CHAPTER 10
Cases of biological control restoring natural systems

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The value of case histories

Here we present case histories of selected invasive insects and plants, discussing the damage they caused to native species, ecosystems, or biodiversity and why biological control was the approach chosen to attempt to reverse their effects. Cases have been chosen to include both examples in which biological control was successful and examples in which it failed. We also discuss several projects still in progress against pests of natural areas. Cases chosen focused on those in which the invasive species’ impact on biodiversity or ecosystem function was high. Case histories provide insight into how natural enemies work, what problems might arise and preclude success, and how outcomes can be measured. Assessing the likelihood of non-target impacts of the biological control agents is not the focus of this chapter (rather, see Chapters 5 and 7). Similarly, while control of the invader per se is sometimes not sufficient for ecosystem restoration, which may require replanting of missing native plants or re-introduction of missing native animals, it is a critical first step that must precede such further efforts and is the focus here. For most chapters, one or more authors were among the scientists who carried out the biological control project and thus have personal familiarity with the events discussed.

Successes

These projects clearly met their ecological goals. In each case we discuss the ecological values at risk, the evidence for successful protection of these values, and any known evidence of unintended damage to the native ecosystem from the agents released.

Everglades preservation through biological control of Melaleuca quinquenervia

Paul D. Pratt, Ted D. Center, Min B. Rayamajhi, Phil W. Tipping, and Mary Purcell

Located in a transition zone between temperate and tropical ecosystems, the Florida Everglades is a 500,000 ha subtropical freshwater wetland (Craft et al., 1995). The topography is flat with a slight elevation change from the north to the south of only about 3–5 cm/km, creating a slowly southward-flowing system (ca. 0.8 km/d) emanating from the
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southern end of Lake Okeechobee and terminating in the mangrove estuaries of Florida Bay (Kushlan, 1990). It is one of the largest freshwater marshes in North America and the largest single body of organic soils in the world (Loveless, 1959), encompassing marshes, sloughs, wet prairies, and tree islands. The global importance of the Everglades is reflected in its designations as an International Biosphere Reserve, a World Heritage Reserve, and a Wetland of International Importance (Maltby and Dugan, 1994).

Everglades plant communities contain species from both tropical (primarily Caribbean) and temperate floras along with many endemic species (Gunderson, 1994). These communities are largely defined by their hydrology, that is, the depth and duration of inundation (hydroperiod), which is governed by slight differences in elevation. Sawgrass (*Cladium jamaicense* Crantz), the quintessential Everglades plant community, covers about 70% of the area, either as a monoculture or intermixed with other emergent species (Loveless, 1959). Shallow-water sloughs, which traverse sawgrass marshes, are flooded year round and are dominated by floating and emergent aquatic species. Tree islands (small areas of higher elevation with diverse trees) are interspersed within a matrix of shorter vegetation, primarily sawgrass prairie (Rader and Richardson, 1992). Upland, drier habitats include tropical hardwood hammocks and pinelands (Gunderson, 1994).

Historically, Everglade habitats were drier in winter and wetter in summer. Drainage and water conservation programs, however, have largely reversed this pattern by retaining water during dry periods and discharging water through drainage canals during high rainfall events to meet urban and agricultural needs (Rader and Richardson, 1992). This reversal significantly harmed the flora and fauna and increased community susceptibility to invasion by non-indigenous species (Doren et al., 2009). Adjacent urban neighborhoods provide staging areas for the invasion of many non-native plant and animal species into Everglade ecosystems (Bodle et al., 1994; Gordon, 1998). While many of these invaders are seemingly benign, some are transformer species capable of altering the structure and function of the systems they invaded (Williamson and Fitter, 1996). The Australian tree *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtales, Myrtaceae) is one such example owing to its ability to alter ecosystem structure and function (Gordon, 1998).

*Melaleuca quinquenervia* is native to northeastern Australia, New Caledonia, and parts of New Guinea. It has been present in south Florida (Figure 10.1) since the late

![Figure 10.1 Melaleuca island in an invaded wetland. Photo courtesy of Francois Laroche, South Florida Water Management District. (See insert for the color representation of this figure.)](image-url)
nineteenth century (Dray et al., 2006), and dispersal was assisted by nurserymen who are believed to have spread seeds deliberately into natural areas as a means of propagation (Austin, 1978). The US Army Corps of Engineers planted trees in the marshes of Lake Okeechobee during 1938–41 to create offshore tree islands to protect the southern levee from erosion (Dray et al., 2006). Altered hydrology from flood control and drainage projects during the 1950s undoubtedly contributed to the tree’s invasion success. Stand coverage expands exponentially after initial colonization of suitable habitat (Laroche and Ferriter, 1992) so, by the late 1990s, Melaleuca infested about 200,000 ha and the Everglades was at risk of being totally overwhelmed (Laroche, 1998).

Although data are scant and some of the putative effects are dubious (e.g., increased transpiration [Allen et al., 1997]), M. quinquenervia clearly alters the vertical structure of plant communities, recruitment of native species, light availability, soil biogeochemistry, and nutrient availability (Gordon, 1998; Turner et al., 1998; Martin et al., 2009). Another negative ecological consequence of the plant’s introduction is its effect on Everglade fire regimes. Sawgrass marshes are shallow-water communities that are well adapted to fire. They recover quickly after burning so long as water levels in the soil are not too deep and the organic soils do not burn (Kushlan, 1990; Lodge, 2004). However, M. quinquenervia, by virtue of its thick corky bark, also resists fire. Fires fueled by stands of this tree are very different in character from those fueled by sawgrass. In dense M. quinquenervia stands, flames are quickly and explosively carried into the canopy as volatile essential oils in the foliage ignite (Flowers, 1991). These crown fires are extremely hot, kill other mature trees (pines and cypress), and ignite underlying muck soils, which can burn for weeks. The intense heat kills sawgrass and other native plants that normally survive the cooler ground fires that often occur in sawgrass-dominated areas. Intense fires induce massive seed release from M. quinquenervia, which retains seeds in persistent serotinous capsules on branches with individual trees storing millions of viable seeds (Rayamajhi et al., 2002). Lacking competition and surface litter, the dense carpets of M. quinquenervia seedlings that emerge prevent establishment of other plant species (Wade, 1981) (Figure 10.2). These recruitment events often give rise to nearly pure stands of mature trees with densities of up to 10,000 mature trees/ha (Rayamajhi et al., 2006, 2009).

Figure 10.2 Few to no plants can survive in the sterile habitat under melaleuca stands. Photo credit, Paul Pratt, USDA/ARS. (See insert for the color representation of this figure.)
Community transformation by *M. quinquenervia* in long-hydroperiod areas is driven by melaleuca’s ability to accelerate soil accretion. As mentioned above, slight elevation differences determine hydroperiod durations and lead to large differences in plant communities. Individual *M. quinquenervia* trees growing in flooded environments produce adventitious “water” roots surrounding the base of the trunks up to the water line (Gomes and Kozlowski, 1980; Myers, 1983; McJannet, 2008). These roots directly add to the organic accumulation at the base of the tree, while also binding soil and trapping sediments (McJannet, 2008). In addition, litterfall adds as much as 12–25 MT/ha of undecomposed organic matter, which accumulates on the forest floor (Rayamajhi et al., 2010), leading to increased soil elevation. Soil accretion inevitably produces shorter hydroperiods over extensive areas, thus creating conditions conducive to further invasion. This “legacy effect” persists long after the trees are removed, so that while site rehabilitation may be possible, restored sites continue to differ, in varying degrees, from pre-invasion conditions.

Alarm over the deterioration of the Everglades led to a widespread desire to preserve and restore the system. Re-establishment of hydrological regimes was widely recognized by engineers as an essential foundation of restoration. However, biologists argued that correcting water flow patterns alone would not restore ecosystem function (Weaver, 2000) without addressing the invasive species problem (Doren et al., 2009). Chief among these was the need to reduce the effects of *M. quinquenervia*. Accordingly, a task force was assembled during the late 1980s to formulate a plan to reduce infestations of *M. quinquenervia*. This plan included biological control as one component of an overall management strategy. The plan called for traditional weed control measures (e.g., herbicide applications and mechanical harvesting) to remove the massive standing biomass and thus eliminate the tree from infested areas. However, anything done to kill the trees caused seed capsules to desiccate, resulting in mass seed releases, thus exacerbating the problem. To impede the re-invasion of cleared areas and to slow the rate of spread to new areas, a biological control program was designed with a primary goal of inhibiting stand regeneration. The biological control program, therefore, required herbivores that could prevent seed production or increase mortality of seedlings and saplings.

Preliminary surveys to find suitable candidate species for introduction against *M. quinquenervia* began in 1986, but the most intensive faunal studies were done from 1989 to 1995, when more than 400 species of plant-feeding insects were recorded in field surveys (Center et al., 2012). Based on study of these insects and selection of species deemed both safe and potentially effective (for the goals described above), three biological control agents were released and established against the exotic tree in Florida: the weevil *Oxyops vitiosa* Pascoe (Figure 10.3), the psyllid *Boreioglycaspis melaleucae* Moore, and the gall midge *Lophodiplosis trifida* Gagné.

*Oxyops vitiosa* established readily at dry and seasonally wet sites but establishment failed at permanently flooded sites (Center et al., 2000). Initially, the weevil dispersed relatively slowly (Pratt et al., 2003), but it is now widely distributed (Balentine et al., 2009). Populations increased at rates comparable to other effective weed biological control agents but were influenced by availability of young shoots (Pratt et al., 2002, 2004). Damage to the stem tips dramatically reduced flowering and seed production (Pratt et al., 2005; Tipping et al., 2008). Coppicing from stumps was severely curtailed (Center et al., 2000), growth of saplings was markedly reduced, and termination of apical growth produced a bushier shape (Tipping et al., 2008). However, larvae became abundant mainly during winter and spring, coincident with seasonal production of young foliage (Center et al., 2000; Pratt et al., 2004). This allowed some “escape” at other times of the year. After attainment of large populations, weevils

Figure 10.3 The melaleuca weevil, *Oxyops vitiosa*, destroys seed production by more than 95%. Photo courtesy of Steve Ausmus, USDA/ARS. (See insert for the color representation of this figure.)
regularly moved into flooded sites, causing significant damage. Although many fully grown larvae drowned, some managed to find pupation sites, allowing small populations to persist in permanently wet habitats (Center, pers. obs.).

