dry mass of litterfall (g/m^2/day) over the study period at a restoration site (Koa2) and both forest sites (Mix1 and Mix2). Points are means ±1 SE. Maximum defoliation occurred on 20 June at Mix1 and Koa2 and on 27 June at Mix2

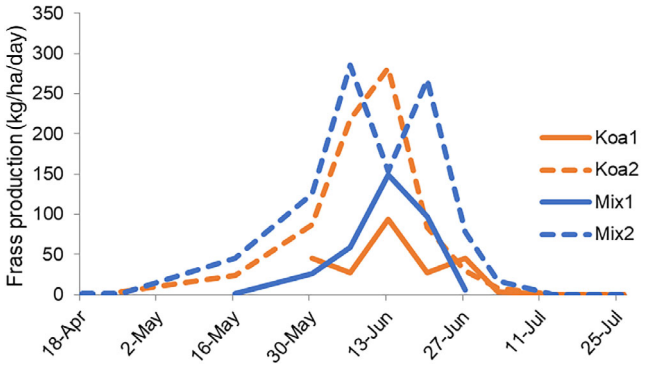


FIGURE 7 Estimated frass production (dry kg/ha/day) over time at reforestation sites (Koa1 and Koa2) and forest sites (Mix1 and Mix2) during 2013. Maximum caterpillar abundance occurred on 20 June at Koa1, Koa2, and Mix1 and on 27 June at Mix2. A Gaussian curve explained almost half of the variability in the data ($R^2 = 0.48$), indicating a distinct pulse in frass production

TABLE 6 Estimated caterpillar mass and daily frass production by caterpillar instars 2–5 under laboratory conditions at 15°C.

Item	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5
Caterpillar	0.0633	0.2767	1.0133	2.7933	7.6733
Frass	<0.01	0.4698	2.1455	6.1945	17.295

Note: Frass production over 24 h was estimated as dry mg/individual. Average dry mass of caterpillars was estimated as mg/individual from 30 individuals pooled for each instar.

TABLE 7 Effects of time and habitat on resin available soil N and P.

Nutrient	Site	F_t	p_t	F_h	p_h	$F_{t\times h}$	$p_{t\times h}$
N	Koa2	8.61	0.040*	12.04	<0.001***	7.80	0.049*
	Mix1	52.15	0.003**	3.68	<0.001***	10.70	0.061
	Mix2	5.48	0.173	5.72	<0.001***	1.30	0.719
P	Koa2	17.86	0.025*	4.29	<0.001***	13.50	0.041*
	Mix1	10.82	0.060	0.34	0.079	1.22	0.746
	Mix2	5.23	0.185	0.01	0.990	2.95	0.374
N:P	Koa2	12.66	0.046*	0.21	0.153	11.96	0.051
	Mix1	27.63	0.011*	0.33	0.085	0.95	0.827
	Mix2	4.18	0.248	1.10	0.005**	1.42	0.686

Note: F and p values are from repeated-measures analyses of variance for soil nutrients during the outbreak in different habitat types (koa vs. grass). Sampling occurred at one reforestation site (Koa2) and both natural forest sites (Mix1, Mix2) at Hakalau. F and p values are displayed with subscripts for time (t), habitat (h), and time × habitat ($t \times h$). A significant time × habitat interaction is indicative of a nutrient pulse. Significance levels: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

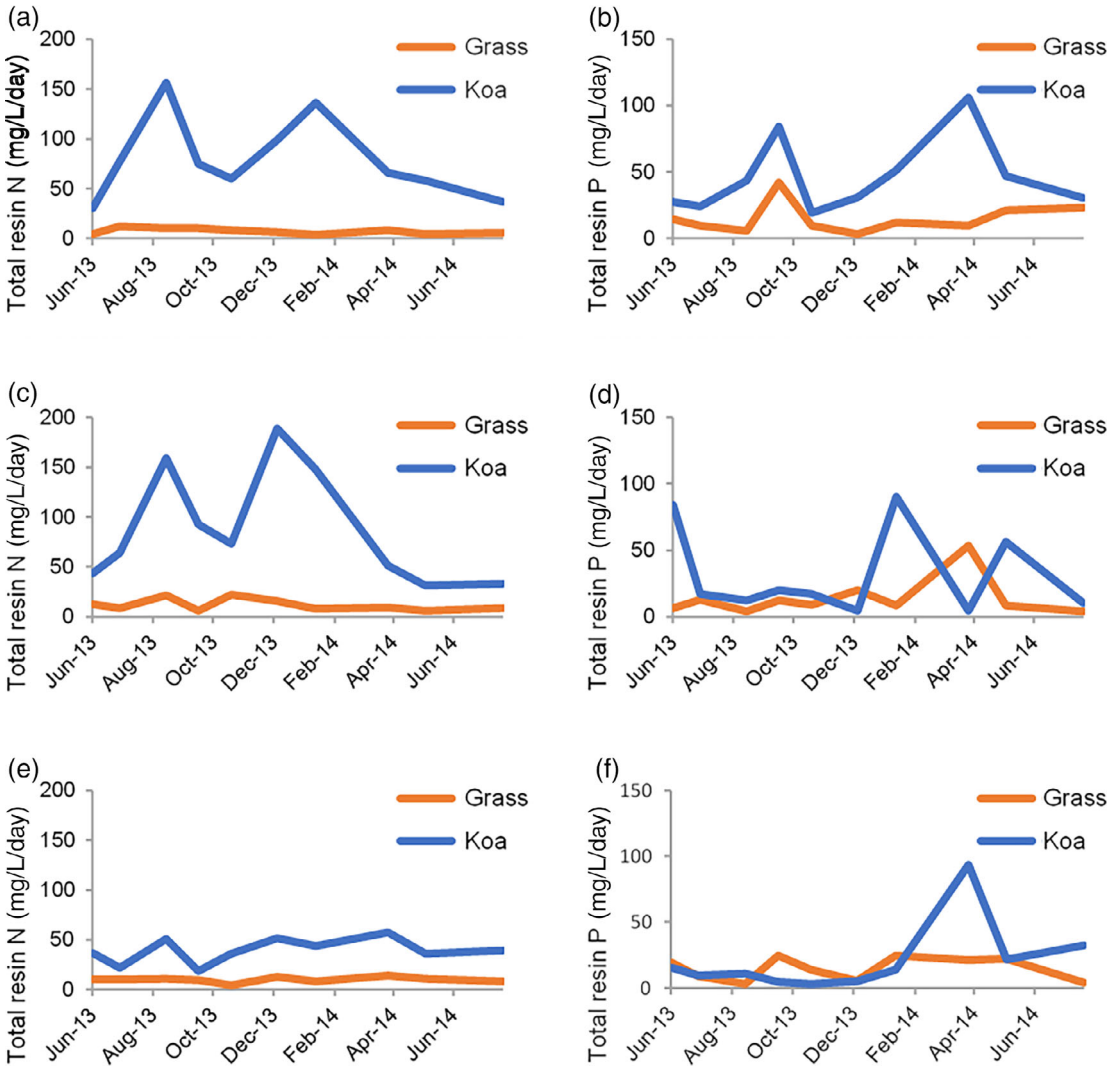


FIGURE 8 Resin available nitrogen (NH_4^+ plus NO_3^-) under koa canopies and in open grass plots at one reforestation site (a) Koa2 and both forest sites (c) Mix1 and (e) Mix2. Resin available phosphorus is shown in panels (b) Koa2, (d) Mix1, and (f) Mix2. N and P measured in mg/L/day. Dates represent starting points for resin bag burial intervals, beginning on 6 June 2013 and ending on 25 July 2014. For reference, sampling began on 6 June 2013 and caterpillar biomass peaked on 13 June at Koa2 and Mix1 and on 20 June at Mix2

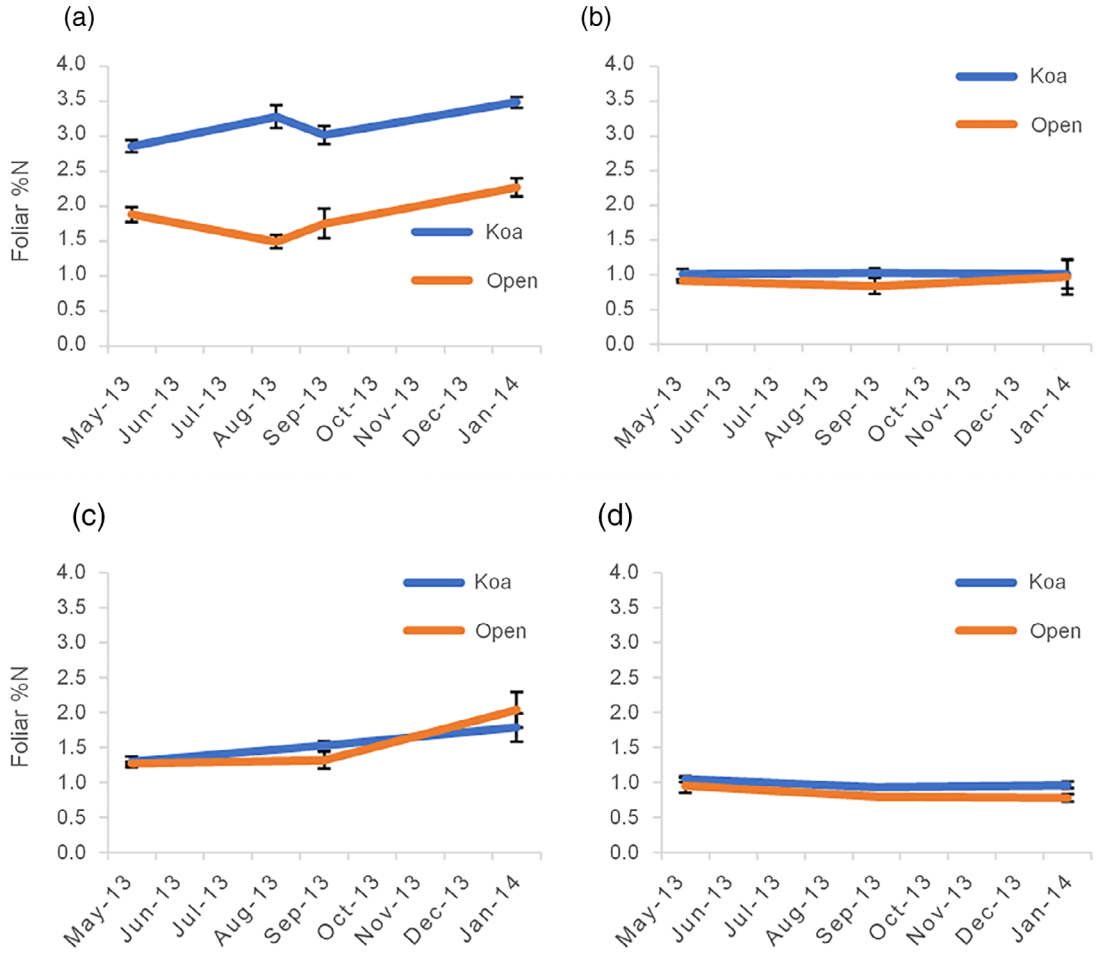


FIGURE 9 Mean (±1 SE) percent foliar nitrogen over time for koa understory species, including (a) alien grasses and the native woody species, (b) ʻōhiʻa (*Metrosideros polymorpha*), (c) ʻōhelo (*Vaccinium calycinum*), and (d) pūkiawe (*Leptecophylla tameiameiae*)

Nitrogen redistribution

Cumulative frass and N redistribution were highest at the Koa2 reforestation site and the Mix2 natural forest site, where about 5600 kg/ha of frass (equivalent to about 180 kg N/ha) fell to the ground during about 2 months from April through July 2013 (Figures 1d and 7). High frass deposition in these two sites was due to high caterpillar density and high foliar biomass. At the two reforestation sites, where foliar biomass was similar (~500 g/m), caterpillar abundance was higher, and more frass fell at Koa2 than at Koa1. By comparison to N falling in frass, there was 160 ± 37 kg N/ha in the pre-defoliation koa canopy foliage at Koa2 and 86 ± 30 kg N/ha at Mix2.

Soil nitrogen (N) and phosphorus (P)

Resin available N in soils under koa canopies in both reforestation sites and the Mix1 natural forest site pulsed distinctly, while in open grass plots it did not, although this interaction was stronger in Koa2 than in Mix1 (Table 7, Figure 8). We did not detect a distinct N pulse at the Mix2 natural forest site. Nitrogen at the Mix1 natural forest site and the Koa2 reforestation site peaked once in summer (from 3 July to 19 August 2013) and again in winter (from about 23 October 2013 to February 2014), but with some variation in timing between sites (Figure 8). The midpoint of the first peak occurred ~43 days after maximum caterpillar biomass at Mix1 and Koa2. Soil resin N was higher on all dates in plots under koa compared to grass plots not under koa, and this difference was most pronounced when resin N was at its peak. In late March 2014, when the N pulse seemed to have dissipated, there were 12, 5, and 3 times as much resin N in koa plots as in grass plots in Koa2, Mix1, and Mix2, respectively. By contrast, at peak N for each site, there were 33, 19, and 4 times as much resin available N in koa plots as in grass plots in Koa2 (December 2013), Mix1 (October 2013), and Mix2 (May 2013). Available N under koa was first detected as both NH_4^+ and NO_3^-,

TABLE 8 Birds observed during 2-min observation periods in koa ($n = 492$) and ʻōhiʻa ($n = 525$) trees in reforestation (reforest) and natural forest (forest) habitats at Hakalau sites on 12 weekly surveys from 22 May to 15 August 2013.

Species[a]	Reforest Koa (242)	Reforest ʻŌhiʻa (159)	Forest Koa (250)	Forest ʻŌhiʻa (366)	Total
No bird	196	93	196	206	691
Unidentified bird	64	80	73	218	435
WAWE	13	51	3	9	76
IIWI (Threatened)	3	3	7	59	72
HAAM	11	20	3	13	47
APAP	0	2	5	36	43
HAEL	3	3	0	2	8
OMAO	0	0	2	1	3
HCRE (Endangered)	0	0	0	1	1
AKIA (Endangered)	0	0	1	0	1
Total birds	94	159	94	339	686

Note: Values for "No bird" indicate the number of trees in which no bird activity was observed. All other values indicate the total number of birds of each species observed. All species are endemic to Hawaiʻi except WAWE, which is invasive.

[a]WAWE (warbling [Japanese] white-eye, *Zosterops japonicus*); IIWI (ʻiʻiwi, *Drepanis coccinea*); APAP (ʻapapane, *Himatione sanguinea*); HAAM (Hawaiʻi ʻamakihi, *Chlorodrepanis virens*); HAEL (Hawaiʻi ʻelepaio, *Chasiempis sandwichensis*); OMAO (ʻōmaʻo, *Myadestes obscurus*); HCRE (Hawaiʻi creeper [ʻalawī], *Loxops mana*); AKIA (ʻakiapōlāʻau, *Hemignathus wilsoni*).

although this quickly converted to an all nitrate signal 1 month after the initial pulse (data not shown).

For resin available soil P, only the Koa2 reforestation site had greater levels under koa than grass, and no differences were found at other sites. Similarly, soil P peaked distinctly under koa only at Koa2, where we observed a double peak that was similar to the double peak of N but offset by 30–60 days (Figure 8). Ratios of resin available N:P fluctuated at two sites, pulsing only at Koa2 toward the end of the study period (March 2014) and after the pulses in N and P alone.

