North Atlantic regions but returning to the eastern Mediterranean to breed. These large-scale movements between feeding and spawning grounds are comparable to those of Pacific and Southern bluefin tuna (*13, 20, 28*). Pacific bluefin migrate from the western Pacific to the North American continental shelf and remain residents for 2 to 5 years before returning to the western Pacific to spawn (*13, 28*). Rapid movements of thousands of kilometers are common in tunas and other highly migratory species. This suggests that the metabolic costs for endothermic fish swimming across ocean basins are low in comparison to the ecological benefits.

The recovery of Atlantic bluefin tuna breeding stocks is linked to the extent of contemporary mixing of mature Atlantic bluefin, as well as to their spawning site fidelity. The electronic tagging data indicate that mixing between the two management units exists at a higher level than ICCAT has incorporated into base-case stock assessments. Although mixing occurs on western and eastern feeding grounds, bluefin tuna may be sorting to major spawning grounds in the eastern Mediterranean and Gulf of Mexico. Extensions to the western breeding area may include the Bahamas, Caribbean, and offshore Carolina waters in late spring and early summer. Future assessments of stock status should evaluate the new information and reassess the management strategies applied to Atlantic bluefin tuna.

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Infiltration of a Hawaiian Community by Introduced Biological Control Agents

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To examine the community-wide effects of introduced biocontrol agents on Kauai Island, Hawaii, we constructed quantitative food webs showing interactions among plants, moths, and moth parasitoids in a native forest. Eighty-three percent of parasitoids reared from native moths were biological control agents, 14% were accidental immigrants, and 3% were native species. Although parasitism by biological control agents reached 28% in some species of moth, all biocontrol agents reared had been released before 1945. This study highlights the importance of considering the potential damage caused by an introduced control agent, in addition to that caused by the target alien species.

The ecological impact of intentionally introduced biological control agents of insect pests is controversial. Some blame the practice for extinctions of native species (*1*), some call for increased regulation (*2*), and some insist that biological control is safe (*3*). The debate is fueled largely by anecdotal reports (*4–6*). A major point of contention surrounds the question of whether nontarget effects, such as those of the snail *Euglandina rosea* on Pacific islands (*7*) and of the lady beetle *Coccinella septempunctata* in North America (*8*), represent isolated events or more general impacts. A few studies address nontarget effects quantitatively at the community level. Louda *et al.* (*9*) measured the attack rate on native thistles by *Rhinocyllus conicus*, a weevil introduced to the United States and Canada to control exotic thistles. They concluded that the amount of seed destroyed by this biological control agent could potentially threaten some native thistles and consequently their native seed predators. The effects of the exotic moth *Cactoblastis cactorum* on native *Opuntia* species in Florida have been quantified (*10*);

potential long-term effects include lower survivorship of younger plants.

Quantifying the mortality of insects from alien parasitoids and predators is more difficult because parasitoids and predators are hard to observe in the field. Boettner *et al.* (*11*) deployed, in the field, "sentinel" larvae of two native silk moth species in New England to measure the attack rate by *Compsilura concinnata*, a parasitoid fly originally introduced for control of gypsy moths. They found high levels of parasitism, up to 100% in some cases, and suggested that nontarget effects could potentially be responsible for extinctions, at least locally, of native species.

Indirect effects on native species are the most difficult to assess. An insect herbivore introduced to control a weed could be attacked by generalist native parasitoids that also have native hosts (*12*). If the weed biological control agent is abundant, then there is the potential for apparent competition (*5, 13*) between the agent and native herbivores, mediated via shared native parasitoids. Thus, even the introduction of an entirely species-specific herbivore, presumed to have no nontarget effects, still could have a community-wide impact. Only by understanding how invasive species interact within the context of the entire community can we hope to

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assess the risks to native species, whether they be direct effects on single species or indirect effects on several species across trophic levels.

Our goal was to understand how alien insect species, particularly those introduced for purposes of biological control, interact with native species within the context of a quantitative food web. Despite potential biases (*14*), quantitative webs, which describe the magnitudes of trophic interactions, are a powerful tool for establishing the level to which alien species have infiltrated a native community and for predicting direct and indirect effects of biological control agents on native species (*15*).

