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Supressing Over-abundant Invasive Plants and Insects in Natural Areas by Use of Their Specialiazed Natural Enemies

Edited by Roy G. Van Driesche and Richard C. Reardon

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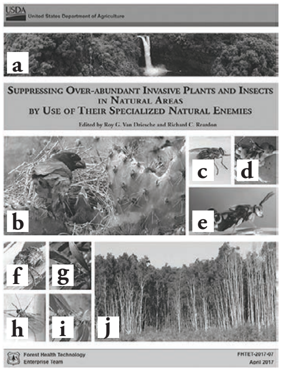

Cover Photos: (a) Rainbow falls, Hawaii (Credit: Kyle Hawton); (b) healthy brood of vegetarian ground finches, *Platyspiza crassirostris* (Credit: George Heimpel); (c) *Philornis downsi*, an invasive parasitic fly (Credit: David L. Hansen, University of Minnesota); (d) dead vegetarian ground finch chick killed by *P. downsi* (Credit: Jody O'Connor and Sonia Kleindorfer); (e) *Conura annulifera*, a parasitoid of *P. downsi* (Credit: David L. Hansen, University of Minnesota); (f) the melaleuca weevil, *Oxyops vitiosa* (Credit: Ellen C. Lake, USDA ARS); (g) *O. vitiosa* adult and feeding scars on melaleuca foliage (Credit: Willey Durden, USDA ARS, bugwood.org); (h) the melaleuca psyllid, *Boreioglycaspis melaleucae* (Credit: Paul D. Pratt, USDA ARS); (i) waxy flocculence produced by *B. melaleucae* nymphs on melaleuca foliage (Credit: Susan A. Wright, USDA ARS); (j) melaleuca infestation (Credit: Randy Westbrooks, bugwood.org)

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SUPPRESSING OVER-ABUNDANT INVASIVE PLANTS AND INSECTS IN NATURAL AREAS BY USE OF THEIR SPECIALIZED NATURAL ENEMIES

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INTRODUCTION

Summary. Biological control has long been used against invasive plants and, less often, invasive insects, in forests, aquatic systems, grasslands, coastal areas, riparian areas, islands, and other biomes or habitats of conservation concern. Historically, motivation for such efforts has shifted gradually away from economic interests toward ecological protection for its own sake. Future projects of this type will require better integration of biological control into conservation practice, a better understanding by societies of the reasons for such work and its possible risks and benefits, as well as continued, consistent public funding. Examples of successful projects in high-value conservations areas (Everglades, Galápagos, oceanic islands, wetlands, forests) are discussed, and future challenges and caveats mentioned.

Keywords biological control, natural areas, conservation, parasitoids, historical trends

CHAPTER 1. HISTORY OF BIOCONTROL IN NATURAL AREAS AND ISSUES AFFECTING ITS USE

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Like crops, plant communities in natural areas are increasingly subject to pressures from invasive insects and plants that directly attack native species or displace them through competition for resources (Foxcroft et al., 2013). While some of these problems can be relieved at the local level through traditional methods for control of invasive species – cutting, pulling, burning, flooding, use of herbicides, or use of poison baits – the limitations of such approaches are becoming increasingly obvious: (1) often they do not work, (2) many species cannot be eradicated and so treatments, even if effective in the year of application, must be repeated, causing an unsustainable burden on management budgets, and (3) treatment is economically feasible only for small areas (hundreds of hectares), while many damaging invasive species require control at much larger scales over whole landscapes, which also increase risks to nontarget species.

Consequently, there is a need for more frequent consideration of biocontrol as an option for managing invasive species in natural areas (see Van Driesche et al., 2016a). To determine if biological control is an appropriate response to any given invasive species problem, the following points need to be considered: (1) Natural areas are often strongly affected at the landscape level by invasive plants and insects, and many species in these groups are suitable for suppression with biological control. (2) However, before considering biological control, it should be determined whether high densities of the invasive species are promoted by anthropogenic disruptions of habitat-shaping processes such as changes in fire or hydrological regimes, changes in grazing or nutrient levels in soils or water bodies (the "drivers vs. passengers" argument). If so, ecologists should determine if those influences can be reversed. Anthropogenic eutrophication of water bodies, for example, is commonly linked to proliferation of fast-growing invasive plants and reduction of nutrient input is important to improve the balance among native and invasive plants in such water bodies. Similarly, lack of large grazing animals may affect competitive balances between native and introduced plants in grasslands. (3) The physical scale over which control of the invasive species is desired should be determined. If control is only desired at the preserve level, then active controls (cutting, burning, use of herbicides, traps, poison baits, etc.) may suffice and biological control may not be needed. (4) For the residual group of invasive species that are not driven by disturbances to habitat-forming processes, that cannot be eradicated, and whose landscape-level control is desired, biocontrol should be considered.

A few biological control agents have strongly damaged populations of conservation concern (Stiling and Moon, 2001; Russell and Louda, 2004; Elkinton and Boettner, 2012), and frequent attention to these cases (Strong, 1997; Stiling, 2000; Louda et al., 2003) has conveyed the impression that risk is common and significant. This perception of high, general risk has lingered and has damaged relations between conservation biologists and biological control scientists in some parts of the world. However, reviews of the level of non-target impacts have shown that weed biocontrol is quite safe (Pemberton, 2000; Suckling and Sforza, 2014) and has become increasingly so over the last 30 years. The risk from insect biological control, while lower than generally assumed, is somewhat higher than for weed biocontrol (Van Driesche and Hoddle, 2017); recent efforts have been made to improve this situation (Van Driesche et al., 2016a). To promote such improvement, the following actions have been advocated:

- Step 1. Agree on good targets. The goal of the use of biological control in a conservation context is ecological restoration, not invasive species suppression per se. Suppression of the invasive species may be required, or not, depending on circumstances, and if suppression is required, biocontrol may or may not be the best approach. Such decisions need to be based on discussion among all concerned parties before initiation of projects against particular invaders.

- Step 2. Agree on which tools to use. If invasive species need to be controlled, all possible options, including biological control (or not) and its integration with any other activities as appropriate (a strategy sometimes called Integrated Ecosystem Pest Management) should be considered.

- Step 3. Build a common set of information by sharing experiences. To promote more frequent consideration of the use of biological control in natural areas, conservation biologists need opportunities to observe restoration of systems that incorporate biological control, through the sharing of information and visits to field sites.

- Step 4. Plan projects holistically with active conservation partners. Once a decision has been taken to use biological control, a system is needed to holistically plan the project. Several questions will need to be answered. For example, is reduction of the pest alone enough to restore the ecosystem, or will other actions also be needed (before, during or after) to mitigate aspects of the biocontrol project or to enhance ecosystem recovery as the invasive species' density decreases?

- Step 5. Anticipate possible conflicts. Conflicts should be anticipated and consensus developed in support of desired actions. This may involve enlisting partners to undertake information-sharing or consensus-building activities. Additional time and effort will likely be needed to convince external audiences rather than just knowledgeable internal ones of the merits of the proposed projects or introductions. The active support of partners often will play a critical role in developing consensus.

HISTORICAL PERSPECTIVE

With the above as a rationale for the use of biological control in natural areas, here we summarize past experiences.

Previous Summaries

While benefits from biological control projects have accrued to natural areas since the earliest days of biological control, particularly of weeds invasive in forests and grasslands (e.g., Dodd, 1940), projects were justified to societies in economic rather than ecological terms until about the 1990s. Chronologically, some key publications highlighting use of biological control in natural areas include the following:

In 2010, Van Driesche et al. reviewed previous benefits of biological control in natural areas and documented benefits to many biomes, including **aquatic and wetland habitats** (Buckingham, 2002; Landis et al., 2003; Ajuonu and Neuenschwander, 2003; Pratt et al., 2005; Denoth and Myers, 2005; Grevstad, 2006; Rayamajhi et al., 2008; Coetzee et al., 2009; Heard and Paynter, 2009; Hill and McConnachie, 2009; Julien et al., 2009; Neuenschwander et al., 2009; Tipping et al., 2009; Boughton and Pemberton, 2009, 2011 [see Smith et al., 2014]) for update of previous reference], **boreal and temperate forests** (Embree, 1971; Embree and Otvos, 1984; Ryan, 1990; Fielding and Evans, 1997; Hough-Goldstein et al., 2009; see also Van Driesche and Reardon [2014] for an update on North American forest projects), **subtropical and tropical forests** (Barton et al., 2007), **grasslands** (Huffaker and Kennett, 1959; McEvoy et al., 1991; McCaffrey et al., 1995; Vogler and Lindsay, 2002; Tomley and Evans, 2004; Samuel et al., 2008), **deserts and arid shrublands** (Dodd, 1940; Zimmermann et al., 2009), **coastal areas and dunes** (Holtkamp, 2002; Edwards et al., 2009), and **oceanic islands** (Fowler, 2004; Grandgirard et al., 2008; Meyer et al., 2008a; Calderón Alvarez et al., 2012; Hoddle et al., 2013), with benefits occurring to biodiversity or ecosystem services.

In 2012, a special issue of *BioControl "Conserving Nature with Biological Control"* published selected papers from a meeting on this topic held in Northampton, Massachusetts, 3-7 October, 2010. This issue highlighted the benefits of biological control to such world premier conservation sites as the South African fynbos (Moran and Hoffman, 2012), the Florida Everglades (Center et al., 2012), the Galápagos National Park (Calderón Alvarez et al., 2012), and the native forests of Tahiti (Meyer et al., 2012). Other papers discussed risks to natural areas or native species from introduced natural enemies (Simberloff, 2012, Elkinton and Boettner, 2012) and management of conflicts that arise in some cases (Dudley and Bean, 2012).

In 2013 in the forward to *Plant Invasions in Protected Areas* (Foxcroft et al., 2013), Ian Macdonald stated "Who could have foreseen that the greatest long-term threat to the integrity of the ecosystems "protected" in these national parks, game reserves and state forests would turn out not to be the axeman, the hunter or the land developer, but rather the inexorable spread of alien species. But this is the situation that protected area managers throughout the world find themselves in today." A chapter in this book (Van Driesche and Center, 2013) laid out the role for plant biological control in conserving such protected areas, including a table documenting the contributions to natural area protection of biocontrol projects against 71 invasive plant species, worldwide.

Following the 2010 meeting in Northampton, Massachusetts, on protecting natural areas through the use of biological control, a group of the meeting's participants began collaboration on a book on this topic, eventually entitled *Integrating Biological Control into Conservation Practice* (Van Driesche et al., 2016a), produced by an editorial group consisting of three biological control scientists (Van Driesche, Hoddle, and Heinz), five conservationists (Simberloff, Blossey, Causton, Marks, and Wagner), and one ethicist (Warner). This collaboration forced each discipline to consider the point of view of the other and engage in conversation until commonly agreed positions emerged. This book discusses issues relevant to biological control's use in natural areas, including (1) design of restoration programs based on understanding of drivers of ecological degradation, (2) review of the tools available for invasive species suppression (mechanical, chemical, biological, etc) and how to manage tradeoffs among them, (4) risks and benefits of biological control and forecasting of risks, (5) use of modern systematics for agent and pest identification, (6) evaluation of natural enemy impacts on target pests, (7) case histories of biological control in natural areas written by original researchers carrying out the work, (8) regulation of biological control in various parts of the world, (9) the ethics and economics of use of biocontrol, and (10) proposals for future reforms of biological control practice.

Critical to growth in the use of biological control in natural areas is better information on nontarget impacts of agents used in past biological control projects, so that the real risks and their likelihood can be more accurately judged by conservationists considering the issue before beginning biological control projects. Recently, this topic has been addressed for both weed (Suckling and Sforza, 2014) and arthropod targets (Van Driesche and Hoddle, 2017). Such summaries replace speculation or generalizations based on atypical cases. Suckling and Sforza, (2014) found the risk of use of non-target plants to be very low currently and to have occurred historically only for two groups of projects, one directed at thistles and the other at cacti. Van Driesche and Hoddle (2017) found that the parasitoids and predators used against invasive insects and mites historically have been less specific than weed biocontrol agents, and these agents can be expected to attack some non-target hosts. Population-level impacts on non-target species are relatively uncommon but do occur, and the average level of host specificity of parasitoids and predators released has narrowed since 1985.

Historical Development of Biocontrol for Protection of Nature

1880-1975: Spill-over benefits from economic projects. Classical biological control of pest insects is generally traced to California in the 1880s when it was used successfully to protect citrus crops (Caltagirone and Doutt, 1989). Weed biocontrol was effectively launched (through its first large scale success) in Australia in the 1920s when vast areas of grazing and forest lands were cleared of dense stands of invasive *Opuntia* cacti through introductions of natural enemies (Dodd, 1940). The goal of pest control through release of natural enemies in most of the method's first century (up to ca 1975) was to improve the economic circumstances of groups or regions. Economics was the measure of value of most activities of societies in this period of history. Protection of intact natural areas as national parks or wildlife refuges had begun in this period and the ideas that their protection embodied slowly broadened societies' views on the conservation and protection of natural areas, especially in the 1960s when many key environmental laws were first enacted. Nevertheless, for biological control projects done before 1975, economic gain was their purpose in nearly all cases. That said, even in this early period, some biological control efforts had spill over benefits to natural areas. This was particularly true for weed biological control projects. Removal of dense thickets of exotic cacti in New South Wales in the 1920s was done to promote ranching and forestry, but perforce permitted native plants to reclaim much lost ground, as not all the 20 million infested hectares were converted to farms or tree plantations as cactus stands declined. On land that remained undeveloped, reduction in cactus density must have resulted in better growth of native plants, although no one thought it worthwhile to document it at the time. Similarly, pre-1975 projects of biocontrol of European invasive forbs in North America, Australia, and other parts of the world also benefitted native grassland plants, although these project's goals were to improve grazing. In the United States, these rangeland projects started with the control of St. Johnswort (*Hypericum perforatum* L.) in California in the 1940s, followed by control of tansy ragwort (*Senecio jacobaea* L., currently given as *Jacobaea vulgaris* Gaertn.) in California and Oregon (US), and puncture vine (*Tribulus terrestris* L.) in California and the southwestern US (Andres et al., 1976). Further projects against other grassland species with similar dual benefits (economic and ecological) were initiated in subsequent decades in North America (Nechols et al., 1995; see also Winston et al., 2014). During this same general period, programs were also started in the eastern United States against two floating aquatic invasive plants: alligator weed (*Alternanthera philoxeroides* [Mart.] Griseb.) and waterhyacinth (*Eichhornia crassipes* [Mart.] Solms.-Laubach) (Andres et al., 1976), and later expanded to other pests of water bodies, wetlands, or surrounding habitats in the southern United States (Van Driesche et al., 2002). These projects, which were justified in terms of economics (reduction in herbicide use, preservation of navigation, protection of electrical generating facilities on rivers), produced benefits that were overwhelmingly ecological.

Historically, insect biological control was most frequently done in support of agriculture and as such did not often provide benefits to natural areas, except for projects directed against invasive pests of native forest trees, especially in North America (e.g., Embree, 1971; Embree and Otvos, 1984; Ryan, 1990; see also Van Driesche and Reardon, 2014 for a review of the use of classical biological control in North America to protect native forests). Also, because some insect pests that feed on crops are polyphagous, they may also attack native plants in natural areas. In this case, release of natural enemies against them, for their control in crops, may lead to the natural spread of the controlling natural enemies into areas of native vegetation, providing benefits there, as occurred in Australia when parasitoids of *Ceroplastes* wax scales moved into forests and controlled the scales there, as discussed by Sands in Van Driesche et al. (2010).

1975-present: Infrastructure expansion and benefits of new projects. By 1971, in the United States, three agencies of the Department of Agriculture were involved in carrying out biological control projects: ARS (Agricultural Research Service), APHIS (Animal and Plant Health Inspection Service) and FS (Forest Service) (Vail et al., 2001). Overseas laboratories to support collection of natural enemies were established in various locations, including most enduringly in Europe (France, Greece, and Italy), South America, Australia, and China (Vail et al., 2001). Establishment of USDA weed biocontrol laboratories in Albany, California, and Sidney (initially in Bozeman), Montana, supported expansion of work on invasive plants in grasslands, and one in Ft. Lauderdale (first in Gainesville), Florida, supported work on aquatic weeds. Insect biological control occurred at a USDA laboratory in Newark, Delaware (with work on both crop and forest pests), and in various U.S. land-grant universities (especially those in California, Hawaii, Florida, and Texas). Other facilities supplemented these, including weed biocontrol work at the Beltsville, Maryland laboratory, and various others constructed to support specific projects.

Facility development also occurred in the other major countries involved in classical biological control, including various laboratories in the UK's CABI system and a multi-country facility developed in Montpelier, France. These new or refurbished locations increased the capacity of countries to address invasive insect and plant problems through natural enemy introductions.

In Australia, biological control research is undertaken by CSIRO and the Queensland, New South Wales, and Victorian Departments of Agriculture, with quarantine facilities in each state. From the 1960s onward, temporary overseas laboratories were established in various countries to support collection of natural enemies for projects. The first opened in 1960 in the UK and focused on *Sirex* wood wasp biological control. Others followed: Brazil, 1965-1982 (weeds of South American origin); Mexico, 1984-2010; Montpelier, France, 1966 (skeleton weed, *Chondrilla juncea* L.); Iran, 1978-79; Portugal (millipedes) and Spain (dung beetles) in the 1980s; South Africa, 1970-1994 (dung beetles and weeds); and Argentina, 1996-1999 (South American weeds). Of these, all have closed except the CSIRO European Laboratory at Montpellier, France, which is based on a joint biocontrol research campus with the USDA at that location (Andrew Sheppard, CSIRO, pers. comm.).

In South Africa, before 1970, several successful but isolated weed biological control projects were carried out against cacti, with little institutional development or broad organizational support. In the early 1970s, the Weed Research Division of the Plant Protection Research Institute (PPRI) was established under the Department of Agriculture and Technical Services (later the Agricultural Research Council), and, in collaboration with Rhodes University, this Division began to more systematically target invasive cacti, waterweeds, and woody invasive plants (especially species of *Acacia* and *Hakea*). In the 1980s, the University of Cape Town established a biological control research group targeting invasive woody plants. In 1995, with the formation of a governmental program called Working for Water (initially in the Department of Water Affairs but later the Department of Environmental Affairs), funding available for weed biocontrol in South Africa increased greatly. PPRI currently has three research laboratories (Pretoria, Cedara – KwaZulu-Natal Province, and Stellenbosch). Separately, the University of Cape Town, Rhodes University, the University of the Witwatersrand, and the University of KwaZulu-Natal all engage in biological control research. The Working for Water Program employs biological control implementation officers in all nine of the provinces of the country (Martin Hill, pers. comm.). All weed biocontrol projects in South Africa are directed against environmental weeds.

In New Zealand, weed biocontrol was carried out from 1975 by the Department of Scientific and Industrial Research until its disestablishment in 1992. Since then Landcare Research (a new crown research institute) has been largely responsible for weed biocontrol (Hayes et al., 2013). New Zealand does not maintain any overseas biocontrol laboratories, but rather partners with other organizations such as CABI to do overseas work. Funding for weed biocontrol comes from both national and local governments and has been relatively stable. New quarantine containment facilities have been built. Regulation of biocontrol is through Environmental Protection Authority (EPA) under the Hazardous Substances and New Organisms Act of 1996, which provides a clear framework for decision-making on applications to release new weed biocontrol agents, uses formal risk assessment and cost-benefit analyses, has statutory time frames for decision-making, ensures public participation, and maintains the independence of the EPA (Hill et al., 2013). Biocontrol targeting arthropod pests affecting the natural environment has been limited to one project against yellow jackets (*Vespula* wasps) (Ward and Schnitzler, 2013). However, further interest has emerged recently as part of a new multi-agency Bioheritage National Science Challenge (http://www.biologicalheritage.nz/home).

In Canada, no system of overseas laboratories was established. Rather, many projects were conducted using the resources of the Commonwealth Agricultural Bureaux (CAB), now CABI, in the UK, an organization that had laboratories of its own in Europe, India, the Caribbean, and other parts of the world. In addition, some Canadian projects were continuations of projects begun in the United States.

Collectively, these new facilities supported many new projects after 1975, many of which benefited natural areas. For details on projects on western US weeds and insects see Nechols et al. (1995), for projects against invasive plants in the eastern United States see Van Driesche et al. (2002), for invasive forest insect pests see Van Driesche and Reardon (2014), and for weeds in South Africa see Impson et al. (2011). While no clear line exists, gradually projects' goals for weed biocontrol, and to a lesser degree for insect biocontrol, became increasingly focused on ecological benefits, either alone or in conjunction with economic goals. A partial sampling of these projects is briefly noted here, arranged by the biome gaining the project's benefits (Table 1-1). Nine examples are presented at greater length in the next section as case histories and are not included in Table 1-1.

Table 1-1. Selected examples of additional biological control projects producing benefits for natural areas, not including those presented as case studies.