The psyllid *B. melaleucae* (Figure 10.4) established quickly (Center et al., 2006) and dispersed rapidly throughout the range of *M. quinquenervia* in Florida. Populations spread at a rate of approximately 7 km/year and are now widely distributed (Balentine et al., 2009). Enormous populations developed during the spring dry season in all habitat types, but populations declined during the summer rainy season. This was probably more of an effect of high temperatures rather than of precipitation (Chiarelli et al., 2011). Psyllids caused high mortality of seedlings and premature leaf drop from mature trees (Franks et al., 2006; Morath et al., 2006). Mortality of coppicing stumps also increased in conjunction with infestations of *O. vitiosa* (Center et al., 2007).

The stem-galling midge *L. trifida* was initially released at 24 sites distributed throughout southern Florida in *M. quinquenervia* stands of varying sizes and hydrology. Both small and large numbers of individuals were used in an attempt to determine an optimal release strategy. Establishment was universally successful (Pratt et al., 2013). Areas where *M. quinquenervia* stands were regenerating from seed or coppicing stumps were heavily galled with a high percentage of the plants being killed, possibly because of interactions with fire or frost. While galls occurred most abundantly in the lower strata, they were also found as high as 13 m in the upper canopy (Pratt et al., 2013). Dispersal occurred at 20 km/year.

Various metrics can be used to quantify the cumulative efficacy of the introduced *Melaleuca* biological control agents. The program’s primary objective was to curtail seed production, and the introduced herbivores met this goal by reducing the tree’s reproductive capacity by as much as 99% (Pratt et al., 2005; Tipping et al., 2008). Seed suppression improved cost efficiency of conventional control tactics because post-herbicide follow-up treatments to remove recruited seedlings were less costly or unnecessary. *Melaleuca*-infested lands adjacent to cleared sites previously provided seed sources for re-invasion and were often inaccessible to land managers, but attack by introduced herbivores markedly limited seed movement into treated areas (Tipping et al., 2012).

Equally as important, no significant feeding on non-target species occurred (Center et al., 2007; Pratt et al., 2009, 2013). Reductions in reproduction and recruitment led to change in the population growth rate of *M. quinquenervia* in Florida. A demographic analysis of seven different *M. quinquenervia* stands showed negative regional population growth rate (Sevillano, 2010), indicating that mortality rates now outpace recruitment. These findings

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**Figure 10.4** (a). The melaleuca psyllid, *Boreiglycaspis melaleucae* Moore (adult) was the second agent released. Photo courtesy of Steve Ausmus, USDA/ARS. (b). Psyllid flocculence, showing a colony of the insect. Photo credit, Paul Pratt, USDA/ARS. (See insert for the color representation of this figure.)
were further confirmed by a five-year study that found ca. 50% reduction in seedling and sapling density as a result of chronic feeding by the introduced herbivores (Tipping et al., 2009). In a third study, it was found that feeding by natural enemies accelerated mortality rates of *M. quinquenervia* growing in dense monocultures (Rayamajhi et al., 2007). Most importantly, this decline in melaleuca density was associated with a concurrent fourfold increase in plant species diversity within the study area (Rayamajhi et al., 2009) (Figures 10.5, 10.6).

Overall, this biological control program provided a sustainable pathway to the restoration and conservation of a unique ecosystem. Because *M. quinquenervia* has been suppressed at both the individual and population levels, habitat disturbances (fire intensity/frequency and soil accretion) will be mitigated as tracts of lands are revegetated by native species. Although full implementation of the restoration plan will take decades, it is clear that biological control has been a critical and necessary component in the conservation and restoration of the Florida Everglades.

**Recovery of native vegetation in New Zealand forests following control of mist flower**

Simon Fowler

Mist flower, *Ageratina riparia* (Regel) R. King and H. Robinson, was a weed in the northern part of North Island (New Zealand) in forest margins, open places, poorly managed pasture, wetlands, and river systems (Barton et al., 2007). Along tracks and riparian areas in native forests it was capable of forming large, dense mats of semi-woody stems that smothered native plants and prevented forest regeneration (Barton et al., 2007). In two specific examples, mist flower was a threat to the survival of two endemic plants, *Hebe bisho-piana* (Petrie) Hatch and *H. acutiflora* Cockayne (Figure 10.7) (Barton et al., 2007). Mist flower was controlled biologically in Hawaii in the 1980s, and research indicated the program could be transferred to New Zealand (Morin et al., 1997).

Figure 10.5 Recovery of native vegetation in a melaleuca-dominated plot, following successful biological control, of melaleuca; note the dead trees and open canopy. Photo courtesy of Min Rayamajhi, USDA/ARS. (See insert for the color representation of this figure.)
Releases of the white smut fungus *Entyloma ageratinae* Barreto and Evans began in New Zealand in 1998 and were followed by release of the gall fly *Procecidochares alani* Steyskal in 2001 (Barton et al., 2007). The monitoring results from 1998 to 2003 presented here are summarized from Barton et al. (2007) with a 10-year update in 2008 (Landcare Research, unpublished data). Infection of mist flower by the fungus increased dramatically in the first few years after its release, peaking at a mean of 67% of live leaves with lesions. Ten years after release the mean percentage of live leaves infected by the fungus was still 55% despite very large reductions in the

![Figure 10.6](image-url) Decline in melaleuca density and increase in species diversity as biological control agents exerted their effect at a Florida research site. Unpublished data of Paul Pratt and Min Rayamajhi.

![Figure 10.7](image-url) Control of mist flower (*Ageratina riparia*) by the introduced white smut fungus, *Entyloma ageratinae*, showing the same location (a) about a year after fungus release when plants were infected but not yet killed (January 27, 2000–summer) and (b) two years later when mist flower shrubs had died and been replaced by mostly native vegetation, particularly ferns and grasses (November 8, 2001–spring); site is Brookby on the edge of the Hunua Ranges (an important water catchment and biodiversity area, just southeast of Auckland, New Zealand), and (c) endangered New Zealand endemic plant, *Hebe acutiflora* Cockayne, no longer threatened by mist flower. Photos courtesy of Jane Barton/Landcare Research (a, b) and Gillian Crowcroft (c). (See insert for the color representation of this figure.)
percentage cover of mist flower. The gall fly, released three years after the fungus, spread more slowly than the fungus and had a much less dramatic impact on the target weed. However, two years after release it had reached a mean level of 1.96 galls/stem. In 2008, mean attack levels of 0.57 and 2.29 were measured in two areas. All these levels of attack for the gall fly were above the mean level of 0.46 galls/stem reported in Hawaii as contributing to mist flower suppression (Hapai, 1977; Barton et al., 2007). By 2008, mean plant height was reduced by 33% (compared to 1998) and the percentage of nodes showing regrowth to <2%, showing that the weed did not have the capacity through compensatory growth to overcome the agents’ attack. In plots selected for high levels of mist flower infestation, mean percentage cover declined from >80% in 1998 to 1.5% in 2003. In randomly selected plots, mist flower cover was 6.1% in 1999, 0.86% in 2003, and 0.1% in 2008.

Mean species richness of native plants was initially 9.3 per plot where cover of mist flower was ≥70%, which was lower (by 44%) than the mean of 16.5 in paired plots that had not been invaded by mist flower. Between 1998 and 2003, the mean percentage cover of mist flower in the plots invaded by the weed decreased to 1.5%. Over the same period, both the species richness and percentage cover of native plants increased, and by 2003 these measures did not differ significantly from those in the paired plots that had never been invaded by mist flower. In contrast, there were no significant differences in the species richness or percentage cover of exotic plants species (excluding mist flower) between plots that were originally invaded by the weed and plots that had never been invaded. Many plant species colonizing the plots were important native mid- or late-successional shrubs or trees. The exotic plant species common in the plots were mostly not weeds that threatened native forest habitats. An exception was African club moss, Selaginella kraussiana (Kunze) A. Braun, which was invading the plots, and appeared to reduce the species richness of native plants. However, S. kraussiana was also invading the plots that had never had any mist flower present, and where mist flower had been suppressed by the fungus there was only a weak, non-statistically significant, “replacement weed effect.”

Both of the endemic New Zealand plant species threatened by mist flower, H. bishopiana and H. acutiflora, are now considered under reduced threat because of the successful biological control of mist flower (P. de Lange, pers. comm.).

Protecting Galápagos plants from cottony cushion scale

Charlotte Causton, Mark S. Hoddle, and Roy G. Van Driesche

The Galápagos archipelago, a UNESCO World Heritage Site and Biosphere Reserve, is renowned for its unique fauna and flora. Geographic isolation and ongoing seismic and volcanic activity have led to the evolution of many species found nowhere else in the world, including 180 flowering plants and ferns. Galápagos plants, like other endemic species in the archipelago, however, are facing an increasingly uncertain future because of threats from invasive species and diseases (Gardener and Grenier, 2011). Three plant species are already extinct, and according to a 2006 evaluation using the threat categories of the International Union for Conservation of Nature (IUCN), more than half of the endemic plant species are in serious decline with at least 20 species facing possible extinction (Tye, 2008). Sixteen of these critically endangered species are restricted to the inhabited islands, which are undergoing severe ecological change as a result of invasive species (Tye, 2008).