Understory foliar response

Understory species responded variably to frass deposition (Figure 9). Grasses under koa responded strongly across all sites, with a 15% increase in foliar N from May through August 2013, ~1 month after soil N started to pulse. At the same time, the foliar N of grasses decreased by 21% in plots away from koa, leading to a significant time × habitat interaction in a repeated-measures analysis of variance (*time* effect, $F = 10.73$, $p < 0.01$; *habitat* effect, $F = 4.17$, $p < 0.01$; *time* × *habitat* interaction, $F = 1.75$, $p < 0.01$). Native woody species, ʻōhiʻa, ʻōhelo, and pūkiawe, also changed slightly in foliar N at this time, although time, habitat, or interaction effects in repeated-measures models were not significant.

Response of birds

General activity and response to habitat variables

Unidentified species composed 63% of the total number of birds observed (Table 8). Among the species we identified most frequently, ʻiʻiwi and ʻapapane were primarily in natural forest habitat, whereas Hawaiʻi ʻamakihi and warbling white-eye were mainly in reforestation habitat. We often could not identify the behavior of birds in the focal trees, but we sometimes observed active foraging on caterpillars, which occasionally escaped predation by suddenly dropping from phyllodes on silk threads.

Logistic regression indicated that overall bird activity in tree species was influenced primarily by the degree of ʻōhiʻa flowering, severity of koa defoliation, and observer (relatively few observers contributed most of the observations). These factors and habitat type also affected activity levels of the four most frequently observed bird species (Appendix S1: Table S4).

ʻŌhiʻa phenology was similar in natural forest and restoration habitats. About one-third of ʻōhiʻa trees were flowerless before (33%, $n = 100$) and after (36%, $n = 402$) defoliation, but trees bore medium to heavy flower crops more frequently before (14%) compared to after (3%) defoliation ($\chi^2 = 21.47$; df = 1, $p < 0.001$).

Changes in use of tree species

We expected birds in both habitats to be present more frequently in koa than ʻōhiʻa during the buildup of caterpillars but then visit ʻōhiʻa more frequently after peak defoliation. Instead, birds visited ʻōhiʻa at least as often as koa before and after defoliation in both habitats. In natural forest habitat, birds were observed at similar frequencies in ʻōhiʻa and koa before defoliation (ʻōhiʻa 57%, koa 44%; $\chi^2 = 2.77$, df = 1, $p = 0.096$) and more frequently in ʻōhiʻa after defoliation (ʻōhiʻa 39%, koa 14%; $\chi^2 = 33.79$, df = 1, $p < 0.001$). In reforestation habitat, birds were present in ʻōhiʻa at least twice as often before defoliation (ʻōhiʻa 66%, koa 33%; $\chi^2 = 8.64$, df = 1, $p = 0.003$) and after defoliation (ʻōhiʻa 35%, koa 15%; $\chi^2 = 18.42$, df = 1, $p < 0.001$). These results also indicate that the magnitude of change in the use of tree species varied according to habitat type. When caterpillars became scarce after defoliation, bird presence in ʻōhiʻa declined from 57% to only 39% in natural forest but it fell from 66% to 35% in reforestation habitat. The magnitude of change in koa use indicated a reversed trend as bird frequency declined from 44% to 14% in natural forest and from 33% to only 15% in reforestation habitat after defoliation. Additionally, the significant drop in the use of both koa and ʻōhiʻa after koa defoliation (Appendix S1: Table S5) may indicate post-defoliation dispersal to other areas not yet or less affected by the outbreak or a coincidental seasonal decrease in bird activity due to a change in other resources, such as ʻōhiʻa flowers, as noted above.

In weak alignment with the general effect of tree species on bird presence or absence, bird activity in koa (both habitats combined) averaged 0.33 birds/min ± 0.05 SE before defoliation and 0.15 birds/min ± 0.03 after defoliation ($z_{1\text{-tail}} = 1.26$, $p = 0.10$). Bird activity was also twice as great in koa that had been defoliated lightly or not at all (≤25%; 0.20 birds/min ± 0.06 SE) compared to more severely defoliated koa (>25%; 0.10 birds/min ± 03; $z_{1\text{-tail}} = 2.40$, $p = 0.008$). Bird activity also declined in ʻōhiʻa, averaging 0.74 birds/min ± 0.10 before and 0.39 birds/min ± 0.03 after koa defoliation ($z_{2\text{-tail}} = 3.24$, $p < 0.001$).

Changes in diet

As predicted from the pulse of high-quality prey, caterpillars increased in bird diets during the outbreak, but limited sampling prevented us from comparing diets of birds in different habitats or evaluating the diets of more than just two species. In the case of the native, omnivorous Hawaiʻi ʻamakihi, we identified 689 individual prey from 19 fecal samples collected before the outbreak (from 26 February to 25 April) and 128 prey items from 15 samples collected during the outbreak (22 May–27 June). Hemiptera and Lepidoptera were the only taxa comprising >15% of prey items in both pre-outbreak and outbreak periods. Small-bodied Hemiptera, especially psyllids (Psyllidae) comprised 93% of prey items before the outbreak and 44% during the outbreak. Based on leg segments, juvenile wing buds, and adult wings, the primary psyllid prey species was the invasive Acacia psyllid (*Acizzia uncatoides*), itself an irruptive species on koa. Caterpillars, much larger prey than psyllids, comprised 4% of prey items before and 43% during the outbreak. Caterpillar fragments were found in 79% of samples before the outbreak and in all samples during the outbreak ($\chi^2 = 3.58$, df = 1, $p = 0.059$). The number of individual caterpillars, as represented by paired sets of mandibles and unpaired mandibles, averaged 1.5/sample ± 0.28 SE before the outbreak and 3.7/sample ± 0.75 SE during the outbreak ($t_{1\text{-tail}} = -2.55$, df = 18, $p = 0.008$).

For the warbling white-eye, 796 individual prey from 28 samples were identified prior to the outbreak and 292 prey were identified from 35 samples during the outbreak. Psyllids and other Hemiptera comprised 87% of prey items before but 26% during the outbreak. Caterpillars comprised 5% of prey items before and 51% during the outbreak. Other taxa comprised <15% of the diet in both periods. Caterpillar parts were observed in 79% of samples before and in all samples during the outbreak ($\chi^2 = 8.29$, df = 1, $p = 0.004$). The number of caterpillars in warbling white-eye samples averaged 1.6/sample ± 0.38 SE before and 4.3/sample ± 0.84 SE during the outbreak ($t_{1\text{-tail}} = -2.91$, df = 47, $p = 0.003$).

In the Hawaiʻi ʻamakihi, koa moth caterpillars were identified in 19% of 19 samples before and 93% of 15 samples during the outbreak ($\chi^2 = 5.15$, df = 1, $p = 0.023$). The abundance of koa moths was 0.32 caterpillars/sample ± 0.13 SE before and 3.0 caterpillars/sample ± 0.61 SE during the outbreak ($t_{1\text{-tail}} = -4.30$, df = 15, $p = 0.0003$). Koa moths were identified in 38% of 24 warbling white-eye samples before and 71% of 35 samples during the outbreak ($\chi^2 = 3.78$, df = 1, $p = 0.052$). The abundance of koa moth caterpillars in warbling white-eye samples was 0.88 caterpillars/sample ± 0.36 SE before and 3.5 caterpillars/sample ± 0.88 SE during the outbreak ($t_{1\text{-tail}} = -2.81$, df = 15, $p = 0.0036$).

Changes in mass

Sampling limitations did not allow us to evaluate changes in mass by habitats, so weights were pooled across sites. A total of 573 individuals from six common forest bird species and the endangered Hawaiʻi creeper (ʻalawī; *Loxops mana*) were captured and measured at the Koa1 reforestation site and the Mix1 natural forest site in 2013 (Table 9). The mass

TABLE 9 Mass (g) of seven common forest bird species at the Koa1 and Mix1 banding sites at Hakalau.

Species	Guild	Period	*n*	Mean	SE	95% CI	*F*	*p*	Adjusted *p*
APAP	Nectar	Pre	38	15.5	0.25	15.0–16.0	5.96	0.019*	0.076
		Out	6	13.9	0.63	12.6–15.2			
HAAM	Omnivore	Pre	102	13.7	0.01	13.5–13.9	6.23	0.014*	0.070
		Out	26	14.3	0.20	13.9–14.7			
HAEL	Arthropod	Pre	20	14.7	0.22	14.2–15.2	9.13	0.006**	0.036*
		Out	9	15.9	0.33	15.2–16.6			
HCRE	Arthropod	Pre	28	14.9	0.13	14.7–15.2	20.91	<0.001***	0.007**
		Out	5	16.5	0.31	15.8–17.1			
IIWI	Nectar	Pre	61	19.0	0.26	18.5–19.5	1.19	0.279	0.558
		Out	5	20.0	0.90	18.3–21.8			
JAWE	Omnivore	Pre	130	11.1	0.06	10.9–11.2	5.03	0.026*	0.078
		Out	70	11.3	0.09	11.1–11.5			
RBLE	Fruit	Pre	53	20.8	0.19	20.4–21.2	0.319	0.574	0.574
		Out	20	21.0	0.31	20.4–21.6			

Note: For each species and period (pre-outbreak and outbreak), foraging guild, number of birds captured, mean, standard error, and 95% CI of mass are presented. Statistical significance for change in mass before and after the outbreak is shown as *F* ratio and associated significance level followed by the significance level adjusted for multiple tests (Holm, 1979). Significance levels: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. RBLE = red-billed leiothrix (*Leiothrix lutea*; see Table 8 footnote for key to other bird identification codes).

TABLE 10 Hawaiian hoary bat activity patterns at Hakalau and Laupāhoehoe.

Station	Hakalau PD1	Hakalau PD2	Hakalau PA1	Hakalau PA2	Laupāhoehoe LA1	Laupāhoehoe LA2
Elevation (m)	1645	1722	1929	2000	1069	1122
Nights sampled	77	77	42	79	74	63
Call events	0.31	0.03	0.05	0.18	14.32	2.83
Echolocation pulses	2.47	0.42	0.17	1.19	204	18.95
Feeding buzzes	0.08	0.01	0	0	0.45	0.27

Note: Call events, echolocation pulses, and feeding buzzes were calculated and standardized per recording night at each station. At Hakalau, four detectors were operated from May to August 2013, with two stations along Pedro Road (PD1 [near Mix1] and PD2 [near Koa1]) and two along Pua Akala Road (PA1 and PA2 [in and near Mix2]). At Laupāhoehoe, two detectors (LA1 and LA2) were operated along Blair Road from July through September 2013.

of only one species (ʻiʻiwi) was significantly different between the two sites, and the difference was consistent for pre-outbreak (26 February–21 May) and outbreak (22 May–30 June) periods, so sites were combined for analysis.

The more frequent consumption of caterpillars was expected to result in increased mass of birds generally. The direction and magnitude of change in pre-outbreak and outbreak mass varied among species and foraging guilds, but most species tended to gain mass (Table 9). Mass gain was unequivocal for the Hawaiʻi ʻelepaio (*Chasiempis sandwichensis*) and Hawaii creeper. Arthropods are important in the diet of all species (Banko et al., 2015), but the Hawaiʻi ʻelepaio and Hawaiʻi creeper are primarily insectivorous whereas the Hawaiʻi ʻamakihi and warbling white-eye are omnivorous (arthropods and nectar), the red-billed leiothrix (*Leiothrix lutea*) is frugivorous, and the ʻiʻiwi and ʻapapane are nectarivorous. Mass remained relatively unchanged during the outbreak only for the nectarivorous ʻiʻiwi and frugivorous red-billed leiothrix.

Response of bats at Hakalau and Laupāhoehoe

Moths are important prey of the Hawaiian hoary bat, and we expected their feeding behavior to change in response to the pulse of koa moths. Due to the large area over which bats forage and the limitations of our sampling design, we could not evaluate whether bat feeding behavior was influenced by differences in koa density and moth abundance in the two habitat types.

We recorded bat call events (number of times a microphone recorded a calling bat), echolocation pulses (number of discrete sound pulses in a call event), and

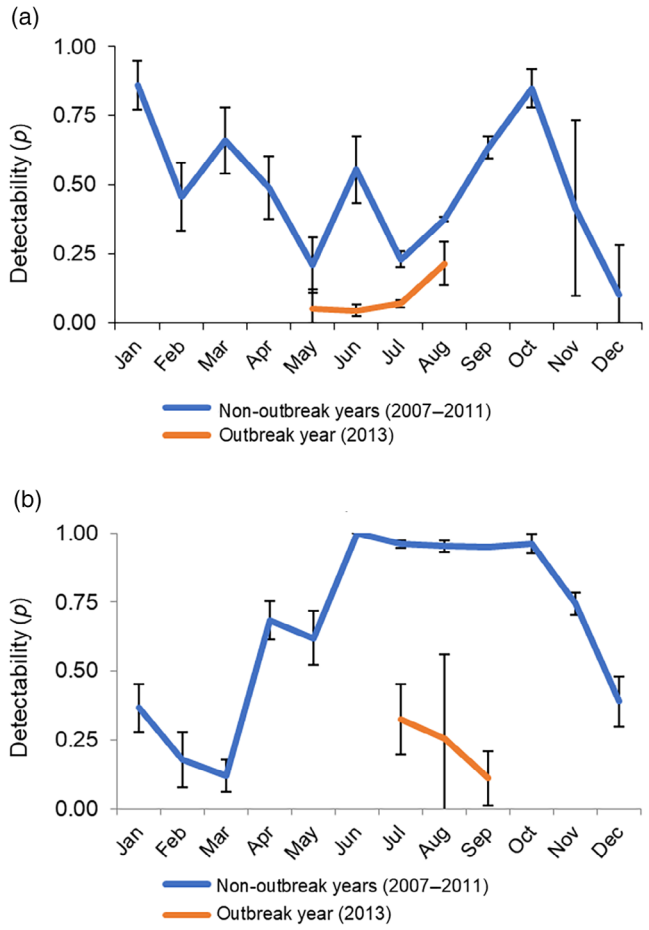


FIGURE 10 Mean (±1 SE) monthly bat detectability at (a) Hakalau [Mix2] and (b) Laupāhoehoe from 2007 to 2011, when koa moths were not irrupting, and during the 2013 outbreak. Bat data for 2013 were collected from May through August at Hakalau and from July through September at Laupāhoehoe. Moth abundance peaked during August and September at Mix2 (Figure 5) and in April and August at Laupāhoehoe (Banko et al., 2014)

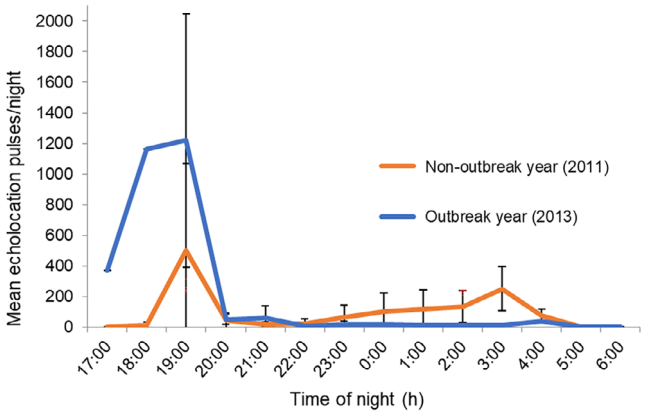


FIGURE 11 Mean (±1 SE) hourly echolocation pulses recorded at night from Hawaiian hoary bats at Laupāhoehoe sites from July through September 2013 (koa moth outbreak) and during the same months in 2011 (non-outbreak). Insufficient data were available for analysis at Hakalau sites

feeding buzzes (rapid increases in rate and number of echolocation pulses, indicating attacks on prey) at Hakalau (upper koa belt) and Laupāhoehoe (lower koa belt, see Figure 2). Acoustic surveys in both areas were conducted during a 5-year period (2007–2011) before the koa moth outbreak and during the summer of 2013, when large tracts of koa were being defoliated and moth abundance was high. The frequency of call events, echolocation pulses, and feeding buzzes was at least one order of magnitude greater at Laupāhoehoe compared to Hakalau during the outbreak year (Table 10). At both sites, bat detectability was higher during the 5-year, pre-outbreak period compared to the outbreak period (Figure 10).