Biome/ location benefitted	Target pest (**P** = plant; **I** = Insect)	Principal biocontrol agents	Examples of species or processes benefitted	References
Grasslands (G) Western US	Tansy ragwort, **P** *Senecio jacobaea L.* (Asteraceae)	Two *Chrysolina* spp. (Chrysomelidae)	In Oregon coastal prairies, lower tansy ragwort numbers allowed a rare plant (*Sidalcea hirtipes* C.L. Hitchc.) to increase by 40% (Gruber and Whytemare 1997). In California, native plant populations increased in coastal prairies following biocontrol, benefitting California poppy (*Eschscholzia californica* Cham.), beach strawberry (*Fragaria chiloensis* [L.] Mill.), Alameda County thistle (*Cirsium quercetorum* [A. Gray] Jeps.), coyote mint (*Monardella villosa* Benth.), and coyotebrush (*Baccharis pilularis* DC.) (Pemberton and Turner 1990).	Coombs et al., 1996; Gruber and Whytemare 1997; McEvoy et al., 1991; Pemberton and Turner 1990; Turner and McEvoy, 1995
(G) Western US	Leafy spurge, **P** *Euphorbia esula* L. (Euphorbiaceae)	Various species of *Aphthona* (Chrysomelidae)	Butler and Wacker (2010) found that in an experimental context in Montana, biocontrol agents reduced leafy spurge density by 80-90%. However, the vegetation that took its place was dominated by nonnative grasses rather than the mix of native forbs and grasses representative of non-infested areas. Setter and Lym (2013) found similar or higher reductions in leafy spurge stems and seedbank numbers at two sites in North Dakota over a ten-year interval, which led to partial recovery of native species. Recovery was slowed, however, by increases in non-native grasses, and seeding of native species may be needed to enhance restoration. Anderson et al. (2015) found that over an 18-yr period in the mountain foothills of Utah, leafy spurge declined 96% due to biocontrol agents, but it was replaced largely by European grasses. This change, while not benefitting native plants, did increase forage quality for native elk (*Cervus canadensis*) in the region. Lesica et al. (2016) identified suitable native forbs for reseeding into leafy spurge-infested areas during or following its biocontrol. Other noted benefits include the recovery of the threatened western prairie fringed orchid (*Plantathera praeclara* Cheviak and Bowles) (Lym, 2005) and of a native *Euphorbia* (*E. robusta* Engelm.), predicted to be within the host range of one of the leafy spurge control agents (*Aphthona nigriscutis* Foudras). In the latter case, increases in population of the native species occurred because lowered competition pressure from leafy spurge was a stronger effect on the native species than feeding by the biocontrol agent (Baker and Webber, 2008).	Anderson et al. 2015; Baker and Webber, 2008; Butler and Wacker 2010; Lesica et al. 2016; Lym, 2005; Setter and Lym 2013
(G) Queensland, Australia	Rubber vine, **P** *Cryptostegia grandiflora* (Roxb.) R. Br. (Apocynaceae)	*Maravalia cryptostegiae* (Cummins) Ono (Pucciniales)	Increased growth of local grasses.	Evans and Tomley, 1994; Vogler and Lindsay, 2002

Table 1-1 (continued). Selected examples of additional biological control projects producing benefits for natural areas, not including those presented as case studies.

Biome/ location benefitted	Target pest (**P** = plant; **I** = Insect)	Principal biocontrol agents	Examples of species or processes benefitted	References
Aquatic or wetland habitats (AW)	Purple loosestrife, **P** *Lythrum salicaria* L. (Lythraceae)	Two *Galerucella* spp. (Chrysomelidae); *Hylobius transversovittatus* Goeze (Curculionidae); *Nanophyes marmoratus* (Goeze) (Brentidae)	In many areas where loosestrife has been suppressed, native species have returned (Landis et al., 2003). Suppression of loosestrife and increase in native plants occurred at one of three sites in Virginia subjected to long term monitoring (McAvoy et al., 2016).	Boag and Eckert, 2013; Denoth and Myers, 2005; Grevstad, 2006; Landis et al., 2003; McAvoy et al., 2016; St. Louis, 2013
(AW) Various, East Africa Lake Victoria	Waterhyacinth, **P** *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae)	Two *Neochetina* spp. (Curculionidae)	In Benin, populations of fish in the genus *Citarhinus* returned to normal levels after biological control of waterhyacinth (Ajuonu et al., 2003; P. Neuenschwander, pers. comm.).	Anon. 2000; Beshir and Bennett 1985; Center et al., 2002; Coetzee et al., 2009; Wilson et al., 2007
(AW) Various countries, including Papua New Guinea and Australia	Giant salvinia, **P** *Salvinia molesta* D. Mitchell (Salviniaceae)	*Cyrtobagous salviniae* Calder and Sands (Curculionidae)	Better light penetration into aquatic systems; Reduced use of herbicides for aquatic weed management in conservation areas (Julien and Storrs, 1996)	Diop and Hill, 2009; Mbati and Neuenschwander, 2005; Room et al., 1981; Thomas and Room, 1986
(AW) South Africa and Zimbabwe	Red fern, **P** *Azolla filiculoides* Lam. (Azollaceae)	*Stenopelmus rufinasus* Gyllenhal (Curculionidae)	Red fern invaded much of South Africa by the 1990s, matting over still water bodies (Hill, 1999), which affected native biodiversity in various parts of southern Africa (Gratwicke and Marshall, 2001). The rare fish *Sandelia bainsii* Castelnau was nearly driven to extinction due to alteration of it last habitat (J. Cambray, Albany Museum, pers. comm.). *Stenopelmus rufinasus* was released in 1997, established and dispersed widely, and rapidly suppressed the weed (McConnachie et al., 2004), allowing recovery (Hill and McConnachie, 2009).	Gratwicke and Marshall, 2001; Hill, 1999; Hill and McConnachie, 2009; McConnachie et al., 2004
(AW) Northern Territory, Australia	*Mimosa*, **P** *Mimosa pigra* L. (Fabaceae)	Various, but especially *Carmenta mimosa* Eichlin & Passoa (Sesiidae) and *Neurostrota gunniella* (Busck) (Gracillariidae)	In some areas, agents have reduced seed rain and seedling regeneration, lowered seed banks, and caused the retreat of mimosa at stand edges in wetlands (Heard and Paynter, 2009), opening space for native plant regeneration.	Heard and Paynter, 2009
Temperate forests (TempF) US mid-Atlantic	Mile-a-minute weed, **P** *Persicaria perfoliata* (L.) H. Gross (Polygonaceae)	*Rhinoncomimus latipes* Korotyaev (Curculionidae)	With reseeding, areas freed of mile-a-minute weed by biological control reverted to native vegetation, both seeded and spontaneous species (Cutting and Hough-Goldstein, 2013; Lake et al., 2014)	Cutting and Hough-Goldstein, 2013; Hough-Goldstein et al., 2009, 2012; Lake et al., 2011, 2014a

Table 1-1 (continued). Selected examples of additional biological control projects producing benefits for natural areas, not including those presented as case studies.

Biome/ location benefitted	Target pest (**P** = plant; **I** = Insect)	Principal biocontrol agents	Examples of species or processes benefitted	References
(TempF) New Zealand	Mist flower, **P** *Ageratina riparia* (Regal) R. King and H. Robinson (Asteraceae)	*Entyloma ageratinae* Barreto and Evans (Entylomatales) and *Procecidochares alani* Steyskal (Tephritidae)	Native plant species richness and cover increased after decline of mist flower due to biological control, with no increase in invasive plants, except a weak response by African club moss (*Selaginella kraussiana* [Kunze] A. Braun). Many plants colonizing plots were native mid- or late-successional shrubs or trees (Barton et al., 2007)	Barton et al., 2007
(TempF) Eastern Canada, Western USA	Larch casebearer, **I** *Coleophora laricella* (Hübner) (Coleophoridae)	*Agathis pumila* (Ratz.) (Braconidae) and *Chrysocharis laricinellae* (Ratz.) (Eulophidae)	Repeated defoliation of western larch (*Larix occidentalis* Nutt.) in northern Idaho reduced tree growth by 80%, but growth returned to normal after successful biological control (Long, 1988). Other biodiversity impacts were not investigated	Long, 1988; Ryan, 1990; Webb and Quednau 1971
Tropical or subtropical forest (TropF) Florida, USA	Old World climbing fern, **P** *Lygodium microphyllum* (Cav.) R.Br. (Lygodiaceae)	*Neomusotima conspurcatalis* (Warren) (Pyralidae) and *Floracarus perrepae* Knihinicki & Boczek (Eriophyidae)	Some areas defoliated by *N. conspurcatalis* have been re-occupied by native plants (Boughton and Pemberton, 2009)	Boughton and Pemberton 2009, 2011; Smith et al. 2014; Lake et al. 2014b
Dunes or coastal habitats (DCH) New South Wales and Western Australia	Bridal creeper, **P** *Asparagus asparagoides* (L.) Druce (Asparagaceae)	Undescribed leafhopper (Tribe Erythroneurini, formerly referred to as *Zygina* sp.) (Cicadellidae) and *Puccinia myrsiphylli* (Thuem.) Wint. (Pucciniales)	Bridal creeper is a threat to four endangered ecological communities in New South Wales – littoral rainforest, river-flat eucalypt forest on coastal floodplains, swamp-oak floodplain forest, and sub-tropical coastal floodplain forest (Downey 2006) and many native plants (Sorensen and Jusaitis 1995, Willis et al., 2003). The rust fungus is currently effectively controlling bridal creeper in many areas, but dead tuber mats persist and can prevent native plant root growth, unless additional measures are taken. Therefore, current benefits are largely in reducing rates of spread.	Downey 2006; Morin and Edwards 2006; Morin et al. 2006; Sorensen and Jusaitis 1995; Willis et al., 2003
Riparian Areas (RE) Rivers and adjacent area in Cape and Fynbos regions, South Africa	Rattlebox, **P** *Sesbania punicea* (Cav.) Benth. (Fabaceae)	*Trichapion lativentre* (Bèguin-Billecocq) (Brentidae); *Rhyssomatus marginatus* Fåhraeus (Curculionidae); *Neodiplogrammus quadrivittatus* (Olivier) (Curculionidae)	Following more than >95% decline in sesbania density due to the biological control agents (Hoffmann and Moran, 1998), many stretches of rivers once clogged with the plant returned to a free-flowing state (Hoffmann, personal observations).	Hoffmann and Moran 1991, 1998
(RE) South Africa	Long-leaved wattle, **P** *Acacia longifolia* (Andr.) Willd. (Fabaceae)	*Trichilogaster acaciaelongifoliae* (Frogatt) (Pteromalidae) and *Melanterius ventralis* Lea (Curculionidae)	Agents reduced seed production of *A. longifolia* >95%, allowing increased in stream water flow (Dennill et al 1999).	Dennill et al. 1999

Table 1-1 (continued). Selected examples of additional biological control projects producing benefits for natural areas, not including those presented as case studies.

Biome/ location benefitted	Target pest (**P** = plant; **I** = Insect)	Principal biocontrol agents	Examples of species or processes benefitted	References
(RE) South Africa	Port Jackson willow, **P** *Acacia saligna* (Labill.) H. Wendl. (Fabaceae)	*Uromycladium tepperianum* (Sacc.) McAlpine (Pucciniales)	From 1991 to 2005, *A. saligna* declined 87-98% at five monitored sites (Wood and Morris 2007). In many areas, dead *A. saligna* trees are being replaced by native fynbos plants, or other weeds and grasses (Lennox et al. 2004)	Wood 2012; Wood and Morris 2007
(RE) South Africa	Golden wattle, **P** *Acacia pycnantha* Benth. (Fabaceae)	*Trichilogaster signiventris* (Girault) (Pteromalidae)	This plant was brought under biological control before it had caused great damage to biodiversity, based on previous experience with the similar but more extensive infestation of *A. longifolia*, as a preventative measure. As such, its benefits are not in the way of correction of actual existing damage, but in its prevention.	Hoffmann et al. 2002; Impson et al. 2011
Oceanic Islands (OI) Seychelles	*Icerya seychellarum* (Westwood), **I** (Monophlebidae)	*Rodolia chermesina* Mulsant (Coccinellidae)	Following this scale's invasion of Aldabra around 1968, native plants, including the endemic *Sideroxylon inerme* ssp. *cryptophlebium* (Baker) J. H. Hemsl., were heavily damaged (Newbery and Hill 1985; Newbery 1988; Gery 1991) and some rare species were on the point of extinction (Friedmann 1994). Following the 1989 release of *R. chermesina* (Gery 1991), scale density was shown to decline and native plants recover over a 5 yr monitoring effort (Johnson and Threadgold 1999.).	Friedmann 1994; Gery 1991; Johnson and Threadgold 1999; Newbery 1988; Newbery and Hill 1985
(OI) Ascension Island, South Atlantic	*Icerya purchasi* Maskell, **I** (Monophlebidae)	*Rodolia cardinalis* (Mulsant); released in 1976 (Coccinellidae)	The ladybird beetle protected a rare endemic spurge, *Euphorbia origanoides* L., whose populations were observed by Cronk (1980) to be declining due to cottony cushion scale (Cronk, 1980). By 1995 (19-yr after release of predator), the scale was not present on sampled spurge populations, including one site documented as infested by Cronk (1980) (Fowler, unpub.). A second survey in 1997 confirmed that *E. origanoides* was no longer attacked (Ashmole and Ashmole, 1997).	Ashmole and Ashmole 1997; Cronk 1980
(OI) Western Pacific atolls of Kiribati, Federated States of Micronesia, and Marshall Islands	*Icerya aegyptiaca* (Douglas), **I** (Monophlebidae)	*Rodolia limbata* (Blackburn) (Coccinellidae)	*Icerya aegyptiaca* invaded various western Pacific atolls (Beardsley 1955, Waterhouse 1993) and attacked various native plants, including *Casuarina equisetifolia* L., *Calophyllum inophyllum* L., and the sand dune plants *Scaevola koenigii* Vahl. and *Scaevola frutescens* K. Kraus (Manser 1974, Maddison 1976). Following its 1994-99, introduction, *R. limbata* controlled the scale (Brancatini and Sands 1997, Sands et al., 1999) allowing recovery of affected plants.	Beardsley 1955; Brancatini and Sands 1997; Maddison 1976; Manser 1974; Sands et al. 1999; Waterhouse 1993

Table 1-1 (continued). Selected examples of additional biological control projects producing benefits for natural areas, not including those presented as case studies.

Biome/ location benefitted	Target pest (**P** = plant; **I** = Insect)	Principal biocontrol agents	Examples of species or processes benefitted	References
(OI) Guam and other Pacific Islands	Cycad scale, **I** *Aulacaspis yasumatsui* Takagi (Diaspididae)	*Rhyzobius lophanthae* Blaisdell (Coccinellidae)	The scale *Aulacaspis yasumatsui* Takagi, along with several other non-native insects, has killed 94% of the cycads in Guam's limestone forests. Consequently, *Cycas micronesica* K.D. Hill has been listed as Endangered by IUCN since 2006, and Threatened by U.S. Fish & Wildlife Service since 2015. The coccinellid *Rhyzobius lophanthae* Blaisdell was introduced from Hawaii, established widely in 2005, and suppressed the scale on mature cycads. This predator was also established on Rota, Koror, and Babeldaup as the scale spread in Micronesia. However, this predator did not suppress the scale adequately on seedlings. The parasitoids *Aphytis lingnanensis* Compere and *Coccobius fulvus* (Compere and Annecke) have been introduced to Guam on numerous occasions. Establishment of these parasitoids has not been confirmed, and cycad plants continue to die every year on Guam and Rota. (Marler, pers. comm.). It is predicted that the population of cycads in western Guam will soon be extinct unless this trend is reversed (Marler and Lawrence 2012). More effective agents are needed, requiring work in the scale's native range in southeast Asia.	Marler and Lawrence 2012

In addition to projects listed in Table 1-1 or discussed below, other projects initiated more recently have ecological goals but have not yet suppressed the pest or achieved demonstrable ecological benefits. Some of these projects likely will provide important benefits in the future and are mentioned here for completeness. While we do not list all such unfinished or in-progress projects, we call attention to the following: (1) hydrilla, *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae) (Grodowitz et al., 2003; Bownes, 2015); (2) Japanese knotweed, *Fallopia japonica* (Houtt.) Ronse Decraene (Polygonaceae) and related species and hybrids (Shaw et al., 2009; Djeddour and Shaw, 2010; Grevstad et al., 2013) (3) cat's claw creeper, *Macfadyena unguis-cati* A.H. Gentry (currently given as *Dolichandra unguis-cati* [L.] L. G. Lohmann) (Bignoniaceae), in Australia and South Africa (L.) (Dhileepan et al., 2007ab, 2013; King et al., 2011); (4) Brazilian peppertree, *Schinus terebinthifolius* Raddi (Anacardiaceae) in Florida (Cuda et al., 2012; Wheeler et al., 2016); (5) air potato, *Dioscorea bulbifera* L. (Dioscoreaceae), in the southeastern US (Overholt et al., 2016); (6) Madeira vine, *Anredera cordifolia* (Ten.) Steenis (Basellaceae), in Australia (Westhuizen, 2011); (7) diffuse (*Centaurea diffusa* Larmarck) and spotted (*Centaurea stoebe* L.) knapweeds (Asteraceae) in western North America (Smith, 2004; Story et al., 2000, 2006, 2008; Seastedt et al., 2007; Myers et al., 2009; Harris, 2011; Newman et al., 2011; Gayton and Miller, 2012); (8) *Parthenium hysterophorus* L. in Queensland, Australia (Dhileepan, 2003); (9) saltcedars, *Tamarix ramosissima* Ledeb., other *Tamarix* species, and hybrids (Tamaricaceae), in the southwestern USA (Hudgeons et al., 2007; Carruthers et al., 2008; DeLoach et al., 2008; Tracy and Robbins, 2009; Pattison et al., 2011; Dudley and Bean, 2012); (10) hemlock woolly adelgid, *Adelges tsugae* Annand (Adelgidae), in the eastern United States (Havill et al., 2014; Mausel and Salom, 2014); (11) winter moth, *Operophtera brumata* (L) (Geometridae), in New England (Elkinton and Boettner, 2014; Elkinton et al., 2015); and (12) emerald ash borer, *Agrilus planipennis* Fairmaire (Buprestidae) (Bauer et al., 2014; Van Driesche and Reardon, 2015) in eastern North America.

ISSUES AFFECTING DEVELOPMENT OF BIOCONTROL PROGRAMS FOR NATURAL AREAS

The further development of biological control projects against pests of natural areas will be affected by several social and financial influences that vary strongly among the various countries developing such projects, including the ability of biological control scientists and conservationists to agree on goals, the willingness of governments to pay for such projects as part of their support for the common good, social beliefs about the merits or offenses of biological control, and the goals and efficiency of whatever regulatory agency must approve the introduction of biological control agents.

Common Cause with Conservation Biologists

To succeed, natural-area biocontrol projects must in the future have support from local conservation biologists. Currently, the degree to which this occurs varies widely and can increase or decrease depending on local events. In Galápagos, for example, an area with no previous history of use of biological control, the invasion of a scale (*Icerya purchasi* Maskell) that proved highly destructive to local plants, stimulated the park service to consider the use of biological control. Successful completion of the project, with large benefits and high safety to local species (see details below in case history) cemented the view that use of biocontrol in the park was potentially suitable, stimulating consideration of further consideration of its use against invasive blackberry (*Rubus niveus* Thunb.) and a parasitic fly (*Philornis downsi* Dodge & Aitken) destroying populations of native land birds. In Hawaii, conservationists recognized the destructive influence of strawberry guava (*Psidium cattleyanum* Sabine) on native forests and strongly supported a biological control project against the invasive tree despite social controversy against it arising from an alliance of pig hunters and anti-government, anti-biological control individuals (Johnson, 2016). In contrast, in the southwestern United States, efforts to suppress vast stands of invasive saltcedars (*Tamarix* spp.) dominating native riparian areas were severely impeded by controversy despite wide agreement of the high level of damage to native riparian plant communities due to *Tamarix* (Van Driesche et al., 2016b). On the surface, this controversy was based on the use of *Tamarix* as nesting habitat by an endangered subspecies of bird (*Empidonax traillii extimus* Phillips); however, this alone does not account for the degree of rancor that developed since (1) the needs of the bird were, in the long term, consonant with saltcedar reduction, that plant being poor habitat compared to willow/popular stands found in uninvaded riparian stretches in the region and (2) the short term effects of biological control could likely be managed by replanting native trees, fencing, and better management of river dam releases and grazing intensity. Rather, it seems that the rancor reached the level of intensity it did due to dislike and distrust between conservation groups and those carrying out the biocontrol project. With that as motive, the bird's status under the Endangered Species Act was used to stop the project.

The degree of trust, rancor, or mutual ignorance of each other between conservation biologists and biological control scientists varies by location. In South Africa, a relatively small group of conservation biologists and biological control scientists have shown a high level of cooperation resulting in many effective projects against environmentally damaging plant invaders, in part because of a clear national understanding of the importance of weed biocontrol to protect water supplies.

In New Zealand, a rigorous new-organisms regulatory act (HSNO) required extensive assessments for biological control introductions. While one might suppose that this would impede the introduction of new biological control agents, it has not. Rather, it has allowed introductions of higher quality agents (safer, more likely to be effective) to proceed. This favorable outcome likely stems from several factors, including the relatively smaller bureaucracy of a small country, social and cultural conditions that allow rapid development of consensus on values, and the small insect and plant biotas requiring assessment. The success of HSNO has stimulated the belief that a similar law might be effective in other countries. This extrapolation, however, may fail in practice in countries like the United States, due to more complex bureaucracy, greater social and political diversity, and larger continental insect and plant biotas, which likely would make it more difficult to reach consensus during safety assessment of biocontrol agents.

In Canada, historically there has been a similar divide between conservation biologists and biocontrol researchers, although the increasing focus on urban areas and issues of invasive species in recent years has raised awareness for the need of ecological restoration with minimal disruption. Consequently, conservation authorities and municipalities have started to see biological control as a viable management option; a case in point is the recent introduction of *Hypena opulenta* Christoph (Lep.: Noctuidae) for biocontrol of invasive swallow-worts (*Vincetoxicum* spp.) (MacQuarrie et al., 2016) (Sandy Smith, pers. comm.).

Governmental Policies on Funding Projects

The study and introduction of biological control agents is of necessity a government-funded activity done in support of the common good. As such, its support requires both a social and governmental belief that the money would be well spent, producing tangible benefits. The use of biological control in natural areas competes poorly for funds against projects aimed to reduce losses from invasive agricultural or forestry pests because there is no obvious interest group to promote the project and plead for funds. For projects in natural areas, this role can potentially be played by NGOs or "friends" groups, but often such influence is not brought adequately to bear.

Trends in funding and support for scientists and laboratories dedicated for biological control work in various countries are not rigorously compiled. However, in several key countries, disinvestment from public sector activity, particularly research, has been a dominant theme in politics over the last several decades. In contrast, in South Africa, the Working for Water Program has provided considerable, stable funding for weed biological control (Martin Hill, pers. comm.).

Future funding for biological control is not knowable, but if a broad social consensus on the utility of biological control for management of certain invasive pests at the landscape level can be developed through a better understanding between conservation biologists and biological control scientists, and then conveyed successfully to the public, prospects for funding would be improved.