Endemic Galápagos plants and other indigenous plants of conservation value are at high risk from invasive herbivorous insects, particularly the cottony cushion scale, Icerya purchasi Maskell (Hemiptera: Monophlebidae) (Figure 10.8), a cosmopolitan plant pest native to Australia and possibly New Zealand. Most widely known as a pest of citrus, this scale insect feeds on over 200 different plant species (Caltagirone and Doutt, 1989; Causton, 2001). Known locally as “el pulgon,” it was first

![Figure 10.8 White mangrove infested with cottony cushion scale. Photo credit, Mark Hoddle. (See insert for the color representation of this figure.)](image-url)
discovered in the Galápagos Islands in 1982, where it was probably accidentally imported on plant material from mainland South America. Within 14 years of its discovery, this scale insect had spread by wind currents and the inter-island movement of plants to 15 of the 18 larger islands and had affected the growth and survival of many plant species of importance (Causton, 2001; Causton et al., 2004). High density *I. purchasi* populations can be especially damaging to native plants with restricted ranges, such as those found in the Galápagos Islands. Immature and adult *I. purchasi* cause damage directly to host plants by sucking sap and removing nutrients, and indirectly through the excretion of a sticky honeydew, which provides a substrate for black sooty molds that grow on leaves and stems disfiguring plants and preventing photosynthesis. Honeydew, a rich carbohydrate source, is also highly attractive to invasive ants (including the little fire ant, *Wasmannia auropunctata* [Roger], and the tropical fire ant, *Solenopsis geminata* [Fabricius]), which harvest this waste product for consumption and in turn help scale insect populations thrive by defending scale colonies from predators and transporting them between plants (Causton, 2001; Hoddle et al., 2013).

To prevent further damage to plants of conservation value, in 1996 conservation scientists at the Charles Darwin Foundation and Galápagos National Park Service managers formed a Technical Advisory Committee to evaluate the threats of the *I. purchasi* invasion and to develop a management strategy for the scale’s control. Surveys across islands indicated that high-density populations of *I. purchasi* were restricting plant growth and possibly killing individuals of at least 62 native and endemic plant species, 16 of which were listed as threatened in the IUCN Red List of Threatened Species, including six Endangered or Critically Endangered species (Causton, 2001; Causton et al., 2004). Of particular concern was the high mortality reported on the native white mangrove (*Laguncularia racemosa* [L.] Gaertn. F.) (Figure 10.8), an important refuge for native freshwater and terrestrial invertebrates, and some birds, including the critically endangered mangrove finch, *Camarhynchus heliobates* Gould, which is restricted to small pockets of mangroves on the western coast of Isabela Island (Fessl et al., 2010). Experimental trials, in which potted plants were artificially infested with *I. purchasi*, confirmed that this scale insect was having a measurable impact on the leaf, shoot, and root growth of white mangrove and at least two other native plant species in the Galápagos Islands (*Acacia macracantha* Humb. & Bonpl. ex Willd. and *Phaseolus mollis* Hook f.) and was likely damaging others (Causton, 2001).

Several endemic daisy genera unique to Galápagos (*Darwiniothamnus* and *Scalesia*) (Figure 10.9) also appeared

![Figure 10.9](image-url)
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to be heavily damaged by *I. purchasi*, including nine threatened species (Causton, 2001; Calderón Alvarez et al., 2012). Moreover, studies suggested that the damage caused by *I. purchasi* was affecting endemic plant-feeding Lepidoptera that are specialist feeders on some of these endemic plant species. For example, the local extirpation of three species of endemic Lepidoptera (*Platyptilia vilema* B. Landry, *Semiothisa cerussata* Herboulot, *Tebenna galapagoensis* Heppner & B. Landry) associated with *Darwiniothamnus tenuifolius* (Hook. f.) Harling (Darwin’s Aster) on Alcedo Volcano may have been caused by *I. purchasi*-induced mortality of plants (Roque-Albelo, 2003).

The Technical Advisory Committee concluded that there was enough evidence to show that *I. purchasi* was having a significant impact on Galápagos ecosystems. Following an evaluation of management options, the committee decided that classical biological control using the coccinellid beetle *Rodolia cardinalis* Mulsant (Figure 10.10), a natural enemy of *Icerya* in its native range and a biological control agent used globally for the control of this pest in citrus (Bartlett, 1978), offered the best prospect for reducing the impact of *I. purchasi* on Galápagos plants. Biological control was considered to be the best option as it was the only management tool that was likely to cause a permanent and widespread suppression of this pest throughout the archipelago on both inhabited and uninhabited islands with minimal risk to non-target species. Studies in agricultural systems where *R. cardinalis* had been deliberately introduced (e.g., California) (Quezada and DeBach, 1973) and in its native range (Prasad, 1989) suggested that the beetle has a high degree of host specificity and can be very effective at suppressing *I. purchasi* populations. Nevertheless, the deliberate importation and release of an exotic species that had the capacity to spread unassisted throughout the Galápagos Archipelago, a World Heritage Protected Area with a wealth of endemic species, was controversial (Causton, 2009). Rigorous host-specificity trials were considered necessary to determine whether the introduction of this beetle would pose risks to native and endemic insects.

In 1999, *R. cardinalis* was imported from Australia into a quarantine facility at the Charles Darwin Research Station for feeding trials. In quarantine, 16 insect species from three different orders (Hemiptera, Coleoptera, and Neuroptera) and nine families (Ortheziidae, Monophlebidae, Pseudococcidae, Eriococcidae, Coccidae, Diaspididae, Aphididae, Coccinellidae, and Chrysopidae) were tested for their suitability as prey for larvae and adults of *R. cardinalis*. The native species tested included those presumed to be at high risk of being preyed upon by *R. cardinalis* (Causton et al., 2004). Studies were also carried out to eliminate the possibility of toxic effects of the beetles on birds that might feed on them. This risk exists because some species of coccinellids produce a defensive fluid that contains an alkaloid that can be toxic to some vertebrates if ingested (e.g., Pasteels et al., 1973). Ornithologists were concerned that Darwin’s finches and other passerines could be at risk should they consume *R. cardinalis* (Lincango et al., 2011). The results of these studies and a risk analysis suggested that *R. cardinalis* would not present a significant threat to either non-target insects or insectivorous birds (Lincango et al., 2011).

Following rigorous review, the Galápagos National Park Service approved release from quarantine, and between 2002 and 2005, 2206 *R. cardinalis* were released onto 10 different islands in the archipelago. This was the first time that Galápagos authorities had approved the introduction of a biological control agent. Follow-up studies soon after its introduction were considered important to document results for local stakeholders and community members who had participated in the release program. Directly after the release of *R. cardinalis*, a predator exclusion study and field observations were carried out on scale insect populations on white mangrove (*L. racemosa*) on Santa Cruz Island to document impact (Calderón Alvarez et al., 2012). In addition to this study, local residents and high school students participated in surveys to detect *R. cardinalis* on host plants in different habitat zones on Santa Cruz.

![Figure 10.10](image-url) Adult *Rodolia cardinalis* preying on cottony cushion scale. Photo credit, Mark Hoddle. (See insert for the color representation of this figure.)
In less than three months after *R. cardinalis* was released, populations of *I. purchasi* on white mangrove that were exposed to the predator in the exclusion experiment, or were monitored in the field, had declined by 99–100% (Calderón Alvarez et al., 2012). Results suggested that *R. cardinalis* played a key role in this decline, possibly in combination with high rainfall that occurred around the same time. The coccinellid was also found on 10 other host plants infested by *I. purchasi* and by 22 weeks it had spread to the other side of Santa Cruz Island (45 km) and to the neighboring island of Baltra (separated from the northern coast of Santa Cruz by an ocean channel approximately 200 m wide) without human assistance (Calderón Alvarez et al., 2012).

In October 2009, seven years after the release of *R. cardinalis*, the biological control program was evaluated more fully to determine if there was successful continued suppression of the target pest, *I. purchasi*, and whether there had been any non-target impacts (Hoddle et al., 2013). The evaluation was carried out over two years and had three major objectives: (1) to survey islands for the presence of *I. purchasi* and *R. cardinalis* in urban, agricultural, and natural areas; (2) to measure the degree of suppression of *I. purchasi* by *R. cardinalis*; and (3) to investigate under field-like conditions the hypothesis that *R. cardinalis* has a limited prey range as predicted by quarantine laboratory studies. Results from this evaluation indicated that *R. cardinalis* survived and spread after its introduction in 2002. It is now widely present in many areas and habitats on at least six islands where it was released, and without purposeful human assistance it has colonized two other islands infested with *I. purchasi*. Furthermore it is found on a wide range of the plants infested by *I. purchasi* in the archipelago (at least 48 of the 112 known host plants) (Calderón Alvarez et al., 2012).

Monthly monitoring over a two-year period on Santa Cruz and San Cristóbal Islands in relatively undisturbed habitats (five study sites) and in a disturbed habitat (one study site) suggested that overall most *I. purchasi* populations were low and that *I. purchasi* has been suppressed to non-damaging levels on several important native host plants, including white mangrove, several *Acacia* species, *Waltheria ovata* Cav., *Prosopis juliflora* (Sw.) DC., and *Parkinsonia aculeata* L. (~60–98% reduction in *I. purchasi* densities depending on host plant and habitat when compared to comparably assessed pre-*Rodolia* pest densities) (Hoddle et al., 2013). For example, before the release of *R. cardinalis*, white mangroves were heavily infested with *I. purchasi*. Following the release of *R. cardinalis* in 2002, *I. purchasi* populations declined on white mangroves (Calderón Alvarez et al., 2012) and continued to be very low on white mangroves over the two-year survey period between 2009 and 2011 (Hoddle et al., 2013) (Figure 10.11).

In some areas and on certain host plants, *I. purchasi* populations persisted at higher densities. The most noteworthy was the *I. purchasi* infestation on sea grape, *Scaevola plumieri* (L.) Vahl, at Tortuga Beach, Santa Cruz Island. At that study site, *I. purchasi* was always present, but the percentage of infested plants increased and decreased over the two-year survey period. As pest densities increased, *R. cardinalis* populations rebounded, and approximately two to six months later *I. purchasi* populations would decline again as predator populations peaked. Other notable exceptions existed when honeydew-collecting ants were present and guarded *I. purchasi* from *R. cardinalis* (Hoddle et al., 2013).