We conducted the study on the island of Kauai, Hawaii. There have been at least 122 releases of parasitic wasps and flies against agricultural pest Lepidoptera in Hawaii within the past 100 years (*3, 16–18*), providing high potential for nontarget effects, particularly on leaf-feeding caterpillars, on which we focused the study. We also included carnivorous caterpillars in the genus *Eupithecia* (Geometridae), because they are not only endemic but fill a niche unique to Hawaii. The Alakai Swamp, designated by the state of Hawaii as a wilderness preserve, was chosen as the study site because it is isolated geographically, altitudinally, climatically, and ecologically from agricultural areas (*19*). Temperatures can range from 10° to 30°C over a day, and rainfall can exceed 10 m per year. We

assumed that any nontarget effects found would represent a minimum for native habitats on Kauai, because the extreme climate may resist invasion; for example, plant invaders are limited to a few species.

To quantify the mortality of native moths caused by alien parasitic wasps in the Alakai Swamp, we constructed quantitative food webs based on quantitative samples of caterpillars from two plots, each measuring 200 m by 25 m, separated by about 2 km. Leaf-feeding caterpillars were collected by beating vegetation along transect lines, with 13 sets of collections made from each plot between April and September over 2 years. Foliage from all plant species was accessible in both plots. We collected 2112 caterpillars from the plots and reared them individually in the laboratory to establish parasitoid associations. With the use of the rearing data, food webs were constructed for each plot over both years (Fig. 1) (*20*). All the webs were similar in structure, indicating that the interactions we found were relatively constant in space and time. Fifty-eight moth species (4 alien and 54 endemic) were reared from 60 plant species (47 endemic, 6 indigenous, and 7 alien) (*21*). Out of 216 parasitoids reared from 2112 caterpillars collected, most (83%) were biological control agents introduced against lowland agricultural pests (*16*), followed by accidentally introduced ("immigrant") wasps (14%). Native

parasitoids were relatively rare (3%). The most common parasitoid species were the generalist braconid biocontrol agents *Meteorus laphygmae*, reared from at least 12 species of moths in six different families, and *Cotesia marginiventris*, reared from at least nine species in three families. The most common immigrant species, the ichneumonid *Diadegma blackburni*, was reared from three species in two families. Thus, although immigrant species are present in the Alakai Swamp, their current infiltration into the native moth community is much lower than that of the biological control agents (Fig. 1).

Not all endemic Lepidoptera taxa are attacked by biological control agents. Four species of carnivorous *Eupithecia* yielded no parasitoids at all. In addition, we made some preliminary collections of at least 15 species of case-bearing leaf-surface-grazing caterpillars from the large endemic genus *Hyposmocoma* (Cosmopterigidae). From 800 *Hyposmocoma* collected, we reared five native parasitoid species but no introduced species. These groups of moths may be protected from attack by biological control agents by occupying a niche that is sufficiently dissimilar to those of agricultural pests.

The small number of native parasitic wasps reared, both in number of species and in absolute numbers (Fig. 1), is difficult to interpret. There is the potential for displacement of native parasitoids by aliens (*22*), especially if native