Social Beliefs about Merits and Offenses of Biological Control Agents

For biological control to be widely applied to conservation biology problems, the social understanding of the process, its risks, and the potential to alleviate risks from invasive species, must be improved, as controversy among groups is itself, in many cases, enough to prevent its use. A particular problem affecting this concern is that many people reason by reference to categories (e.g.: “Pesticides are bad. This material is a pesticide. Therefore, it is bad.”). Given the tendency of many people to think in this style, being able to impose a label on a thing defines its perception. Category labels are often based on familiar examples. Therefore, whether groups perceive biological control as good or bad will depend on the examples they know. Knowledge of biocontrol successes fade over time, while its failures or mistakes remain visible and influential.

Given these ways in which groups perceive and judge biological control, the future of biological control’s use in natural areas will be affected by the degree to which agencies, NGOs, conservation groups, or others disseminate messages and stories about biological control – either as a force for ecological restoration or as an ecologically risky practice to be shunned. In Hawaii, efforts to communicate reasons for biological control of strawberry guava were initially not well and widely conveyed to the broader public, and, consequently, difficulties arose getting permits for release of the agent (*Tectococcus ovatus* Hempel) (Hemiptera: Eriococcidae) on state land (Johnson, 2016). When local conservation groups in favor of suppression of this invasive tree became engaged, communication about the project – its need, its methods, its benefits and risks – better reached more people, and views of the project became more widely favorable and permits were issued. Countries and agencies that partner with such conservation groups to undertake such public outreach on their behalf will benefit from improved social understanding and acceptance of their projects.

Goals and Efficiency of Regulatory Agencies

Regulatory mandates for the agencies that pass judgment on biological control agent introductions matter to outcomes. All such agencies seek to ensure safety but may not be charged to also actively seek the potential benefits from such introductions (performing a risk/benefit analysis of introductions). Mandates for natural enemy introduction reviews vary considerably among countries (Sheppard and Warner, 2016). Features of good systems include (1) clear goals, (2) clear and not overly complex procedures for reviews and consultations, (3) mandated time periods for completion of reviews, and (4) ability to obtain scientific input from all relevant sources. Rigorous systems with prompt time frames (e.g., HSNO, New Zealand) appear to function smoothly, while vague, complex systems with no time frames (e.g., United States) may find themselves seriously confounded when required to change procedures or adopt new goals. Indeed, in the United States, recent efforts to include food web effects in weed biocontrol agent reviews caused authorities charged with protection of wildlife to virtually cease reviews for several or more years. Ideas for improvement have been articulated by Blossey (2016).

CHAPTER 2. IMPROVING HEALTH OF NATIVE GALÁPAGOS PLANTS BY INTRODUCING A SPECIALIZED PREDATOR OF THE INVASIVE COTTONY CUSHION SCALE

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

The Galápagos archipelago, a UNESCO World Heritage Site and Biosphere Reserve, is renowned for its high levels of endemic flora and fauna, a result of its isolation from other land masses and late colonization by humans. These ecosystems are so unique that they have recently been recognized as one of the 137 most irreplaceable protected areas in the world (Le Saout et al., 2013). A fast-growing tourist destination, this archipelago has seen a rapid a rise in visitors and residents since the 1990s, and the Galápagos are increasingly becoming more connected to the rest of the world. With this, pathways for alien species have multiplied, and the threats associated with these bio-invasions are increasing.

The accidental introduction on plant material of the cottony cushion scale, *Icerya purchasi* Maskell (Hemiptera: Monophlebidae) (Figure 2-1), a cosmopolitan plant pest native to Australia (and possibly New Zealand), brought new threats to endemic Galápagos plants and other indigenous plants of conservation value. This insect is known to feed on over 200 different plant species, although it is best known as a pest of citrus (Caltagirone and Doutt, 1989; Causton, 2001). *Icerya purchasi* feeds on plant phloem, removing nutrients required for plant growth, and its honey dew promotes sooty mold that reduces photosynthesis.

Figure 2-1. Cottony cushion scale, *Icerya purchasi* (Credit: Mark Hoddle)

Icerya purchasi was first recorded in the Galápagos Islands in 1982 and by 1996 had spread to 15 of the 18 larger islands either by wind currents or movement of plants between islands (Causton, 2001; Causton et al., 2004). By 1996, the Charles Darwin Foundation (CDF) and the Galápagos National Park Service (GNPS) had received reports that *I. purchasi* appeared to be affecting the growth and survival of plant species of importance, including endemic plants with restricted ranges. In response, a Technical Advisory Committee was formed to oversee research to confirm observations that *I. purchasi* was causing substantial harm to Galápagos flora, and if so, to develop a control plan.

Figure 2-2. (a) Cottony cushion scale, *Icerya purchasi*, on seagrape, *Scaevola plumieri*, a dunes dominant much affected by the scale; (b) assessing scale abundance (Credits: a,b Mark Hoddle)

Surveys found that at least 62 native and endemic plant species were fed on by the scale (Figures 2-2 and 2-3), of which 16 were on the IUCN Red List of Threatened Species, including six in the two highest threat categories (Endangered and Critically Endangered) (Causton, 2001; Causton et al., 2004). Many introduced and cultivated species were also identified as hosts, some of which increased scale density in natural areas. Scale density and damage varied among host plants, and high infestations caused plant die back or death. One heavily infested native plant was white mangrove (*Laguncularia racemosa* [L.] Gaertn. F.), a dominant species along the islands' coastline that creates important habitat for native invertebrates, fish, and birds, including the critically endangered mangrove finch, *Camarhynchus heliobates* (Snodgrass & Heller), which is restricted to a small stand of mangroves on the western coast of Isabela Island (Fessl et al., 2010). Other plants that were heavily infested included species of the endemic daisy genera *Darwiniothamnus* and *Scalesia* (Family Asteraceae), many of which are red listed because of their vulnerable status (Causton, 2001; Calderón Alvarez et al., 2012). The rapid decline of *Darwiniothamnus tenuifolius* (Hook. f.) Harling (Darwin's

Figure 2-3. Assessing density of cottony cushion scale on *Acacia macracantha* in the arid zone (Credit: Mark Hoddle)

Aster) on Alcedo Volcano on Isabela Island was associated with heavy *I. purchasi* infestations, and this plant's decline may also have harmed its specialist feeders; three endemic Lepidoptera (*Platyptilia vilema* B. Landry, *Semiothisa cerussata* Herbulot, *Tebenna galapagoensis* Heppner & B. Landry), previously found on the flanks of the volcano, were not recorded in the years following the invasion of *I. purchasi* and may have become locally extinct (Roque-Albelo, 2003). Also, honey dew produced by the scale may have facilitated population expansion of invasive ants (including *Wasmannia auropunctata* [Roger] and *Solenopsis geminata* [Fabricius]). These ants defend scale colonies from predators and transport scales between plants (Causton 2001; Hoddle et al., 2013).

Despite many reports of plants being affected by *I. purchasi*, proving that scale infestations harmed or killed field-grown plants was difficult because of the co-occurrence of other stress factors such as drought or poor nutrition. To resolve this uncertainty, in 1999 experimental trials were set up using potted plants to compare growth rates of scale-free vs scale-infested plants. Four native plants known to be hosts of *I. purchasi* in the wild were tested. Growth of leaves, shoots, and roots of three species (white mangrove, *Acacia macracantha* Humb. & Bonpl. ex Willd., and *Phaseolus mollis* Hook f.) was reduced by medium or high scale infestations. In contrast, growth of the endemic species *Scalesia helleri* B. L. Rob was not affected significantly by *I. purchasi*, and this plant consistently had only low densities of scale in the wild, suggesting it has some level of resistance to attack compared to other *Scalesia* (Causton, 2001; ML Johnson et al., unpub.).

WERE OTHER CONTROLS FEASIBLE?

With the data from these trials and plant surveys, the Technical Advisory Committee concluded that there was enough evidence to show that *I. purchasi* was having a significant impact on Galápagos ecosystems and measures should be undertaken archipelago-wide to reduce *I. purchasi* populations. The extensive distribution of the scale insect and the inaccessibility of some invaded sites meant that mechanical or chemical control methods (Causton and Van Driesche, 2016) were not feasible. Consequently, the committee decided that classical biological control was the best option as it was the only management tool that was likely to cause permanent and widespread suppression of this pest on both inhabited and uninhabited islands. Fortuitously, biological control had been used against *I. purchasi* previously to protect citrus plants, eliminating the need to conduct exploratory surveys and providing relevant information for evaluating the safety of importing natural enemies of the pest to the Galápagos.

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

The coccinellid beetle *Rodolia cardinalis* Mulsant (Figure 2-4a,b), a natural enemy of *Icerya* in its native range and the most commonly used species in earlier biological control programs against the pest, appeared best matched to survive the conditions of Galápagos. Furthermore, studies in agricultural systems where *R. cardinalis* had been deliberately introduced (e.g., California) (Quezada and DeBach, 1973) and in its native range in Australia (Prasad, 1989) suggested that the beetle would pose little risk to non-target species and effectively suppress *I. purchasi*. Nevertheless, most control programs with *R. cardinalis* were conducted before strict screening protocols were put in place to evaluate the risks of introducing an alien species to control an alien pest, and no or few post-release evaluations had been conducted to evaluate non-target impacts. Additional studies were therefore considered necessary to determine whether the importation of this beetle would pose risks to native and endemic insects or jeopardize Galápagos ecosystems in other ways.

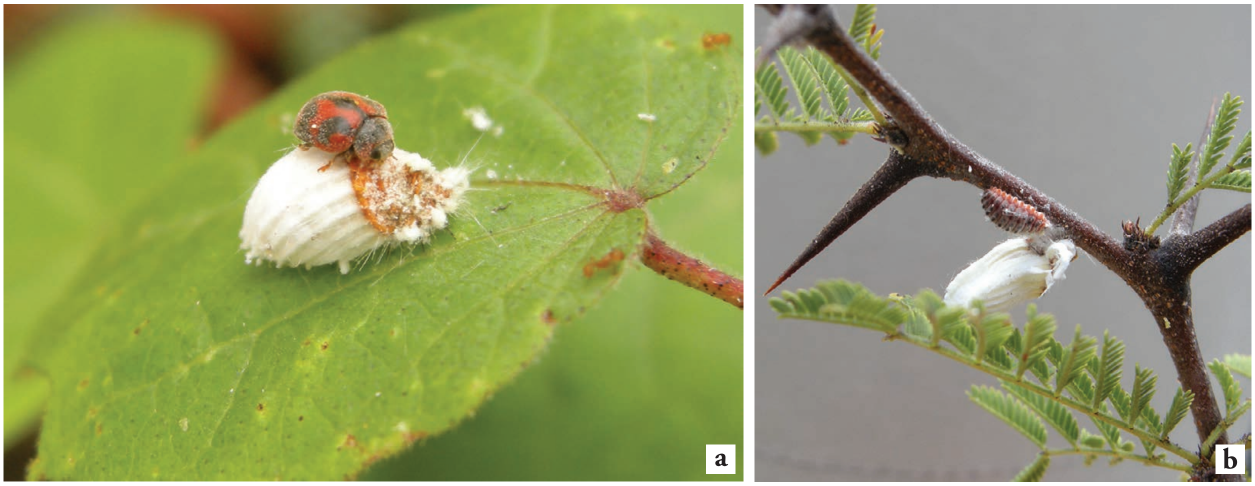

Figure 2-4. An adult (a) and larva (b) of *Rodolia cardinalis* feeding on cottony cushion scale, *Icerya purchasi* (Credits: a,b Mark Hoddle)

In 1999, with the help of CSIRO Entomology, *R. cardinalis* beetles were collected from Brisbane, Australia and imported into a quarantine facility at the Charles Darwin Research Station (CDRS) on Santa Cruz Island, Galápagos. This facility was specially built to conduct tests after a cost analysis demonstrated that it would be prohibitively expensive and logistically difficult to do testing outside Galápagos. From 1999 to 2000, 16 insect species from three orders (Hemiptera, Coleoptera, and Neuroptera) and nine families (Aphididae, Coccidae, Coccinellidae, Chrysopidae, Diaspididae, Eriococcidae, Monophlebidae, Ortheziidae, Pseudococcidae) were tested as prey for *R. cardinalis* larvae or adults. Species tested were those presumed to be at high risk of being preyed upon by *R. cardinalis* in the event of its release (Causton et al., 2004). For all trials, no-choice tests were used in which adults or larvae were exposed only to non-target prey (but not *I. purchasi*).

Non-target impact studies were later extended to evaluate the potential risk of *R. cardinalis*, if eaten, to endemic, insectivorous vertebrates, especially birds, because when attacked coccinellids produce a repellent fluid containing an alkaloid that might be toxic to some species. Although, no evidence exists to suggest that fluids secreted by *R. cardinalis* are toxic, the precautionary principle was applied and experimental studies were carried out to test the consequences of feeding immature stages or adults of *R. cardinalis* to two species of Darwin's finches (Lincango et al., 2011).

The results of these studies suggested that *R. cardinalis* would not present any significant threat to non-target insects or insectivorous birds (Causton et al., 2004; Lincango et al., 2011). In the host-specificity trials, immature and adult stages of *R. cardinalis* did not feed on any of the insect species presented to them except for an endemic ground pearl, *Margarodes similis* Morrison, a scale in the same family as *I. purchasi*. This species, however, is typically encased in a hard shell and found 40 cm below ground and was unlikely to be at risk from predation. Furthermore, *R. cardinalis* was not able to complete its life cycle on this species. When evaluating the effects of feeding *R. cardinalis* adults to species higher up the food chain, we found that beetles were distasteful to the two species of finch tested and were actively avoided or rejected. Symptoms of toxicity (mortality, deterioration, critical weight loss) of birds that had been hand-fed *R. cardinalis* were not observed in either species while in captivity; long-term monitoring could not be conducted because of ethics issues regarding time to keep the birds in captivity.

In 2001, a risk assessment was submitted to the Technical Advisory Committee, and subsequently GNPS approved release of *R. cardinalis* from quarantine. From 2002 to 2005, over 2200, *R. cardinalis* were released on 10 islands. A strong emphasis was placed on community involvement in the release and post-introduction program to raise awareness about biological control and how it works and to emphasize the years of studies that are needed before importation to ensure the safety of the biological control agent.

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

A monitoring program was initiated on Santa Cruz Island soon after the release of *R. cardinalis*, and we found that *R. cardinalis* quickly established in urban, rural, and natural areas. Within 10 weeks, it was found on at least 10 plant species in Puerto Ayora, and within three months, *R. cardinalis* had dispersed without human assistance some 45 km across Santa Cruz Island and reached the neighboring island of Baltra (separated from Santa Cruz by a 200 m channel) (Calderón Alvarez et al., 2012), demonstrating a strong dispersal capacity. Direct observations and predator-exclusion cages were used to evaluate the efficacy of the beetle in reducing scale populations on the badly damaged white mangroves on Santa Cruz Island, and these studies showed a rapid decline of cottony cushion scale density, together with an increase in *R. cardinalis* (Calderón Alvarez et al., 2012). Within three months, scale on mangrove in the experiment declined >99% (Calderón Alvarez et al., 2012). These results suggested that *R. cardinalis* by itself was sufficient to reduce scale insect numbers, at least on some host plants, and that other restoration actions (see Causton and Van Driesche, 2016) were not needed in the short-term. A decision was made to carry out a more extensive evaluation after enough time had passed to allow outcomes to become apparent.

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

Seven years after the first release of *R. cardinalis*, a second evaluation was initiated through a collaborative effort of scientists from CDF, UMASS Amherst, University of California Riverside, technical staff from Galápagos Biosecurity Agency and the Galápagos National Park Directorate, and naturalist guides. The objectives of the evaluation were (1) to determine how widely *R. cardinalis* had established and whether additional releases were needed, (2) to evaluate whether *R. cardinalis* was successfully limiting *I. purchasi* densities, (3) to determine if damaged plant species had recovered, and (4) to see if *R. cardinalis* was feeding on any non-target species. In 2009, nine islands were surveyed for the presence of *I. purchasi* and *R. cardinalis*, in urban, agricultural, or natural areas. In addition, from late 2009 through late 2011 selected species of plants were monitored monthly at six study sites on Santa Cruz or San Cristobal islands to measure the degree of suppression of *I. purchasi* by *R. cardinalis*. Results indicated that *R. cardinalis* had survived and spread after its introduction in 2002 and that it was found in a wide range of habitats. Establishment of *R. cardinalis* was confirmed for six of the ten islands (Fernandina, Floreana, Isabela, Marchena, San Cristobal, and Santa Cruz) where it had been released and on two additional islands (Baltra and Champion). In 2016, *R. cardinalis* was also found on Genovesa Island, where only 22 beetles had been released (in 2003). Genovesa, is a small (14 km^2), isolated, low elevation, arid island, and this recovery suggests that *R. cardinalis* can survive for long periods of time under harsh conditions.

In 2009, *R. cardinalis* was found on 48 of 112 plant species reported as hosts of *I. purchasi* (Calderón Alvarez et al., 2012). Monthly counts on plants at four sites on Santa Cruz and two sites on San Cristobal islands during 2009-2011 found that *I. purchasi* populations were at relatively low densities on most plant species, and overall, these were lower than levels observed before *R. cardinalis* was released (Hoddle et al., 2013). On Santa Cruz Island, densities of *I. purchasi* were extremely low on white mangrove over the whole 26-month survey, and scale insects were rarely detected during one-minute timed searches (Hoddle et al., 2013) compared to more than 100 adult females per branch in 2002 before the predator's release (Calderón Alvarez et al., 2012). Results were similar though less dramatic on three plant species monitored pre- and post-liberation in two arid-zone sites on Santa Cruz Island, and varied with host plant and habitat (Hoddle et al., 2013). Consistently low *I. purchasi* densities were found on palo verde (*Parkinsonia aculeata* L.) and *Acacia insulae-iacobi* L. Riley; however, infestation rates on *A. macracantha* varied between sites, suggesting that differences in vegetation diversity or density, and the level of moisture in the habitat influenced the efficacy of *R. cardinalis*. The highest *I. purchasi* densities were found in dunes on *Scaevola plumieri* (L.) Vahl, at Tortuga Beach, Santa Cruz Island, where over the 2-yr survey, infestation rates ranged from 20 to 90%. However, plant condition remained consistently good (Hoddle et al., 2013), despite strong predator-prey cycling. Scale densities also remained relatively high in urban areas on San Cristobal, on pigeon pea (*Cajanus cajan* [L.] Millsp.) and gooseberry tree (*Phyllanthus acidus* [L.] Skeels), where scales were heavily tended by invasive ants that interfered with *R. cardinalis* foraging (Hoddle et al., 2013) (Figure 2-5).

Figure 2-5. Tending of cottony cushion scale by invasive ants promotes high scale density by interfering with predation by the biocontrol agent, *Rodolia cardinalis* (Credit: Mark Hoddle)

Lack of resources prevented us from monitoring the response of the threatened *D. tenuifolius* populations on the flanks of Alcedo Volcano to the introduction of *R. cardinalis*; however, in 2011 park rangers confirmed the presence of *R. cardinalis* in the area and reported healthy populations of *D. tenuifolius*.

To determine if *R. cardinalis* fed on nontarget species, we conducted some field observations, but most observations were made by exposing *R. cardinalis* adults to potential prey in large, outdoor cages (ca 1.5 x 2 x 2 m) at CDRS in 2009. Potted endemic or native plants (e.g., *A. macracantha*, *Gossypium* sp., *P. aculeata*, and *Waltheria ovata* Cav.) were placed in the cages and infested with *I. purchasi* (the target) and nontarget prey species (e.g., *Coccus viridis* [Green], *Ceroplastes* spp., local mealybugs, aphids, and spider mites, as available) (Figure 2-6). Thirty-one field-collected or laboratory-reared *Rodolia* that had been starved for 24 hrs were released individually into

Figure 2-6. Field cage used to measure reaction of *Rodolia cardinalis* to nontarget insects offered as prey, when presented to starved adult beetles in field cages stocked with native plants infested with potential prey species (Credit: Mark Hoddle)

these cages and each beetle was observed for ~1 hr. Behaviors that were noted included encounters with nontargets and foraging activity. During more than 22 h of observations, free-ranging *R. cardinalis* adult beetles only fed on the target, *I. purchasi*, and were not observed to feed on non-target insects, despite frequent encounters. Furthermore, we found no evidence of *R. cardinalis* attacking non-*Icerya* prey species during field surveys, even when non-target insect species were close to *I. purchasi* (Hoddle et al., 2013). These results support pre-introduction work conducted under quarantine showing that *R. cardinalis* has high host fidelity and is unlikely to feed on nontarget species in the Galápagos. Finally, we evaluated the search efficiency of *R. cardinalis* by placing 15 sticky trap cards in *Icerya*-infested plants and 15 sticky traps in non-infested plants. Very few *Rodolia* beetles were trapped on non-infested plants, suggesting that *R. cardinalis* readily locates *I. purchasi*-infested plants from a distance and that encounters are not random. This suggests that *R. cardinalis* can detect isolated populations of *Icerya* in the wild.

FUTURE OF THE SYSTEM

Additional surveys are needed to confirm establishment of *R. cardinalis* on all islands and to determine whether threatened plant species on some of the outer islands have recovered. In areas that have been surveyed, results indicate (1) that the importation of a single natural enemy of the invasive scale *I. purchasi* has been sufficient to restore plant communities and (2) that additional interventions, such as efforts to replant native species, are not needed. The level of control, however, varies with the plant species, habitat, and season, and may also be influenced by the presence of invasive ants.

ACKNOWLEDGMENTS

The success of this program was due to a large collaborative effort (see participants listed in Calderón Alvaréz et al., 2012 and Hoddle et al., 2013), and we thank everybody who contributed to this project. We would like to express our special appreciation and thanks to the Galapágos National Park Directorate for their support and help with this project. This article is contribution number 2153 of the Charles Darwin Foundation for the Galapágos Islands.