The feeding preferences and predation behavior of *R. cardinalis* were evaluated in a large walk-in field cage (Figure 10.12) at the Charles Darwin Research Station, October–December 2009. The cage held potted native plants (e.g., *P. aculeata*, *Gossypium* spp., *Acacia macroacantha* Humb. & Bonpl. ex Willd., and *W. ovata*) that were infested with *I. purchasi* (the target) and non-target prey species (e.g., *Coccus viridis* [Green], *Ceroplastes* spp., mealybugs, aphids, and spider mites). Thirty starved
Field-collected or laboratory-reared adult *R. cardinalis* were released individually into the cage and their foraging behaviors and prey choices were recorded visually for up to 60 min. There was no evidence of attack by free-ranging *R. cardinalis* adult beetles on non-target insects during more than 22 h of behavioral observations, and all recorded predation was solely on *I. purchasi*, the intended prey species of the biological control project. Furthermore, during separate field surveys, no evidence was found of *R. cardinalis* attacking non-*Icerya* prey species, even when non-target insect species were in close proximity to *I. purchasi* (Figure 10.13) (Hoddle et al., 2013). These results suggest that this program is unlikely to have had any significant adverse impact on non-target invertebrate fauna in the Galápagos Islands.

From the results of two years of population monitoring of *Icerya* in several distinct habitats of the Galápagos Islands, it appears that *I. purchasi* populations are being maintained at relatively low densities and are lower than those observed before the release of *R. cardinalis*. The level of control, however, depends on the plant species, habitat, season, and possibly on tending by invasive ants. The biological control program is successfully suppressing pest populations below non-damaging levels on many plant species in the Galápagos Islands, which in turn should facilitate restoration of the affected native ecosystems. Most noteworthy is the complete recovery of stands.

**Figure 10.12** Walk-in field cage (right) stocked with native plants and adult *Rodolia cardinalis*. Photo credit, Mark Hoddle. (See insert for color representation of this figure.)

**Figure 10.13** *Rodolia cardinalis* larva faced with a choice: cottony cushion scale or *Ceroplastes* sp. scale (top), attacks the cottony cushion scale (bottom). Photo credit, Mark Hoddle. (See insert for the color representation of this figure.)
of white mangroves on Santa Cruz Island that were severely damaged by *I. purchasi* and were declining before the introduction of *R. cardinalis* (Van Driesche et al., 2010). Populations of Darwin’s aster, *D. tenuifolius*, also appear to be recuperating on the flanks of Alcedo Volcano according to observations by park rangers. Continued monitoring will allow us to understand better the benefits of this biological control program, but in the meantime, the results from rigorous studies before release, as well as considerable post-release assessment, show that biological control was an effective and safe tool for managing invasive species in natural ecosystems of high conservation value.

**Preserving Hawaiian dry forests by protecting wiliwili trees from erythrina gall wasps**

Leyla Kaufman and Russell H. Messing

Hawaii’s dryland forests were once a source of great biotic diversity, hosting over 20% of all native plants in the Hawaiian Islands (World Wildlife Fund, 2013). However, impacts such as fire, grazing, agricultural and pasture development, and invasive weeds and ungulates have decimated these ecosystems. It is estimated that over 90% (and perhaps as much as 99%) of Hawaii’s dry forest habitat has been lost (Cabin et al., 2000), and more than 25% of the species in this ecosystem are on the Federal Endangered Species List. Nevertheless, there is still hope for the preservation and recovery of some of these native communities, and many dryland restoration projects are in progress (Allen, 2000).

In the remaining stands of native dry forest, the endemic coral tree, or wiliwili (*Erythrina sandwicensis* O. Deg.) is a major overstory tree (Figure 10.14). It was once a dominant component of ancient endemic Hawaiian dryland forests. It is one of the few native trees in Hawaii that are deciduous, regularly losing its leaves during the summer in order to conserve water, and putting out new leaves in the fall. It grows up to 15 m tall, on leeward slopes of all the main islands, at elevations from sea level to just over 600 m. The trees form nitrogen-fixing symbioses with *Bradyrhizobium* species, thus naturally enriching forest soils.

**Figure 10.14** Remnant patch of lowland dry forest, with wiliwili tree, *Erythrina sandwicensis*, in foreground at Puuwaawaa, Big Island, Hawaii. Photo credit, Leyla Kaufman. (See insert for the color representation of this figure.)
The wiliwili tree played an important role in native Hawaiian culture, and it is mentioned in many Hawaiian legends and proverbs. Its wood was used for surfboards, canoe outriggers, and fish net floats, and the bright red seeds were used for making leis (Wagner et al., 1990). Currently, however, the wiliwili is subject to sustained competitive pressure from non-native plants (such as *Pennisetum setaceum* [Forssk.] Chiov., *Melia azedarach* L. and *Grevillea robusta* A. Cunn. ex R. Br.), seed predation by an exotic bruchid weevil (*Specularius impressithorax* [Pic]), and herbivory by introduced ungulates.

Recently, the invasive Erythrina gall wasp, *Quadrastichus erythrinae* Kim (Hymenoptera: Eulophidae), (Figure 10.15) emerged as a new, serious threat to the endemic wiliwili and, by extension, the web of endangered native plants, birds, and insects that inhabit remaining stands of dryland forest (Heu et al., 2005). This species, which invaded Hawaii in 2005, was first described based on specimens from Mauritius, Reunion, and Singapore. The gall wasp occurs in East Africa, although its exact native range remains unknown (Rubinoff et al., 2010). Within a few months of its arrival in Hawaii, the gall wasp colonized all major islands, causing widespread damage to endemic *E. sandwicensis*, as well as exotic species of *Erythrina* occurring on the islands (Messing et al., 2009). The exotic ornamental *Erythrina variegata* L. was an important component of Hawaii’s urban landscape; but since the gall wasp invasion, the City and County of Honolulu have had to remove over 1000 dead *Erythrina* trees.

*Figure 10.15* Adult of erythrina gall wasp, *Quadrastichus erythrinae* (left, photo courtesy of M. Tremblay) and galled leaves from Koko Crater (right, photo credit, Leyla Kaufman). (See insert for the color representation of this figure.)
Female gall wasps deposit eggs in leaves, petioles, stems, inflorescences, and young seed pods, where subsequent larval feeding induces gall formation, which in heavy and or chronic infestations leads to defoliation and tree mortality (Kim et al., 2004; Heu et al., 2008). Given the extent of damage, dramatic reduction in flowering owing to high stress, and the fact that tree mortality was observed within a few months of the invasion, University of Hawaii researchers and staff at the Hawaii Department of Agriculture initiated efforts to search for biological control agents in Africa (Figure 10.16). In 2006, two agents were successfully reared and maintained under quarantine conditions in Hawaii: *Eurytoma erythrinae* Gates and Delvare (Hymenoptera: Eurytomidae) (Figure 10.16) and *Aprostocetus nitens* Prinsloo and Kelly (Hymenoptera: Eulophidae). These species were also previously unknown and were subsequently described by Gates and Delvare (2008) and Prinsloo and Kelly (2009), respectively.

After host-specificity testing and risk assessment were completed, *E. erythrinae* was released in November 2008. Female *E. erythrinae* lay their eggs in galled tissue, where the larvae feed externally on gall wasp larvae and pupae. Each *E. erythrinae* consumes 1 to 5 hosts to complete its larval development and then pupates inside a gall chamber. Monitoring sites were selected on the islands of Kauai, Oahu, Maui, and Hawaii. Pre-release monitoring data were collected for six months, and post-release evaluation continued for five years (through 2013). Several different monitoring techniques were used to assess the effectiveness of *E. erythrinae* in controlling gall wasp populations. These included ratings of infestation level in young shoots.
using a 4-point scale (Messing et al., 2009), rearing parasitoids or gall wasps from galls, dissection of galled tissues, tagging and monitoring development of young shoots and inflorescences, and running germination tests on collected seeds.

The biological control agent became well established in the field within three to six months after release. Establishment of the biological control agent took longer at sites that had previously been treated with systemic insecticides; therefore, additional releases were made at those sites. Infestation levels of the gall maker in young shoots decreased significantly at all sites after release of the biological control agent. During the pre-release monitoring period, on average <10% of young shoots were rated as uninfested by the pest gall wasp (i.e., healthy). This figure changed dramatically post-release, with >80% of shoots rated as uninfested by the pest in the fourth year after release. Dissections of galled tissues revealed significant numbers of the biological control agent, confirming that they were indeed responsible for the reduction in foliage infestation levels.

Pest infestation levels in inflorescences also decreased post release, though this was at a slower rate compared to ratings in young shoots and varied significantly among sites. In order to evaluate the level of control, inflorescences were tagged early in the season and followed until mature seed pods were formed. Drier sites exhibited poor control by *E. erythrinae* in inflorescences. At some of these dry sites, 100% of the inflorescences tagged early in the season were rated as infested, with the highest infestation levels occurring at the end of the season. Tagged inflorescences that produced seeds were used in germination tests. Results from these tests showed that levels of infestation in mature seed pods were negatively correlated with germination rate (i.e., the higher the infestation level in seed pods, the lower the germination rate). There was no significant correlation between the level of infestation in seed pods and the number of seeds produced per seed pod; highly infested seed pods sometimes produce similar numbers of seeds as lightly infested or uninfested seed pods.