When we had enough samples, we observed a temporal shift in feeding behavior when comparing summer months of the pre-outbreak and outbreak periods. Echolocation pulses of bats at Laupāhoehoe from July through September 2011 (pre-outbreak) were recorded during all hours of darkness between 5:00 PM and 6:00 AM, with a peak during 7:00 PM and 8:00 PM, when 41% of pulses occurred (Figure 11). In comparison, during the koa moth outbreak in 2013, echolocation pulses were heavily concentrated early in the night, with 94% occurring from 5:00 PM through 8:00 PM and relatively few occurring later.

Response of parasitoid wasps at Hakalau and Laupāhoehoe

We expected parasitoid attack rates to increase with the abundance of caterpillars due to their relatively fast rates of reproduction. Instead, we found that the overall rate at which koa moth caterpillars (all instars) were parasitized at Hakalau decreased significantly ($\chi^2 = 18.58$, $p < 0.0001$) from 13.3% ($n = 255$) before the outbreak (18–25 April) to 2.3% ($n = 215$) during the outbreak (16 May–20 June). Before the outbreak, the parasitism rate was highest in caterpillars collected during the fourth instar (25%, [$n = 36$]). Parasitism rates of caterpillars collected during the second and third instars were about half that amount (12.5% [$n = 64$] and 11.1% [$n = 117$], respectively) while only one parasitoid emerged from caterpillars collected in the fifth instar (3% [$n = 33$]). Of the pre-outbreak parasitoids, *Hyposoter exiguae* (Hymenoptera: Ichneumonidae) comprised 76.5% of all parasitoids while *Meteorus laphygmae* (Hymenoptera: Braconidae) made up 11.8%. Four additional parasitoids (11.8%) pupated but failed to emerge as adults and were

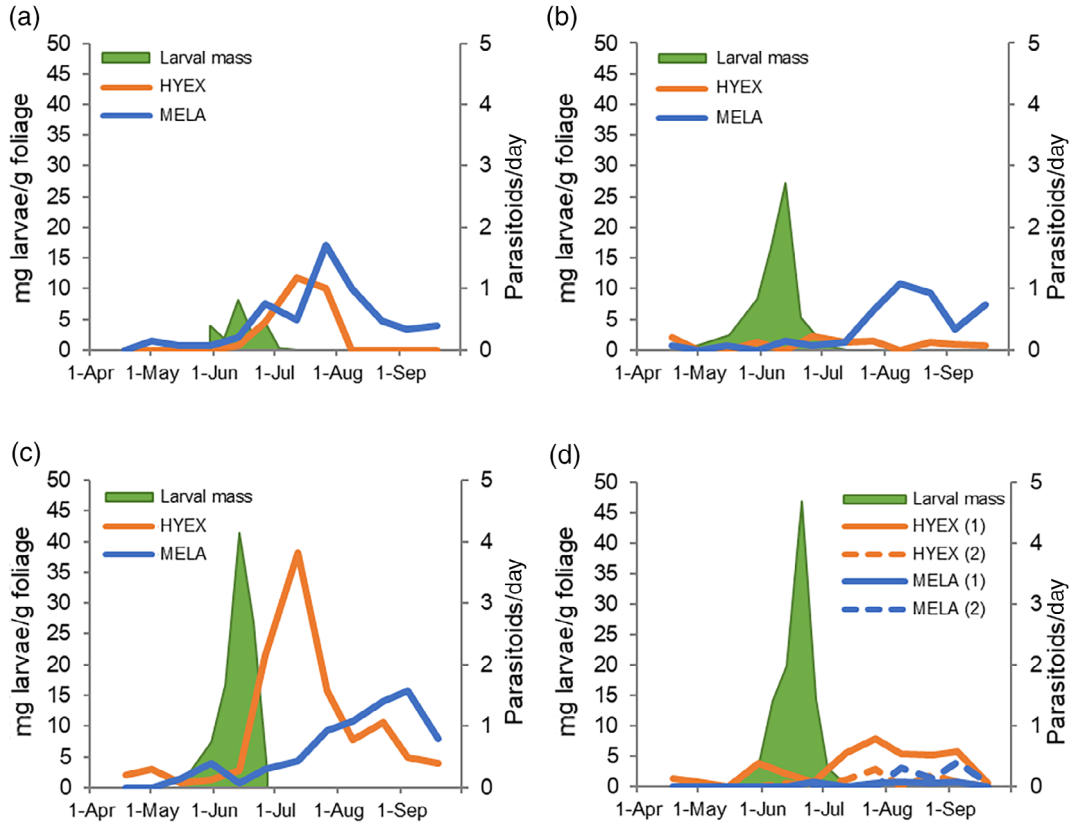


FIGURE 12 Biomass of koa moth larvae collected from koa foliage (mg larvae/g foliage) and abundance of parasitoids, *Hyposoter exiguae* (HYEX) and *Meteorus laphygmae* (MELA), collected in malaise traps (individuals/day) during 2013 at reforestation sites (a) Koa1 and (b) Koa2 and forest sites (c) Mix1 and (d) Mix2

not identified. Parasitoids emerged most often from instar 4 (64.5%) but also sometimes from instars 3 (25.8%) and 5 (9.7%). During the outbreak, only three *H. exiguae* and two *M. laphygmae* were reared from 215 caterpillars collected during instars 3 ($n = 31$), 4 ($n = 119$), and 5 ($n = 58$); the instar of an additional seven individuals could not be determined. Of these five parasitoids, one emerged each from instars three and four while the instar of three others was ambiguous (likely instar 4, but possibly 5).

Although attack rates declined during the buildup of caterpillars, the numbers of *H. exiguae* and *M. laphygmae* tracked caterpillar abundance at the four study sites, generally increasing in abundance about 1–2 months following peak caterpillar biomass (Figure 12). We found no pattern of abundance relative to habitat type. The magnitude of the response varied between species and among sites, with *H. exiguae* increasing in abundance most at the Mix1 natural forest site and the Koa1 reforestation site and *M. laphygmae* increasing at all sites except the Mix2 natural forest site.

From the 105 koa moth pupae ($n = 95$) and prepupae ($n = 10$) collected at Laupāhoehoe, 70 (67%) emerged as moths (45 male, 25 female), 12 (11%) were parasitized, and 23 (22%) died from unknown causes. Parasitoids were represented by *Vulgichneumon diminutus* (Ichneumonidae; $n = 9$) and *Chaetogaedia monticola* (Diptera: Tachinidae; $n = 3$). All parasitoids emerged from the koa moth's pupal stage, and though they have been reported to attack the larval stage (Beardsley & Perreira, 2000; Bess, 1974), making them larval–pupal parasitoids, we did not observe this.

DISCUSSION

We addressed several hypotheses common to insect outbreaks generally, but the rarity and unpredictability of koa moth outbreaks (Haines et al., 2009) make them difficult to investigate with a statistically robust study design. For this reason, we focused our study in an area where we already had or could quickly collect pre-outbreak data on tree and foliage density, tree size, and understory vegetation; koa moth abundance; litterfall and soil nutrient levels; bird habitat use, diet, and body mass; bat feeding activity; and parasitoid wasp abundance and caterpillar attack rates. As the outbreak spread to our relatively remote study area, we were able to

evaluate its dynamics and impacts on host trees, nutrient cycling, and insect consumers. Despite the limited statistical power of representing our two habitat types with only two sites each, our results provide insights into outbreak ecology generally and specifically into the dynamics, complexity, and consequences of outbreaks in low-diversity tropical island forests.

Koa moth abundance patterns

Insect outbreaks likely occur more frequently and with greater impact where host trees are dominant or distributed in large, dense stands (Carson & Root, 2000). Many examples support this idea, but outbreaks can also defoliate small, scattered populations and individual trees (Nair, 2007; Sutton et al., 2021). According to the resource concentration hypothesis, we predicted that the outbreak would occur earlier and result in higher herbivore densities in the koa-dominated reforestation stands due to rapid discovery by moths and superabundant food for caterpillars (Carson & Root, 2000; Root, 1973), and we found that the age structure of caterpillars was initially more advanced at the reforestation sites. Although we lack fine-grained temporal estimates of caterpillar abundance, caterpillar numbers and biomass apparently peaked first at the two reforestation sites but also at the Mix1 natural forest site. Caterpillar abundance peaked about a week later at the Mix2 natural forest site, but its distance from the three Pedro sites could indicate an effect of spatial variation. Nevertheless, because the outbreak spread upward from the lower koa belt, it seems unlikely that moths encountered the higher-elevation reforestation stands before reaching the lower-elevation natural forest stands. The timing of peak defoliation occurred about a week after the peaks of caterpillar biomass at each site.

Contrary to the resource concentration hypothesis, caterpillar numbers (per branch sample) were high at both natural forest sites, where koa density and foliar biomass per unit area were relatively low. In line with expectations, caterpillar numbers were also high at the Koa2 reforestation site, but they were unexpectedly low at Koa1. Caterpillar biomass (per unit of foliage) was highest at the two natural forest sites, intermediate at Koa2, and low at Koa1.

We were unable to evaluate temporal trends before the buildup of caterpillars, but strong peaks occurred later at the Koa2 reforestation site and the Mix1 natural forest site. In contrast, peaks at the other sites were relatively weak and indistinct, indicating lower rates of caterpillar survival or less synchronous development.

Defoliation patterns

Following trends in caterpillar abundance, defoliation was heavier at the two natural forest sites and the Koa2 reforestation site compared to Koa1. Foliar biomass was reduced significantly more (78%–93%) at natural forest sites compared to reforestation sites (64%–79%). All size classes were heavily defoliated in both habitats but more so for large koa in natural forest.

How leaf quality and phenology may have interacted with the koa moth outbreak is unclear, but the tendency of insects to feed preferentially on new leaves can exert selective pressure on the timing of leaf production (Aide, 1993; Coley, 1983; Coley & Barone, 1996), and variation in the chemical and physical quality and availability of new leaves may affect herbivore fitness (Barton & Haines, 2013; Feeny, 1970) and population variability (Forkner et al., 2008; Koricheva et al., 2012; Visser & Holleman, 2001). Heavier defoliation at natural forest sites may indicate an inverse relationship between koa density and the quality of foliage for caterpillars. Although koa is a symbiotic N-fixer, it typically obtains most of its N from soil, particularly as stands reach canopy closure (Pearson & Vitousek, 2001). As a result, koa foliage in dense stands may be less nutritious or palatable due to competition for resources among trees (Stein & Scowcroft, 1984), resulting in lower N content and higher C:N ratio (Kula et al., 2020). It was surprising, therefore, that among the reforestation sites defoliation was heavier at Koa2, where koa density was higher. In this instance, however, differences in the age of phyllodes between the two sites may have influenced caterpillar consumption rates and development times. Anecdotally, phyllodes at Koa1 seemed older (more chlorotic and tougher to the touch) than phyllodes at Koa2. In experimental feeding trials, caterpillars consumed more plant tissue and developed faster when placed on young phyllodes compared to old phyllodes (Barton & Haines, 2013). Therefore, differences in phyllode age, presumably due to variation in koa phenology, might account for some of the variability in defoliation severity among sites. Early caterpillar instars are expected to be less able to consume tougher phyllodes; consequently, a stand with older foliage would have been less attractive to ovipositing moths and therefore less likely to support a severe outbreak. At Hakalau, we observed that caterpillars also preferred phyllodes over true leaves, as predicted from laboratory feeding trials (Barton & Haines, 2013). Nevertheless, seedlings were heavily defoliated despite having a greater proportion of true leaves. For all size classes, foliage consumed during the outbreak consisted mostly of phyllodes, whereas foliage that remained after the outbreak consisted mainly of leaves (about 50% of remaining foliage) and what

seemed to be older phyllodes. Illustrating how limited koa foliage became as the intensity of defoliation increased, we observed caterpillars on several other native plant species that had not been previously reported (Haines et al., 2009). Additionally, a stand of the widespread invasive N-fixing tree, *Falcataria moluccana* (Fabaceae), was defoliated, and feeding trials demonstrated that the koa moth can complete development on this species (Haines et al., 2013). Several ʻōhiʻa trees were defoliated at Laupāhoehoe, but we did not determine whether the caterpillars completed development.

Response of koa to defoliation

Because palatability varies with foliage type (Barton & Haines, 2013), we expected defoliated koa to initially produce less palatable true leaves as a defense against subsequent attack by koa moths. Before defoliation, phyllodes comprised nearly all the foliage of small and large koa. After defoliation, true leaves were produced in greater proportion relative to phyllodes by small koa (dbh ≤ 8 cm) in both habitats (81%–89% of foliage), whereas large koa produced true leaves in similar proportion to phyllodes in natural forest habitat (55%) and smaller proportion in reforestation habitat (32%). True leaves also promote faster plant growth due to their higher gas exchange per dry mass and per C and N investment compared to phyllodes (Pasquet-Kok et al., 2010), which would especially benefit small koa (dbh ≤ 8 cm), whose growth might be limited by their relatively small reserves of carbohydrates (Nykänen & Koricheva, 2004; Stevens et al., 2008). Assuming that large koa were less constrained by carbohydrate reserves, the ratio of true leaves to phyllodes may have been more strongly influenced by light levels following defoliation. In shaded habitat, koa tends to produce higher proportions of true leaves whereas phyllodes predominate in sunnier habitat (Baker et al., 2009). Possibly due to closed ʻōhiʻa cover, the foliage of large koa in natural forest habitat may have been slightly skewed toward true leaves compared to foliage in reforestation habitat, where there was little ʻōhiʻa cover. Haines et al. (2009) noted that defoliated koa on Maui during the 2003–2004 outbreak initially produced high proportions of leaves that were replaced months later by phyllodes. The same pattern was reported for the 1977 koa moth outbreak on Maui (Stein & Scowcroft, 1984).

Compared to small trees, severely defoliated large trees survive at higher rates (Davidson et al., 1999), grow more quickly (Jacquet et al., 2012), and refoliate faster (Nakajima, 2018), likely due to their higher concentrations of carbohydrates (Nykänen & Koricheva, 2004; Stevens et al., 2008). At Hakalau, small and almost entirely defoliated trees suffered relatively high mortality and refoliated slowly, whereas greater nutrient reserves may have enabled nearly all defoliated large trees to survive and refoliate quickly. Nitrogen fixation rates were also likely to have declined following defoliation as biomass allocation to nodules decreased with defoliation severity (Ruess et al., 2006), but large koa may have been better able to compensate for this reduction due to their greater root biomass and ability to mobilize N from the soil.

Competition for nutrients among koa in relatively dense stands may have contributed to temporary differences in refoliation rates between habitats. Although small trees in both habitats produced similar amounts of new foliage, large koa in natural forest stands initially produced more than twice the amount foliage compared to trees in reforestation stands. New foliage in reforestation stands was also often patchily distributed and concentrated on large branches as epicormic growth rather than near branch tips. Overall, reforestation koa seemed to recover more slowly and suffered more branch mortality. Dense stands of koa defoliated on Maui in 1977 also produced new foliage very slowly, with <1% of the stand canopy being replaced 6 months after a koa moth outbreak (Stein & Scowcroft, 1984). Although they observed greater foliar recovery in young (about 15 years) stands that had been thinned and fertilized 3 years before the outbreak, tree growth had already stagnated due to overstocking and was further reduced by 71% 1 year after defoliation. Koa density was 2100/ha on control stands and 490/ha on treated stands on Maui, whereas at Hakalau, koa density was 732/ha on reforestation stands and 125/ha on forest stands. Even considering the presence of ʻōhiʻa, overall tree density at Hakalau was much higher in reforestation stands, which may make them less resilient to defoliation and other stress factors.