CHAPTER 3. POTENTIAL FOR BIOLOGICAL CONTROL OF A PARASITE OF DARWIN'S FINCHES

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

Philornis downsi (Figure 3-1) is a parasitic fly (Diptera: Muscidae) that was first recorded in the Galápagos archipelago in 1964 where it likely invaded from mainland Ecuador (Bulgarella et al. 2015). *Philornis downsi* poses a major threat to the passerine fauna of the Galápagos Islands due to the way in which its larvae feed. Adult females lay their eggs in bird nests, and first-instar larvae feed in the nares of nestlings while the second and third instars feed on nestlings externally by rasping at the skin and ingesting blood and fluid from the wounds, causing death or deformity of nestlings (Figure 3-2) (Fessl et al., 2006a).

Figure 3-1. *Philornis downsi* is an invasive parasite of nestling birds threatening to cause extinction of many of Darwin's finches in the Galápagos Islands (Credit: David L. Hansen, University of Minnesota)

Parasitism by *P. downsi* causes delayed growth and development, anemia, and death of nestlings (Fessl et al., 2006a). Nestling mortality of up to 100% has been reported for some of the ten species of Darwin's finches affected by *P. downsi* in the Galápagos (O'Connor et al., 2010; Kleindorfer et al., 2014; Heimpel et al., 2016; Koop et al., 2016). Depending on host species and year, 64-98% of nests are infested by *P. downsi,* and on average there are over 40 pupae per nest (Fessl and Tebbich, 2002). This is a stark contrast to the same estimates for *P. downsi* recorded on mainland Ecuador, where, in any given year, 34.6% of nests were infested and on average there were 12.4 *P. downsi* pupae per infested nest (Bulgarella et al., 2015).

Figure 3-2. When the nestlings of ground finches are attacked by *Philornis downsi*, healthy brood, as in this vegetarian ground finch, *Platyspiza crassirostris* (a) are replaced by dead chicks (b) or ones with gross deformities (c) (Credits: a George Heimpel; b,c Jody O'Connor and Sonia Kleindorfer)

Philornis downsi is now considered the greatest threat to the persistence of the adaptive radiation of passerines that was instrumental to the development of evolutionary theory by Charles Darwin (Causton et al., 2013). Until now, none of the 13 species of Darwin's finches have gone extinct in Galápagos since human colonization (Grant and Grant, 2008). However, extinction is a very real threat for several of these species as a result of the invasion of *P. downsi*, in particular the critically endangered Mangrove Finch (*Camarhynchus heliobates* [Snodgrass & Heller]) and Medium Tree Finch (*Camarhynchus pauper* Ridgway) (Fessl et al., 2010; O'Connor et al., 2010). Currently, Mangrove Finches are being protected from exposure to *P. downsi* by a practice known as 'head-starting', in which eggs are removed from nests in the field and reared in a biosecure facility. The reared fledglings are released into their native habitat. This is a very time- and labor-intensive procedure and is being used as a stop-gap measure while long-term solutions are developed (Cunninghame et al., 2013; Fessl et al., 2017).

WERE OTHER CONTROLS FEASIBLE?

Several strategies for the suppression of *P. downsi* populations are currently being considered. These include short-term measures, such as the treatment of nests with insecticides and mass trapping using lures, and long-term measures, such as importation (classical) biological control, release of sterile males, and pheromone disruption. As with head-starting, the short-term control tactics are considered primarily stop-gap measures while long-term measures are developed. Before discussing biological control, we briefly outline developments in strategies employing insecticides and the release of sterile males.

Pyrethroid insecticides such as permethrin have been used to treat the nests of several species of finches. Such treatments can greatly reduce the intensity of *P. downsi* infestation, resulting in increased nestling growth and fledging success (e.g., Fessl et al., 2006b; Koop et al., 2013). This work has been extended to include a novel study by Knutie et al. (2014) that demonstrated that birds can self-fumigate nests when permethrin-treated cotton is made available to birds. Permethrin is considered safe to birds as

LD_{50} doses are exceptionally high for various species including chickens, ducks, pheasants, and starlings (Causton and Lincango, 2014). Furthermore, Causton and Lincango (2014) carried out a case-specific risk assessment using data from Galápagos and concluded that there is no evidence that permethrin has detrimental effects on the mortality of adult and juvenile birds, but the authors point out that the potential for longer-term effects on reproductive function or fitness needs to be evaluated. This work is currently being extended using the zebra finch (*Taeniopygia guttata* Reichenbach) as a model species with the hope that the long-term safety of permethrin for birds as small as Darwin's finches will be corroborated (M. Bulgarella, unpublished).

The sterile insect-release technique (SIT) is based on the release of large numbers of sterile male insects, and it has been successfully implemented for the control of several fly species including the new world screw worm (*Cochliomyia hominivorax* [Coquerel]) (Diptera: Calliphoridae) and several species of tropical fruit flies (Klassen and Curtis, 2005). The basic premise of SIT is that introducing many sterile males into a population prevents the production of offspring by any female that mates with such a male. Although the use of SIT has been suggested for *P. downsi*, the feasibility and likely efficacy of this technique for this species are questionable. The main impediment is that *P. downsi* flies do not mate readily under laboratory conditions. Fertile eggs can be obtained by capturing mated female flies in the field, however, and methods have been developed to raise the resulting larvae on a chicken blood-based diet (Lahuatte et al., 2016). Unfortunately, these procedures together are far too labor-intensive to offer a realistic basis for SIT at this time. Due to the difficulty of rearing *P. downsi* in the laboratory, it has not been determined how *P. downsi* males respond to the ionizing radiation typically used to obtain male sterility in SIT programs. If ionizing radiation has a detrimental impact on male mating success, then success of SIT releases would be reduced (see Calkins and Parker, 2005). Furthermore, the mating behavior of *P. downsi* females is likely to strongly influence the success of the sterile insect technique. Indeed, polyandry (mating with multiple males) would not only dilute the effectiveness of releases but would place sperm of irradiated males in competition with that of normal males. Although there are few data on the mating system of *P. downsi*, Dudaniec et al. (2010) demonstrated a moderate degree of polyandry in *P. downsi* (females produced progeny from 1.9 different sires on average).

Among the methods of intervention currently being used or contemplated, only head-starting and insecticide use have demonstrated protection of Darwin's finches from *P. downsi* parasitism (Fessl et al., 2017). However, neither of these measures has any potential for long-term suppression of *P. downsi* populations. Currently, the most promising long-term management strategy is importation of specialized parasitoids of the fly.

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

No biological control agents have yet been released into the Galápagos for the control of *P. downsi*. However, recent studies in the native range of *P. downsi* (mainland Ecuador and Trinidad & Tobago) have revealed parasitism of *Philornis* puparia (of several species) by five parasitoid species. Ecuadorian parasitoids include *Conura annulifera* (Walker) (Hymenoptera: Chalcididae) (Figure 3-3), a *Brachymeria* species (Hymenoptera: Chalcididae), a *Trichopria* species (Hymenoptera: Diapriidae), a *Spalangia* species (Hymenoptera: Pteromalidae), and an *Exoristobia* species (Hymenoptera: Encyrtidae) (Bulgarella et al., 2015, 2017). In Trinidad & Tobago, the parasitoid *Brachymeria philornisae* n. sp. Delvare was recently recovered from *Philornis trinitensis* Dodge & Aitken in Tobago and the species described (Delvare et al., 2017).

Of these species, the most information is available for *C. annulifera*, which has been recovered exclusively from *Philornis* species (including *P. downsi*) in Trinidad, Brazil (Burks, 1960; Delvare, 1992;

Figure 3-3. Parasitoids of *Philornis downsi*, such as the chalcidid *Conura annulifera*, attack larvae or pupae of the fly and occur in South America, where the fly is native, but are absent from the invaded range of the fly (Galápagos) (Credit: David L. Hansen, University of Minnesota)

Couri et al., 2006), and Ecuador (Bulgarella et al., 2017). This suggests that it may be a specialist on *Philornis* species. Indeed, laboratory host-specificity studies done in quarantine in the U.S. support the hypothesis that *C. annulifera* is a *Philornis* specialist. While puparia of *P. downsi* were readily attacked, the puparia of five non-target fly species including other muscids, sarcophagids, and calliphorids were not (Bulgarella et al., 2017).

Before the release of *C. annulifera* can be considered, host-use tests must be conducted on the non-target species that would be most at risk in the Galápagos. The greatest priority is to test endemic species belonging to the cyclorrhapan Diptera – a taxonomic level that contains various superfamilies, including the Muscoidea, Oestroidea, Hippoboscoidea, Syrphoidea, and Platypezoidea (Griffiths, 1972). The life history of *C. annulifera* suggests that it is these species that represent the most likely non-target hosts. *Conura annulifera* is a solitary pupal ectoparasitoid that lays a single egg in the gap between the hard external puparium and the soft body of the developing *Philornis* pupa. The Cyclorrhapha are the only group of insects that exhibit this gap (Whitten, 1957), and comparative analyses suggest that parasitoids that exploit this niche are restricted to ovipositing there (Bulgarella et al., 2017). In summary, our empirical investigations and the historical record suggest that *C. annulifera* is a specialist on the genus *Philornis.* Furthermore, the life history traits of this species suggest that it is physiologically restricted to the cyclorrhaphan Diptera. However, to move the project forward, it is critical that the host specificity of *C. annulifera* be assessed more extensively on endemic species in the Galápagos.

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

Whether unanticipated problems might occur from releases of *Philornis* parasitoids cannot be foretold now, since none have yet occurred.

WOULD INVADER SUPPRESSION BE SUFFICIENT FOR RESTORATION?

Since releases have not been made, we can only speculate about the potential efficacy of *C. annulifera* or other species as biological control agents of *P. downsi*. Currently, it is unknown how much they might depress fly populations or if any measures would need to be integrated with a biological control program. With respect to the potential effects of release of *C. annulifera*, we can only say that limited field sampling done to date has revealed a maximum of 11% parasitism of *Philornis* at one field site in mainland Ecuador (Bulgarella et al., 2017). While successful biological control agents used in other projects have often caused higher parasitism than this in their native ranges (Hawkins and Cornell, 1994), it would be premature to conclude that *C. annulifera* would be ineffective.

Mortality of the exact host stage attacked by *C. annulifera* (the pupa) is likely to have the strongest negative effect on *P. downsi* populations. *Philornis downsi* larvae presumably experience strong density-dependent, intraspecific competition (Kleindorfer et al., 2014), and so adding mortality to the post-larval stages (i.e., of pupae) avoids problems of potential redundant mortality or alleviation of host density-dependence. Population models have illustrated this principle (May et al., 1981; Abrams, 2009), and a population model developed for *P. downsi* confirmed that raising mortality of pupae should indeed be more effective in suppressing populations than raising mortality of eggs or larvae (G.E. Heimpel unpublished).

Additional parasitoids beyond *C. annulifera* are currently being considered for biological control against *P. downsi,* should they prove necessary. An unidentified species of *Trichopria* has been found to parasitize *Philornis* in mainland Ecuador (Bulgarella et al., 2017). This species attacks and emerges from the pupal stage, and preliminary studies suggest specificity to *Philornis* (M. Bulgarella, I. Ramirez and G.E. Heimpel, unpub. data). Some characteristics of the life history of this species suggest that it may be an efficient biological control agent if used alongside *C. annulifera*. Unlike *C. annulifera*, *Trichopria* sp. is a gregarious species, laying multiple eggs per host. Theoretical work by Heimpel (2000) highlights how gregarious vs. solitary development can influence host population suppression by parasitoids. These models suggest that egg limitation is more likely to reduce the efficacy of control by gregarious species such as *Trichopria* sp., whereas host resources are more likely to become limiting for solitary species like *C. annulifera*. Although it has been suggested that gregarious species are likely to be more effective biological control agents due to their higher fecundity and rapid recruitment (Heimpel, 2000), it may be that egg limitation results in lower population suppression when hosts are abundant. Host limitation may, on the other hand, become more of a problem for a solitary biological control agent if the host species is successfully suppressed. As such, it may be that the complementary introduction of a solitary and a gregarious parasitoid would buffer against failure of biological control should either hosts or eggs be limiting at any given time.

Evolution should also be at least considered as a theoretical solution to this problem. Several studies suggest that the potential exists for at least some bird species to become resistant or tolerant to *P. downsi* through natural selection (see Huber et al., 2010; Koop et al., 2013; Knutie et al., 2016). Coevolution of hosts and their parasites is, however, a slow process, and one that usually favors the faster-reproducing parasites (Damore and Gore, 2012). But birds can also adapt behaviorally, and this may allow resistance to develop more rapidly if these behaviors are socially transmitted. For example, adult and nestling Darwin's finches engage in preening behaviors that may result in removal of *P. downsi* larvae from nestlings (Koop et al., 2013). In addition, Cimadom et al. (2016) have shown that three finch species preen using the leaves of an endemic Galápagos plant, *Psidium galapageium* Hook. f., and experimental work has demonstrated that extracts of this plant repel adult *P. downsi*. The possibility of natural resistance, whether it is conferred genetically or socially is appealing, but relying on this possibility alone to protect vulnerable populations seems unwarranted, particularly given the rapidity with which *P. downsi* is causing population declines in finch species (Koop et al., 2016).

FUTURE OF THE SYSTEM

The reasons behind the greater abundance of *P. downsi* on birds in the Galápagos Islands compared to the mainland are likely complex and multifaceted, but a paucity of natural enemies in the introduced range is almost certainly a contributing factor. In mainland Ecuador, overall parasitism of *P. downsi* by parasitoids typically ranges from 10-20% (Bulgarella et al., 2015, 2017), but parasitism in the Galápagos has never exceeded 5%, and then only by introduced generalist species (Fessl et al., 2017), suggesting that eventually, parasitoid introductions, if safe, may be beneficial. Classical biological control of *P. downsi* in the Galápagos Islands is a promising means of suppressing the population of this invasive species. Although the immediate aim would be to suppress the current population of *P. downsi*, introducing a highly specific biological control agent could also serve to protect vulnerable bird populations from invasions of other similar brood parasites, which may occur in the future. In addition to *P. downsi* there are at least three other *Philornis* species (*P. niger* Dodge & Aitken, *P. falsificus* Dodge & Aitken, and an additional unidentified species) in mainland Ecuador (Bulgarella et al., 2017). Ensuring that appropriate specialized natural enemies are present on the archipelago may minimize the impacts of future invasions of more *Philornis* species. Preventative measures such as this may be particularly prudent in this case, given the increasing popularity of the Galápagos as a tourist destination and the demand for transport links between the islands and the mainland (Causton et al., 2006).

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CHAPTER 4. RESTORING GUMWOOD FORESTS ON ST HELENA: THE CONTRIBUTION OF BIOCONTROL OF ORTHEZIA SCALE

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

The small South Atlantic island of St Helena has a highly degraded but internationally significant terrestrial biota. For example, St Helena's flowering plants include 30 endemic species in 23 genera, of which 10 genera are endemic (Pearce-Kelly and Cronk, 1990). However, this indigenous flora now covers only 1% of the island's land area of 122 km^2 (Cronk, 1989). In the past there would have been extensive forests of arborescent daisies such as the 8-10 m high gumwood tree, *Commidendrum robustum* (Roxb.) DC. (Asteraceae). By the 1980s, this important part of the relic flora was represented by just 2500 trees, mostly in just two natural stands (Cronk, 2000) (Figure 4-1).

Figure 4-1. Last gumwood, *Commidendrum robustum*, relic arborescent daisy woodland at Peak Dale – about 2500 trees (Credit: Simon Fowler)

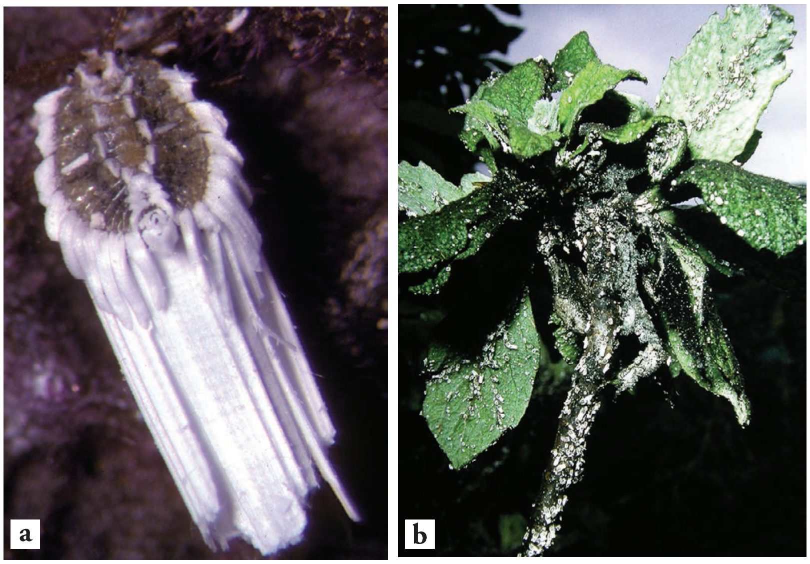

Figure 4-2. *Orthezia insignis* (a) and its damage on gumwoods (b) (Credits: a United States National Collection of Scale Insects Photographs, USDA ARS, bugwood.org; b Simon Fowler)

A scale insect was noticed on these gumwoods in 1991 and identified as *Orthezia insignis* Browne (Hemiptera: Ortheziidae) (Figure 4-2). This was the first record on St Helena of this South American scale insect, which is a pest throughout the continental tropics. Tree deaths started occurring in 1992. By 1993, the scale's infestation of the gumwoods was a source of extreme concern to island conservationists, with over 100 gumwood trees having died (ca 5% of all existing individuals in two years) (Fowler, 2004). If the observed exponential increase in the rate of tree deaths had been unchecked, it was estimated that all 2500 trees would have died by 1995 (Figure 4-3) (Fowler, 2004). This outcome was likely given the lack of natural enemies and the abundance of alternative hosts for the scale, such as the abundant weed *Lantana camara* L. (Verbenaceae) (Fowler, 2004).

This potential extinction of the gumwood trees of St Helena followed a long history of environmental degradation that began with the island's discovery in the 16th century by Portuguese mariners and their release of goats, which by the early 18th century was thought responsible for the near complete destruction of the low altitude forests (as recorded by Darwin [1845]). Human settlement, from 1659 on, led to over-exploitation of all but the very high altitude vegetation zones for timber and firewood, and unrestrained grazing by domestic and feral animals prevented regeneration (Cronk, 2000). Finally, from the late 1800s large areas of the highest altitude vegetation were cleared for plantations of New Zealand flax, *Phormium tenax* Forst. & Forst. (Asphodelaceae), a fiber crop (Cronk, 2000). The scale *O. insignis* was therefore acting on an already highly degraded landscape, threatening the last wild stands of the endemic *C. robustum* and other *Commidendrum* species with extinction (Fowler, 2004).

Because St Helena was geopolitically important to colonial powers in the 17 through 19th centuries, detailed studies on its invertebrates were made incidentally by Europeans based there (Ashmole and Ashmole, 2000). The island's invertebrates showed remarkable evolutionary

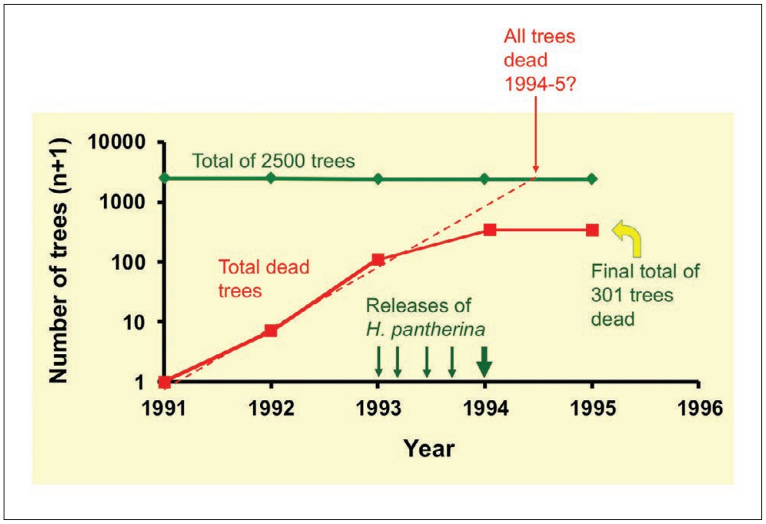

Figure 4-3. Rapid loss of gumwood trees following invasion of Orthezia scale (1991-1993) occurred but losses stabilized following biological control of scale (1993 and following) (Simon Fowler, unpublished data)

radiation, furthered detailed in the 20th and 21st centuries (e.g., Basilewsky, 1972, 1976). As a result, the invertebrates that are dependent on *Commidendrum* species on St Helena are well known, and their loss would be predicted if *Commidendrum* species were to go extinct in the wild. Three insect orders (Coleoptera, Lepidoptera, and Hemiptera) on St Helena include families that have particularly impressive evolutionary radiations. These groups are well studied and include most of the *Commidendrum*-dependent species (Figure 4-4). For analysis of the impacts of Orthezia scale, only fully identified, well described species were included here, and any species likely to have become extinct before the invasion of *O. insignis* were excluded. Detailed collections made from 1800 to present give reasonable confidence in assessing the island's insect fauna. Species were considered extinct pre-Orthezia if they had not been collected since 1960 and were in a group that was sufficiently well known, with available experts, for species to be identified/determined. The host specificity of the insects was based on observations, deductions, and host-records in published sources (Melliss, 1875; Wollaston, 1877; Wollaston TV (Mrs.), 1879; Basilewsky, 1972, 1976; Ashmole and Ashmole, 2000; Mendel et al., 2008). Some modifications were based on modern findings where this was deemed authoritative and thorough, e.g., *Longitarsus helenae* Wollaston (Coleoptera; Chrysomelidae), originally thought to be from "cabbage trees" (Wollaston 1877) but determined by the Belgian expeditions (Basilewsky, 1972) to be host specific on *Trimeris scaevolifolia* (Roxb.) Mabb. (Campanulaceae). Species only recorded rarely on single host plants were assumed to be host specific: in this case, it was assumed that the recent, very thorough surveys would have recorded these insect species from other host plants if the insects were not host specific. *Commidendrum*-dependent species that were oligophagous, i.e., ones recorded from more than one *Commidendrum* species, were also included in Table 4-1 as these would also have become extinct if all *Commidendrum* species on the island were driven to extinction in the wild by *O. insignis*.