A census of several wiliwili tree populations conducted across the islands in 2012, four years after the release of the biological control agent, showed that 30–35% of the trees studied died because of the gall wasp invasion. This percentage could have been much higher if the biological control agent had not been released so promptly. Results from the census also showed that younger trees, or trees with smaller diameters, experienced higher mortality rates than trees with greater trunk diameters. Surviving trees exhibited improved health and more trees were able to flower. During our surveys, little-to-no tree recruitment was observed at any site, which may be caused by factors such as poor control by *E. erythrinae* in inflorescences at many sites that renders seeds inviable. Other factors that may also play a role include widespread seed damage by the bruchid *S. impressithorax*, competition with invasive weeds such as fountain grass (*P. setaceum*), or seedling predation by feral ungulates (such as goats, pigs, and deer). The importance of these other factors has yet to be assessed, but if they prove important, it may take more than biological control alone to restore healthy populations of *E. erythrinae* in the Hawaiian Islands. The second biological control agent, *A. nitens*, is still (2014) under quarantine in Hawaii, and tests are being conducted to determine compatibility of the two agents.

In summary, while the biological control project has improved the health status of tree foliage dramatically, seed suppression caused by flower galling remains high. Further study of the system is required to promote recovery of the wiliwili tree at the population level.

**Failures**

**Destruction of Fraser fir by balsam woolly adelgid in Appalachian “sky-island” forests**

Michael E. Montgomery

Fraser fir, *Abies fraseri* (Pursh) Poir., is endemic to the Appalachian Mountains of the southeastern United States. It has a disjunct distribution of only 26,610 ha that is limited to elevations above 1600 m on six massifs in southwestern Virginia, western North Carolina, and eastern Tennessee. It is associated with red spruce, *Picea rubens* Sargent, and these two conifers along with an assortment of northern hardwoods, shrubs, and herbaceous species form the southern Appalachian spruce-fir “sky-island” forests. This unique ecosystem was listed as the second most endangered in the United States (Noss and Peters, 1995). The main threats to the ecosystem are air pollution and the balsam woolly adelgid, *Adelges piceae* (Ratzburg) (Hemiptera: Adelgidae) (Figure 10.17) (Dull et al., 1988).

Three decades after the discovery of *A. piceae* in the southern Appalachians, mortality of Fraser fir ranged from 44% to 91% among the six isolated “sky-island” populations of Fraser fir (Figure 10.18) (Dull et al., 1988).
Figure 10.17  Balsam woolly adelgid on trunk (left) and gouty twigs resulting from twig infestation (right). Photograph by William M. Ciesla, Forest Health Management International, Bugwood.org. (See insert for the color representation of this figure.)

Figure 10.18  Fraser fir killed by balsam woolly adelgid, together with regenerating young trees not yet old enough to be susceptible. Photo credit, Michael Montgomery, USDA Forest Service. (See insert for the color representation of this figure.)
Red spruce is also affected because it cannot survive the high winds that blast higher elevations without the protection of the much sturdier Fraser fir. Without the thick canopy of spruce and fir, the understory dries out, input of coarse woody debris is changed, and the vegetative state is permanently altered (Stehn et al., 2011). Thus, the loss of Fraser fir has a cascading effect on the entire ecosystem.

While it seems unlikely that the Fraser fir will be extirpated, the forest type remains imperiled with an uncertain future. The young, understory fir trees grew rapidly following the initial wave of mortality. Currently, they are producing seed, but are also becoming susceptible to the adelgid (Lusk et al., 2010). Mortality of regrowth trees, however, is patchy, unlike the widespread mortality that occurred earlier. In the first wave of mortality, there was a complete loss of the overstory (McManamay et al., 2011), which caused the previously mesic to wet, much-shaded understory to be exposed to greater solar insolation and desiccating winds, covered only by dense stands of young trees. Air pollution and climate change also place additional stress on this ecosystem; thus, the future of this forest type hinges on the frequency and intensity of these three exogenous disturbances (Stehn et al., 2013).

Although the southern Appalachian spruce-fir forest resembles the northern boreal forests of North America, it differs in the species of spruce and fir, a denser and more diverse understory, and a warmer and wetter climate. Further, it is an ice age relic, a remnant of the vast spruce-fir forest that covered the southern United States during the last ice age, whereas the boreal forest is younger, forming after the retreat of the glaciers. The southern Appalachian spruce-fir ecosystem supports more than 30 endemic plant and animal species, as well as many disjunct species more common in boreal forests (DENR, 2010). Four of these are listed as federally endangered: the Carolina northern flying squirrel, *Glaucomys sabrinus coloratus* Handley; the spruce-fir moss spider, *Microhexura montivaga* Crosby & Bishop; the spreading avens, *Geum radiatum* Michx.; and the rock gnome lichen, *Gymnoderma lineare* (A. Evans) Yosham & Sharp. The ghost moth, *Gazoryctra sciophanes* (Ferguson) (Lepidoptera: Hepialidae), another globally rare taxon, is restricted to these forests and just a few sky islands in West Virginia (USA). Likely there are many additional unknown species of insects that are endemic to this ecosystem, since systematic surveys have been made only for some Lepidoptera (Scholtens and Wagner, 2007) and carabid beetles in the genus *Trechus* (Barr, 1962). The latter is a group of flightless ground beetles restricted to cool, moist microhabitats such as caves, sink holes, moss carpets, and deep humus. Of the several species that Barr (1962) described, sixteen are each restricted to only one or two of the six “sky islands” above 1500 m in the southern Appalachians. The *Trechus* ground beetles are an example of the speciation and diversity that can occur in isolated habitats by species with low dispersal capability.

The balsam woolly adelgid is considered to be native to Europe and was first discovered in North America in 1908 in Maine. It was first detected in the southern Appalachians in 1957, and by 1968 it was in all naturally occurring Fraser fir stands. The adelgid attacks all native North American fir species causing a hypersensitive response at its feeding sites that blocks translocation vessels (Balch, 1952). Feeding on the twigs causes gout (Figure 10.18), whereas feeding on the bole produces “rotholz” deformities. The thin bark of Fraser fir makes it especially vulnerable. In the southern Appalachians, the adelgid has two or three parthenogenic generations each year (Arthur and Hain, 1984). It overwinters as a first instar nymph under the bark or bud scales and becomes active in April, going through two more nymphal instars before becoming an adult, with peak egg laying in mid June. The crawlers that hatch from these eggs find a feeding site, settle, and aestivate until mid July, then resume development and, in mid August, peak production of the second batch of eggs occurs. In developing a biological control strategy for *A. piceae*, it is important to recognize that it has two well separated periods of egg production and that both periods should be targeted.

Biological control programs targeting the balsam woolly adelgid in Canada and the United States began in 1933 and more than 700,000 individuals representing 33 predator species were released before the project ended in 1966 (Montgomery and Havill, 2014). Worldwide, the family Adelgidae has no known parasitoids and no significant diseases. In the southern Appalachians, releases of 2914 individuals of 22 predator species were made from 1959 through 1966 (Amman, 1961; Amman and Speers, 1964, 1971). At the end of the program, the species considered to be established in both Canada and the United States were...
Aphidecta obliterata (L.), Aphidoletes thompsoni (Moehn), Crematogaster nigrocellulata Czerney, Laricobius erichsonii Rosenhauer, Neoleucopis obscura Haliday, and Symmyrus impexus (Mulsant) (Clausen, 1978; Schooley et al., 1984). Except for C. nigrocellulata, these species were also released in the southern Appalachians, and A. obliterata, A. thompsoni, and L. erichsonii were reported as established (Amman and Speers, 1965), but a survey in 1968 found only a few L. erichsonii and that native mites were the most important predators (Fedde, 1972).

Many of the imported species released to control A. piceae may have been confused with native species. Aphidoletes thompsoni is likely a junior synonym of Aphidoletes abietis (Kieffer), a common, widespread species considered native to North America (Gagné, 2010). Aphidoletes abietis was reported in New York State (Felt, 1917) and has been collected recently from A. piceae in Canada and the United States (Gagné, 2010) and from A. tsuga in the eastern United States (Wallace and Hain, 2000). Laricobius erichsonii may have been confused with the native Laricobius rubidus (LeConte) since the adults are very similar in appearance and no morphological features distinguish larvae in the genus. Clark et al. (1971) considered the Leucopis/Neoleucopis released in North America to be a mixture of five species, two of which may be confused with native North American species. After N. obscura was released in New Brunswick, it was reported to have spread rapidly, including to neighboring Maine. Chamaemyiid flies native to eastern North America include Neoleucopis pini-cola Malloch, Leucopis americana Malloch, and Leucopis piniperda Malloch. Later it was determined from vouchers that Leucopis hexagonata McAlpine and Leucopis atratula Ratzburg were also released in the Maritimes and that the former may be native to North America (McAlpine, 1971). The species most represented in Canadian museums from field collections made during the program are L. atratula and L. piniperda (McAlpine, 1971, 1978; Tanasijshuk, 2002). The native North American predator L. americana was reported to have been displaced by N. obscura in New Brunswick and Newfoundland (Balch, 1952; Bryant, 1963). However, both of these entities are dubious (Tanasijshuk, 2002). The “N. obscura” released in the southern Appalachians were field collected in Maine (Amman, 1961; Amman and Speers, 1964) and the identity of these remains uncertain. Until a revision of the taxonomy of the Chamaemyiidae is completed, voucher specimens studied, and a survey of existing predators made, it will remain unclear which imported species in this family were released and established, and which native species have made a host shift to A. piceae.