Leaf area 100,000 cm² per 100 m³   100 Lepidoptera   10 Parasitoids
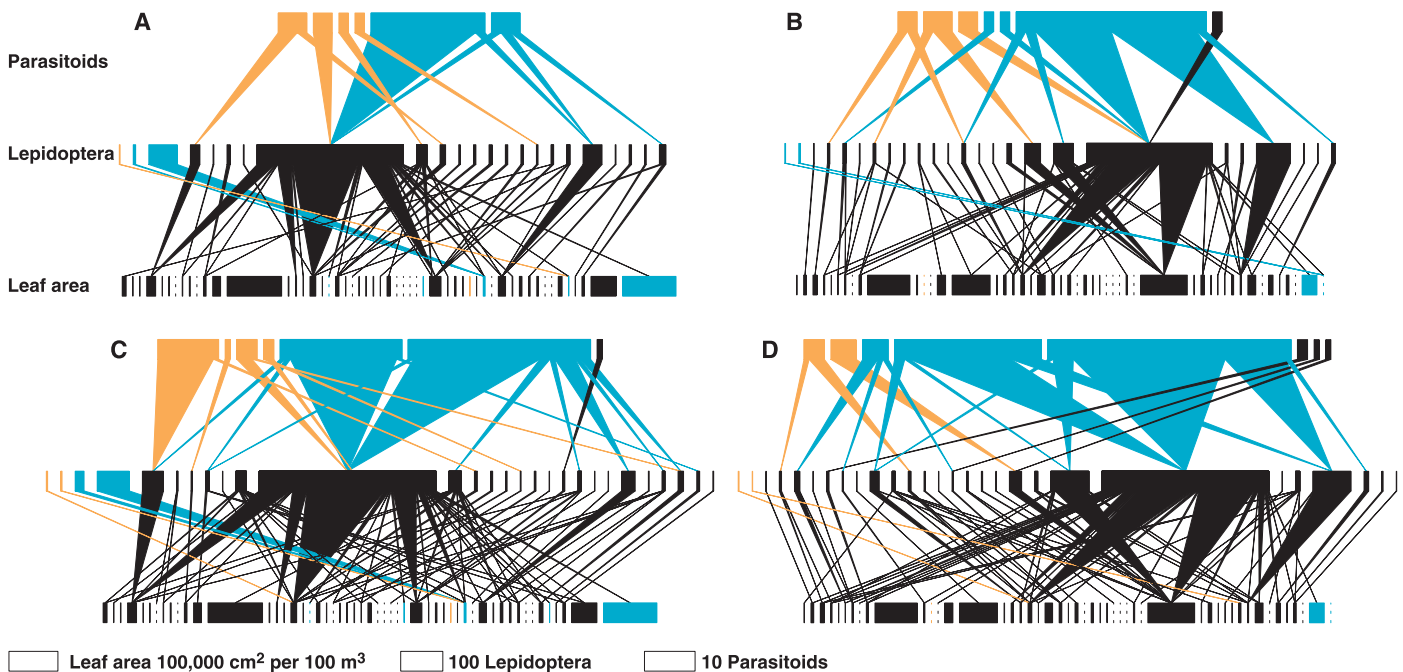
Fig. 1. Quantitative food webs for two plots over 2 years in the Alakai Swamp. Plant species are on the bottom, moths in the middle, and parasitoids on top. Each bar represents a species, and its width represents its relative abundance among all individuals collected. Relative plant abundance was measured using leaf area per 100 m³ and was assessed by counting leaves of all plant species along four arbitrary transects in each plot and by measuring average leaf area for all species. The scale bar for leaf area represents 100,000 cm² per 100 m³ of forest; the bar for Lepidoptera represents 100 individuals; and the bar for parasitoids represents 10 individuals. The width of the lines connecting trophic levels represents the relative numbers of the upper species attacking the lower species. Plants represented by dotted lines were in the plots but did not occur on these transects. Native species are black, accidental immigrants are yellow, and intentionally introduced species are blue. In the case of insects, intentionally introduced species are biological control agents; in the case of plants, intentionally introduced species are ornamentals and trees that were originally planted for erosion control. (**A**) Plot 1, 1999. (**B**) Plot 2, 1999. (**C**) Plot 1, 2000. (**D**) Plot 2, 2000. All webs are drawn at the same scale. See supplemental material (*20*) for figure detail and species names.

parasitoids (such as those in the ichneumonid genus *Enicospilus*) attack later larval stages than those attacked by aliens (all alien wasps in our study emerged from their hosts before the final instar). Unfortunately, native Hawaiian parasitoids are not well studied, so it is unknown whether competitive displacement has occurred. It is also possible that the native parasitoid fauna was historically impoverished, because presumably it is difficult for relatively specialized, higher-trophic-level organisms to invade remote islands (*23*).