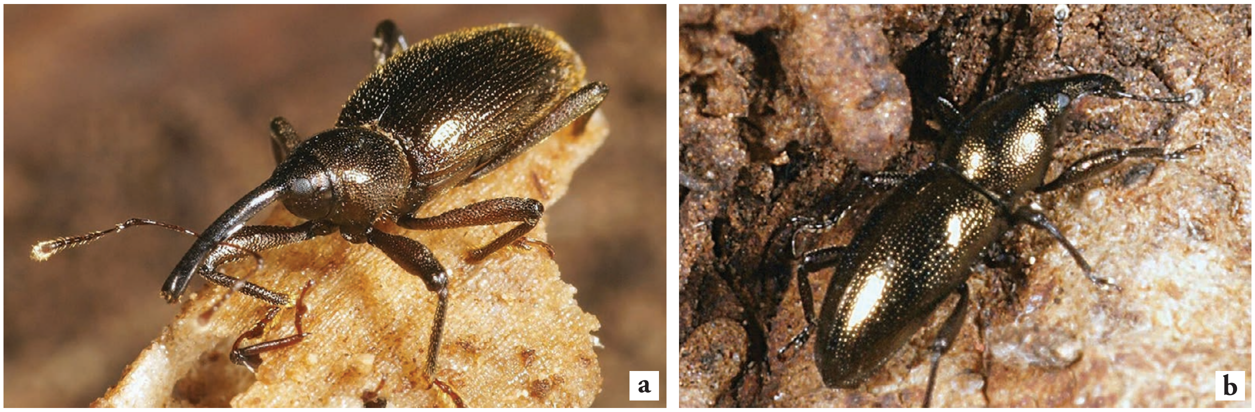

Figure 4-4. The endemic insects of St Helena that are dependent on *Commidendrum* species that would have been destroyed by Orthezia scale include 12 beetles, 15 moths, and 7 hemipterans; among them, the two weevils illustrated here: *Lamprochrus cossonoides commidendri* Decelle (a) and *Acanthinomerus* sp. (b). All of this biodiversity was threatened by the pending destruction of their host plants by the invasive scale. (Credits: a,b Roger Key)

Failure to suppress *O. insignis* through biological control would not only have driven a major component of the endemic flora extinct in the wild, but would have caused the co-extinction of a further 14% of the endemic insect fauna of St Helena in the orders Hemiptera, Coleoptera, and Lepidoptera (Table 4-1). Given the likely loss of further endemic species, such as associated parasitoids or other specialized natural enemies of the plant-associated insects in Table 4-1, this is likely to be a low estimate of the total predicted co-extinctions if *Commidendrum* species had become extinct in the wild on St Helena.

Table 4-1. The predicted loss of dependent species in the main insect orders associated with *Commidendrum* spp. on St Helena should these plant species become extinct in the wild as a result of the invasion of the exotic scale insect, *O. insignis*. Percentage losses used total numbers of endemic species from Ashmole and Ashmole (2000).

Taxonomic group	Predicted number of species lost	Percentage loss of endemic species
Hemiptera	7	18%
Coleoptera	12	8%
Lepidoptera	15	28%
Total	34	14%

WERE OTHER CONTROLS FEASIBLE?

Foliage-applied insecticides can control *O. insignis* on individual gumwood trees, but effective use over whole stands in steep terrain subject to persistent southeast trade winds would have been extremely difficult. Perhaps more probably, soil-applied insecticides, which can be used to control *O. insignis* (Crop and Plant Protection Unit, 2009), might be applied, but the abundance of alternative host plants for the pest would have promoted frequent re-invasion that would have required an ongoing program of pesticide application. Furthermore, use of chemical control, while conceivably protective to the plants, would have caused severe non-target effects on the many endemic arthropods feeding on treated gumwoods (Table 4-1). Finally, the option of natural control by local native natural enemies was discarded as there appeared to be no existing natural enemies of *O. insignis* on St Helena, as shown by the fact that none were seen in a two-year study of the scale in gumwood stands on the island (Fowler, 2004).

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

The biological control agent released on St Helena from 1993-95 was *Hyperaspis pantherina* Fürsch (Coleoptera: Coccinellidae) (Figure 4-5), which had previously been used successfully to control *O. insignis* in Hawaii and in several countries in Africa (Booth et al., 1995). The only report of any prey other than *O. insignis* being attacked by *H. pantherina* is from the host range testing carried out before its release on St Helena: when deprived of *O. insignis*, adult *H. pantherina* did attack mealybugs (*Pseudococcus* and *Planococcus* spp.). However, oviposition and successful development only occurred in the presence of *O. insignis* prey (Booth et al., 1995). At the time of the release of *H. pantherina* on St Helena, there were no known indigenous mealybugs or scale insects on St Helena (Fowler, 2004). The mealybug *Ripersiella mediatlantica* Matile-Ferrero (Hemiptera: Pseudococcidae) is now regarded as an endemic species on St Helena (Ashmole

Figure 4-5. *Hyperaspis pantherina*, the predator that controls Orthezia scale on St Helena (Credit: www.discoverlife.org)

and Ashmole, 2000; Key, 2014), but the Belgian entomologists who collected and described the only four specimens ever collected (found together with an exotic mealybug and an exotic scale on dead cabbage trees on the High Central Ridge in the 1960s) state it was not possible to say whether it was native or not (Matile-Ferrero, 1976). Whether *H. pantherina* has any impact on endemic mealybugs on St Helena is unknown, but it is highly unlikely to establish a breeding population on such prey. In contrast, the generalist mealybug predator *Cryptolaemus montrouzieri* (Mulsant) (Coleoptera; Coccinellidae), which was released in 1971 (St Helena Government, 2013) would be a greater threat to any indigenous mealybugs on St Helena, as it has a wide prey range (Kairo et al., 2012). However, any harm *C. montrouzieri* might do to putative indigenous mealybugs would have to be balanced against the beneficial effects it has by attacking exotic pest species of mealybugs on St Helena: these pest mealybugs severely damage crop and ornamental plants (St Helena Government, 2016) and critically endangered endemic plants such as *Mellissia begoniifolia* (Roxb.) Hook.f. (Solanaceae), the St Helena boxwood (Lambdon and Ellick, 2016).

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

There have not been any specific surveys to assess whether the introduction of *H. pantherina* and the successful suppression of the exotic scale *O. insignis* have had any unexpected ecosystem effects. However, there have been substantial surveys of invertebrates as part of recent conservation initiatives, and none of these reports show any unexpected presence of the predator in native habitats in the absence of *O. insignis* prey (Mendel et al., 2008).

There were concerns that the weed *L. camara* might become more abundant once *O. insignis* was suppressed as this was one of the scale insect's preferred host plants. Suppression of *L. camara* on St Helena has been suggested as an essential prerequisite for the natural regeneration of scrubwoods, *Commidendrum rugosum* (Dryand.) DC. (Asteraceae), following the near-eradication of goats (Ashmole and Ashmole, 2000). Fortunately, other introduced biocontrol agents (e.g., lantana lacebug, *Teleonemia scrupulosa* Stål [Hemiptera: Tingidae]) appear to be maintaining *L. camara* under sufficient biological suppression (Ashmole and Ashmole, 2000; Jill Key, pers. comm.).

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

Reduction of *O. insignis* by *H. pantherina* was >95% (Figure 4-6), but this is probably an underestimate because it is hard in the field to distinguish live scales from fragments left after attack by the beetle (Fowler, 2004). Indeed, rearing of *H. pantherina* ended on St Helena in 1995 because sufficient *O. insignis* could not be collected on the island to support the colony, presumably because biocontrol had been so successful (Fowler, 2004). More recently, occasional outbreaks of the scale on the island have been reported, but these outbreak patches are rapidly colonized by *H. pantherina* and the scale suppressed (Mendel et al., 2008). The only exceptions to this successful suppression have been noted at some low-altitude restoration sites where tending ants appear to be protecting *O. insignis* from predation by *H. pantherina,* resulting in the scale persisting as a nuisance pest (Roger Key, pers. comm. 2013). After a visit to St Helena in 2015, Quentin Cronk, an authority of the endemic flora of St Helena (Cronk, 2000) commented "*Orthezia* is still about, as is *Hyperaspis* – the two seem to have settled down into a stable co-existence with *Orthezia* no longer a serious problem, just a minor nuisance. This is an extraordinary success story" (Q. Cronk pers. comm. 2015).

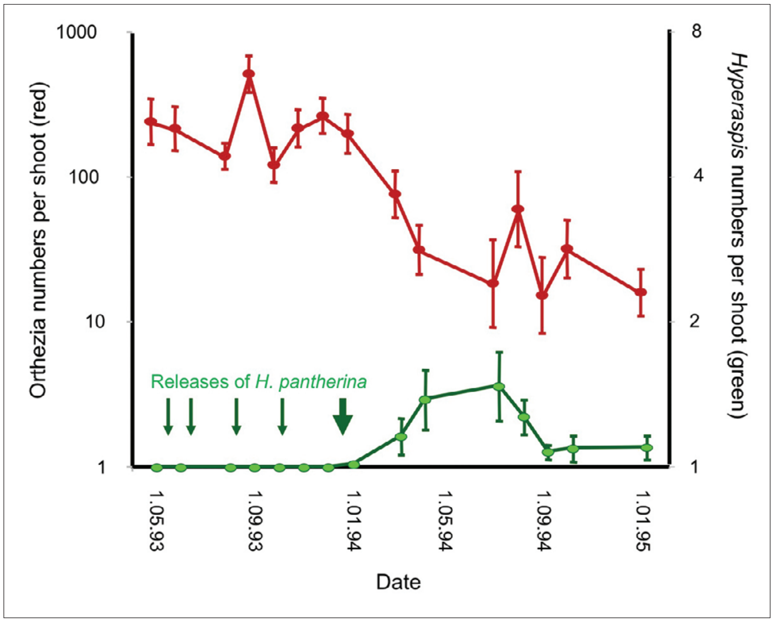

Figure 4-6. Control of Orthezia scale by the ladybird beetle *Hyperaspis pantherina* on the island of St Helena

WERE OTHER MEASURES NEEDED?

Controls over domestic and feral stock, rabbits, and weeds have all been essential for protection of both naturally regenerating stands of *Commidendrum* and for planted stands established under the Millennium Forest Project, which aims to expand the area of natural forest on the island (Thompson, 2008; IUCN, 2011). Some invertebrates still cause minor problems on new plantings, such as mollusks, lepidopteran larvae, and the root mealybug *Pseudococcus viburni* Signoret (Hemiptera: Pseudococcidae), but *O. insignis* has never caused any damage to the Millennium Forest (Figure 4-7) (Rebecca Cairns-Wick, pers. comm., 2013).

FUTURE OF SYSTEM

St Helena has a dismal history of failed conservation efforts stretching back to at least 1709 (Ashmole and Ashmole, 2000; Cronk, 2000). Recent conservation initiatives include the Millennium Forest (IUCN, 2011), which is a substantial re-planting project aiming to re-create part of the Great Wood that once existed in mid-altitude parts of St Helena. The Millennium Forest, which predominately is comprised of restoration plantings of gumwood trees, currently covers 38 ha, with a total planned area of 250 ha. The main difference between the modern-era programs and past failures seems to be the current high level of community engagement, which was often markedly absent in the past (Ashmole and Ashmole, 2000; Cronk, 2000; IUCN, 2011). For example, virtually every islander has purchased at least one tree to plant in the Millennium Forest (Thompson, 2008), and there are extensive volunteer and education programs focused on this restoration project (IUCN, 2011). Substantial financial support for this work has been contributed by the UK government (e.g., Darwin Initiative). After centuries of biodiversity loss on St Helena, interspersed by many failed conservation attempts, there finally seems some hope. Although continued pest and weed control efforts, as well as restoration planting, are still needed, many restorations are succeeding that would

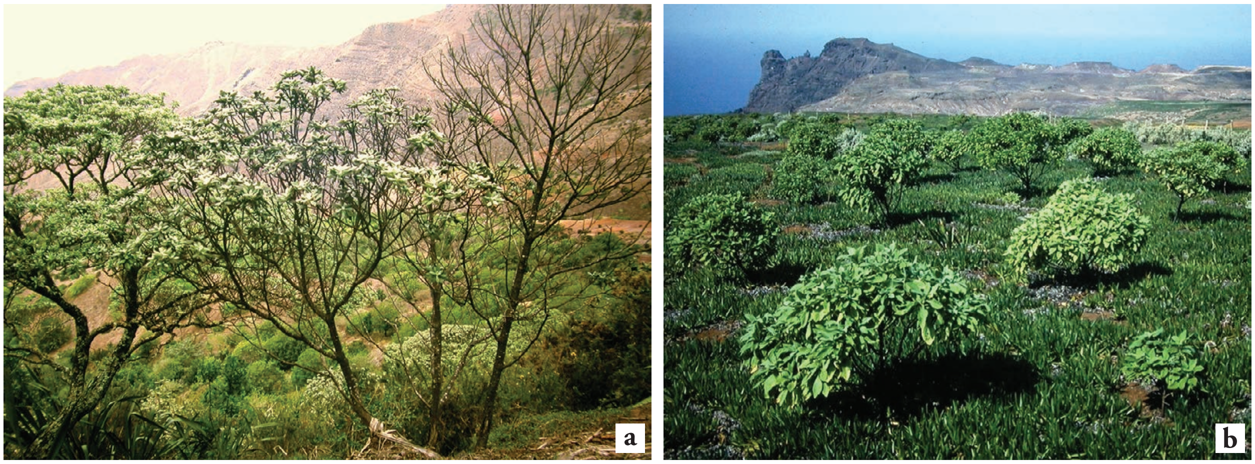

Figure 4-7. New restoration initiatives to expand gumwood stands are now possible due to suppression of Orthezia scale by the introduced biocontrol agent, allowing for recovery of surviving gumwoods (a) or planting of gumwoods in additional areas (b) (Credits: a,b Simon Fowler)

have failed had biological control of *O. insignis* not been achieved (Fowler, 2004). To quote a past president of the St Helena National Trust "The introduction of *Hyperaspis* to St Helena and its biocontrol of *Orthezia* is a conservation success story; we would be in a very different situation had *Orthezia* not been brought under control" (Rebecca Cairns-Wick, pers. comm. 2013).

ACKNOWLEDGMENTS

Rebecca Cairns-Wick, Quentin Cronk, Jill Key, and Roger Key provided up-to-date information from St Helena. The Agriculture and Forestry Dept., St Helena Government, funded and operated the project on St Helena. The project was started by CAB Bioscience using quarantine facilities licensed by the Ministry of Agriculture, Fisheries and Food, UK (Licence PHF 873A/667/73) and funding from the British Government (ODA Project OMC 92/94 349/053/001A). Landcare Research, New Zealand, provided funding for analysis and writing up.

CHAPTER 5. PROTECTION OF WILIWILI TREES, THE FOUNDATION OF HAWAIIAN DRY FORESTS, THROUGH SUPPRESSION OF AN INVASIVE GALL WASP

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

The endemic tree *Erythrina sandwicensis* O. Deg. (Fabaceae), locally known as wiliwili, is one of the few native deciduous species in Hawaii (Rock, 1913). It is considered a keystone species of lowland dry forests, one of the most endangered habitats in the Hawaiian archipelago (Cabin et al., 2000). It grows on leeward slopes on all of the main islands, from sea level to 600 m in elevation (Wagner et al. 1990).

This tree has faced many threats over the last several decades, which have reduced its abundance (Bruegmann, 1996). The most recent of these has been the invasion of the erythrina gall wasp (EGW), *Quadrastichus erythrinae* Kim (Hymenoptera: Eulophidae) (Figure 5-1a), which put *E. sandwicensis* at risk of extinction. The gall wasp was first reported from Reunion Island, Mauritius, and Singapore in 2003, and was formally described by Kim et al. (2004). The gall wasp was first reported on Oahu, Hawaii in April 2005, and by August it was found on all the main Hawaiian Islands (Heu et al., 2006). The gall wasp was first observed infesting the ornamental and windbreak forms of the exotic species *Erythrina variegata* L. Both forms of this tree species were extremely susceptible to the gall wasp, and they suffered nearly 100% mortality statewide. The Department of Parks and Recreation of the City and County of Honolulu removed over 1,000 dead *E. variegata* trees (Vorsino, 2006). Soon thereafter, the gall wasp was reported infesting several other exotic species of *Erythrina* growing in botanical gardens around the islands (Messing et al., 2009), as well as the endemic *E. sandwicensis* in both urban and natural areas. Nearly 100% of endemic wiliwili trees had some level of galling in urban and natural areas. Over 65% of shoots inspected during pre-release months were rated as heavily galled (infestation ratings of 2 or 3 out of a 4-point scale from 0-3).

Female EGW insert their eggs into young plant tissues such as leaves, petioles, stems, flowers, and seedpods. Larval feeding causes galling of infested tissues (Figure 5-1b). Severe galling induces defoliation,

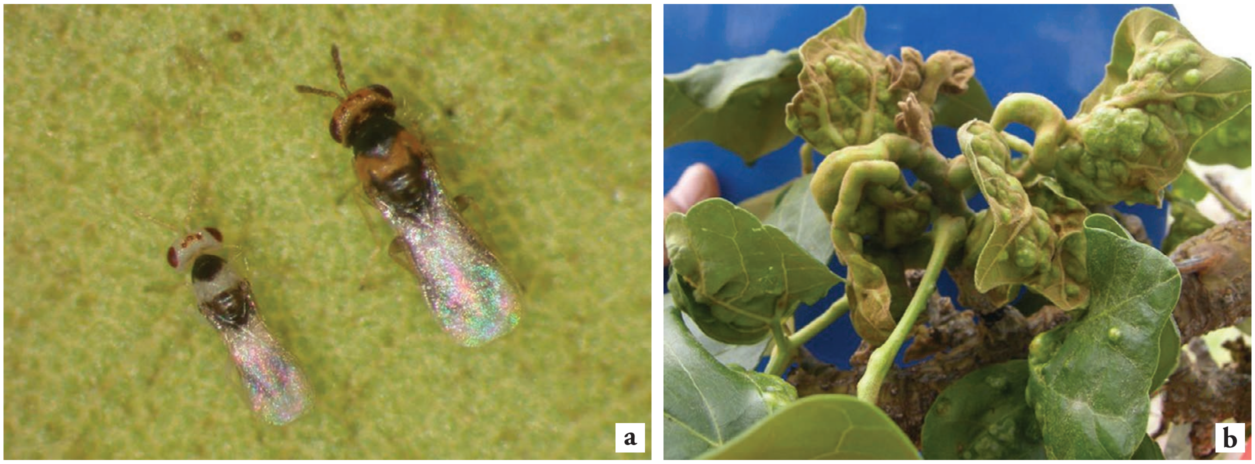

Figure 5-1. Adults of the erythrina gall wasp, *Quadrastichus erythrinae* (a); galled foliage of the wiliwili tree (b) (Credits: a,b Hawaii Department of Agriculture)

which in turn reduces growth and plant vigor, and potentially causes tree mortality (Kim et al., 2004; Heu et al., 2006). Within months of the invasion of EGW, heavy infestations and tree mortality were observed in natural habitats, which caused great concern among conservationists and local communities. A statewide seed bank program was established in 2007 to preserve the species in the event of extinction in the field (Hollier, 2007). Concurrently, feasible short and long-term control methods were sought.

WERE OTHER CONTROLS FEASIBLE?

Initial efforts to slow the spread of the gall wasp included removal and disposal of infested material, but this was quickly recognized as impractical due to the small size of the wasp, its rapid dispersal, and the occurrence of overlapping generations.

Applications of systemic insecticides, as trunk injections or soil drenches, were assessed for preservation of ornamental trees at irrigated urban sites (Xu et al., 2008). It was concluded that trunk injection with imidacloprid was the most effective treatment under those conditions. Daccola et al. (2009) tested the effectiveness of two stem-injected insecticides (imidacloprid and emamectin benzoate) in a natural, dryland site on Maui; they concluded that imidacloprid was the better treatment and that control lasted about one year.

Insecticide treatments were used mainly in urban settings, golf courses, and botanical gardens. Occasionally this approach was used in natural areas. Even though pesticides were found to be effective in some cases, they were not considered useful as a cost-effective, long-term, self-sustaining option to suppress EGW in natural dryland areas in Hawaii. Consequently, a classical biological control program was initiated in 2005.

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

The Hawaii Department of Agriculture (HDOA) and the University of Hawaii undertook a search for possible biological control agents in several parts of Africa, the most plausible area of origin of the gall wasp. The parasitoid *Eurytoma erythrinae* Gates and Delaware (Hymenoptera: Eurytomidae) (Figure 5-2a) was reared from galled leaves of *Erythrina abyssinica* Lam. ex DC., which had been collected in Tanzania in 2006. A colony of this parasitoid was successfully established in quarantine in Hawaii.

Eurytoma erythrinae was also unknown to science at the time of collection and was formally described by Gates and Delvare (2008). Studies on the basic biology and host specificity of this species were done at the HDOA Insect Quarantine Facility. Females of *E. erythrinae* lay their eggs inside EGW galls, and parasitoid larvae feed externally on up to five EGW larvae or pupae to complete their development.

Host specific studies examined potential risks to seven gall-forming non-target species: one Hawaiian endemic psyllid, four beneficial species (three tephritids and one eriococcid used for weed biological control), and two immigrant wasps (one agaonid and one eulophid) (HDOA, unpublished data). Studies concluded that *E. erythrinae* did not pose a risk to any of the non-target species tested, and the parasitoid was approved for release in late 2008, which occurred at several sites on all main Hawaiian Islands.