Despite a comprehensive 30-year biological control program, the balsam woolly adelgid remains a serious pest not only of Fraser fir but also other fir species in North America. Although it is generally accepted that biological control of A. piceae in North America has not been successful (Clark et al., 1971; Schooley et al, 1984), there is no conclusive explanation for the lack of success. The failure of several species can be attributed to poor climate matching and not vetting specificity to the target species. The first imported predators were collected in Great Britain, from adelgids on pine, and only one of the six species was specific to adelgids: None of the 15 species from India and Pakistan that were released in the southern Appalachians established (Amman and Speers, 1971). These Asian predators were mainly generalist species and included many species of uncertain identity. On the other hand, the importations made through the biological control laboratory of CABI in Switzerland exemplify a well run classical biological control program where the natural enemy complex on the target host was studied and the most promising species were exported in large numbers. Although several of these species established, at least temporarily, none have provided effective control. That the European climate is warmer and drier than the release sites in North America has been suggested as a factor (Clark et al., 1971; Schooley et al., 1984). It should not be surprising, however, that the predators did not bring the adelgid below damaging thresholds, since in Europe the population dynamic of the entire predator complex is largely inversely density dependent and not regulative (Eichhorn, 1969a), and tree resistance and weather both have strong influences on the pest’s population dynamics (Franz, 1956; Pschorn-Walcher and Zwölfer, 1956).

The ineffectiveness of the predators exported from Europe has also been attributed to poor synchronization with one or both adelgid generations, and predator preferences for adelgids on the stem versus on the twigs (Pschorn-Walcher and Zwölfer, 1956; Eichhorn, 1968). A main weakness of the predaceous beetles L. erichsonii, A. obliterata, and S. impexus is that they are univoltine, whereas the adelgid has two to three generations per year. These predators also appear after the adelgid has started to lay eggs in the spring (Pschorn-Walcher and Zwölfer,
1956). The chamaemyiid flies, however, are multivoltine, appear earlier in the spring, and attack both generations. One of these, _C. nigrocellulata_ was not released in the southern Appalachians, and it is not certain what fly species was actually released because of problems with identification. Thus, there does seem to be an opportunity for additional introductions to establish biological controls that could reduce the damage to Fraser fir.

After the end of the balsam woolly adelgid biological control program, the Caucasus Mountains were explored for natural enemies, as it was felt that this may be the ancestral home of _A. piceae_ (Eichhorn, 1969a, b). In this region of Turkey, Georgia, and Russia, _Adelges nordmanniana_ (Eckstein), which is closely related to _A. piceae_, occurs on _Abies nordmanniana_ (Steven) Spach (Ravn et al., 2013). These authors confirmed Eichhorn’s (1969b, 2000) observation that the chamaemyiid _L. hennigata_ is the most important predator of the fir adelgid in Turkey. This is in contrast to North America and Europe, where the predator is also native, but seems to be uncommon. It is unknown if this different dynamic reflects differences in habitat, prey species, or genetic differences among populations of the fly.

Another source of potential biological control agents for the balsam woolly adelgid may be the hemlock woolly adelgid ( _Adelges tsugae_ [Amann]), currently the target of an active biological control program in the eastern United States (Onken and Reardon, 2011). _Laricobius nigrinus_ Fender (Coleoptera: Derodontidae) and _Sasajiscymnus tsugae_ Sasaji & McClure (Coleoptera: Coccinellidae) have been successfully established and are widespread. In laboratory tests, the lady beetle _S. tsugae_ fed and oviposited equally on the balsam and hemlock adelgids, although survival of beetle larvae was higher on the hemlock woolly adelgid (Jetton et al., 2011). The lady beetle’s life history may be better synchronized with _A. piceae_ since both are inactive during the winter and active during the summer, whereas _A. tsugae_ is active from fall until late spring and is in diapause during the summer.

A prerequisite to new biological control efforts is to resurvey the natural enemies now present and to make positive identifications of both established and candidate species. The confusion over identity of the chamaemyiid species that were released and recovered points to the importance of taxonomy in biological control (see also Chapter 6). There are several species of Chamaemyiidae in North America recovered from adelgids feeding on fir and hemlock (McAlpine, 1987; Humble, 1994; Ross et al., 2011). Finding biological control candidates in Oregon, Washington, or Maine (rather than in foreign countries) would greatly simplify legal issues related to transporting insects and obtaining permits for their release. Since the Fraser fir seedlings that survived the first wave of _A. piceae_ attack are now maturing and becoming susceptible to the pest, it seems timely to reassess the possibilities for biological control of balsam woolly adelgid.

**A century of unsuccessful *Lantana camara* biological control effort in Australia**

Rieks van Kinken

The neotropical shrub lantana, _Lantana camara_ L. _sensu lato_, is listed among the world’s worst 100 invasive species because of its impacts on biological diversity and human activities (Lowe et al., 2000). It has been distributed pantropically, largely as an ornamental, and is now considered invasive in approximately 60 countries or island groups (Day et al., 2003). Invasive lantana grows as individual clumps or dense monospecific stands, typically 1–4 m tall. As an environmental weed it invades disturbed natural forests and woodlands (Figure 10.19), including rainforest margins, where it disrupts succession, decreases biodiversity, and hinders regeneration efforts (Day and Zalucki, 2009, and references therein). This in turn can facilitate higher fire frequency and intensity, further favoring lantana (Fensham et al., 1994). Harm to native species richness occurs above a 75% cover threshold in wet sclerophyll forest in southeastern Australia (Gooden et al., 2009). One analysis suggests that lantana threatens more than 1400 native species in Australia, including 279 plants and 93 animals listed under state or national threatened species legislation, and 100 threatened ecosystems (Turner et al., 2007). Its primary impact as a weed of pastures is displacement of desirable species, but it also interferes with stock management, increases maintenance expenditure, fatally poisons stock under some circumstances, and reduces land values (Day et al., 2003; AEC Group, 2007; Day and Zalucki, 2009). It is estimated to cost the pastoral industry Aus $104,000,000 per year (2005–06 value) in lost productivity and management costs (AEC Group, 2007). It also affects Australian silviculture, accounting for an estimated 30% of establishment costs and up to 50% of the harvesting costs (Wells, 1984).
Lantana was first introduced into Europe from the Americas in 1636 (Day and Zalucki, 2009). Subsequent centuries of hybridization and selection among several American taxa have resulted in over 650 varieties that vary in morphology and ecology (Zalucki et al., 2007). As a result, the taxonomy is complicated and remains disputed. Morphological studies suggest it could be a single highly variable hybrid swarm (Sanders, 2012). Alternatively, recent genetic analyses suggest invasive lantana in Australia could be from a single, morphologically variable species with primary genetic influences from the Caribbean and Venezuela (R. Watts, unpublished data), which would be a subset of the native distribution of the plant in the larger sense, which extends from Florida and Texas through to northern Argentina and Uruguay (Zalucki et al., 2007).

In Australia, lantana has a relatively broad ecological niche. It is able to become dominant in habitats from temperate regions to wet-dry tropics and across a broad rainfall gradient (750–3000 mm) (Day et al., 2003). It does best in high-light environments. Although it can become dense in open woodlands, it performs poorly in forests. Furthermore, lantana requires disturbance to invade and become dominant, such as through feral and domestic animal activity, fire, or clearing (Fensham et al., 1994; Day et al., 2003). Seeds have fleshy endocarps and are dispersed by birds and animals (Day et al., 2003). In Australia lantana probably occurs across most of its potential range, although infilling continues.

Many management tools are available, including herbicides, mechanical control, and fire (Stock et al., 2009). However, they are often not practical or economical, especially on steep hillsides, in extensive natural forests, pastures with low productivity, or along waterways (Haseler, 1963). It was even harder to manage in the early 1900s when management was largely restricted to manual control. Lantana, therefore, became one of the first targets for biological control in 1902, starting in Hawaii (Davis et al., 1992). It is also the longest running biological control program, with the search for new agents continuing (Day and Zalucki, 2009), and one of the most active, with 42 agents released in at least 41 countries (Zalucki et al., 2007).

In Australia, the biological control program began in 1914, and it has so far resulted in the release of 32 agents, with further species still being considered (Day,
growth and annual seed production have not been quantified. Plant deaths have only occasionally been reported in Australia, but even then other contributing stressors such as drought are generally also implicated (Day, 2012).

Lack of evidence of population-level effects from biological control is not unique to Australia. For example, biological control has been demonstrated to cause high levels of leaf damage and loss of viable seed in Guam (Muniappan et al., 1996), but demographic consequences have not been quantified. An exception is the Big Island of Hawaii where lantana is no longer considered to be a problem in arid areas, apparently because of the combined effect of several biological control agents (Davis et al., 1992). All of those agents were also released in Australia, but to minimal effect (Zalucki et al., 2007).

Of the 32 agents released in Australia, 18 (58%) established, which is similar to weed biological control in general (60–64%) (Zalucki et al., 2007), and most of these (15 species) reached high densities at least somewhere and sometimes. Of those, nine caused at least seasonal and local damage (typically reported as significant defoliation or seed damage), but only one species, the sap-sucker Aconophora compressa Walker (Hemiptera: Membracidae) (Figure 10.20), resulted in sustained damage through the season in at least some years and places. Established agents are typically only patchily abundant (Day et al., 2003), so negative interactions between agents are considered unlikely (Day and Zalucki, 2009), and additive effects, for example on defoliation, are localized (Day, 2012).

So why has lantana biological control been apparently ineffective in Australia despite a century of effort, the release of 32 agents, and so many agents (48%) reaching high densities? There are two parts to this question. First, what damage to lantana plants is required to sustain the required demographic effects? Second, why are agents not reaching and sustaining the densities required to achieve that level of damage? Recent demographic modelling suggests that large effects on mortality and reproduction are required to regulate lantana populations (Osunkoya et al., 2013). This is supported by general observations that lantana plants are resilient to severe disturbances including hot fires, mechanical damage, and considerable and frequent defoliation (Day, 2012; Osunkoya et al., 2013) and that natural mortality is rare (Osunkoya et al., 2013; Yeates, 2013). For example, plants recovered...
even after 100% of lantana leaves were removed manually every month for a one to two year period (Broughton, 2000). Demographic impacts in the absence of other stressors such as drought will therefore require prolonged, systemic damage such as can only be achieved through galling or pathogen attack. Alternatively, it will require prolonged loss of leaves throughout the growing season, although even this will not necessarily result in mortality (Broughton, 2000). Seed predation is unlikely to affect demography significantly unless most seeds are killed (van Klinken and Flack, 2008). These requirements contrast with the types of agents released in Australia: only 29% of agents attack the plant structurally (1 pathogen, 5 sap-suckers, 2 stem borers and 1 galler). In contrast, 48% (15 species) are leaf feeders (including leafminers) and 23% (7 species) are flower or fruit feeders. Most agents would therefore not be expected to cause the required demographic impacts, unless populations maintained exceptionally high densities for prolonged periods.