Defoliation reduces tree growth (Piper et al., 2015; Rozendaal & Kobe, 2014; Stein & Scowcroft, 1984), and further reductions in growth (linear or curvilinear) and survival (exponential) occur with multiple episodes of defoliation (Foster, 2017). Koa that produced little or no foliage after 24–25 weeks had been heavily defoliated (≥80%), included all size classes, and occurred in both habitats. Koa mortality was apparently low on Maui during 2003 and 2004 (Haines et al., 2009), but Stein and Scowcroft (1984) reported 35% mortality of trees 20 months after the 1977 Maui outbreak. Experimentally induced, repeated defoliation can reduce growth, increase the rate of top dieback, and impact tree physiology in various ways (Kosola et al., 2001), and we observed many dead trees after the third round of defoliation at the Laupāhoehoe study area. Although single or multiple defoliations occurring in rapid succession can affect tree

survival and growth in the short term, little is known about the longer-term consequences for outbreak survivors, some of which may experience defoliation at periodic or irregular intervals over their lifetime.

Nutrient cycling and alien grass

The koa moth outbreak was expected to release nutrients into the soil and potentially become absorbed by woody understory plants if not taken up primarily by alien grasses. Pulses of litterfall and frass during the outbreak increased soil N and P at some sites, with subsequent uptake of foliar N in alien grasses. The litterfall rates measured at the start of our study were higher than baseline rates, likely due to damaged phyllodes falling into litter traps. Indeed, koa foliage biomass in the canopy was declining due to the increases in caterpillar biomass and herbivory. Other work shows that daily koa litterfall can range from 0.08 to 2.25 g/m (Baker et al., 2009), which generally falls below the rates in our sites at the start of the study.

Frass deposition during defoliation quickly redistributed large quantities of N to the forest floor, similar to studies from other ecosystems (Grüning et al., 2017; Hollinger, 1986; Lovett et al., 2002). Between 1500 and 5500 kg/ha of frass, equating to between 48 and 184 kg/ha of N, were deposited over only 3 months, an amount similar to annual litterfall N in typical years (Baker et al., 2009). The resulting N pulse in soils under koa at two of three sites appeared ~43 days after peak caterpillar biomass and consisted of two peaks that were loosely correlated with elevated rainfall (Banko et al. 2014), indicating that rain washed frass from foliage or enhanced N movement to resins, or both (Hart & Firestone, 1989; Lajtha, 1988). Additionally, initial frass deposition may have increased decomposition rates of existing koa litter layers. Koa litter, despite having a low C:N ratio compared to ʻōhiʻa and other native trees, decomposes slowly (Scowcroft, 1997), resulting in thick litter layers in the forest understory. Therefore, labile C and nutrients in frass may have "primed" the koa litter layer to stimulate decomposition, leading to a delayed peak in N mineralization and release (Hobbie, 2000).

Although N pulses were detected at the Koa2 restoration site and the Mix1 natural forest site, no pulse was observed at the Mix2 natural forest site, despite it receiving four times the amount of frass as recorded at Mix1. Soil properties at the Mix2 site may have affected the N pulse. Whereas both Pedro sites are on Puu Oo highly organic hydrous silty clay loam, Mix2 is on Keamoku extremely cobbly medial loam (Soil Survey Staff, 2014). Frass N inputs to the coarse-textured Mix2 soils are likely to result in rapid N leaching loss, as has been shown with rapid N pulses and subsequent leaching in other Hawaiian forest sites with coarse-textured soils (Lohse & Matson, 2005), as well as in widespread observations of elevated N leaching following defoliation in other systems (Grüning et al., 2017; Lovett et al., 2002; Webb et al., 1995). However, soil texture alone does not always determine how well resins capture available N in soil (Hook & Burke, 2000), raising the possibility that frass inputs at Mix2 did not increase available N to the degree observed at Mix1 and Koa2.

Understory species responded variably to frass deposition. Alien grasses under koa responded most dramatically, with foliar N increasing by 15% whereas foliar N in grasses in open plots decreased by 21%. In contrast, native woody species did not respond during our short sampling period. Grasses tend to have higher growth rates than woody species, as well as dense fibrous root systems in the upper soil layers (Scholes & Archer, 1997). In contrast, woody plants adapted to low N conditions may exhibit low flexibility in N uptake following nutrient additions (Chapin et al., 1986). Consequently, alien grasses may have been better able than native woody species to exploit the N pulse after the outbreak. Similar results were found in a northern California grassland, where an insect outbreak led to widespread mortality of native bush lupines (*Lupinus arboreus*), followed by an N pulse and subsequent exotic annual grass invasion (Maron & Connors, 1996; Maron & Jefferies, 1999).

Potentially, woody species did increase N uptake during the nutrient pulse, but foliar N concentrations may not have increased due to the allocation of the extra N to higher biomass production or fruit set rather than to leaves (Yang, 2004). Also, high N uptake may not be evident for over 1 year in long-lived, woody species (Lovett et al., 2002), which would require additional sampling to detect a response to the N pulse. If high soil N levels increase alien grass growth, the reestablishment of native woody species may be hindered where koa has been planted to restore Hawaiian montane forests (Funk & McDaniel, 2010; McDaniel & Ostertag, 2010). Thus, our results indicate that alien grasses benefited quickly from the deposition of frass, whereas the long-term consequences of the N pulse for understory vegetation dynamics are unclear. It is also possible that frass deposition increased foliar P more than N, as commonly occurs following nutrient fertilization (Ostertag, 2010), but our lack of foliar P data and the relatively small changes observed in soil resin P at most sites make this difficult to evaluate.

The dense grass cover at Hakalau may also have reduced the amount of frass-derived nutrients available to koa recovering from defoliation, resulting in the slow regrowth of crowns compared to our anecdotal observations at the Laupāhoehoe and Kīpuka sites, where grass cover was relatively sparse. Repeatedly defoliated trees at

these warmer, wetter, lower-elevation sites renewed their crowns in only 18 weeks, whereas trees at Hakalau regrew only about half their crowns after 34 weeks. In a mesocosm study, Frost and Hunter (2007) found that after experimental herbivory or mechanical removal of 21%–24% of the total leaf area of potted red oak (*Quercus rubra*) saplings, a portion of ^{15}N-enriched caterpillar frass added to the pots was quickly recovered in the foliage and subsequently assimilated by late-season caterpillars. This indicates an interaction between grass cover and climate whereby frass interception by dense grass at Hakalau slowed refoliation and reduced koa foliar N, both of which might have suppressed another outbreak. Experimental studies might resolve how grass cover interacts with allocations of N to koa foliage and woody tissue and subsequently to rates of herbivory.

Response of consumers to the resource pulse

Resource pulses can affect consumers and communities directly and indirectly at various levels, including changes in the behavior, distribution, physical condition, fecundity, and survival of individuals; population dynamics and epidemiology; food web and trophic interactions; and community structure and dynamics (Ostfeld & Keesing, 2000; Yang et al., 2008, 2010). Nevertheless, the short-term unpredictability of the spread of the koa moth outbreak and the large area over which it occurred precluded us from investigating landscape-level responses and interactions of consumers. The scope of our study was, therefore, limited to relatively local observations of short-term changes in the feeding behavior, diet, and mass of birds; the feeding behavior of bats; and the population dynamics of parasitoid wasps and changes in their caterpillar attack rates.

Response of birds to outbreak

Perkins (1903) noted that large numbers of birds were attracted to koa moth outbreaks, but we did not observe unusually high bird activity perhaps because caterpillars were distributed widely across the landscape. Bird activity was affected primarily by the abundance of ʻōhiʻa flowers, severity of koa defoliation, and habitat type. Time spent in ʻōhiʻa or koa changed in response to caterpillar abundance, but the direction of change differed according to habitat type. Additionally, birds increased their consumption of koa moth caterpillars as they became more abundant, and most species gained weight.

Birds occupied ʻōhiʻa, which hosts many arthropods (Gruner, 2004) and is a major source of nectar (Banko & Banko, 2009), equally or more frequently than koa in both habitats, but the proportional use of tree species changed after defoliation, when both caterpillars and flowers became scarce. Relative to koa, bird activity increased in ʻōhiʻa in natural forest habitat but declined in reforestation habitat after defoliation. As we expected, therefore, birds in natural forest habitat were attracted to koa when caterpillars were abundant, despite the relatively low density of koa. Contrary to our expectations, birds in reforestation habitat were more active in ʻōhiʻa during the outbreak, despite the low density of ʻōhiʻa. Although we have no supporting data, this suggests that birds might have readily obtain caterpillars in the high-density koa stands, allowing them more time to forage in ʻōhiʻa for nectar and perhaps arthropods less available in koa.

Although caterpillars are the most frequent arthropod prey of birds generally at Hakalau (Banko et al., 2015), the availability of ʻōhiʻa nectar strongly influences the foraging behavior and movements of nectarivorous species (Baldwin, 1953; Carothers, 1986; Carpenter & MacMillen, 1976; Pimm & Pimm, 1982), some of which likely dispersed as flowers became increasingly scarce during the outbreak. Many ʻiʻiwi disperse from Hakalau from May through August, when ʻōhiʻa flowering typically decreases (Guillaumet et al., 2017; Kuntz, 2008), and in later months some ʻiʻiwi and ʻapapane, the most abundant species in natural forest habitat, move to subalpine habitat during the flowering peak of māmane (*Sophora chrysophylla*; Fabaceae; Hess et al., 2001). Hawaiʻi ʻamakihi and warbling white-eye, the most abundant species in reforestation habitat, may have responded to changes in flower abundance with relatively localized movements. Birds spent less time in heavily defoliated trees compared to lightly defoliated trees, indicating that they were responding to reduced caterpillar availability. Birds also may have avoided defoliated trees to reduce their exposure to raptors, such as ʻio (*Buteo solitarius*). Although birds were affected by defoliation for a relatively short time at Hakalau, koa stands in the lower koa belt (e.g., Laupāhoehoe and Kīpuka) were defoliated repeatedly, with potentially greater impacts on regional bird populations. Whisson et al. (2018) found that Australian bird species richness was reduced and that birds used fewer microhabitats in defoliated trees, indicating that reduced resource availability can affect community structure, at least temporarily. Although we did not observe changes to the Hakalau bird community, native *Plagithmysus* (Cerambycidae) beetles may increasingly infest the many koa branches killed during defoliation (Goldsmith et al., 2007), and this could increase foraging opportunities for the endangered ʻakiapōlāʻau

(*Hemignathus wilsoni*; Ralph & Fancy, 1996) and other insectivores.

The response of bird populations to insect outbreaks depends largely on the palatability of the irruptive insect (Paxton et al., 2011), and birds readily exploit some outbreaking insects (McMartin et al., 2002) or not (Hogstad, 2005). We expected birds to feed heavily on *S. paludicola* during the outbreak because *Scotorythra* spp. are important in the diets of Hawaiian birds generally (Banko & Banko, 2009; Perkins, 1903, 1913). Opportunistic species are expected to be especially prone to switching to a superabundance of palatable prey (Yang et al., 2008), and we found that two insectivorous/nectarivorous generalists, the Hawai'i 'amakihi and warbling white-eye, responded dramatically to the abundance of caterpillars during the outbreak. Both species shifted from a diet dominated by an invasive, irrupting psyllid before the koa moth outbreak to one dominated by koa moth caterpillars during the outbreak. Although the change may have been due to a seasonal decrease in psyllid abundance coinciding with the outbreak, the shift from other caterpillar taxa to *S. paludicola*, particularly by the Hawai'i 'amakihi, indicates opportunistic utilization of this temporarily abundant and valuable prey species.

In parallel with these dietary shifts, omnivorous and insectivorous bird species gained mass during the outbreak. Changes in mass were significantly positive for at least two (Hawai'i 'elepaio, endangered Hawai'i creeper) of the four smallest and most insectivorous species (also including warbling white-eye, Hawai'i 'amakihi). Mass was unchanged for the frugivorous red-billed leiothrix and nectarivorous 'i'iwi, and mass apparently declined for the nectarivorous 'apapane. Because sample sizes were small for 'apapane, Hawai'i 'elepaio, Hawai'i creeper, and 'i'iwi during the post-outbreak period, the influence of foraging guild or other factors potentially accounting for patterns of mass change is not clear.

Apart from increased mass, we were unable to evaluate other measures of fitness associated with the outbreak at Hakalau. The outbreak occurred during the later stages of the nesting season for most species (Ralph & Fancy, 1994; Woodworth & Pratt, 2009), when the abundance of highly nutritious food may have increased fledgling survival or possibly enabled additional nesting attempts. Nevertheless, following defoliation and the crash of caterpillars on koa, parent birds and fledglings would have had to rely more heavily on 'ōhi'a resources, especially in reforestation stands.

Predation by birds may reduce populations of foliar-feeding caterpillars under non-outbreak conditions (Barbaro & Battisti, 2011; Glen, 2004; Holmes, 1990), but it is ineffectual at preventing high densities (millions/ha) of caterpillars (Crawford & Jennings, 1989), levels that we observed during the peak of the outbreak. We identified caterpillars of *Scotorythra* spp. in fecal samples collected from 1994 to 1997 from Hakalau bird species (Banko et al., 2015), but if birds have a role in suppressing *Scotorythra* populations, it is likely restricted to the upper koa belt, where bird diversity and abundance, especially of insectivores, are much higher than at lower elevation (Camp et al., 2010; Scott et al., 1986). The single defoliation event at Hakalau raises the question of whether bird predation may have helped suppress subsequent irruptions, even if it failed to suppress the first. Caterpillars are more likely to be vulnerable to attack by predators, parasites, and pathogens at higher elevations, where larval development is slower, but slower larval development itself may have contributed to there being only one defoliation event.

Response of bats to outbreak

Where bats are diverse and abundant, they have been shown experimentally to limit arthropod populations and herbivory in natural and agroforestry habitats (Kalka et al., 2008; Kalka & Kalko, 2006; Williams-Guillén et al., 2008). Given the relatively low abundance of the Hawaiian hoary bat, it seems doubtful that they suppress insect populations in native forests or play an important role in the dynamics of insect outbreaks. Although Hawaiian hoary bat detectability at both Hakalau and Laupāhoehoe was notably lower during the outbreak year than in any year of the 5-year study conducted by Gorresen et al. (2013), this was likely due to the relatively short amount of foraging time required to reach a digestive bottleneck each night. Echolocation calls associated with searching and attacking insect prey peaked abnormally early in the night during the outbreak at Laupāhoehoe (no comparison of this type from Hakalau data is made because of insufficient bat calling activity). Bats actively foraged over longer portions of the night and presumably at lower success rates during non-outbreak times when moth densities were orders of magnitude lower. The timing of feeding among bat species varies relative to the activity and abundance of preferred prey species (Rydell et al., 1996). Furthermore, moth activity is strongly affected by temperature and wind with fewer moths collected in light traps on cold and windy nights (Jonason et al., 2014; Yela & Holyoak, 1997). We expect that koa moths were active well after sunset, based on personal observations and communications from others of moth activity at house lights many hours after sunset and "blizzards of moths crossing Saddle Road" (W.P. Haines, public communication in Stewart, 2013). With lower feeding

efficiency, bats also are expected to have to call more (more call events and sound pulses) over longer portions of the night, which we observed during the non-outbreak years. Although the activity and frequency of feeding buzzes of some continental bat species increased when local densities of a pest moth were experimentally enhanced with synthetic sex pheromone lures, their behavior was not observed during a large-scale outbreak (Charbonnier et al., 2014).