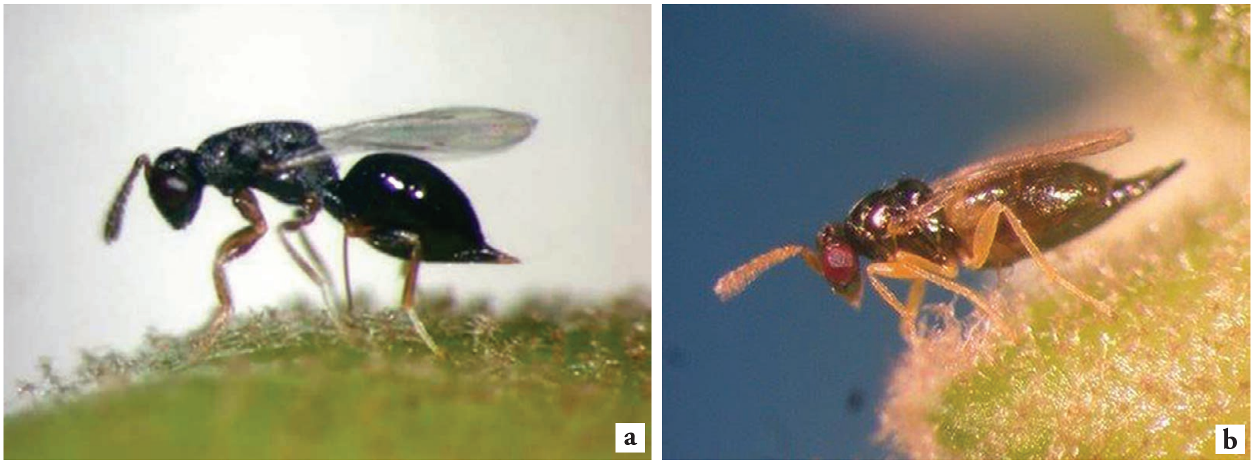

Figure 5-2. Two parasitoids have been studied for biocontrol of the erythrina gall wasp in Hawaii: (a) the eurytomid *Eurytoma erythrinae* and (b) the eulophid *Aprostocitus nites* (Credits: a,b Hawaii Department of Agriculture)

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

Eurytoma erythrinae quickly established in natural habitats and now occurs on all the main Hawaiian Islands. Pre- and post-release monitoring data show that this biocontrol agent has reduced infestation levels in foliage and improved the health of wiliwili trees in both urban settings and natural stands. Only a year after the release of the biocontrol agent, trees showed a significant reduction of infestation level in leaves, stems, and petioles. An increase in flowering was also observed after release. Nevertheless, galling of inflorescences is still high and reduces seed production (Figure 5-3). Galling is particularly high on young inflorescences and seedpods at drier sites on Maui and Hawaii. Monitoring showed that heavily infested young inflorescences die before blossoming. Germination studies show that seeds from heavily infested pods have lower germination rates compared to seeds from lightly infested or uninfested pods.

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

A multi-site survey throughout the state done in 2012 found that approximately 30-35% of the wild wiliwili trees had been killed by the gall wasp, and little-to-no recruitment of seedlings was observed.

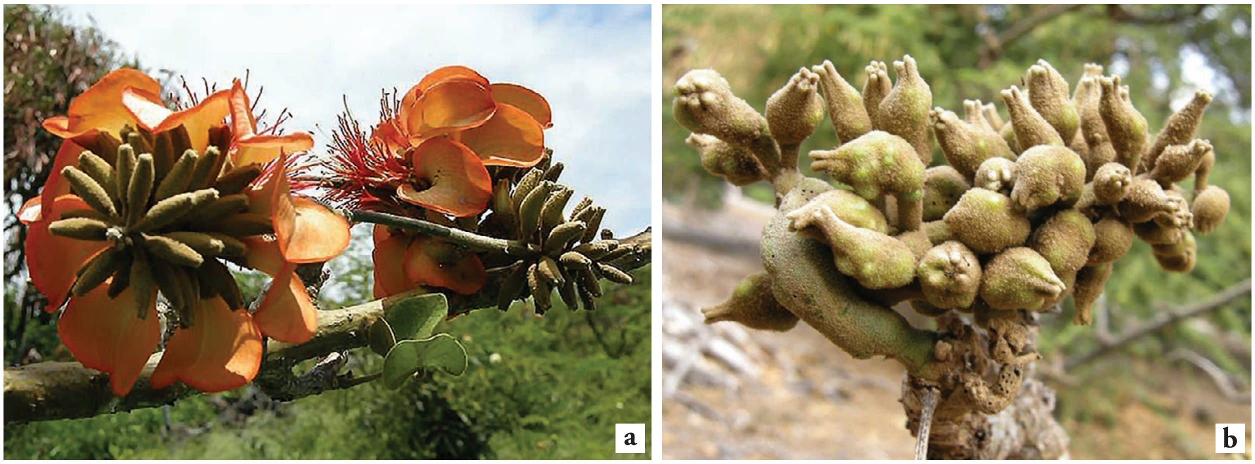

Figure 5-3. Uninfested flowers of the wiliwili tree (a) versus a galled inflorescence (b) (Credits: a,b Hawaii Department of Agriculture)

Release in 2008 of the parasitoid *E. erythrinae* reduced the risk of mortality for wiliwili trees and supported the continued use of the wiliwili tree in dryland restoration efforts in Hawaii. Nevertheless, these efforts are not yet self-sustaining because of the continued reduction in tree seed production due to the gall wasp, coupled with pre-existing threats to the tree such as habitat destruction, changes in the fire regime, seed predation by the bruchid *Specularis impressithorax* (Pic), competition with invasive weeds such as fountain grass, *Pennisetum setaceum* (Forssk.) Chiov., as well as severe browsing pressure by feral ungulates. The combined effect of these threats, together with poor control of the EGW in inflorescences may be preventing plant recruitment in natural areas in Hawaii. Monitoring showed that over 50% of seedpods collected only three weeks after maturity have seeds already infested with *S. impressithorax* eggs. Germination tests indicated that uninfested seeds have an average germination rate of about 45-50%. Seeds with at least one bruchid exit hole have less than 10% chance of germination, whereas seeds with two or more exit holes do not germinate. More research is needed to elucidate how these threats affect wiliwili recruitment in dryland forests in Hawaii.

WERE OTHER MEASURES NEEDED?

Currently, *E. eryhrinae* is the only control agent that has been released in Hawaii against EGW. Nevertheless, it is evident that additional control measures are needed to prevent heavy galling of inflorescences and seedpods. Another biological control agent, the parasitoid *Aprostocitus nites* Prisloo and Kelly (Hymenoptera: Eulophidae) (Figure 5-2b), which has potential to provide additional control, is currently being considered for release. The HDOA has finished studies on the biology and host specificity on this prospective agent. Additional studies were also conducted to address any potential negative interactions of this second parasitoid with the first parasitoid, *E. erythrinae*. Results from these studies suggest that there is no risk to potential nontarget species and that there is no evidence for negative interactions between the two biocontrol agents. Results also suggested that the two agents together could provide additional protection to inflorescences and seedpods (Yalemar, pers. comm.).

The HDOA has completed an Environmental Assessment for *A. nites* to propose its release into the environment, and concluded that this species poses no significant impacts to the environment. Pending state and federal approvals, this biocontrol agent could be released soon.

FUTURE OF SYSTEM

The first biological control agent released against the gall wasp has provided enough control to prevent mortality of existing wiliwili trees in Hawaii. This measure alone, however, is not enough to restore self-sustaining tree populations. The second biological control agent is expected to provide better suppression of galling on inflorescences, which should increase production of viable seeds. This and the reduction of other threats to the wiliwili tree are needed to ensure the long-term survival of this endemic Hawaiian tree.

ACKNOWLEDGMENTS

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CHAPTER 6. CAN ASH COMMUNITIES AND THEIR DEPENDENT SPECIES BE PARTIALLY PROTECTED THROUGH BIOLOGICAL CONTROL OF EMERALD ASH BORER?

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

Ash trees (*Fraxinus* spp.) are important components in many hardwood forests in the United States and Canada (Federal Register, 2003; Nowak et al., 2003). There are 16 species of *Fraxinus* native to North America (Harlow et al., 1996; USGS, 2014), each adapted to different ecological habitats across a range of climates zones, soil types, and moisture gradients (Eyre, 1980). These diverse ash communities provide not only economic benefits, with US ash timber alone valued at $282 billion (Nowak et al., 2003), but also serve as food, cover, nesting sites, and habitat for mammals, birds, arthropods, and other organisms (Poland and McCullough, 2006; Gandhi and Herms, 2010; Koenig et al., 2013, Wagner and Todd, 2016). Any significant reduction in the abundance and/or diversity of the ash community would inevitably result in both economic losses (e.g., reduction of lumber production) and cascading ecological degradation in North American natural forests.

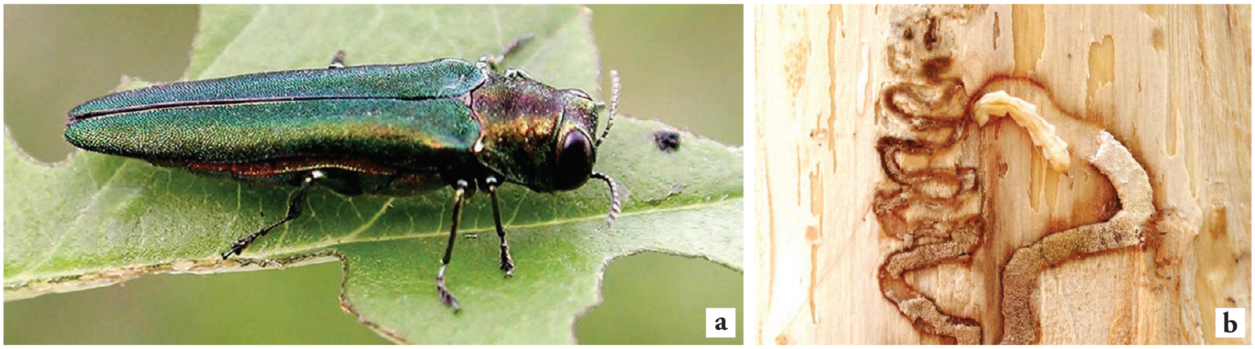

Figure 6-1. Emerald ash borer, perhaps the most destructive invasive pest affecting North American forests today (a) adult; (b) typical gallery showing a mature larva digging into wood for pupation (Credits: a Debbie Miller, USDA Forest Service, bugwood.org; b Jian Duan)

Figure 6-2. Dead and dying ash trees in heavily damaged forest in south central Michigan, showing the ecological impact of emerald ash borer (Credit: Jian Duan)

Emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (Figure 6-1a), is an invasive forest insect native to northeastern Asia (China, the Korean Peninsula, and the Russian Far East), whose larvae kill trees by tunneling in the phloem (Figure 6-1b). Since emerald ash borer was first detected in southern Michigan and Ontario in 2002 (Haack et al., 2002), it has killed hundreds of millions of North American ash trees in 32 US states (Herms and McCullough, 2014; Emerald Ash Borer Information, 2016) and two Canadian provinces. While the economic cost of the EAB invasion is estimated to be $1 billion per year for the next decade (Kovacs et al., 2010), the ecological impacts of the EAB invasion on North American forests are already severe and widespread (Figure 6-2). EAB has killed 99% of healthy ash trees in some early-infested forests and has the potential to functionally extirpate ash from the continent (Klooster et al., 2014). The loss of ash diversity and abundance in natural forests in the earliest-invaded regions (e.g., Midwestern and Mid-Atlantic States) has already harmed native plants and has the potential to affect populations of native, ash-dependent insects (Figure 6-3), as well as changing nutrient cycling and other ecological proecesses (Ulyshen et al., 2011, 2012; Flower et al., 2013; Stephens et al., 2013; Gandhi et al., 2014; Jennings et al., 2016a).

WERE OTHER CONTROLS FEASIBLE?

As discussed above, EAB is driving the ecological degradation in ash-dominated forests in North America, and taking no action against it is not a sensible option. Initial efforts to contain EAB damage focused on eradication of incipient populations from newly infested areas by destroying all infested trees within these areas, while at the same time restricting the movements of EAB-infested live trees or firewood in or out of the eradication area. However, the eradication effort was abandoned by 2009 because EAB populations in many infested areas (such as Michigan, Ohio, and Maryland) were already too high and too widespread (Herms and McCullough, 2014). Subsequently, efforts were shifted towards slowing the spread of EAB into new areas by regulatory restriction of movement of EAB-infested wood or plant materials, insecticide treatment of susceptible trees (either artificially girdled or naturally stressed as trap trees), and biological control via introduction and releases of natural enemies collected from EAB's native range. Because it is impractical to treat all susceptible trees with insecticides in natural forests, classical biological control via establishment of introduced (non-native) natural enemies is needed to protect ash resources against EAB in North American (Bauer et al., 2015).

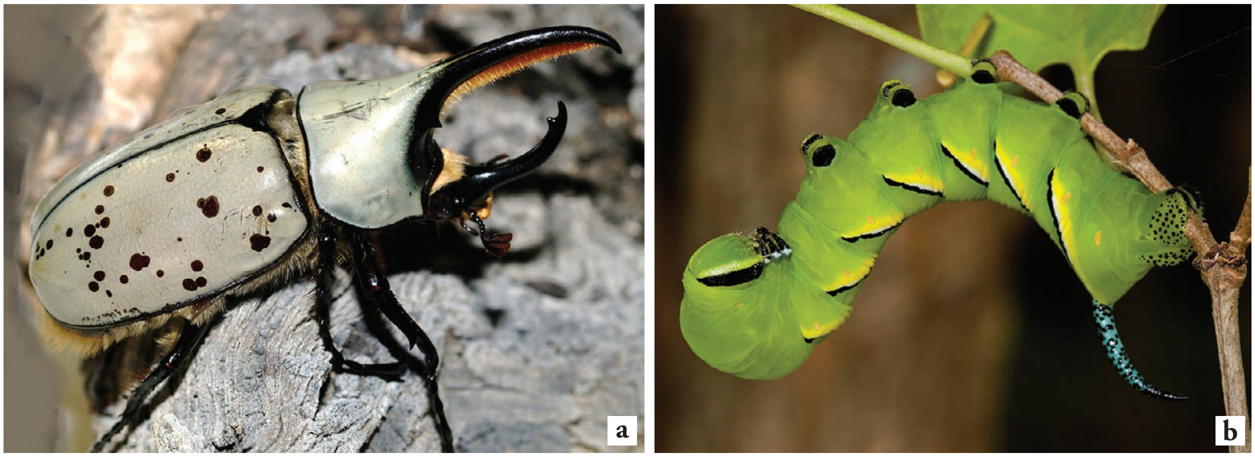

Figure 6-3. Two of nearly 100 species of ash-dependent insects threatened by loss of ash: (a) the scarabaeid beetle *Dynastes granti* and (b) the sphingid moth *Sphinx franckii* (Credits: a Margarethe Brummerman; b Colin Gillette)

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

Foreign exploration for natural enemies in northeastern China (part of the native range of the pest) began in 2003 (Liu et al., 2003, 2007) and was later extended into the Russian Far East (Duan et al., 2012a; Yao et al., 2016). Between 2003 and 2007, four species of hymenopteran parasitoids were found in northeastern China: (1) *Sclerodermus pupariae* Yang et Yao (Bethylidae), an ectoparasitoid of larvae, prepupae, and pupae (Wu et al., 2008, Yang et al., 2012); (2) *Spathius agrili* Yang (Braconidae), an ectoparasitoid of late instar larvae (Liu et al., 2003; Yang et al., 2005); (3) *Oobius agrili* Zhang and Huang (Encyrtidae), an egg parasitoid (Figure 6-4a) (Zhang et al., 2005; Liu et al., 2007), and (4) *Tetrastichus planipennisi* Yang (Eulophidae) (Figure 6-4b,c), an endoparasitoid of late instar larvae (Liu et al., 2003; Yang et al., 2006). Field surveys conducted in the Russian Far East between 2008 and 2012 found three additional species of hymenopteran parasitoids: (5) *Spathius galinae* Belokobylskij and Strazanac (Braconidae) (Figure 6-4d), an ectoparasitoid of late instar larvae (Belokobylskij et al., 2012; Duan et al., 2012a); (6) *Atanycolus nigriventris* Vojnovskaja-Krieger (Braconidae), an ectoparasitoid of late instar larvae (Belokobylskij et al., 2012; Duan et al., 2012a); and (7) *Oobius primorskyensis* Yao & Duan, a recently described new species of egg parasitoid (Yao et al., 2016).

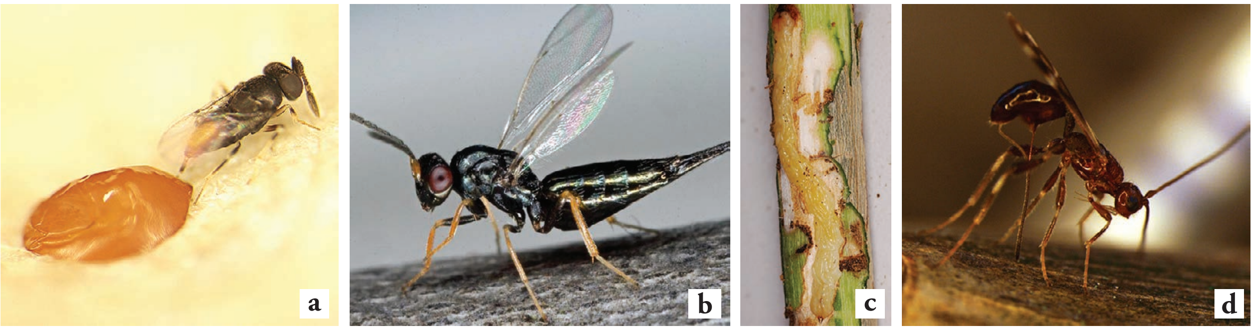

Figure 6-4. Parasitoids: (a) *Oobius agrili*, a parasitoid of emerald ash borer eggs imported from China; (b) *Tetrastichus plannipenisi* adult, an internal larval parasitoid of emerald ash borer imported from China; (c) brood of *T. plannipenisi* parasitoid larvae in gallery of host; (d) *Spathius galinae*, an external parasitoid of emerald ash borer larvae imported from the Russian Far East (Credits: a,c,d Jian Duan; b David Cappaert, bugwood.org)

Of these, the host range of *S. pupariae* was deemed too broad based on studies in China (Yang et al., 2012), and it was not considered further as a potential biological control agent. The other three Chinese parasitoids (*T. planipennisi*, *S. agrili,* and *O. agrili*) were proposed for introduction, and after extensive host range testing and safety evaluation, a petition for their release was approved in 2007 (USDA APHIS, 2007). Separately, similar work was done with the Russian parasitoids *S. galinae* and *O. primorskyensis*. The petition for release of *S. galinae* was approved in 2015 and one for release of *O. primorskyensis* is under review (as of November, 2016). Although importation of *A. nigriventris* from the Russian Far East was considered, the difficulty in maintaining a colony of this species under quarantine laboratory conditions prevented conducting host range studies for further evaluation (JJD, unpublished data).

The safety of Asiatic parasitoids petitioned for environmental releases in North America was assessed with data collected from both field surveys of other wood-boring insects in the parasitoids' native range (China and Russian Far East) and quarantine testing with North American wood-boring insects. Data from these studies shows that host specificity of these Asian parasitoids in general is highly constrained by the phylogenetic relationship of nontarget hosts to their co-evolved host, *A. planipennis* (USDA APHIS, 2007, 2015; Yang et al., 2008; Duan et al., 2015a). Field data from China and the Russian Far East show that these parasitoids do not attack other wood-boring insects in ash, such as bark beetles (Scolytinae) or longhorned beetles (Cerambycidae) (Yang et al., 2008; Duan et al., 2015a). However, host specificity studies in quarantine laboratories further showed that three of these introduced parasitoids – *O. agrili*, *S. agrili,* and *S. galinae* – do attack some North American *Agrilus* species (Table 6-1). In contrast to the attack on EAB, however, their attack rates in these nontarget *Agrilus* species is much lower, even under laboratory conditions that promote maximum parasitism (USDA APHIS, 2007, 2015; Yang et al., 2008; Duan et al., 2012a, 2015a). Based on both laboratory and field host range studies, the potential non-target impact from introduction of these Asian parasitoids for EAB biocontrol, if any, would be only a low level of parasitism of some non-target *Agrilus* species in North America.

Table 6-1. Numbers of non-target insect taxa tested with Asian parasitoids petitioned in North America for environmental release against emerald ash borer (*Agrilus planipennis*).

Parasitoids	Insect orders	Families	Non-target species	Non-target *Agrilus*	Non-target species attacked
Oobius agrili [1]	2	6	18	6	3/18
Tetrastichus planipennisi [1]	3	6	13	5	0/13
Spathius agrili [1]	2	6	19	9	4/19
Spathius galinae [2]	3	6	15	6	1/15

[1] Data compiled from USDA APHIS (2007)

[2] Data compiled from USDA APHIS (2015) and Duan et al. (2015a)

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

There are approximately 800 *Agrilus* species in North America, with 175 species in the United States (Bellamy, 2008; Nelson et al., 2008). It would be extremely difficult, if not impossible, to test every single North American *Agrilus* species with the introduced EAB parasitoids for safety assessment. It may be possible that these introduced EAB parasitoids (e.g., *O. agrili* and *S. agrili*) may occasionally attack some of the non-target *Agrilus* species in North America. However, recent host-finding studies also show that these parasitoids are strongly attracted to volatiles from ash trees (Yang et al., 2008; Johnson et al., 2014), indicating their strong affinities to the host's food plants. Thus, it can be reasonably predicted that the level of these attacks of non-ash feeding *Agrilus* species, if any, would be limited. Field surveys of non-target insects associated with ash trees following field releases of introduced EAB parasitoids in Maryland have not found any evidence of non-target attack from these introduced parasitoids (Jennings et al., 2016a,b; JJD unpub. data). In contrast, arthropod diversity associated with ash trees is significantly reduced because of EAB invasion in Maryland (Jennings et al., 2016b). Therefore, introduction of EAB parasitoids from Asia is not likely to cause any unexpected, negative system responses, but may be expected to induce positive system responses from the protection of ash trees against EAB infestation in North America.