There is precedence for agents reaching and maintaining high densities, resulting in demographic impact on even long-lived resilient species (Van Driesche et al., 2010). Why then have agents not achieved this on lantana? A primary reason given is a poor climate match (Day and Neser, 2000; Day et al., 2003). This seems an unlikely reason for biological control failing throughout Australia given the diverse climates and environments in which lantana grows. Certainly most agents have been able to reach high densities in particular climate regions and habitats (under canopy or in the open). Nonetheless, climate does appear to be the primary factor preventing most agents from sustaining high densities, either directly or through their effects on plant quality. Most agents have multiple generations in a year and apparently emerge in low numbers at the start of the season, taking much of the season to reach high densities. Furthermore, for most species, high densities are typically reached in late summer and early autumn as the temperature drops or plant quality declines.

**Figure 10.20** Lantana defoliated by the tree hopper Aconophora compressa in southeast Queensland, Australia and close up of insect. Photo courtesy of Michael Day, QDAFF. (See insert for the color representation of this figure.)
allowing plants to then recover. Densities also drop following extreme weather events, such as drought, heavy rainfall, or heat waves. The sap-sucker *A. compressa* is the least coupled to season, but populations crash after heat waves (Day et al., 2003).

Another commonly cited reason for poor or variable agent performance is differences in host varietal preferences. Certainly differences have been observed in the laboratory in at least 10 biological control agents (Day et al., 2003), but observations in the field remain largely anecdotal (e.g., Day and Neser, 2000) and are easily misinterpreted. Predation and parasitism of agents is also a possible explanation. Although not considered important in Australia (Day et al., 2003), some biological control agents have reached high densities soon after release, only to crash subsequently, so it is nonetheless worth further investigation. For example, the leafminer *Calicomyza lantanae* (Frick) (Diptera: Agromyzidae) caused significant damage within four years of its release in 1974, but populations subsequently declined (Julien and Griffiths, 1999). Finally, host associations in the native range are likely to contribute to some failures or poor performance, with agents collected off *L. camara* and *Lantana urticifolia* Mill. establishing better than those from other *Lantana* species (Day and Zalucki, 2009, and refs therein). The centuries of artificial selection of lantana means that exact genetic matches may not exist in the field, although further searches in the putative source of genetic lineages (the Caribbean and Venezuela) may well yield further agents.

Lantana is clearly a difficult target for biological control, because of its demographic resilience and, perhaps, its genetic complexity. Nonetheless it does occur in diverse climates even within Australia. Is failure then the consequence of a lack of suitable agents or the difficult nature of the target? Or have the wrong agents been introduced? Certainly further agents are being considered, and further surveys in the native range may well yield additional agents. With the benefit of hindsight, the lantana biological control program has suffered from poorly defined goals, for example regarding whether the objective was to reduce lantana densities in open fields or in forest understories, and in which climatic region. Furthermore, there was limited explicit consideration of the likely ability of potential agents to achieve these outcomes through demographic impacts (but see Day and Urban, 2004), and relatively few follow-up studies to understand why biological control agents have been largely unsuccessful. The biological control program is still ongoing. These limitations therefore need to be considered to maximize its likelihood of success and should be guided by recent demographic studies (Osunkoya et al., 2013), an improved understanding of why previous agents have been ineffective, and quantitative, long-term evaluation of the biological control program. It is yet to be seen whether an effective agent for lantana biological control in Australia can be found, that is, one that will cause the type and duration of damage necessary to achieve stated objectives for lantana biological control.

**Projects still unfolding**

These projects are not yet finished and may or may not achieve their ecological goals fully, but they illustrate the kind of cases in which biological control has potential to benefit damaged ecosystems.

**Preserving ash-dependent biodiversity through biological control of emerald ash borer**

Jian J. Duan

Ash trees (*Fraxinus* spp.) are dominant or subdominant forest components in many forest stands in the northeastern and midwestern United States as well as in the Pacific Northwest and other states. There are sixteen species of native ash in the United States (USDA PLANTS Database, 2013). Each *Fraxinus* species is adapted to a slightly different habitat within forest ecosystems. Several species tolerate poorly drained sites and wet soils, protecting environmentally sensitive riparian areas (D’Orangeville et al., 2008; Rockermann, 2011); for instance, pure stands of black ash (*Fraxinus nigra* Marshall) grow in bogs and swamps in northern areas, where they provide browse, thermal cover, and protection for wildlife such as deer and moose (*Alces alces* [L.]). The ecological effects of emerald ash borer (EAB) (Figure 10.21), *Agrilus planipennis* Fairmaire, are likely to include both loss of habitat and food resources for vertebrates and habitat loss for ash-specialized herbivorous insects and their specialized predators and parasitoids (Wagner, 2007; Wagner and Todd, 2015). First detected in North America in Michigan in 2002 (Haack et al., 2002), emerald ash borer is a highly
A destructive invasive beetle that attacks and kills North American ash (Figure 10.22) (Cappeart et al., 2005). While adults feed on mature ash leaves and rarely cause any significant damage to the host tree, EAB larvae feed on phloem, creating extensive galleries under the bark (Figure 10.23). When emerald ash borer populations are high, larval consumption of tree phloem is substantial, resulting in tree girdling and death in three to five years (Poland and McCullough, 2006; McCullough et al., 2009; Poland et al., 2010; Mercader et al., 2011). Although none of these approaches alone appear to be sufficiently effective in containing the spread of EAB, biological control via self-propagating and dispersing natural enemies has the potential to reduce EAB populations in forests, nurseries, and urban ash plantings.

Initial efforts to reduce or contain emerald ash borer damage focused on eradication. However, because the population in the originally infested area (Michigan) was already high and widespread when first recognized, eradication proved both ineffective and cost-prohibitive and by 2009 efforts were abandoned. Subsequently, efforts focused on slowing the invasion of new areas (Poland et al., 2010; Mercader et al., 2011) by restricting movement of EAB-infested wood or plant materials, insecticide treatment or physical destruction of infested trees (including use of artificially girdled EAB trap trees), and biological control via introduction and release of natural enemies collected from EAB’s native range (e.g., Liu et al., 2007; USDA APHIS, 2007; McCullough et al., 2009; Poland et al., 2010; Mercader et al., 2011). Although none of these approaches alone appear to be sufficiently effective in containing the spread of EAB, biological control via self-propagating and dispersing natural enemies has the potential to reduce EAB populations in forests, nurseries, and urban ash plantings.

The EAB biological control program began in 2007 with the release of three Asian hymenopteran parasitoids: Spathius agrili Yang (Braconidae), Tetrastichus planipennisi Yang (Eulophidae) (Figure 10.24a, b), and Oobius agrili Zhang and Huang (Encyrtidae) (Figure 10.25) (Yang et al. 2005, 2006; Zhang et al., 2006; Liu et al., 2007; USDA APHIS, 2007; Bauer et al., 2008, 2009, 2010). While the former two parasitoid species attack EAB larvae, the latter (O. agrili) parasitizes EAB eggs. With the establishment of the USDA APHIS EAB biological control rearing facility in Brighton, Michigan, in 2009, large numbers of these parasitoids have been released in ash-dominated forests in 16 EAB-infested states. All three parasitoid species have been recovered following their release in the United States; however, only T. planipennisi and O. agrili have been recovered consistently more than one year after release. At two sites in Michigan, parasitism by O. agrili increased from 3–4% in the year of release to 20–28% two years later. Establishment and spread of the stronger flying T. planipennisi has been
even more impressive. At six intensively studied sites in Michigan, 92% of the trees at the release site contained at least one brood of *T. planipennisi* four years after release, and parasitism levels increased steadily to an average of over 21% four years after the field releases (Figure 10.26) (Duan et al., 2013a). Parasitism levels at the six control sites (at least 1 km away) also increased yearly to an average level of 13%. It is hoped that populations of these exotic parasitoids will continue to establish themselves in more EAB-infested areas, increase over time, and exert significant control of EAB populations within the next few years in the United States.

However, the effectiveness of *T. planipennisi* in controlling EAB is affected by the thickness of tree bark (Figure 10.27), which is directly related to tree size. Data from the earlier EAB parasitoid surveys in northeast China (Liu et al., 2007) and the Russian Far East (Duan et al., 2012b), as well as from areas in the United States where the parasitoid has recently been released (Duan et al. 2012a, 2013a), show that *T. planipennisi* is indeed more prevalent in smaller diameter ash trees. The reason for this apparent bias was identified in a field experiment that showed that *T. planipennisi* rarely parasitizes EAB larvae in larger, thick-barked trees (>3.2 mm thick bark, typical of trees with >12 cm dbh) owing to the parasitoid’s relatively short ovipositor (average 2–2.5 mm) (Abell et al., 2012). The thick bark of large ash trees provides a refuge for EAB larvae from attack by *T. planipennisi* (Abell et al., 2012). Abell et al. (2012) further suggest that *T. planipennisi* will be more effective in stands with younger trees (<12 cm dbh) such as in the Michigan study sites, or in natural ash regeneration found in some EAB-affected stands.