During the 2013–2014 outbreak, Hawaiian hoary bats remained uncommon at Hakalau relative to their presence at Laupāhoehoe, as was observed by Gorresen et al. (2013) from 2007 to 2011. This is evidenced by the relative number of call events, echolocation pulses, and the detectability indices from the two locations. Thus, even during a period when koa moths were superabundant at Hakalau (see video link within https://doi.org/10.5066/P9HE9WKK), we did not detect an increase in bat foraging activity. Because koa moths were abundant and widespread during the 2013–2014 outbreak, there would have been little adaptive benefit to bats moving into Hakalau from surrounding areas. Some bat species track and exploit the local availability of prey within regional landscapes (McCracken et al., 2012), but aggregating behavior is more likely to occur in open habitats rather than in closed forest (Müller et al., 2012).

Response of parasitic wasps to outbreak

Hymenopteran parasitoids can drive moth population cycles in temperate, continental regions (Klemola et al., 2010; Turchin et al., 2003), but their role in tropical and insular environments is unclear. Koa moth outbreaks may at one time have occurred more frequently in the Hawaiian Islands (Haines et al., 2009; Perkins, 1913), but interactions between Hawaiian moths and their native predators and parasitoids are complicated, if not disrupted, by a diverse, abundant, and widespread invasive parasitoid community (Henneman & Memmott, 2001; Oboyski et al., 2004; Peck et al., 2008). Nevertheless, we expected to see increased numbers and attack rates of some members of this novel parasitoid community in response to the koa moth outbreak.

Consistent with previous reports (Davis, 1954; Haines et al., 2009; Zimmerman, 1958), *H. exiguae*, a long-established adventive parasitoid, was most frequently reared from koa moth caterpillars, and *Meteorus laphygmae*, introduced in 1942 to control sugarcane pests, also was reared. Both have broad host ranges and are widespread on Hawai‘i Island (Funasaki et al., 1988; Peck et al., 2008). Although malaise trap data indicate that both species tracked caterpillar abundance during the outbreak, the rate of parasitism (3.2%) was not proportional to caterpillar abundance. The rate was also less than that found during the late stage of the 2003–2004 Maui koa moth outbreak (20% [12 of 60], Haines et al., 2009), for caterpillars generally in Kaua‘i forests (20% [12 of 60], Henneman & Memmott, 2001), and for endemic *Cydia* spp. (Tortricidae) in subalpine woodland on Mauna Kea (39.5%; Oboyski et al., 2004). Our finding that 15% of pupae and pre-pupae at Laupāhoehoe were parasitized indicates that overall parasitism at Hakalau may be greater than the rate we observed only in caterpillars.

We did not assess mortality rates of koa moth eggs due to parasitism, predation, or pathogens, but predators can destroy many eggs of some outbreaking species (Castagneyrol et al., 2014). Host associations of egg parasitoids are poorly known in Hawai‘i, but the endemic *Trichogramma semifumatum* (Hymenoptera: Trichogrammatidae) has been reported to attack *Scotorythra* spp. eggs (Swezey, 1929). Other species of *Trichogramma* are often released as biocontrol agents of agricultural pests and can be a significant cause of Lepidoptera egg mortality (Smith, 1996). We could not attribute caterpillar mortality in the field or laboratory to pathogens, but entomopathogenic fungi or other factors may have gone undetected during the egg stage. Unidentified diseases were suspected of killing many caterpillars being reared in the laboratory during the 2003–2004 koa moth outbreak on Maui (Haines et al., 2009), and microorganisms may affect insect outbreak dynamics in a variety of complex ways and in concert with other factors (Cardoza et al., 2012; Elderd et al., 2013; Ewald, 1987; Páez et al., 2017; Royama et al., 2017).

It is unclear what level of parasitism might be necessary to suppress a koa moth outbreak, but non-native parasitoids did little to dampen the 2013–2014 irruption. Moreover, we found no evidence of parasitism by endemic species of *Enicospilus* (Ichneumonidae), despite earlier reports of *Enicospilus* attacking *Scotorythra* spp. (Swezey, 1929). Neither was *Enicospilus* reared from *S. paludicola* during the 2003–2004 outbreak on Maui, likely because *Enicospilus* attacks later instars than do *H. exiguae* and *M. laphygmae* (Haines et al., 2009). In an experimental study of the temperate, continental autumnal moth (*Epirrita autumnata*; Geometridae), a caterpillar parasitism rate of 88% was associated with a rapid decline in numbers to below initial outbreak levels (Klemola et al., 2010). Top-down factors may be important in limiting the frequency and scope of outbreaks (Dwyer et al., 2004; Letourneau, 2012; Ostfeld & Keesing, 2000; Symondson et al., 2002) even if they are not critical in stopping them, but quantifying the effects of native and non-native enemies on koa moth dynamics is challenging due to the unpredictable timing of

outbreaks. Even in the intensively studied spruce budworm (*Choristoneura fumiferana*) outbreak system, Royama et al. (2017) were unable to identify a dominant effect of a single agent of mortality among the number they investigated.

Outbreak dimensions and dynamics

Across Hawai'i Island, >280 km^2 of forest was defoliated at least once (Haines et al., 2013), affecting about 36% of the island's koa-associated forest (789 km^2 total; Baker et al., 2009). The outbreak was the largest ever recorded (by a factor of 18), the first reported on windward Hawai'i Island since 1901 (Henshaw, 1902), and the first anywhere on the island since 1953 (Davis, 1954; Haines et al., 2009).

Frequent, large, or prolonged defoliator outbreaks are not expected where seasonality is low, tree diversity is high, and leaves are heavily defended against herbivory, such as in some continental tropical forests (Dyer et al., 2012). Sporadic irruptions of the koa moth provide valuable, if rare, opportunities to investigate outbreak dynamics and consequences in tropical forests with low seasonality and low tree diversity. The 2013–2014 koa moth outbreak was massive and long-lasting, but other large, extended outbreaks have occurred on Maui and Hawai'i Islands in the past (Haines et al., 2009; Perkins, 1896; Swezey, 1931). Our results confirm that these large irruptions can result in enormous pulses of prey for vertebrate and invertebrate consumers, abrupt and severe defoliation of large tracts of forest, and sudden infusions of nutrients into the soil that far exceed background levels of resource variability and community function. The ecological factors that trigger and terminate koa moth irruptions are not understood, although our results can help to develop a framework for understanding the roles of environmental variability, herbivore–host plant interactions, predator–prey dynamics, and disease–host relationships (and see Barton & Haines, 2013; Haines et al., 2009, 2013).

The outbreak arrived at the Hakalau site 6 months after being initially detected in the lower koa belt. Caterpillar numbers increased over 8 or 9 weeks at Hakalau before koa trees were defoliated, indicating that cooler temperatures in the upper koa belt slowed caterpillar development. Our experimental results support this idea because caterpillars reared at lower temperature consumed less foliage (indicated by lower frass production), indicating slower growth. Other factors, such as foliage type (true leaf or phyllode) and age of phyllode, may also have affected caterpillar survival and developmental rates (Barton & Haines, 2013).

The 2013–2014 Hawai'i Island outbreak was notable also because some tracts of koa were repeatedly defoliated in rapid succession. We observed complete defoliation of the same koa stands on three occasions at the Laupāhoehoe study site and twice at the Kīpuka site in 2013. Koa was reportedly also defoliated on three occasions in the Kaiwiki area over 12 km northwest of Hilo (J. Pang-Ching, University of Hawai'i at Hilo, oral communication, 2014). Other multiple defoliations in the same location have occurred within a single year (Henshaw, 1902), during consecutive years (Perkins, 1903) and separated by 4 years (Evenhuis, 2007; Haines et al., 2009; Swezey, 1926). Although forest stands can be defoliated repeatedly over short multi-year intervals by the koa moth and in some other outbreak systems, multiple within-year defoliations, as we and Henshaw (1902) observed, are unusual. We propose that multiple factors affected the frequency of defoliation within the koa stands we observed.

Repeated defoliation may be partly due to relatively slow rates of egg and larval development, which may allow defoliated stands to refoliate before being revisited by waves of koa moths dispersing from other defoliated areas. Additionally, reduced seasonality in Hawai'i (Giambelluca & Schroeder, 1998) enables koa to regrow foliage year-round, providing fresh resources for repeated rounds of mass herbivory. The broad gradient of elevation over which the outbreak occurred may also have contributed to the temporal patchiness of the defoliation through local variability in rainfall and temperature (Giambelluca et al., 2013). At a finer scale, young phyllodes are highly palatable to *S. paludicola* caterpillars (Barton & Haines, 2013) and their abundance in the forest canopy could be an important trigger for repeated outbreaks. Although induced chemical changes following defoliation may reduce growth and fecundity in the following generation of herbivores, increased N content (derived from frass) in the new foliage may counteract any putative defensive compounds (Nykänen & Koricheva, 2004), potentially allowing new, vigorous cohorts of koa moths to repeatedly defoliate stands. Interception of N by the dense alien grass cover at Hakalau may have reduced the quality of new foliage, reducing herbivory and the potential for subsequent defoliation.

Although koa moths irrupted in various locations on Hawai'i Island over many months, we observed a relatively high degree of temporal synchronicity across large areas of forest. At Laupāhoehoe, defoliation was essentially simultaneous across 2 km and a 250-m gradient of elevation during each of the three outbreaks. At Hakalau, we collected caterpillars representing two to four instars in our branch samples during the peak of caterpillar abundance, but the cohorts of fourth- and fifth-instar larvae were overwhelmingly abundant, resulting in widespread, rapid defoliation and a cohort of moths that could then disperse more or less together to oviposit in

new, unaffected or recovered areas, thus reinforcing synchronicity at local to regional scales. At a local scale, caterpillar biomass and abundance peaked around 20 June at the three northernmost sites, which were clustered within 2 km of one another and across an elevation gradient of 200 m. A week later and 4 km to the south, caterpillars peaked at Mix2, indicating relatively close temporal synchronization over an approximately regional spatial scale. We assume that synchronization between the four Hakalau study sites was partly a result of the enormous numbers of moths dispersing from the larger, earlier outbreak in the lower koa belt below Hakalau. Nevertheless, as for most insect outbreaks (Bjørnstad et al., 2008; Kessler et al., 2012), we could not identify the biotic and environmental factors that triggered the initial outbreak and promoted regional synchronization. The role of synchronicity in ending the outbreak due to large, if temporary, declines in koa foliage across large areas also remains uncertain, but trees with any remaining foliage near our study areas were scattered and unlikely to support even a local outbreak.

Consequences of koa moth outbreaks for koa and forest dynamics

Insect outbreaks may have profound ecological consequences when they affect dominant species or occur in low-diversity ecosystems (Carson & Root, 2000; McBrien et al., 1983), such as those typical of the Hawaiian Islands and other remote islands (MacArthur & Wilson, 1967; Price, 2004). Theory suggests that high diversity ecosystems are more resilient to disturbance (i.e., they return more quickly to equilibrium) than are low-diversity systems (Hooper et al., 2005; Peterson et al., 1998; Tilman & Downing, 1994). Although determining how diversity affects food webs depends upon the structure and connectivity of different linkages within the ecosystem (Proulx et al., 2005), experimental evidence indicates that reduced diversity can decrease and destabilize interaction webs and ecosystem processes (Rzanny & Voigt, 2012). Furthermore, biodiversity effects on food web resilience are likely mediated through complex pathways, which may be obscured by variable life-history traits of species and indirect interactions both within and between trophic levels (Downing & Leibold, 2010). Although we did not investigate impacts of the outbreak to the Hakalau forest food web specifically, our study examined outbreak dynamics and species interactions at three trophic levels (koa host trees, koa moth herbivores, and predators and parasitoids of herbivores). Despite the massive short-term increase in herbivory and large pulse of nutrients and high-value prey, there was no indication that food web structure and function would be affected in the long term.

By 2018, 4 years after the outbreak, evidence of widespread koa defoliation had become difficult to detect, although seedpod production remained extremely low even into 2020 (S. Kendall, U.S. Fish and Wildlife Service, written communication, 10 February 2020). A lack of long-lasting impacts would point to the likely coevolution between the outbreak herbivore and its host plant species (Yang, 2012). Furthermore, specific resource pulses seldom, if ever, result in permanent transitions of communities to alternative stable states (Yang et al., 2010). The extensive defoliation of koa indicates low resistance to koa moth herbivory, but trees at Hakalau regenerated their crowns within about 1 year, indicating a relatively high degree of resilience. The repeated recovery of many tree crowns in lowland areas after serial defoliation (e.g., Laupāhoehoe and Kīpuka) also indicates relatively high resiliency of koa to outbreaks, despite apparently greater mortality and crown dieback. Outbreak dynamics may be sustainable between koa and koa moths partly because outbreaks are infrequent at local scales. Nevertheless, seven outbreaks occurred across portions of windward East Maui from 1894 to 2003, with some degree of spatial overlap (Haines et al., 2009). Consequently, individual trees and patches of forest likely experienced repeated defoliation during their lifetimes. Additionally, small outbreaks could easily be overlooked, suggesting that outbreak frequency may be underestimated, at least at the stand level.

Koa may also tolerate defoliator outbreaks because of their capacity for relatively fast growth and flexible phenology. Koa grows rapidly, particularly during the first decade (Pearson & Vitousek, 2001). Moreover, despite the occurrence of a general seasonal pattern, new leaves or phyllodes can be produced throughout the year, as observed when light levels are experimentally altered (Baker et al., 2009). Above 1650-m elevation, we observed that koa produced new phyllodes in any month but usually more prolifically during winter and spring (Lamoureux et al., 1981). In contrast, defoliation of other native tree species by native or non-native caterpillars has rarely been reported and has not been observed over large areas. Koa also recovers or regenerates quickly from wind damage and fire (Baker et al., 2009; Herbert et al., 1999). Generally, koa responds to herbivory and other physical damage in ways that support the hypothesis that resistance and resilience are inversely related (Herbert et al., 1999). Furthermore, the different responses of koa to herbivory and defoliation in reforestation (high-density) and natural forest (low-density) stands indicates an influence of nutrient limitation, although we did not assess site differences in the

nutritional value of foliage and our baseline estimates of nutrient stores were made after rather than before high levels of frass deposition. The lower biomass of caterpillars per unit of foliage and the lower intensity of defoliation in reforestation stands may indicate lower nutritional value of the foliage, and the slower regrowth of foliage soon after defoliation and greater mortality of trees in reforestation stands may indicate nutrient limitation in the soil. It also was found for ʻōhiʻa, for example, that resistance to hurricane damage decreased and resilience increased as the supply rate of a limiting resource (P) increased (Herbert et al., 1999).

In some continental forests, periodic outbreaks of defoliators can influence stand structure through tree mortality and gap initiation (Filion et al., 2006). Even in koa-dominated stands, however, the increase in light penetrating to the forest floor following defoliation may be only a temporary benefit to gap-adapted or weedy species. The amount of light intercepted even by intact koa crowns is relatively low due to the vertical orientation typical of the phyllodes (Baker et al., 2009), and, as we found, crown mortality is low and crown regeneration is relatively rapid, especially where grass cover is sparse. Our observations support the idea that koa forests are resilient to perturbations of many kinds (Baker et al., 2009), but at Hakalau the pulse of N resulting from caterpillar frass deposition was readily taken up by the dense cover of alien grasses. Nevertheless, even in tropical forests where grasses do not dominate the forest floor, nutrient pulses (e.g., following hurricanes) are short-lived (Ostertag et al., 2003). Longer-term studies would be needed, however, to fully understand whether nutrient pulses lead to increased biomass of exotic grasses, or what effect this may have on subsequent forest dynamics. Thick alien grass layers lead to an almost complete lack of understory regeneration in koa restoration stands, even in the absence of nutrient pulses (Yelenik, 2017); thus, an increase in grass biomass due to excess N may have no net negative effect on these somewhat degraded secondary forest systems.