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

Following regulatory approval, environmental releases of the three Chinese parasitoids (*S. agrili*, *T. planipennisi,* and *O. agrili*) began with very small numbers (a few hundred per species) in 2007 in Michigan, the epicenter of EAB invasion. However, large releases (tens of thousands per species) did not start until 2010 when the USDA APHIS mass-rearing facility was established in Brighton, Michigan (Gould et al., 2015). By the summer of 2016, 24 EAB-infested states had received releases of one or more species of these agents (MapBiocontrol, 2016). All three biocontrol agents have been recovered following their releases in most release areas in the U.S.; however, only *T. planipennisi* and *O. agrili* have been consistently recovered more than one year following their release.

At six study sites in Michigan, EAB egg parasitism by *O. agrili* increased from 1-4% in the first few years (2007–2011) during or after their release (which occurred thru 2010) to 20-28% in 2014 (Abell et al., 2014). However, the role of the introduced egg parasitoid *O. agrili* in suppressing EAB population growth remains to be determined because of the difficulty of measuring EAB egg densities under the loose bark or bark crevices of infested ash trees in the field. In contrast, *T. planipennisi* appears to have spread much faster and became a dominant larval parasitoid of EAB in the Michigan study sites shortly after its release (Duan et al., 2012b, 2013, 2015b). The parasitism rate of EAB larvae by *T. planipennisi* increased from 1.0-5.6% in the first three years (2008-2011) after the start of field releases to 26-30% in both release and control sites four or five years later (by 2014). Recent life table analyses of seven years of data collected from the six Michigan study sites following the releases of these biocontrol agents show that parasitism by *T. planipennisi* has contributed significantly to the reduction of net EAB population growth rates in these sites since 2012, approximately four years after the initial release (Duan et al., 2015b). With additional mortality from woodpeckers and native parasitoids (primarily braconids in the genus *Atanycolus*), EAB larval densities declined nearly 90% in infested ash trees at both parasitoid-release and control plots between 2009 and 2014 (Duan et al., 2015b). Findings of the life table study in Michigan further indicate that successful biocontrol of EAB may involve suppression of EAB abundance both by local, oligophagous natural enemies (such as *Atanycolus* spp.) and by introduced specialist parasitoids (such as *T. planipennisi*) (Figure 6-5).

However, the effectiveness of *T. planipennisi* in protecting ash trees against EAB is affected by bark thickness, which increases with tree size. Data from field surveys in *T. planipennisi*'s native range (China and Russian Far East) and in the U.S. show that parasitism by *T. planipennisi* is concentrated in smaller ash trees (Liu et al., 2007; Duan et al., 2012a; Jennings et al., 2016b). A recent survey of randomly selected ash saplings (2-5 cm DBH [Diameter at Breast Height]) at the Michigan study sites found that *T. planipennisi* was the dominant mortality factor, causing 36-85% parasitism of older (3rd-JL) EAB larvae and that this

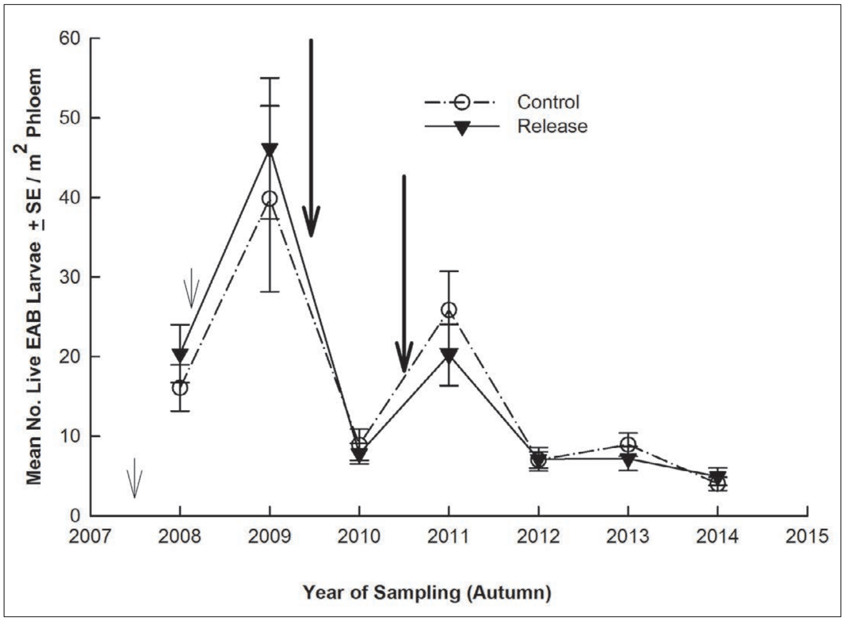

Figure 6-5. Reduction in emerald ash borer intensity (rate of attack on surviving trees) over a seven year period at 12 plots in Michigan, reflecting lower attack rates by the borer. Arrows represent the time and number of parasitoid releases, with big arrows being major (>11,00 wasps) and small arrows being minor (<700 wasps) releases (from Duan et al., 2015)

parasitoid protects ash saplings effectively from attack by EAB (Duan et al., 2017). The reason for this higher parasitism rate in smaller trees is the better match between the parasitoid's ovipositor length (average 2-2.5 mm) and bark thickness, which prevents wasps from attacking EAB larvae in the lower boles of trees that exceed 12 cm DBH and a bark thickness of 3.2 mm (Abell et al., 2012).

To control EAB successfully in larger ash trees, efforts are currently focused on establishing the Russian parasitoid *S. galinae* in North America. This braconid has a longer ovipositor (4-6 mm) than *T. planipennisi*, and it can attack EAB larvae feeding on trees with DBHs up to 25-30 cm (Duan et al., 2012a). Release of *S. galiane* in the U.S. began in the summer of 2016, and more time is needed to assess its effectiveness in protecting large ash trees. In theory, highly effective egg parasitoids from EAB's native range might also be able to protect both small and large ash trees against EAB, as they can kill the pest before larvae bore into the ash cambium. However, the current level of egg parasitism by *O. agrili* (<29%) by itself is not sufficient to protect ash trees. Introduction of other egg parasitoids, such as *O. primorskyensis* may enhance egg parasitism (Larson and Duan, 2016).

WERE OTHER MEASURES NEEDED?

Host tree resistance can have significant effects on EAB survival and development, and hence population growth rates. Thus, levels of ash tree resistance can also affect the degree of success of EAB biocontrol. Field studies in the pest's native range show that EAB is rarely a serious pest on many Asian ash species such as *Fraxinus mandschurica* Rupr. and *Fraxinus rhynchophylla* Hance, largely because of putative tree resistance as well as the prevalence of EAB egg and larval parasitoids (Liu et al., 2007; Duan, 2012a; Wang et al., 2016). In North America, the common species of *Fraxinus*, such as *F. pennsylvanica* Marshall, *F. americana* L., and *F. nigra* Marshall, have little resistance to EAB and are readily killed by even moderate EAB infestations (Rebek et al., 2008; Tanis and McCullough, 2015). However, some North American ash, such as *F. quadrangulata* Michx., appear to have largely escaped EAB infestation in Michigan (Tanis and McCullough, 2012). In addition, some "lingering" healthy (often younger) trees of the susceptible ash species (*F. pennsylvanica* and *F. americana*) have been frequently observed to survive EAB infestation in the epicenter of EAB invasion such as Michigan and Ohio (Tanis and McCullough, 2012). A population dynamics model parameterized with combined parasitism rates of 60% parasitism of EAB eggs and 30% larval parasitism shows that EAB population growth rate in North America can be reduced to the below-replacement level (<1) when accompanied with moderate to high levels of host plant resistance (Duan et al., 2015c). Together, these observations provide hope that some level of host tree resistance in North American ash may facilitate biocontrol in protecting ash and their dependent communities in North America. Resistance in North American ash currently is low but may be higher in the future ash forest due to natural selection (selective survival of partly resistance ash) or outplanting of lines of ash bred for higher levels of resistance (see review in Villari et al., 2015).

FUTURE OF SYSTEM

Following its accidental introduction into the U.S, probably in the 1990s (Siegert et al., 2014), EAB continues to spread and degrade ash communities in North America. The EAB biocontrol program, started nearly a decade ago via introduction and establishment of co-evolved natural enemies from the pest's native range, appears to hold promise to protect North American ash communities. To date, this program has successfully established the egg parasitoid *O. agrili* and the larval parasitoid *T. planipennisi* introduced from China, in most of the areas in the U.S. where these species have been released. While the role of *O. agrili* in reducing EAB population growth requires continued evaluation, the larval parasitoid *T. planipennisi* currently plays a significantly suppressive role in saplings and smaller trees (DBH <12 cm) in aftermath forests in Michigan (Duan et al., 2015b, Duan et al., 2017). This suppressive effect is likely to spread geographically as populations of *O. agrili* and *T. planipennis* increase in density in more EAB-infested areas where they have been released, protecting saplings and small trees. To protect larger trees, however, establishment of more effective egg parasitoids and larval parasitoids with long ovipositors is needed. The most recent introduction of *S. galinae* from the Russian Far East, which has a much longer ovipositor (4-6 mm) than *T. planipennisi*, is one such species. Initial recoveries in New York and Connecticut have been made at promising levels (2016, RGVD and JJD, unpub. data). As EAB densities decline, future studies will be required on (1) growth and survival rates of ash in aftermath forests with self-sustaining and increasing biocontrol agent populations, (2) persistence of key ash-dependent invertebrates (Wagner and Todd, 2016), and (3) repetition of basic population work in new regions as EAB invades southern and western areas in the United States, which will be ecologically distinct from the north central and northeastern US areas on which this discussion is based.

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CHAPTER 7. BIOLOGICAL CONTROL OF WATERHYACINTH RESTORES ECOSYSTEM FUNCTIONING TO AN IMPOUNDMENT IN SOUTH AFRICA

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR THREAT TO NATIVE SPECIES?

Figure 7-1. Waterhyacinth, *Eichhornia crassipes*, is a South American plant that has become invasive worldwide in tropical and subtropical standing or slow moving water, shown here at New Year's Dam in South Africa (Credit: Julie Coetzee)

Eichhornia crassipes (Mart.) Solms-Laub. (Pontederiaceae) (waterhyacinth) (Figure 7-1), from South America, has been considered the most damaging aquatic macrophyte in many of the rivers, manmade impoundments, lakes, and wetlands of South Africa (Hill, 2003). The lack of natural enemies, coupled with eutrophication of many aquatic habitats in South Africa, has facilitated the invasion by this weed. These nutrient-enrichment disturbances are mainly anthropogenic, including agricultural activities and an increase in urbanization due to accelerated human population growth. The management of *E. crassipes* requires site-specific applications where priorities depend on the prevailing climate, the nature and use of the water body in question, extent of the infestation, and the resources available for control activities. Here we present a case study in which we discuss the biodiversity impacts of *E. crassipes* on the environment, including direct effects on aquatic biodiversity and indirect effects of increased evapotranspiration leading to greater water loss, and how these impacts were lessened by biological control of the plant.

Our case system is that of the plant's impact on a small water body created by the New Year's Dam, behind which there was an 80.8 ha impoundment. This site is near the town of Alicedale in the Eastern Cape Province of South Africa. This impoundment predominantly supplies water to the local population for domestic use and irrigation (Doudenski, 2004). Waterhyacinth was first recorded on the reservoir in 1988, and by 1990 the reservoir was 80% covered (Figure 7-2a), affecting water removal and recreational fishing (Hill, 2003), but the infestation's impact on biodiversity and functioning of the system was largely unknown.

The impacts of *E. crassipes* are considerable and have been well reviewed (Villamagna and Murphy, 2010). While the direct and indirect (cost of control) economic impacts of *E. crassipes* are readily measured (Mailu, 2001), its biodiversity impacts are more difficult to define, and very few studies have attempted to do so (Villamagna and Murphy, 2010). At New Year's Dam, Midgley et al. (2006) showed that infestations of *E. crassipes* significantly reduced aquatic benthic biodiversity in comparison to waterhyacinth-free areas. This study, carried out over some 18 months, showed that the number of families and the number of individuals of benthic invertebrates were significantly lower under the mats of *E. crassipes* than areas where the weed had been controlled. Further, standard measures of biodiversity, including the Shannon-Weiner Diversity Index, Margalef's Richness Index, Pielou's Evenness Index, and chlorophyll *a* were all significantly lower under waterhyacinth mats than in waterhyacinth-free zones. *Eichhornia crassipes*-infested areas were characterized by poor water quality specialists such as leeches and midge larvae, while *E. crassipes*-free zones had a significantly higher abundance and diversity of species that are less tolerant of poor water quality, such as mayflies, damselflies, and dragonflies.

Figure 7-2. A small reservoir in South Africa (New Year's Dam) completely covered by waterhyacinth before biological control in 1990 (a) and the same site in 1999 after introduction of a biological control agent suppressed weed density (b) (Credits: a,b Martin Hill)

WERE OTHER CONTROLS FEASIBLE?

Mechanical control or the manual removal of *E. crassipes* is invariably the initial control option tried. While manual removal using rakes and pitchforks can be successful for really small infestations, it is labor-intensive and ineffective in larger infestations. Mechanical harvesters have been used on some of the larger rivers, dams, and wetlands in South Africa, and, while harvesters can be successful, they are expensive (Hill and Olckers, 2001). These control options are, however, impractical for infestations larger than about one hectare because of the weed's rapid rate of increase and the fact that it is more than 90% water (Hill and Cilliers, 1999). Herbicidal control is widely used in South Africa, commonly with application of glyphosate, glyphosphate trimesium, diquat, or terbutryn. Herbicidal control of waterhyacinth depends on skilled operators who maintain a long-term follow-up program to control re-infestation by scattered plants and those germinating from seed. Therefore, any herbicide program against the weed requires a commitment to an ongoing operation of unlimited duration. It is the lack of follow-up that often causes herbicidal programs to fail (Hill et al., 2012).

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

The biological control program against waterhyacinth in South Africa began in 1973. Nine biological control agents have been introduced in the country: (1) the weevil *Neochetina eichhorniae* Warner (Figure 7-3) in 1974 (Cilliers, 1991); (2) the fungus *Cercospora piaropi* Tharp. (Mycosphaerellales: Mycosphaerellaceae) in 1987 (Coetzee et al., 2011); (3) the galumnid mite *Orthogalumna terebrantis* Wallwork in 1989; (4) the weevil *Neochetina bruchi* Hustache in 1990; (5) the crambid moth *Niphograpta albiguttalis* Warren (= *Sameodes albiguttalis* [Warren]) in 1990; (6) the mirid bug *Eccritotarsus catarinensis* (Carvalho) in 1996; (7) the mirid bug *Eccritotarsus* sp. in 2007 (Paterson et al., 2016), (8) the acridid grasshopper *Cornops aquaticum* (Brüner) in 2011 (Winston et al., 2014); and (9) the delphacid *Megamelus scutellaris* Berg in 2013. All these agents have been subjected to extensive host-specificity testing in several countries around the world (Center et al., 2002; Coetzee et al., 2009), and to date no non-target effects have been recorded (Louda et al. 2003) despite the occurrence of closely related species in all the countries where these agents have been released.

Even though there were five biological control agents available for release on *E. crassipes* in South Africa at the time of the infestation on New Year's Dam, only the weevil *N. eichhorniae* was introduced. In January 1990, 200 adults were released, with 1000 more in November of the same year. In contrast, Conlong et al. (2009) suggested that 100,000 adult *Neochetina* weevils were needed per hectare to suppress *E. crassipes* in 2-4 years. Annual field trips were made to New Year's Dam from 1990 to 2016 to evaluate the impact of the biological control. By 1994, weevils had spread throughout the infestation on the reservoir,

Figure 7-3. The weevil *Neochetina eichhorniae,* the agent responsible for biological control of waterhyacinth at the New Years Dam site in South Africa: (a) adult; (b) adult feeding damage (Credits: a Anthony King; b Julie Coetzee)

and they had reduced *E. crassipes* coverage to <20%, and average plant height had been reduced from 60 to 20 cm (Hill and Cilliers, 1999). The percentage cover of the weed on the impoundment was less than 5% by 2000 and has remained at this level (Figure 7-2b) (Coetzee et al., 2011).

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

No unexpected, harmful ecosystem responses to biological control of the invasive plant were observed. Results were beneficial to biodiversity and the general habitat. Indeed, the only unexpected ecosystem response was the rapidity of control. Successful biological control of *E. crassipes* usually takes 3-5 years in tropical areas (Julien et al., 1999), but considerably longer periods are usually required (8-10 years) under more temperate climates such as that at New Year's Dam (Hill and Olckers, 2001). Thus, the complete control of the weed on New Year's Dam in four years was unexpected, especially given the low inoculation density of the agent used. This rapid control has been ascribed to the fact that the system is oligotrophic (see below).

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

The significant reduction of *E. crassipes* coverage on New Year's Dam has resulted in the recovery of the benthic invertebrate community (Midgley et al., 2006), and it has also resulted in water savings for the area. Invasive alien plants have significant environmental and ecological impacts in South Africa, especially in habitats such as riparian zones and freshwater systems (Chamier et al., 2012). The increased evapotranspiration rates associated with invasive alien plants are estimated to result in a loss of about 3,300 million m^3 of water (about 7% of the national total) (Le Maitre et al. 2000), and this impact was the main reason for the establishment of the Working for Water Program (WfW) in 1995, a national program created to reduce the impacts of alien invasive plants on South Africa's critical water resources, while creating jobs at the same time. *Eichhornia crassipes* increases water loss from aquatic ecosystems up to 40% (Penfound and Earl, 1948). More recently, Fraser et al. (2016) conducted analysis of the water loss saving due to the biological control program on New Year's Dam. Published estimates of the water loss due to evapotranspiration from *E. crassipes* vary significantly, and therefore the study used three different rates from the literature, a high, medium and low rate (Allen et al., 1997). It is estimated that without biological control, and thus 80% plant cover of the impoundment's surface, the total annual evaporation rate of the impoundment would vary between 1,477,946 m^3 and 6,545,188 m^3, depending on the evapotranspiration rate estimate used. However, this water loss significantly decreased with biological control once plant cover was reduced to 5% of the impoundment's surface, with the total evaporation rate estimated to be between 1,082,067 m^3 and 1,398,770 m^3 for the low and high evapotranspiration rate estimates, respectively, and thus a water loss saving of nearly 400,000 m^3 at the low evapotranspiration rate and 5 million m^3 at the high rate.

FUTURE OF THE SYSTEM

Many studies have shown that the successful biological control of *E. crassipes* is often limited if water is eutrophic, and the first step towards control should be to reduce nutrient inputs into the system (Coetzee et al., 2007; Coetzee and Hill, 2012). A long-term monitoring program assessing the factors affecting the success of biological control of *E. crassipes* in South Africa suggested that additional control measures are needed in systems where water phosphorus levels are above 0.1 mg l^{-1} (Byrne et al., 2010). Unfortunately, biological control efforts of *E. crassipes* in South Africa are hampered by the adoption of an excessively high water P regulatory standard of 1 mg l^{-1} for all water treatment works (DWAF, 1996). Every invaded system in the country is characterized by P levels greater than this level, all except New Year's Dam (Byrne et al. 2010). Thus, the success of biological control at New Year's Dam using a single agent can be attributed to the fact that the level of P in the water has remained below 0.1 mg l^{-1} (Byrne et al. 2010).

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CHAPTER 8. THE ROLE OF MELALEUCA CONTROL IN EVERGLADES RESTORATION: ACCOMPLISHMENTS AND FUTURE PLANS

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

The Australian tree *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtales: Myrtaceae) was first introduced to south Florida in 1886 (Dray et al., 2006). The tree was sold by nurseries, planted as agricultural windbreaks and forestry crops, and used to stabilize levees (Bodle et al., 1994; Dray et al., 2006). *Melaleuca quinquenervia*, hereafter melaleuca, flowers primarily in the fall and winter months, although it can flower at other times. Flowering spikes are produced on branches that vary between growth and reproductive phases, resulting in an alternating pattern of leaves and flowers or persistent woody seed capsules on a given branch. These seed capsules contain a great many small seeds that are released when the capsule dries (Tomlinson, 1980). Rayachhetry et al. (1998) estimated that a 21-m tall tree could produce 51 million seeds, of which 15%, or 5.6 million, would likely be viable.

Melaleuca was first reported as naturalized in Florida in the mid-1920s (Dray et al., 2006). It invades a variety of areas from disturbed sites such as the sides of roads and ditches to natural habitats, including cypress stands, sawgrass marshes, pine flatwoods, and mesic prairies (Bodle et al., 1994). Melaleuca can outcompete native plants and form dense monocultures (Figure 8-1), changing the vertical structure of communities and converting wetland prairies and marshes into melaleuca forests (Gordon, 1998; Turner et al., 1998). Melaleuca can also alter fire frequency and intensity, affect water table depth and surface flow, and modify above and belowground ecosystem components (Gordon, 1998; Serbesoff-King, 2003; Martin et al., 2009; Center et al., 2012). Laroche and Ferriter (1992) estimated that a small melaleuca population could grow exponentially to infest 95% of a 250 ha patch in just 25 years. By 1998, melaleuca had invaded nearly 400,000 hectares in Florida (Laroche 1998).

Figure 8-1. *Melaleuca quinquenervia* can displace native vegetation in invaded wetlands and forests in Florida (Credit: Paul D. Pratt, USDA ARS)

The hydrology of the Everglades historically consisted of a dry season from November to April and a wet season from May through October (Rader and Richardson, 1992). However, this pattern has been largely reversed by drainage and water conservation programs, which discharge water after high rainfall events and hold it during dry periods (Kushlan, 1987; Rader and Richardson, 1992). Changes in hydroperiod can reduce native flora and fauna and increase susceptibility to invasive species, including melaleuca, which can then cause additional changes in ecosystem structure and function (Myers, 1975; Kushlan, 1987; Gordon, 1998; Turner et al., 1998 and references therein).

The spread of melaleuca and its ecological damage prompted the formation of a Melaleuca Task Force in 1990. This group included local, state, and federal scientists and land managers and was charged with developing a comprehensive plan to manage melaleuca. The first plan was issued in 1990 and it has been periodically updated (Laroche, 1999).

WERE OTHER CONTROLS FEASIBLE?