To control EAB successfully on both small and larger ash trees, other EAB parasitoids from the pest’s native range that have longer ovipositors should be released in EAB-invaded areas in North America. Currently, a new braconid larval parasitoid (*Spathius galinae* Belokobylskij & Strazanac), collected from the Russian Far East, has been evaluated for host specificity and a petition filed for its release against EAB in the United States (Duan et al., 2012b; Gould and Duan, 2013). This Russian parasitoid
is also likely to be more cold tolerant than *S. agrili*, which was collected farther south in Tianjin, China (east of Beijing on the coast) where temperatures are moderated by the China Sea. Climate-matching studies indicated that the central part of the United States is potentially more suitable for *S. agrili* than the more northern areas where most releases have been made to date. Furthermore, climate-matching analysis indicates that the portion of the United States suitable for *S. galinae* extends farther north than is the case for *S. agrili* (Gould and Duan, 2013).

Besides parasitism by *T. planipennisi*, EAB larvae also suffer heavy losses in the United States from other biotic factors, including woodpeckers, mortality from plant defenses, diseases, and other parasitoids, mostly ones native to North America (e.g., Duan, 2010; 2012a, b; 2013a, b). For example, Duan et al. (2013a) report that among the other mortality factors detected across their study sites, woodpeckers were the most abundant factor in Michigan, removing up to 57% of immature and older EAB stages from feeding galleries and/or pupal chambers. Duan et al. (2013a) also show that putative tree resistance killed up to 15% of younger larvae and unknown diseases caused similar levels of mortality of larger larvae throughout the study, while parasitism by North American native parasitoids (*Atanycolus* spp. [Hymenoptera: Braconidae] and *Phasgonophora sulcata* Westwood [Hymenoptera: Chalcididae]) inflicted 18% larval mortality in Michigan. How these North American native parasitoids and other mortality factors will interact with the newly introduced *T. planipennisi* has yet to play out.

Finally, the success of EAB biological control programs in the United States may also hinge on the degree of ash tree resistance to EAB. Field studies in the pest’s native range showed that EAB is rarely a
serious pest on many Asian species of ash trees (e.g., *F. mandschurica* Rupr., *F. rhyncophylla* Hance), largely because of the combination of natural enemies (primarily parasitoids) and putative tree resistance that effectively killed immature stages of EAB (Liu et al., 2007; Duan et al., 2012b). In contrast, EAB frequently becomes a serious pest on introduced North American ash species in Asia (e.g., *F. velutina* Torr., *F. pennsylvanica*, and *F. americana*), and often kills infested trees grown in plantations or as landscape trees even with the presence of abundant parasitoids that may cause >70% parasitism of both eggs and larvae (Liu et al. 2007; Duan et al. 2012b). In North America, the common ash species such as *F. pennsylvanica*, *F. americana*, and *F. nigra* appear to have little resistance to EAB larvae and are readily killed by EAB infestations. However, recent field observations showed that some North American ash, such as blue ash, have not been heavily infested by EAB largely because of their high resistance to EAB larvae (Tanis and McCullough, 2012). In addition, some “lingering” healthy (often younger) trees of the susceptible ash species (*F. pensyvanica* and *F. americana*) have been frequently observed surviving the wave of EAB invasion even in the epicenter of EAB invasions (e.g., in Michigan). Using experimentally established emerald ash borer cohorts, Duan et al. (2010) also showed that healthy young green and white ash trees in fact killed nearly 30% early instars of emerald ash borer larvae, indicating some level of host-tree resistance in those healthy young ash trees. Together, these observations provide hope that some level of host-tree resistance in North American ash may facilitate biological control in protecting North American ash and their dependent communities.

Figure 10.25 *Oobius agrili* ovipositing in an emerald ash borer egg; this is another important parasitoid introduced from China. Photo credits, Jian J. Duan, USDA ARS. (See insert for the color representation of this figure.)

Figure 10.26 Increase in rates of parasitism of emerald ash borer larvae by the introduced parasitoid *Tetrastichus planipennisi* in Michigan, following its introduction in 2008. Reproduced with permission from Duan et al. (2013).
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It is hoped that populations of introduced parasitoids will continue to establish themselves in more EAB-infested areas, increase over time, and exert significant control of EAB populations within next few years in the United States. If they do, the benefit of such a classical biological control program is also likely to extend to other native arthropods that depend on ash resources.

Restoring native vegetation in Tahitian forests dominated by Miconia calvescens

Jean-Yves Meyer

In Tahiti, a small tropical oceanic island located in the South Pacific, the massive invasion of native rainforests by Miconia calvescens DC (hereafter miconia) (Melastomataceae) was considered an intractable management situation in the 1980s. This small tree (6–12 m in height, up to 16 m) native to tropical Central and South America was introduced to Tahiti as a garden ornamental in 1937 for its large (80 × 30 cm) showy leaves with purple undersides (Meyer, 1996). After introduction, it spread to form dense forests, excluding native and endemic trees and preventing new seedling recruitment. A relatively shade-tolerant and fast-growing species (up to 1.5 m of height growth per year), early reproducing (after four to five years of growth), and a prolific fruit producer (millions of seeds produced by a mature tree per reproductive season), miconia is a formidable competitor for the native flora. It is able to penetrate into relatively undisturbed native forests (Meyer, 1998); its rapid spread is aided by natural disturbances such as cyclones that open the forest canopy and promote faster recruitment and growth (Murphy et al., 2008). Frugivorous introduced and native birds facilitate the invasion by dispersing its small fleshy fruits over long distances, and birds consume more miconia where it is abundant, likely accelerating the rate of spread at sites where it is already invasive (Spotswood et al., 2012). Invading miconia density reaches two to four individuals per m², and its basal area attains 30 to 40 m²/ha. Light availability in miconia-invaded forest understories decreases to 0.4–0.6% compared to 1–3% in native forests (Meyer et al., 2007). By 1980, over 80,000 ha were considered invaded (two-thirds of the island’s land surface), from near sea level to about 1400 m elevation. At high elevations, miconia encroaches on montane cloud forest and threatens 40–50 Tahitian endemic plant species (Meyer and Florence, 1996). The understory of miconia-invaded forests typically resembles a “biological desert” with only dead endemic tree fern trunks still standing.

Figure 10.27 Parasitism by Tetrastichus planipennisi is limited by bark thickness relative to ovipositor length, such that only smaller trees are protected. Unpublished data of Jian J. Duan.
Because of the extent of the infestation, the steep mountainous and often inaccessible slopes on Tahiti, and the failure of conventional manual and chemical control owing to the long duration (>15 years) of the plant’s seed bank (Meyer et al., 2011), biological control was chosen as a potentially more effective management approach to reduce the impacts of miconia on native vegetation. However, many questions were asked when the biological control program was officially started in 1997, including whether effective, safe biological control agents existed in miconia’s native range and whether native forests, once cleared of miconia, would be invaded by other weeds. The latter was viewed as a possible risk, based on outcomes of other biological control projects against pests of natural areas (e.g., Barton et al., 2007) and given that more than 420 naturalized exotic plant species are present on Tahiti, about 70 of which pose serious invasion threats (Fourdrigniez and Meyer, 2008).

Several trips to Central and South America to search for potential control agents yielded a fungal pathogen (*Colletotrichum gloeosporioides* [Penz] Sacc. f. sp. *miconiae* Killgore & L. Sugiyama) (Order Melanconiales; Class Coelomycetes; Subdivision Deuteromycetinae; hereafter *Cgm*) that was found to be highly specific to miconia during extensive testing in the quarantine laboratory of the Hawaii Department of Agriculture. The pathogen causes leaf anthracnosis and necrosis, leading to defoliation (Figure 10.28) and death of seedlings. This fungus appeared to be a promising agent (Killgore et al., 1999).

In 2000, a release was performed on Tahiti (Meyer and Killgore, 2000). *Cgm* established successfully and spread across the entire island in less than three years, infecting almost all miconia plants from sea level to high elevation. However, while mortality for very young seedlings was between 70–75% in the laboratory, the mortality rate was much lower under field conditions (30% for seedlings <50 cm in height at release sites [Meyer et al., 2008]). A relatively unexpected effect of the *Cgm* was partial defoliation of miconia canopy trees, with leaf damage of 6–36%, increasing with elevation (Meyer et al., 2008; Meyer and Fourdrigniez, 2011). The cooler climate found above 600 m in Tahiti proved to be the most favorable for *Cgm* reproduction, development, and efficiency.

Having demonstrated that reproductive success and seedling recruitment of some critically endangered endemic trees and subshrubs increased with partial defoliation of miconia by *Cgm* (Meyer et al., 2007; Meyer and Fourdrigniez, 2011), changes were monitored in forest dynamics in permanent plots set up in 2005 at different elevations in rainforests and cloud forests, focusing on plant composition and abundance in the understory. Plant succession over a four-year period showed an increase of total native and endemic species richness and plant cover (mainly fern species) at all sites. The appearance of seedlings of endemic woody species that had been absent for the past decade in our permanent plots (Figure 10.29) located in miconia-invaded forests was noteworthy (Meyer et al., 2012). One of our study sites located at the lowest elevation (about 600 m) was re-invaded by other light-demanding pioneer herbs, shrubs, and trees, while at
higher elevation (above 800 m elevation), most newly recruited species were native and endemic plants. These results demonstrate that biological control can be a useful tool in ecosystem management (Headrick and Goeden, 2001) and should be considered for restoration of highly invaded forests in situations where re-invasion by other weeds is unlikely to occur. Dense monotypic stands of other shade-tolerant invasive trees such as *Psidium cattleianum* Sabine and *Syzygium jambos* L. (Alston) (Myrtaceae), for example, are known to occur on many Indo-Pacific tropical islands (e.g., in the Mascarenes, the Seychelles, and the Hawaiian archipelago) with dramatic impacts on the native flora, and such species might potentially be controlled in a similar manner. However, it must be emphasized that the new plant assemblage after miconia control is different from the pre-invasion stage, and long-term monitoring of forest dynamics will be still needed to study the trajectory of these newly created or “novel habitats.”

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**References**


Stehn, S. E., C. R. Webster, M. A. Jenkins, and S. Juse. 2011. High-elevation ground-layer plant community composition...
Cases of biological control restoring natural systems