Recent koa moth outbreaks on Maui (Haines et al., 2009) and the 2013–2014 outbreak on Hawaiʻi Island raise the question of whether conditions are changing in ways that favor more frequent outbreaks in the future. Although we do not understand the factors that promote koa moth outbreaks, our results indicate that they can alter forest communities and processes in the short term. More frequent large outbreaks could potentially have longer-lasting effects (Yang et al., 2010). Moreover, multiple outbreaks in rapid succession, as we observed in our low-elevation study sites, could have greater consequences for resources that are critically important to conservation managers. Economic interests could also be affected by large outbreaks, given the high commercial value of koa (Baker et al., 2009).

Managers confronted with the 2013–2014 outbreak had no better option than to observe how a massive irruption of native moths could potentially affect their efforts at forest restoration. Attempting to forestall or curtail the outbreak using pesticides, for example, could have had many unintended, harmful consequences for arthropod and vertebrate communities, food webs, and ecosystem processes. Because the causes of most insect outbreaks are not well known, useful management prescriptions for preventing koa moth outbreaks or stopping them once they are underway are unknown. Nevertheless, stocking koa at high densities to restore forest habitat on former pasturelands may increase the disruption to animal and plant communities when outbreaks result in the near total loss of forest canopy over large areas. Although koa is relatively fast-growing and is a valuable resource for many native species, increasing the diversity of canopy tree species in planted forest stands may help reduce the impacts of severe outbreaks in the future.

ACKNOWLEDGMENTS

Funding for this study was provided by the U.S. Geological Survey Environments Program. Robert Hauff of the Hawaiʻi Division of Forestry and Wildlife (DOFAW) and Karl Magnacca (Pacific Cooperative Studies Unit, University of Hawaiʻi at Mānoa, Oʻahu Army Natural Resources Program) assisted with aerial and ground surveys of the outbreak and extent of the defoliation. Cynthia King of the Natural Areas Reserve System (DOFAW) provided support for malaise traps and other logistical assistance. The authors thank Angela Beck, John Diener, Kelsie Ernsberger, Lizzy Goodrick, Jonathan Henn, Steve Kendall, Nolan Lancaster, Sonia Levitt, Danny McCamish, Stacia Near, Josh Pang-Ching, Laura Petteway, Corinna Pinzari, Linda Pratt, and Travis Soward for critical help in the field and laboratory. Will Haines generously shared his extensive knowledge and observations of koa moths during the outbreak. David Foote also provided entomological expertise and field assistance. J. B. Friday of the College of Tropical Agriculture and Human Resources, University of Hawaiʻi, and others provided helpful observations as the outbreak spread. Jim Jacobi provided forest-type GIS layers used in the preparation of Figure 2. The authors appreciate the encouragement and support of Jim Kraus, Manager, and Steve Kendall, Biologist, of Hakalau Forest National Wildlife Refuge. Permits for work at Laupāhoehoe were facilitated by Melissa Dean

and Tabetha Block (Hawai'i Experimental Tropical Forest, Institute of Pacific Islands Forestry) and Steve Bergfeld (DOFAW). The authors are grateful to Becky Ostertag (University of Hawai'i at Hilo) and two anonymous journal reviewers for their thoughtful comments and suggestions for improvement. Editing by Janet Carter improved the manuscript. Endangered and other bird species were captured and handled in accordance with all federal and state permitting requirements. All animal procedures were reviewed and approved by the University if Hawai'i Institutional Animal Care and Use Committee. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Banko et al., 2021; Banko & Peck, 2021; Montoya-Aiona et al., 2020; Peck & Banko, 2021 and Yelenik et al., 2021) used in the analyses are available from ScienceBase: http://www.sciencebase.gov/.

ORCID

Paul C. Banko https://orcid.org/0000-0002-6035-9803
Stephanie G. Yelenik https://orcid.org/0000-0002-9011-0769

REFERENCES

Aide, T.M. 1993. "Patterns of Leaf Development and Herbivory in a Tropical Understory Community." *Ecology* 74: 455–66.

Baker, P.J., P.G. Scowcroft, and J.J. Ewel. 2009. *Koa (Acacia koa) Ecology and Silviculture*. General Technical Report PSW-GTR-211. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Baldwin, P.H. 1953. "Annual Cycle, Environment and Evolution in the Hawaiian Honeycreepers (Aves: Drepaniidae)." *University of California Publications in Zoology* 52: 285–398.

Balzotti, C.S., and G.P. Asner. 2017. "Episodic Canopy Structural Transformations and Biological Invasion in a Hawaiian Forest." *Frontiers in Plant Science* 8: 1256.

Banko, P.C., and W.E. Banko. 2009. "Evolution and Ecology of Food Exploitation." In *Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna*, edited by T.K. Pratt, C. T. Atkinson, P.C. Banko, J.D. Jacobi, and B.L. Woodworth, 159–93. New Haven, CT: Yale University Press.

Banko, P.C., and R.W. Peck. 2021. "Hawaii Island Tree Response to Koa Moth Outbreak, 2013–2014." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9HU5SBC

Banko, P.C., R.W. Peck, K. Brinck, and D.L. Leonard. 2015. *Richness, Diversity, and Similarity of Arthropod Prey Consumed by a Community of Hawaiian Forest Birds*. Hawai'i Cooperative Studies Unit Technical Report HCSU-066. Hilo, HI: University of Hawai'i at Hilo.

Banko, P.C., R.W. Peck, and E.H. Paxton. 2021. "Hawaii Island Bird Response to Koa Moth Outbreak, 2013–2014." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9CKV8QM

Banko, P.C., R.W. Peck, S.G. Yelenik, E.H. Paxton, F.J. Bonaccorso, K. Montya-Aiona, and D. Foote. 2014. *Dynamics and Ecological Consequences of the 2013–2014 Koa Moth Outbreak at Hakalau Forest National Wildlife Refuge*. Hawai'i Cooperative Studies Unit Technical Report HCSU-058. Hilo, HI: University of Hawai'i at Hilo, Hawai'i.

Barbaro, L., and A. Battisti. 2011. "Birds as Predators of the Pine Processionary Moth (Lepidoptera: Notodontidae)." *Biological Control* 56: 107–14.

Barton, K.E., and W.P. Haines. 2013. "Koa Looper Caterpillars (*Scotorythra paludicola*, Geometridae) Have Lower Fitness on Koa (*Acacia koa*, Fabaceae) True Leaves than on Phyllodes." *Proceedings of the Hawaiian Entomological Society* 45: 141–7.

Berryman, A.A. 1987. "The Theory and Classification of Outbreaks." In *Insect Outbreaks*, edited by P. Barbosa and J.C. Schultz, 269–86. New York: Academic Press.

Beardsley, J.W., and W.D. Perreira. 2000. "New Distribution Records of Non-endemic Hymenoptera (Insecta) in Hawaii. Records of the Hawaii Biological Survey for 1999." *Bishop Museum Occasional Papers* 63: 21–30.

Bess, H.A. 1974. "*Hedylepta blackburni* (Butler), a Perennial Pest of Coconut on Wind-swept Sites in Hawaii." *Proceedings of the Hawaiian Entomological Society* 21: 343–53.

Binkley, D., and P. Matson. 1983. "Ion Exchange Resin Bag Method for Assessing Forest Soil Nitrogen Availability." *Soil Science Society of America Journal* 47: 1050–2.

Bjørnstad, O.N., A.M. Liebhold, and D.M. Johnson. 2008. "Transient Synchronization Following Invasion: Revisiting Moran's Model and a Case Study." *Population Ecology* 50: 379–89.

Camp, R.J., T.K. Pratt, P.M. Gorresen, J.J. Jeffrey, and B.L. Woodworth. 2010. "Population Trends of Forest Birds at Hakalau Forest National Wildlife Refuge, Hawai'i." *The Condor* 112: 196–212.

Cardoza, Y.J., R.W. Hofstetter, and F.E. Vega. 2012. "Insect-associated Microorganisms and their Possible Role in Outbreaks." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D. K. Letourneau, and A.A. Agrawal, 155–74. Hoboken, NJ: Wiley-Blackwell.

Carothers, J.H. 1986. "Behavioral and Ecological Correlates of Interference Competition Among Some Hawaiian Drepanidinae." *The Auk* 103: 564–74.

Carpenter, F.L., and R.E. MacMillen. 1976. "Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper." *Science* 194: 639–42.

Carson, W.P., and R.B. Root. 2000. "Herbivory and Plant Species Coexistence: Community Regulation by an Outbreaking Phytophagous Insect." *Ecological Monographs* 70: 73–99.

Castagneyrol, B., H. Jactel, Y. Charbonnier, L. Barbaro, and A.-M. Dulaurent-Mercadal. 2014. "Egg Mortality in the Pine Processionary Moth: Habitat Diversity, Microclimate and Predation Effects." *Agricultural and Forest Entomology* 16: 284–92.

Chapin, F.S., III, P.M. Vitousek, and K. Van Cleve. 1986. "The Nature of Nutrient Limitation in Plant Communities." *The American Naturalist* 127: 48–58.

Charbonnier, Y., L. Barbaro, A. Theillout, and H. Jactel. 2014. "Numerical and Functional Responses of Forest Bats to a Major Insect Pest in Pine Plantations." *PLoS One* 9: e109488.

Christenson, L.M., G.M. Lovett, M.J. Mitchell, and P.M. Groffman. 2002. "The Fate of Nitrogen in Gypsy Moth Frass Deposited to an Oak Forest Floor." *Oecologia* 131: 444–52.

Coley, P.D. 1983. "Herbivory and Defensive Characteristics of Tree Species in a Lowland Tropical Forest." *Ecological Monographs* 53: 209–34.

Coley, P.D., and J.A. Barone. 1996. "Herbivory and Plant Defenses in Tropical Forests." *Annual Review of Ecology and Systematics* 27: 305–35.

Cooray, R.G., and D. Mueller-Dombois. 1981. "Structural Variation of Organism Groups Studied in the Kīlauea Forest: Population Structure of Woody Species." In *Island Ecosystems: Biological Organization in Selected Hawaiian Communities. U.S. International Biological Program Synthesis Series 15.*, edited by D. Mueller-Dombois, K.W. Bridges, and H.L. Carson, 259–68. Stroudsburg, PA, and Woods Hole, MA: Hutchinson and Ross.

Coupe, M.D., and J.F. Cahill. 2003. "Effects of Insects on Primary Production in Temperate Herbaceous Communities: A Meta-analysis." *Ecological Entomology* 28: 511–21.

Crawford, H.S., and D.T. Jennings. 1989. "Predation by Birds on Spruce Budworm *Choristoneura fumiferana*: Functional, Numerical, and Total Response." *Ecology* 70: 152–63.

Davidson, C.B., K.W. Gottschalk, and J.E. Johnson. 1999. "Tree Mortality Following Defoliation by the European Gypsy Moth (*Lymantria dispar* L.) in the United States: A Review." *Forest Science* 45: 74–84.

Davis, C.J. 1954. "Some Recent Lepidopterous Outbreaks on the Island of Hawaii." *Proceedings of the Hawaiian Entomological Society* 15: 401–3.

Downing, A.L., and M.A. Leibold. 2010. "Species Richness Facilitates Ecosystem Resilience in Aquatic Food Webs." *Freshwater Biology* 55: 2123–37.

Dwyer, G., J. Dushoff, and S.H. Yee. 2004. "The Combined Effects of Pathogens and Predators on Insect Outbreaks." *Nature* 430: 341–5.

Dyer, L.A., W.P. Carson, and E.G. Leigh, Jr. 2012. "Insect Outbreaks in Tropical Forests: Patterns, Mechanisms, and Consequences." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D.K. Letourneau, and A.A. Agrawal, 219–45. Hoboken, NJ: Wiley-Blackwell.

Elderd, B.D., B.J. Rehill, K.J. Haynes, and G. Dwyer. 2013. "Induced Plant Defenses, Host–pathogen Interactions, and Forest Insect Outbreaks." *Proceedings of the National Academy of Sciences of the United States of America* 110: 14978–83.

Ellison, A.M., M.S. Bank, C.D. Barton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, et al. 2005. "Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems." *Frontiers in Ecology and the Environment* 3: 479–86.

Esper, J., U. Büntgen, D.C. Frank, D. Nievergelt, and A. Liebhold. 2007. "1200 Years of Regular Outbreaks in Alpine Insects." *Proceedings of the Royal Society of London. Series B, Biological Sciences* 274: 671–9.

Evenhuis, N.L. 2007. *Barefoot on Lava: The Journals and Correspondence of Naturalist R. C. L. Perkins in Hawai'i, 1892–1901*. Honolulu, HI: Bishop Museum Press.

Eveleigh, E.S., K.S. McCann, P.C. McCarthy, S.J. Pollock, C.L. Lucarotti, B. Morin, D.B. Strongman, J.T. Huber, J. Umbanhowar, and L.D.B. Faria. 2007. "Fluctuations in Density of an Outbreak Species Drive Diversity Cascades in Food Webs." *Proceedings of the National Academy of Sciences of the United States of America* 104: 16976–81.

Ewald, P.W. 1987. "Pathogen-induced Cycling of Outbreak Insect Populations." In *Insect Outbreaks*, edited by P. Barbosa and J. C. Schultz, 269–86. New York: Academic Press.

Feeny, P. 1970. "Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars." *Ecology* 51: 565–81.

Filion, L., S. Payette, E.C. Robert, L. Delwaide, and C. Lemieux. 2006. "Insect-induced Tree Dieback and Mortality Gaps in High-Altitude Balsam Fir Forests of Northern New England and Adjacent Areas." *Ecoscience* 13: 275–87.

Forkner, R.E., R.J. Marquis, J.T. Lill, and J. Le Corff. 2008. "Timing is Everything? Phenological Synchrony and Population Variability in Leaf-Chewing Herbivores of *Quercus*." *Ecological Entomology* 33: 276–85.

Foster, J.R. 2017. "Xylem Traits, Leaf Longevity and Growth Phenology Predict Growth and Mortality Response to Defoliation in Northern Temperate Forests." *Tree Physiology* 37: 1151–65.

Frost, C.J., and M.D. Hunter. 2007. "Recycling of Nitrogen in Herbivore Feces: Plant Recovery, Herbivore Assimilation, Soil Retention, and Leaching Losses." *Oecologia* 151: 42–53.

Funasaki, G.Y., P.-Y. Lai, L.M. Nakahara, J.W. Beardsley, and A.K. Ota. 1988. "A Review of Biological Control Introductions in Hawaii: 1890–1985." *Proceedings of the Hawaiian Entomological Society* 28: 105–60.

Funk, J.L., and S. McDaniel. 2010. "Altering Light Availability to Restore Invaded Forest: The Predictive Role of Plant Traits." *Restoration Ecology* 18: 865–72.

Gagné, W.C., and L.W. Cuddihy. 1999. "Vegetation." In *Manual of Flowering Plants of Hawai'i*. Revised edition. Bishop Museum Special Publication 97, edited by W.L. Wagner, D.R. Herbst, and S.H. Sohmer, 45–114. Honolulu, HI: University of Hawai'i Press and Bishop Museum Press.