Alien adult parasitoids were reared from 8.3% of caterpillars collected in 1999 and 11% collected in 2000. These numbers represent the minimum of caterpillars that died as a direct result of parasitoid attack. Eighteen out of 77 caterpillars (23%) that died of unexplained causes (11% of all collected) contained parasitoid larvae, and one of these had been parasitized twice. Most of these larvae appeared to be healthy except for the presence of a recently hatched wasp larva. It is likely that the parasitoids were alien wasps, because the larvae were large endoparasitoids in geometrid hosts, whereas the native parasitoid species were all small nonichneumonoid species, reared from nongeometrids. Based on rearing and dissection data combined, the level of attack by alien parasitoids is estimated to be 19% in 1999 and 22% in 2000.

Although a food web represents a snapshot in time and does not allow us to predict population dynamics, it is possible that the attack rates by alien wasps, though reaching up to 28% for some individual moth species, are sustainable. Hawkins *et al.* (*24*) found that biological control agents causing less than 36% parasitism of target hosts were not effective in suppressing host populations; however, the biology of species that can become pests may allow them to sustain higher parasitism levels than native species in a complex natural environment. Because all of the alien parasitoids reared were introduced to the Hawaiian Islands before 1945 (*25*) (*3*, *26*, *27*) and have likely been established in the Alakai Swamp for many years, it seems probable that the moth species we collected have suffered attack from the parasitoids for decades and will persist. However, it is also possible that some more vulnerable native species disappeared before we began our study (*28*).

The main potential for indirect effects mediated by alien species was in plot 1, which was more deeply infiltrated by alien plant species, notably *Rubus argutus* (blackberry), *Hedychium gardnerianum* (ginger), and *Acacia melanoxylon* (an Australian tree). Several biocontrol agents have been introduced for the control of *R. argutus*, including the moths *Croesia zimmermani* (Tortricidae) and *Schreckensteinia festaliella* (Heliodinidae) (*29*), both of which we reared. Indirect effects could occur if parasitoids attacked *C. zimmermani* and/or *S. festaliella*

heavily, which could lead to larger numbers of parasitoids attacking native host caterpillars. However, no parasitoids, either alien or native, were reared from these agents.

M. laphygmae, *C. marginiventris*, and the ichneumonid *Eriborus sinicus* were originally released more than 50 years ago. At that time, generalist biological control agents were considered superior, because not only did they have the potential to control several pest species (*27*), but native insects could serve as hosts during times of the year when crop pests were rare. Although there has been debate about whether generalist or specialist parasitoids make the best biological control agents (*30*, *31*), it now seems very unlikely, given current regulations, that a known generalist could be intentionally introduced to the islands (*4*). Although tight controls on introductions did not begin until the 1980s, since the 1960s more specialist (that is, known to attack one species of Lepidoptera) than generalist (that is, attacking at least two families of Lepidoptera) biological control agents were released (*32*) (*3*, *16–18*). If newer agents have also been more habitat-specific (that is, unable to survive in native forest), this could partly explain the lack of recently introduced parasitoids in our sample. However, it is possible that *M. laphygmae* and *C. marginiventris* are such dominant members of the community that agents introduced more recently have simply failed to compete with them in the extreme environmental conditions of the Alakai Swamp. Although it is impossible to fully understand the dynamics of this system after only 2 years of study, there is little doubt that the community structure has been altered considerably from its original state.

Increasingly, biological control is being considered for use in conservation as well as agriculture (*33*, *34*). There are clearly important environmental benefits to this practice, as agents may control invasive alien plants or insects that, unchecked, may cause irreparable damage to native communities (*35*). However, this study underscores the critical importance of determining whether the potential damage caused by an introduced agent would be as extensive as that caused by the target pest species (*33*, *36*).

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21. Seven species in the geometrid genus *Scotorythra*, at least five species in the oecophorid genus *Thyrocopa*, and at least three species in the tortricid genus *Pararrhaptica* were combined into three species complexes in the webs, because they are all generalist feeders that are indistinguishable as larvae, when parasitoids emerge and kill them. All other caterpillars could be identified to species.
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