Gagné, W.C., and F.G. Howarth. 1981. "Arthropods Associated with Foliar Crowns of Structural Dominants." In *Island Ecosystems: Biological Organization in Selected Hawaiian Communities*. U.S. International Biological Program Synthesis Series 15, edited by D. Mueller-Dombois, K.W. Bridges, and H.L. Carson, 275–88. Stroudsburg, PA, and Woods Hole, MA: Hutchinson Ross.

Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.-L. Chen, P.-S. Chu, J.K. Eischeid, and D.M. Delparte. 2013. "Online Rainfall Atlas of Hawai'i." *Bulletin of the American Meteorological Society* 94: 313–6. https://doi.org/10.1175/BAMS-D-11-00228.1

Giambelluca, T.W., and T.A. Schroeder. 1998. "Climate." In *Atlas of Hawaii*, Third ed., edited by S.P. Juvik and J.O. Juvik, 49–59. Honolulu, HI: University of Hawai'i Press.

Giambelluca, T.W., X. Shuai, M.L. Barnes, R.J. Alliss, R.J. Longman, T. Miura, Q. Chen, et al. 2014. *Evapotranspiration of Hawai'i*. Final Report Submitted to the U.S. Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai'i.

Giffin, J.G. 2007. "A Comparison of Moth Diversity at Kilauea (1911–1912) and Upper Waiakea Forest Reserve (1998−2000),

Island of Hawaii." *Proceedings of the Hawaiian Entomological Society* 39: 15–26.

Glen, D.M. 2004. "Birds as Predators of Lepidopterous Larvae." In *Insect and Bird Interactions*, edited by H.F. van Emden and M. Rothschild, 89–106. Andover: Intercept.

Goldsmith, S., H. Gillespie, and C. Weatherby. 2007. "Restoration of Hawaiian Montane Wet Forest: Endemic Longhorned Beetles (Cerambycidae: *Plagithmysus*) in Koa (Fabaceae: *Acacia koa*) Plantations and in Intact Forest." *Southwestern Naturalist* 52: 356–63.

Gorresen, M.P., F.J. Bonaccorso, C.A. Pinzari, C.M. Todd, K. Montoya-Aiona, and K. Brinck. 2013. *A Five-Year Study of Hawaiian Hoary Bat (Lasiurus cinereus semotus) Occupancy on the Island of Hawai'i*. Hawai'i Cooperative Studies Unit Technical Report HCSU-041. Hilo, HI: University of Hawai'i at Hilo.

Gruner, D.S. 2004. "Arthropods from 'ōhi'a Lehua (Myrtaceae: *Metrosideros polymorpha*), with New Records for the Hawaiian Islands." *Bishop Museum Occasional Papers* 78: 33–52.

Grüning, M.M., J. Simon, H. Rennenberg, and A. I-M-Arnold. 2017. "Defoliating Insect Mass Outbreak Affects Soil N Fluxes and Tree N Nutrition in Scots Pine Forests." *Frontiers in Plant Science* 8: 954.

Guillaumet, A., W.A. Kuntz, M.D. Samuel, and Eben Paxton. 2017. "Altitudinal Migration and the Future of an Iconic Hawaiian Honeycreeper in Response to Climate Change and Management." *Ecological Monographs* 87: 410–28.

Haines, W.P., K.E. Barton, and P. Conant. 2013. "Defoliation of the Invasive Tree *Falcataria moluccana* on Hawaii Island by the Native Koa Looper Moth (Geometridae: *Scotorythra paludicola*), and Evaluation of Five Fabaceous Trees as Larval Hostplants." *Proceedings of the Hawaiian Entomological Society* 45: 129–39.

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." *Pacific Science* 63: 349–69.

Haney, J.C. 1999. "Numerical Response of Birds to an Irruption of Elm Spanworm (*Ennomos Subsignarius* [Hbn.]; Geometridae: Lepidoptera) in Old-growth Forest of the Appalachian Plateau, USA." *Forest Ecology and Management* 120: 203–17.

Harrison, S., and J.L. Maron. 1995. "Impacts of Defoliation by Tussock Moths (*Orgyia vetusta*) on the Growth and Reproduction of Bush Lupine (*Lupinus arboreus*)." *Ecological Entomology* 20: 223–9.

Hart, S.C., and M.K. Firestone. 1989. "Evaluation of Three In Situ Soil Nitrogen Availability Assays." *Canadian Journal of Forest Research* 19: 185–91.

Heddle, A. L. 2003. "Systematics and Phylogenetics of the Endemic Genus *Scotorythra* (Lepidoptera: Geometridae) in the Hawaiian Islands." Dissertation, University of California at Berkeley.

Henneman, M.L., and J. Memmott. 2001. "Infiltration of a Hawaiian Community by Introduced Biological Control Agents." *Science* 293: 1314–6.

Henshaw, H.W. 1902. *Birds of the Hawaiian Islands, Being a Complete List of the Birds of the Hawaiian Possessions with Notes on their Habits*. Honolulu, HI: Thrum.

Herbert, D.A., J.H. Fownes, and P.M. Vitousek. 1999. "Hurricane Damage to a Hawaiian Forest: Nutrient Supply Rate Affects Resistance and Resilience." *Ecology* 80: 908–20.

Hess, S.C., P.C. Banko, M.H. Reynolds, G.J. Brenner, and L.P. Laniawe. 2001. "Seasonal Changes in Food Resource Abundance and Drepanidine Densities in Subalpine Woodland on Mauna Kea, Hawai'i." *Studies in Avian Biology* 22: 154–63.

Hess, S.C., J.J. Jeffrey, L.W. Pratt, and D.L. Ball. 2010. "Effects of Ungulate Management on Vegetation at Hakalau Forest National Wildlife Refuge, Hawai'i Island." *Pacific Conservation Biology* 16: 144–50.

Hines, J.E. 2006. *Presence 4—Software to Estimate Patch Occupancy and Related Parameters*. Laurel, MD: U.S. Geological Survey Patuxent Wildlife Research Center. http://www.mbr-pwrc.usgs.gov/software/presence.html

Hobbie, S.E. 2000. "Interactions between Litter Lignin and Nitrogen Litter Lignin and Soil Nitrogen Availability during Leaf Litter Decomposition in a Hawaiian Montane Forest." *Ecosystems* 3: 484–94.

Hogstad, O. 2005. "Numerical and Functional Responses of Breeding Passerine Species to Mass Occurrence of Geometrid Caterpillars in a Subalpine Birch Forest: A 30-Year Study." *Ibis* 147: 77–91.

Hollinger, D.Y. 1986. "Herbivory and the Cycling of Nitrogen and Phosphorus in Isolated California Oak Trees." *Oecologia* 70: 291–7.

Holm, S. 1979. "A Simple Sequentially Rejective Multiple Test Procedure." *Scandinavian Journal of Statistics* 6: 65–70.

Holmes, R.T. 1990. "Ecological and Evolutionary Impacts of Bird Predation on Forest Insects: An Overview." *Studies in Avian Biology* 13: 6–13.

Hook, P.B., and I.C. Burke. 2000. "Biogeochemistry in a Shortgrass Landscape: Control by Topography, Soil Texture, and Microclimate." *Ecology* 81: 2686–703.

Hooper, D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, et al. 2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monographs* 75: 3–35.

Howarth, F.G., D. Preston, F. Moretzsohn, and M. McShane. 2003. *Invertebrate Survey of Hakalau National Wildlife Refuge, Hawaii*. Contribution No. 2003-21 to the Hawaii Biological Survey. Honolulu, HI: Bishop Museum.

Jacobi, J.D. 1989. *Vegetation Maps of the Upland Plant Communities on the Islands of Hawai'i, Maui, Moloka'i, and Lana'i*. Cooperative National Park Resources Studies Unit Technical Report 68. Honolulu, HI: University of Hawai'i at Mānoa.

Jacobs, D. 1999. "The Diet of the Insectivorous Hawaiian Hoary Bat (*Lasiurus cinereus semotus*) in an Open and a Cluttered Habitat." *Canadian Journal of Zoology* 77: 1603–8.

Jacquet, J.-S., C. Orazio, and H. Jactel. 2012. "Defoliation by Processionary Moth Significantly Reduces Tree Growth: A Quantitative Review." *Annals of Forest Science* 69: 857–66.

Janzen, D.H. 1981. "Patterns of Herbivory in a Tropical Deciduous Forest." *Biotropica* 13: 271–82.

Jeffrey, J., and B. Horiuchi. 2003. "Tree Planting at Hakalau Forest National Wildlife Refuge—The Right Tool for the Right Stock Type." *Native Plants Journal* 4: 30–1.

Jennings, D.T., H.S. Crawford, Jr., and M.L. Hunter, Jr. 1991. "Predation by Amphibians and Small Mammals on the Spruce Budworm (Lepidoptera: Tortricidae)." *Great Lakes Entomologist* 24: 69–74.

Jonason, D., M. Franzen, and T. Ranius. 2014. "Surveying Moths Using Light Traps: Effects of Weather and Time of Year." *PLoS One* 9: e92453.

Kalka, M., and E.K.V. Kalko. 2006. "Gleaning Bats as Underestimated Predators of Herbivorous Insects: Diet of *Micronycteris microtis* (Phyllostomidae) in Panama." *Journal of Tropical Ecology* 22: 1–10.

Kalka, M.B., A.R. Smith, and E.K.V. Kalko. 2008. "Bats Limit Arthropods and Herbivory in a Tropical Forest." *Science* 320: 71.

Kessler, A.K., K. Poveda, and E.H. Poelman. 2012. "Plant-induced Responses and Herbivore Population Dynamics." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D.K. Letourneau, and A.A. Agrawal, 91–112. Hoboken, NJ: Wiley-Blackwell.

Klemola, N., T. Andersson, K. Ruohomäki, and T. Klemola. 2010. "Experimental Test of Parasitism Hypothesis for Population Cycles of a Forest Lepidopteran." *Ecology* 91: 2506–13.

Koricheva, J., M.J. Klapwijk, and C. Björkman. 2012. "Life History Traits and Host Plant Use in Defoliators and Bark Beetles: Implications for Population Dynamics." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D.K. Letourneau, and A.A. Agrawal, 177–96. Hoboken, NJ: Wiley-Blackwell.

Kosola, K.R., D.L. Dickman, E.A. Paul, and D. Parry. 2001. "Repeated Insect Defoliation Effects on Growth, Nitrogen Acquisition, Carbohydrates, and Root Demography of Poplars." *Oecologia* 129: 65–74.

Kula, A.A.R., M.H. Hey, J.J. Couture, P.A. Townsend, and H.J. Dalgleish. 2020. "Intraspecific Competition Reduces Plant Size and Quality and Damage Severity Increases Defense Responses in the Herbaceous Perennial, *Asclepias syriaca*." *Plant Ecology* 221: 421–30.

Kuntz, W.A. 2008. "The Importance of Individual Behavior to Life History and Conservation: Breeding and Movement Biology in the ʻiʻiwi (*Vestiaria coccinia*)." PhD diss., University of Hawaiʻi at Mānoa.

Lajtha, K. 1988. "The Use of Ion-exchange Resin Bags for Measuring Nutrient Availability in an Arid Ecosystem." *Plant and Soil* 105: 105–11.

Lamoureux, C.H., D. Mueller-Dombois, and K.W. Bridges. 1981. "Temporal Variation of Organism Groups Studies: Trees." In *Island Ecosystems: Biological Organization in Selected Hawaiian Communities*. U.S. International Biological Program Synthesis Series 15, edited by D. Mueler-Dombois, K.W. Bridges, and H.L. Carson, 391–407. Stroudsburg, PA, and Woods Hole, MA: Hutchinson and Ross.

Letourneau, D.K. 2012. "Integrated Pest Management—Outbreaks Prevented, Delayed, or Facilitated?" In *Insect Outbreaks Revisited*, edited by P. Barbosa, D.K. Letourneau, and A.A. Agrawal, 371–94. Hoboken, NJ: Wiley-Blackwell.

Lohse, K.A., and P. Matson. 2005. "Consequences of Nitrogen Additions for Soil Losses from Wet Tropical Forests." *Ecological Applications* 15: 1629–48.

Long, Z.T., C.L. Mohler, and W.P. Carson. 2003. "Extending the Resource Concentration Hypothesis to Plant Communities: Effects of Litter and Herbivores." *Ecology* 84: 652–65.

Lovett, G.M., L.M. Christenson, P.M. Groffman, C.G. Jones, J.E. Hart, and M.J. Mitchell. 2002. "Insect Defoliation and Nitrogen Cycling in Forests." *BioScience* 52: 335–41.

MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maron, J.L., and P.G. Connors. 1996. "A Native Nitrogen-fixing Shrub Facilitates Weed Invasion." *Oecologia* 105: 302–12.

Maron, J.L., and R.L. Jefferies. 1999. "Bush Lupine Mortality, Altered Resource Availability, and Alternative Vegetation States." *Ecology* 80: 443–54.

McBrien, H., R. Harmsen, and A. Crowder. 1983. "A Case of Insect Grazing Affecting Plant Succession." *Ecology* 64: 1035–9.

McCracken, G.F., J.K. Westbrook, V.A. Brown, M. Eldridge, P. Federico, and T.H. Kunz. 2012. "Bats Track and Exploit Changes in Insect Pest Populations." *PLoS One* 7: e43839.

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." *Applied Vegetation Science* 13: 280–90.

McMartin, B., I. Bellocq, and S.M. Smith. 2002. "Patterns of Consumption and Diet Differentiation for Three Breeding Warble Species during a Spruce Budworm Outbreak." *The Auk* 119: 216–20.

Montoya-Aiona, K.M., C.A. Pinzari, and F.J. Bonaccorso. 2020. "Hawaii Island, Hawaiian Hoary Bat Acoustic Data Pre- and Post-koa Moth Outbreak, 2007–2013." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9ZFS101

Müller, J., M. Mehr, C. Bässler, M.B. Fenton, T. Hothorn, H. Pretzsch, H.-J. Klemmt, and R. Brandl. 2012. "Aggregative Response in Bats: Prey Abundance Versus Habitat." *Oecologia* 169: 673–84.

Myers, J.H. 1988. "Can a General Hypothesis Explain Population Cycles of Forest Lepidoptera?" *Advances in Ecological Research* 18: 179–242.

Nair, K.S.S. 2007. *Tropical Forest Insect Pests: Ecology, Impact, and Management*. Cambridge: Cambridge University Press.

Nakajima, H. 2018. "Refoliation of Deciduous Canopy Trees Following Severe Insect Defoliation: Comparison of *Fagus crenata* and *Quercus crispula*." *Plant Ecology* 219: 665–75.

Nykänen, H., and J. Koricheva. 2004. "Damage-induced Changes in Woody Plants and their Effects on Insect Herbivore Performance: A Meta-analysis." *Oikos* 104: 247–68.

Oboyski, P.T., J.W. Slotterback, and P.C. Banko. 2004. "Differential Parasitism of Seed-feeding *Cydia* (Lepidoptera: Tortricidae) by Native and Alien Wasp Species Relative to Elevation in Subalpine *Sophora* (Fabaceae) Forests on Mauna Kea, Hawaii." *Journal of Insect Conservation* 8: 229–40.

Oʻ Rourke, M.E., and M.J. Petersen. 2017. "Extending the 'Resource Concentration Hypothesis' to the Landscape-Scale by Considering Dispersal Mortality and Fitness Costs." *Agriculture, Ecosystems and Environment* 249: 1–3.

Ostertag, R. 2010. "Foliar Nitrogen and Phosphorus Accumulation Responses after Fertilization: An Example from Nutrient-limited Hawaiian Forests." *Plant and Soil* 334: 85–98.

Ostertag, R., F. Inman-Narahari, S. Cordell, C.P. Giardina, and L. Sack. 2014. "Forest Structure in Low-Diversity Tropical Forest: A Study of Hawaiian Wet and Dry Forests." *PLoS One* 9: e103268.

Ostertag, R., F.N. Scatena, and W.L. Silver. 2003. "Forest Floor Decomposition Following Hurricane Litter Inputs in Several Puerto Rican Forests." *Ecosystems* 6: 261–73.

Ostfeld, R.S., and F. Keesing. 2000. "Pulsed Resources and Community Dynamics of Consumers in Terrestrial Ecosystems." *Trends in Ecology & Evolution* 15: 232–7.

Páez, D.J., V. Dukic, J. Dushoff, A. Fleming-Davies, and G. Dwyer. 2017. "Eco-evolutionary Theory and Insect Outbreaks." *American Naturalist* 189: 616–29.

Pasquet-Kok, J., C. Creese, and L. Sack. 2010. "Turning over a New 'Leaf': Multiple Functional Significances of Leaves versus Phyllodes in Hawaiian *Acacia koa*." *Plant, Cell and Environment* 33: 2084–100.

Paxton, E.H., T.C. Theimer, and M.K. Sogge. 2011. "Tamarisk Biocontrol Using Tamarisk Beetles: Potential Consequences for Riparian Birds in the Southwestern United States." *The Condor* 113: 255–65.

Paxton, E.H., S.G. Yelenik, T.E. Borneman, E.T. Rose, R.J. Camp, and S.J. Kendall. 2017. "Rapid Colonization of a Hawaiian Restoration Forest by a Diverse Avian Community." *Restoration Ecology* 26: 165–73.

Pearson, H.L., and P.M. Vitousek. 2001. "Stand Dynamics, Nitrogen Accumulation, and Symbiotic Nitrogen Fixation in Regenerating Stands of *Acacia koa*." *Ecological Applications* 11: 1381–94.

Peck, R.W., and P.C. Banko. 2021. "Hawaii Island Insect Response to Koa Moth Outbreak, 2013–2014." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9HE9WKK

Peck, R.W., P.C. Banko, M. Schwarzfeld, M. Euaparadorn, and K. W. Brinck. 2008. "Alien Dominance of the Parasitoid Wasp Community Along an Elevation Gradient on Hawai'i Island." *Biological Invasions* 10: 1441–55.

Pejchar, L., K.D. Holl, and J.L. Lockwood. 2005. "Hawaiian Honeycreeper Home Range Size Varies with Habitat: Implications for Native *Acacia koa* Forestry." *Ecological Applications* 15: 1053–61.

Perkins, R.C.L. 1896. "A Collecting Trip on Haleakala, Maui, Sandwich Islands." *The Entomologist's Monthly Magazine* 32: 190–5.

Perkins, R.C.L. 1903. "Vertebrata." In *Fauna Hawaiiensis*, Vol 1, Part. 4, edited by D. Sharpe, 365–466. Cambridge: University Press.

Perkins, R.C.L. 1913. "Introduction." In *Fauna Hawaiiensis*, Vol 1. Part 6, edited by D. Sharpe, xv–ccxxvii. Cambridge: University Press.

Peterson, G., C.R. Allen, and C.S. Holling. 1998. "Ecological Resilience, Biodiversity, and Scale." *Ecosystems* 1: 6–18.

Piene, H. 1989. "Spruce Budworm Defoliation and Growth Loss in Young Balsam Fir: Recovery of Growth in Spaced Stands." *Canadian Journal of Forest Research* 19: 1616–24.

Pimm, S.L., and J.W. Pimm. 1982. "Resource Use, Competition, and Resource Availability in Hawaiian Honeycreepers." *Ecology* 63: 1468–80.

Piper, F.I., M.J. Gundale, and A. Fajardo. 2015. "Extreme Defoliation Reduces Tree Growth but not C and N Storage in a Winter-deciduous Species." *Annals of Botany* 115: 1093–103.

Price, J.P. 2004. "Floristic Biogeography of the Hawaiian Islands: Influences of Area, Environment and Paleogeography." *Journal of Biogeography* 31: 487–500.

Proulx, S.R., D.E. Promislow, and P.C. Phillips. 2005. "Network Thinking in Ecology and Evolution." *Trends in Ecology & Evolution* 20: 345–53.

Ralph, C.J., and S.G. Fancy. 1994. "Timing of Breeding and Molt in Six Species of Hawaiian Honeycreepers." *The Condor* 96: 151–61.

Ralph, C.J., and S.G. Fancy. 1996. "Aspects of the Life History and Foraging Ecology of the Endangered Akiapolaau." *The Condor* 98: 312–21.

Redfern, A., and S.L. Pimm. 1987. "Insect Outbreaks and Community Structure." In *Insect Outbreaks*, edited by P. Barbosa and J.C. Schultz, 99–133. New York: Academic Press.

Reich, P.B. 1995. "Phenology of Tropical Trees: Patterns, Causes, and Consequences." *Canadian Journal of Botany* 73: 164–74.

Risch, S.J., D. Andow, and M.A. Altieri. 1983. "Agroecosystem Diversity and Pest Control: Data, Tentative Conclusions, and New Research Directions." *Environmental Entomology* 12: 625–9.

Root, R.B. 1973. "Organization of a Plant-arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica oleracea*)." *Ecological Monographs* 43: 95–124.

Root, R.B., and N. Cappuccino. 1992. "Patterns in Population-change and the Organization of the Insect Community Associated with Goldenrod." *Ecological Monographs* 43: 393–420.

Royama, T., E.S. Eveleigh, J.R.B. Morin, S.J. Pollock, P.C. McCarthy, G.A. McDougall, and C.J. Lucarotti. 2017. "Mechanisms Underlying Spruce Budworm Outbreak Processes as Elucidated by a 14-Year Study in New Brunswick, Canada." *Ecological Monographs* 87: 600–31.

Rozendaal, D.M.A., and R.K. Kobe. 2014. "Competitive Balance among Tree Species Altered by Forest Tent Caterpillar Defoliation." *Forest Ecology and Management* 327: 18–25.

Ruess, R.W., M.D. Anderson, J.S. Mitchell, and J.W. McFarland. 2006. "Effects of Defoliation on Growth and N Fixation in *Alnus tenuifolia*: Consequences for Changing Disturbance Regimes at High Latitudes." *Ecoscience* 13: 404–12.

Russell, C., K. Kosola, E. Paul, and G. Robertson. 2004. "Nitrogen Cycling in Poplar Stands Defoliated by Insects." *Biogeochemistry* 68: 365–81.

Rydell, J., A. Entwistle, and P.A. Racey. 1996. "Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk." *Oikos* 76: 243–52.

Rzanny, M., and W. Voigt. 2012. "Complexity of Multitrophic Interactions in a Grassland Ecosystem Depends on Plant Species Diversity." *Journal of Animal Ecology* 81: 614–27.

Scholes, R., and S. Archer. 1997. "Tree-grass Interactions in Savannas." *Annual Review of Ecology and Systematics* 28: 517–44.

Schowalter, T.D. 2012. "Outbreaks and Ecosystem Services." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D.K. Letourneau, and A.A. Agrawal, 246–65. Hoboken, NJ: Wiley-Blackwell.

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. 1986. "Forest Bird Communities of the Hawaiian Islands: Their Dynamics, Ecology, and Conservation." *Studies in Avian Biology* 9: 1–431.

Scowcroft, P.G. 1997. "Mass and Nutrient Dynamics of Decaying Litter from *Passiflora mollissima* and Selected Native Species in a Hawaiian Montane Rain Forest." *Journal of Tropical Ecology* 13: 407–26.

Scowcroft, P.G., J.E. Haraguchi, and N.V. Hue. 2004. "Reforestation and Topography Affect Montane Soil Properties, Nitrogen Pools, and Nitrogen Transformations in Hawaii." *Soil Science Society of America Journal* 68: 959–68.

Shaw, A.N., and J.L. DeForest. 2013. "The Cycling of Readily Available Phosphorus in Response to Elevated Phosphate in Acidic Temperate Deciduous Forests." *Applied Soil Ecology* 63: 88–93.

Smith, S.M. 1996. "Biological Control with *Trichogramma*: Advances, Successes, and Potential of their Use." *Annual Review of Entomology* 41: 375–406.

Soil Survey Staff. "Web Soil Survey." Natural Resources Conservation Service, U.S. Department of Agriculture. http://websoilsurvey.nrcs.usda.gov/

Stein, J.D., and P.G. Scowcroft. 1984. "Growth and Refoliation of Koa Trees Infested by the Koa Moth, *Scotorythra paludicola* (Lepidoptera: Geometridae)." *Pacific Science* 38: 333–9.

Stephens, D.W., and J.R. Krebs. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Stevens, M.T., E.L. Kruger, and R.L. Lindroth. 2008. "Variation in Tolerance to Herbivory is Mediated by Differences in Biomass Allocation in Aspen." *Functional Ecology* 22: 40–7.

Stewart, C.M. 2013. "Moth Infestation Continues on Isle." *Hawaii Tribune Herald*, June 1. https://www.hawaiitribune-herald.com/2013/06/01/hawaii-news/moth-infestation-continues-on-isle/

Sutton, S., S.C. Pasquini, T. Swanson, and W.P. Carson. 2021. "On the Occurrence of a Highly Localized Outbreak of a Saturniid in Lowland East Ecuador: A Case Study and Literature Review." *Neotropical Biodiversity* 7: 39–44.

Swezey, O.H. 1926. "Reports on Defoliation of Maui Koa Forests by Caterpillars." *Hawaiian Planters' Record* 30: 354–62.

Swezey, O.H. 1929. "Notes on the Egg-parasites of Insects in Hawaii." *Proceedings of the Hawaiian Entomological Society* 7: 282–92.

Swezey, O.H. 1931. "Some Observations on the Insect Faunas of Native Forest Trees in the Olinda Forest on Maui." *Proceedings of the Hawaiian Entomological Society* 7: 493–504.

Swezey, O.H. 1954. *Forest Entomology in Hawaii: An Annotated Check-list of the Insect Faunas of the Various Components of the Hawaiian Forest*. Bernice P. Bishop Museum Special Publication 44. Honolulu, HI: Bishop Museum Press.

Symondson, W.O.C., K.D. Sunderland, and M.H. Greenstone. 2002. "Can Generalist Predators be Effective Biocontrol Agents?" *Annual Review of Entomology* 47: 561–94.

Tilman, D., and J.A. Downing. 1994. "Biodiversity and Stability in Grasslands." *Nature* 367: 363–5.

Tomich, Q.P. 1986. *Mammals in Hawai'i: A Synopsis and Notational Bibliography*, Second ed.. Bernice P. Bishop Museum Special Publication 76. Honolulu, HI: Bishop Museum Press.

Turchin, P., S.N. Wood, S.P. Ellner, B.E. Kendall, W.W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C.J. Briggs. 2003. "Dynamical Effects of Plant Quality and Parasitism on Population Cycles of Larch Budmoth." *Ecology* 84: 1207–14.

Visser, M.E., and L.J.M. Holleman. 2001. "Warmer Springs Disrupt the Synchrony of Oak and Winter Moth Phenology." *Proceeding of the Royal Society of London. Series B, Biological Sciences* 268: 289–94.

Vitousek, P.M., and H. Farrington. 1997. "Nutrient Limitation and Soil Development: Experimental Test of a Biogeochemical Theory." *Biogeochemistry* 37: 63–75.

Wilson, J.M., and R.M. Barclay. 2006. "Consumption of Caterpillars by Bats during an Outbreak of Western Spruce Budworm." *American Midland Naturalist* 155: 244–9.

Yang, L.H. 2004. "Periodical Cicadas as Resource Pulses in North American Forests." *Science* 306: 1565–7.

Yang, L.H. 2012. "The Ecological Consequences of Insect Outbreaks." In *Insect Outbreaks Revisited*, edited by P. Barbosa, D. K. Letourneau, and A.A. Agrawal, 197–218. Hoboken, NJ: Wiley-Blackwell.

Yang, L.H., J.L. Bastow, K.O. Spence, and A.N. Wright. 2008. "What Can we Learn from Resource Pulses." *Ecology* 89: 621–34.

Yang, L.H., K.F. Edwards, J.E. Byrnes, J.L. Bastow, A.N. Wright, and K.O. Spence. 2010. "A Meta-analysis of Resource Pulse-consumer Interactions." *Ecological Monographs* 80: 125–51.

Yela, J.L., and M. Holyoak. 1997. "Effects of Moonlight and Meteorological Factors on Light and Bait Traps Catches of Noctuid Moths (Lepidoptera: Noctuidae)." *Environmental Entomology* 26: 128–1290.

Yelenik, S.G. 2017. "Linking Dominant Hawaiian Tree Species to Understory Development in Recovering Pastures via Impacts on Soils and Litter." *Restoration Ecology* 25: 42–52.

Yelenik, S., S. Perakis, R.W. Peck, and P.C. Banko. 2021. "Hakalau Forest Litter, Frass, Soil, and Understory Foliar Nitrogen during Koa Moth Outbreak, 2013–2014." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9J9QQ96

U.S. Forest Service (USFS). 2007. Forest Inventory and Analysis National Core Field Guide. Volume I: Field Data Collection Procedures for Phase 2 Plots, Version 4.0. U.S. Department of Agriculture. https://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/core_ver_4-0_10_2007_p2.pdf

Webb, J., B. Cosby, F. Deviney, K. Eshleman, and J. Galloway. 1995. "Change in the Acid–Base Status of an Appalachian Mountain Catchment Following Forest Defoliation by the Gypsy Moth." *Water, Air, and Soil Pollution* 85: 535–40.

Whisson, D.A., A. Orlowski, and M.A. Weston. 2018. "Tree Canopy Defoliation Impacts Avifauna." *Forest Ecology and Management* 428: 81–6.

Williams-Guillén, K., I. Perfecto, and J. Vanderneer. 2008. "Bats Limit Insects in a Neotropical Agroforestry System." *Science* 320: 70.

Wolda, H. 1978. "Fluctuations in Abundance of Tropical Insects." *American Naturalist* 112: 1017–45.

Wolda, H. 1980. "Seasonality of Tropical Insects. I. Leafhoppers (Homoptera) in Las Cumbres, Panama." *Journal of Animal Ecology* 49: 277–90.

Wolda, H. 1992. "Trends in Abundance of Tropical Forest Insects." *Oecologia* 89: 47–52.

Wolfe, E.W., and J. Morris. 1996. *Geologic Map of the Island of Hawaii. Miscellaneous Investigation Series, Map I–2524-A, Scale 1:100,000*. Reston, VA: U.S. Geological Survey.

Woodworth, B.L., and T.K. Pratt. 2009. "Life History and Demography." In *Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna*, edited by T.K. Pratt, C.T. Atkinson, P.C. Banko, J.D. Jacobi, and B.L. Woodworth, 194–233. New Haven, CT: Yale University Press.

Zimmerman, E.C. 1958. *Insects of Hawaii. Vol. 7: Macrolepidoptera*. Honolulu, HI: University of Hawaii Press.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Banko, Paul C., Robert W. Peck, Stephanie G. Yelenik, Eben H. Paxton, Frank Bonaccorso, Kristina Montoya-Aiona, R. Flint Hughes, and Steven Perakis. 2022. "Hypotheses and Lessons from a Native Moth Outbreak In a Low-Diversity, Tropical Rainforest." *Ecosphere* 13(2): e3926. https://doi.org/10.1002/ecs2.3926