Removing melaleuca with heavy equipment can be effective in rights-of-way for canals and utilities, but stumps must be treated with herbicide to prevent re-growth. Mechanical removal causes too much disturbance and non-target damage to be useful in natural areas, where hand removal of seedlings is the only appropriate mechanical tool (Laroche, 1998). Herbicides can provide effective control of melaleuca. Hack and squirt and cut-stump treatments are the most effective way to treat individual trees, but these techniques are labor intensive. Aerial applications are more appropriate for large-scale infestations (Laroche, 1998). Melaleuca is adapted to fire, which will kill small saplings but not large trees (Turner et al., 1998).

Melaleuca responds to stress from herbicides, physical damage, fire, frost, or desiccation by synchronously releasing seed held in the capsules (Meskimen, 1962). This can lead to establishment of dense stands of melaleuca seedlings. These seedlings outcompete native vegetation, and after a fire, they can promote the conversion of sawgrass prairies (*Cladium jamaicense* Crantz) (Cyperales: Cyperaceae) into melaleuca forests (Turner et al., 1998). Thus, follow-up treatments are needed to eliminate the seedlings before they reproduce, which can occur in less than three years (Laroche, 1998; Meskimen, 1962).

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

Development of a biological control program to complement the removal of standing biomass with herbicidal, mechanical, and physical controls was a high priority for the Melaleuca Task Force (Laroche, 1998; Center et al., 2012). The goals of the biological control program were to find agents that were host-specific to the genus *Melaleuca,* or below, that would limit stand regeneration by reducing flowering or seed production (targeting inflorescences or seeds) or increasing mortality of seedlings, saplings, or stump sprouts (Center et al., 2012).

Three agents have established on melaleuca in Florida. Releases of the first agent, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), began in 1997 (Figure 8-2a). Adults and larvae feed on melaleuca leaves; larvae cause extensive damage, but prefer young foliage and are most common in the field from October through May (Purcell and Balciunas, 1994; Center et al., 2000). The weevil pupates in the soil and does not establish at permanently flooded sites (Center et al., 2000). The melaleuca psyllid, *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) (Figure 8-2b), feeds on melaleuca leaves but will also attack stem tissue if population densities are high (Wineriter et al., 2003). This phloem-feeder completes its entire life cycle on the plant and is not affected by site hydrology (Wineriter et al., 2003; Center et al., 2006). The psyllid was first released in 2002 and it established at all release sites (Center et al., 2006). The third agent, *Lophodiplosis trifida* Gagné (Diptera: Cecidomyiidae), is a stem-galling midge that disrupts apical and axillary growth of melaleuca (Figure 8-2c). It completes its entire life cycle within galls on melaleuca and is most active during the wet-warm season and in wet habitats in the native range (Pratt et al., 2013). Releases of *L. trifida* began in 2008, and it established readily and dispersed rapidly (Pratt et al. 2013). The ecological host ranges of all three agents were validated in field experiments after their release, confirming that non-target species in Florida were at no risk of attack (Center et al., 2007; Pratt et al., 2009, 2013).

Figure 8-2. (a) The melaleuca weevil, *Oxyops vitiosa*, was the first biocontrol agent released against melaleuca. Feeding by weevil adults and larvae on melaleuca leaves decreases melaleuca's reproductive capacity; (b) the melaleuca psyllid, *Boreioglycaspis melaleucae*, is a phloem feeder that attacks melaleuca leaves and stems; (c) the stem-galling midge *Lophodiplosis trifida* disrupts apical and axillary growth of melaleuca (Credits: a Ellen C. Lake, USDA ARS; b,c Paul D. Pratt, USDA ARS)

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

Melaleuca compensates for damage by *O. vitiosa* by producing replacement foliage and new stems, but this comes at the cost of reproduction. One year following *O. vitiosa* herbivory, damaged trees had only 20% as many reproductive structures as undamaged trees (Pratt et al., 2005). However, in permanently wet habitats, melaleuca escaped persistent attack by the weevil due to insufficient dry substrate for pupation (Center et al., 2000). *Boreioglycaspis melaleucae* attacks both young and old melaleuca leaves, and leaves damaged by the psyllid are 4.7 times more likely to fall off than are undamaged leaves (Morath et al., 2006). Trees attacked by *O. vitiosa* and *B. melaleucae* produced only 1% of the seed formed by control trees protected by insecticide treatments (Tipping et al., 2008). High densities of psyllids also decreased growth and increased mortality of melaleuca seedlings (Franks et al., 2006). Tipping et al. (2012) monitored recruitment and survival of melaleuca seedlings in a seasonally inundated wetland and documented negative population growth of melaleuca at the site. The decline in this population was more likely due to reduction in seed inputs due to agent herbivory than to seedling mortality (Tipping et al., 2012). An insecticide check study that limited herbivory on melaleuca saplings demonstrated that galling by the newest agent, *L. trifida*, significantly reduced above- and below-ground biomass (Tipping et al., 2016).

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

Melaleuca invasion alters above- and below-ground ecosystem components, including decreasing nutrient storage and the concentration of nutrients available in the litter layer. These changes may impede succession of the native plant community after melaleuca is removed (Martin et al., 2009). Rayamajhi et al. (2009) monitored mature melaleuca stands in seasonally flooded and non-flooded sites from 1997, the year the first biological control agent was released, through 2005. A two to four-fold increase in plant diversity was correlated with declines in melaleuca within these sites (Figure 8-3), with greater decreases in melaleuca density and increases in plant diversity at the non-flooded sites (Rayamajhi et al. 2009). Foliar damage by the biological control agents may have accelerated thinning of the melaleuca canopy and increased light penetration to the forest floor, thus facilitating native plant recovery (Rayamajhi et al., 2009).

In an insecticide-check field study, population-level suppression of melaleuca by *O. vitiosa* and *B. melaleucae* was documented (Tipping et al., 2009); however, there was no significant recovery of the native plant community. Several factors, including reduced nutrient levels, reduced soil moisture due to a reduction in leaf litter, or distance from propagules of native plants could account for the lack of recovery at this site (Tipping et al. 2009). The restoration of some invaded sites may require replanting of native vegetation rather than solely relying on passive recolonization by native plants (Rayamajhi et al., 2009; Martin et al., 2011).

Figure 8-3. As melaleuca stands decline under pressure from the introduced biological control agents, native plants recover (Credit: Min B. Rayamajhi, USDA ARS)

Removal of melaleuca can benefit native wildlife. Radio-telemetry data of endangered Florida panthers, *Puma concolor coryi* Bangs, within Big Cypress National Preserve indicated a shift in habitat use and a 16% reduction in panther home range size correlated with landscape-level removal of melaleuca and presumably an increase in habitat quality (Julian et al., 2012).

WERE OTHER MEASURES NEEDED?

Rodgers et al. (2014) conducted aerial surveys in the Everglades between 2010 and 2012 and determined that melaleuca occupied 17,802 out of 728,000 ha mapped. This represented 15% of the 1 km grid cells; however, the infestation level within these cells was less than 10% in 92% of the cells and less than 1% in 79% of the cells (Rodgers et al., 2014). Reductions in the density of melaleuca achieved through integrated weed management now enable targeted treatment of high density patches as well as large areas with low density infestations under a maintenance control program (LeRoy Rodgers, pers. comm.). Herbivory from the suite of biological control agents increases the susceptibility of remaining melaleuca trees to herbicides, fire, and frost, and decreases the ability of melaleuca to recover from these events (Center et al., 2012). Although biological control helps to reduce the impact of melaleuca infestations located on private land adjacent to conservation areas, these infestations remain of concern (LeRoy Rodgers, pers. comm.). Host-range studies are underway on another potential agent, *Lophodiplosis indentata* Gagné (Diptera: Cecidomyiidae), a leaf-galling midge (Center et al., 2012).

FUTURE OF SYSTEM

Interagency collaboration, including The Areawide Management and Evaluation of Melaleuca program (TAME Melaleuca), contributed to the progress in controlling melaleuca (Silvers et al., 2007). TAME Melaleuca promoted regional implementation of biological control as part of the integrated weed management effort to control melaleuca. It included demonstrations of different removal techniques singly and within an integrated strategy, assessing the efficacy of these techniques, and transferring management technologies to land managers and property owners (Silvers et al., 2007).

A new collaborative project is underway between the USDA ARS Invasive Plant Research Laboratory (IPRL), the South Florida Water Management District, and the US Army Corps of Engineers. The “Melaleuca Eradication and Other Exotic Plants (2016) – Implement Biological Controls Project” is a component of the Comprehensive Everglades Restoration Plan (CERP 2016), which was signed into law in the Water Resources Development Act (WRDA) in 2000. This multibillion dollar multi-decade effort outlines a plan to simultaneously restore the ecosystem of south Florida while ensuring a sufficient water supply for agricultural and urban use and providing flood protection. CERP has been called the world’s largest ecosystem restoration effort, encompassing 18,000 square miles over 16 counties in south and central Florida. Construction of a mass-rearing annex at the USDA ARS Invasive Plant Research Laboratory was the first component of CERP to be completed. The role of IPRL within CERP is to mass rear, release, establish, and evaluate the efficacy of biological control agents throughout the area in southern Florida being restored. This biological control effort currently targets additional species, including air potato – *Dioscorea bulbifera* L. (Liliales: Dioscoreaceae), waterhyacinth – *Eichhornia crassipes* (Mart.) Solms (Commelinales: Pontederiaceae), and Old World climbing fern – *Lygodium microphyllum* (Cav.) R. Br. (Schizaeales: Lygodiaceae). The agents and activities will change as additional biological control agents become available for release and new weed problems emerge.

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CHAPTER 9. PARTIAL RESTORATION OF NATIVE RAINFORESTS IN THE ISLAND OF TAHITI (FRENCH POLYNESIA) AFTER INTRODUCTION OF A FUNGAL PATHOGEN TO CONTROL THE INVASIVE TREE *MICONIA CALVESCENS*

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

The tropical forest ecosystems of the high volcanic islands of Hawaii (USA), the Society, and the Marquesas Islands (French Polynesia) in the Pacific Ocean are recognized as biodiversity hotspots (Myers et al., 2012), especially for their plant richness and uniqueness (Olson et al., 2001). Their vascular flora include 1030, 553, and 333 native species, respectively, with an endemism rate of 48 to 88% (Meyer et al., 2014; Lorence et al., 2016). Between 60 and 70% of the endemic taxa found in the Society and the Marquesas Islands are restricted to tropical montane cloud forests (Meyer, 2010a). An alien plant species introduced in these three archipelagoes, *Miconia calvescens* DC. (Melastomataceae) (Figure 9-1), is a direct and important threat to this unique island biodiversity, and its control is viewed as an important priority for conservation.

Figure 9-1. *Miconia calvescens* is a New World tree with large leaves that forms an overtopping, dense canopy on Tahiti, shading out many native plant species (Credit: Eloise Killgore)

Miconia calvescens (hereafter *Miconia*) is a small tree (typically 6-12 m in height, but up to 16 m) native to rainforests of Central and South America that became very popular for horticulture because of its large, brightly colored leaves. It was first introduced to Tahiti in the Society Islands as an ornamental in a private garden in 1937. Within 50 years, *Miconia* had invaded all the native rainforest habitats on the island, from nearly sea-level to montane cloudforests, up to 1,400 m elevation, habitats that cover about 70% of the island (about 80,000 hectares). This fast growing (up to 1.5 m/year) and early reproducing (fruiting after 4-5 years of vegetative growth) species produces thousands of small fleshy berries, each of them containing hundreds of tiny seeds which are dispersed over long distances by frugivorous birds. A single large reproductive tree can produce over 50 million seeds per year, which can germinate in low light conditions such as in undisturbed native rainforest understory. Within a few generations, *Miconia* can form dense almost monotypic stands (up to 3 to 6 individuals per m^2), causing a dramatic reduction in light.

By the 1990s, 40 to 50 of the 107 endemic plants of Tahiti were directly threatened by *Miconia* (Meyer and Florence, 1996). Most of these endemic plants (classified as Critically Endangered, Endangered, or Vulnerable in the IUCN Red List) are understory herbs, subshrubs, shrubs, or small trees that cannot survive or reproduce under the shade of a closed canopy of *Miconia*. Studies conducted on Tahiti have demonstrated that reproduction of several endangered endemic shrubs and subshrubs (*Psychotria* spp. and *Ophiorrhiza* spp., Rubiaceae), and the seedling recruitment of the small endangered endemic tree *Rapanea* (*Myrsine*) *longifolia* (Nadeaud) Mez (Myrsinaceae) both decrease with increase in *Miconia* cover (Meyer et al., 2003, 2008b). The replacement of native forests by dense monotypic stands of *Miconia*, coupled with potentially severe impacts on watersheds (e.g., increase of runoff and reduction in groundwater recharge) and increased soil erosion (Kaiser, 2006), makes the species an "ecosystem transformer" (Richardson et al., 2000). *Miconia* also became invasive in tropical rainforests following later introductions to other islands of the Society archipelago (Moorea, Raiatea, and Tahaa), the Marquesas (Nuku Hiva and Fatu Iva), the Hawaiian Islands (Hawai'i, Kauai, Maui, Oahu), New Caledonia (Province Sud), and the Queensland region in Australia, and it remains a threat to many other tropical islands in the Pacific and Indian Oceans, as well as in the Caribbean (Meyer, 2010b).

WERE OTHER CONTROLS FEASIBLE?

In the Society and the Marquesas Islands, different control strategies were used, depending on the intensity of the *Miconia* invasion. Manual and chemical controls (by hand removal of seedlings and saplings, and cut-stump treatment of large reproductive trees) were carried out in small localized areas of high ecological value (e.g., areas with remnant populations of endangered endemic plants) in the heavily invaded islands of Tahiti and Moorea (>3,500 infested ha). Containment was done on the island of Raiatea where *Miconia* populations were less important (ca 500 infested ha, i.e., less than 3% of the island surface). Eradication was attempted on the islands of Tahaa, Nuku Hiva, and Fatu Iva, where the number of individuals was low and confined to a small area (<10 ha), and with few reproductive trees. On Raiatea where "Miconia removal campaigns" were organized from 1992 to 2008, with total of ca. 3,500 people involved (including the French Army, local nature protection groups and schoolchildren), more than 2.2 million *Miconia* plants were destroyed, including more than 4,500 reproductive trees. There was, however, no significant decrease in the number of plants being removed annually over this period, likely due to the short duration of each control campaign (one or two weeks per year), the relatively low number of participants and volunteers, a long lasting soil seed bank (more than 15 years), and the discovery of new populations in remote areas that were difficult for control teams to reach (Meyer, 2010b).

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

Because manual and chemical control methods had limited effect in heavily invaded islands, especially where *M. calvescens* had already formed dense monospecific stands on steep mountain slopes, investigations on biological control of the plant were begun. In addition, the low genetic diversity of the species suggested it would be unlikely to rapidly evolve resistance to biological control agents (Le Roux et al., 2008).

Exploratory field trips were conducted by the Hawaii Department of Agriculture (HDOA) between 1993-1995 in the native range of *Miconia* (mainly in Costa Rica, Brazil, and Trinidad) in search of its natural enemies. Among the biological control candidates, a fungal pathogen – *Colletotrichum gloeosporioides* forma specialis *miconiae* (Order: Melanconiales, Class: Coelomycetes, Subdivision: Deuteromycetinae, hereafter *Cgm*) – was found in Brazil in 1997, causing *Miconia* leaf anthracnose and plant necrosis (Figure 9-2a,b). Rigorous host-specificity testing conducted at the HDOA quarantine facilities to assess its safety for introduction involved testing species in the same order (Myrtales) and included native and endemic melastomes (*Melastoma denticulatum* D. Don and *Astronidium* spp.) found in the Society Islands. Results indicated that this strain of *C. gloeosporioides* was highly specific to *M. calvescens* (Killgore et al., 1999). *Cgm* causes leaf spots, defoliation, and eventually death of young seedlings under laboratory conditions (up to 74% mortality one month after inoculation) (Meyer et al., 2008a). This fungus was successfully introduced from HDOA quarantine facilities to Tahiti in 2000, with approval of the French Polynesian government, and it was released in two permanent plots located at about 600-620 m elevation with a mean annual rainfall ranging from 3,300 mm to 7,000 mm. About one hundred *Miconia* seedlings or saplings (between 10 cm and 2.8 m in height) were monitored for a period of six years after the inoculation to assess the pathogen's dispersal and its impacts on *Miconia* in the wild. Leaf spots were observed about 30 days after inoculation, and the percentage of plants infected reached 100% after 3 months, with lesions on 90-99% of all leaves. The mortality rate of plants in the monitored group was 15% as a whole, but it reached 30% for seedlings <50 cm tall (Meyer et al., 2008a). Within three years, the fungus had disseminated throughout the island of Tahiti and had infected nearly all the *Miconia* plants up to 1,400 m in montane rainforests. It was also found on the neighbouring island of Moorea located nearly 20 km away, without any intentional release there. *Cgm* has succeeded in infecting nearly all the *Miconia* plants on both islands, particularly at high elevation montane rainforests or cloudforests, by natural means without causing any apparent harm to non-target plant species (Meyer et al., 2008a).

Figure 9-2. (a) Inoculating *Miconia* with the introduced pathogen *Colletotrichum gloeosporioides* forma specialis *miconiae*; (b) the leaf spot fungus causing deterioration of leaves (Credits: a,b Jean-Yves Meyer)

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

Figure 9-3. Partial defoliation of *Miconia calvescens* canopy trees caused by the fungal pathogen (Cgm) in montane cloud forest in Tahiti (Credit: Jean-Yves Meyer)

An unanticipated response of the forest ecosystem after the release and dispersal of the *Cgm* in Tahiti was the partial defoliation (Figure 9-3) of large reproductive *Miconia* trees. Field studies showed that leaf damage on *Miconia* canopy trees increased from 5% to 45% with elevation in study plots set up between 600 and 1,020 m, suggesting that temperature and moisture (as humidity or free water) are important factors for disease development, reproduction and dissemination. This partial defoliation of *Miconia* forests favoured the recruitment of native plants (Figures 9-4, 9-5), including rare threatened endemic plants such as the tree *R. longifolia* (Myrsinaceae) and the subshrub *Ophiorrhiza subumbellata* G. Forst. (Rubiaceae), by enhancing the light availability in the understory (Meyer et al., 2008a; Meyer and Fourdrigniez, 2011).

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

Monitoring plots (10 x 10 m) were set up along elevation gradients located between 600 and 1200 m to study forest dynamics and plant succession over time, noting the taxonomical types (flowering plants, ferns), biogeographical status (native, endemic or alien) and ecological groups (shade-tolerant or light-demanding) of each species. Results collected over 5 years (2005-2010) showed that the number and cover of understory plants increased with time, an effect which was more pronounced for light-demanding pioneer species. Most colonizing understory species (80%) were native trees, shrubs, or ferns, with little reinvasion by other alien plants, which was mainly restricted to the lowest altitude plots (Meyer et al., 2012). Seedlings of rare endemic plants – such as the tree *Pittosporum taitense* Putterlick (Pittosporaceae) and the small terrestrial orchid

Figure 9-4. Threatened endemic plant species such as the shrub *Psychotria speciosa* (a), the small tree *Myrsine longifolia* (b), and the small orchid *Liparis clypeolum* (c) have benefited from the partial defoliation of *Miconia calvescens* caused by the introduced fungal pathogen (Credits: a-c Jean-Yves Meyer)

Figure 9-5. Recruitment of native ferns and shrubs in the understory of a *Miconia calvescens*-invaded rainforest where *Miconia* has been partially defoliated by the introduced fungal pathogen (Credit: Jean-Yves Meyer)

Liparis clypeolum (G. Forst.) Lindl. (Figure 9-4c) – were found in the permanent plot at 600 m elevation in 2014 although they had not been seen in the past 20 years at that site (J-Y Meyer, unpub. data). However, these plant assemblages are certainly different from the pre-invasion stage (which remains unknown), and long-term monitoring of forest dynamics will be needed to study the trajectory of these "novel habitats".

FUTURE OF SYSTEM

Sixteen years after its successful release in Tahiti, the fungal pathogen *Cgm* did not provide complete control of *Miconia,* especially in low elevation rainforests (<600 m) where warmer temperatures seem to decrease the fungus effectiveness. However, long-term monitoring demonstrates that this biological control agent can be considered a tool for partial restoration of heavily invaded rainforests at higher elevation (including montane cloudforests) and contribute to the recovery of native and endemic plant species (Van Driesche et al., 2016c). Other highly specific biocontrol agents are being tested in Brazil, such as the fungus *Coccodiella miconiae* (Duby) I. Hino & Katum. (Ascomycota: Phyllachoraceae), which attacks younger leaves than *Cgm*, and so could be a useful complementary agent (Alves et al., 2014).

In summary, although these fungal pathogens may slow the growth of established *Miconia* plants and cause the dieback of young seedlings, it is unlikely that they will reverse the massive invasion of *Miconia*. On the islands of Raiatea and Nuku Hiva where *Cgm* was released in 2004 and 2007 respectively, as well as in the Hawaiian Islands, manual and chemical control efforts will be still necessary to eradicate or contain this extremely invasive alien plant in tropical island forest ecosystems.

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CHAPTER 10. STRATEGIC RESTORATION OF SALTCEDAR-AFFECTED RIPARIAN ECOSYSTEMS OF THE U.S. SOUTHWEST: INTEGRATION OF BIOCONTROL AND ECOHYDROLOGICAL CONDITIONS IN RESTORATION PLANNING

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WAS THE INVADER A KEY SOURCE OF ECOSYSTEM DEGRADATION OR A THREAT TO NATIVE SPECIES?

Tamarix spp. (saltcedar, or *Tamarix* hereafter) is a complex of semi-deciduous shrub species originating in Eurasia and currently established in wetlands and riparian ecosystems of the arid and semi-arid parts of western North America (Figure 10-1) and other regions with similar climates (Argentina, South Africa, Australia). Although introduced for horticultural purposes (erosion control and shade in desert regions), these shrubs escaped cultivation early in the 20th century in association with the widespread regulation of western US rivers, which inhibited the natural flooding regimes that promote regeneration of native cottonwood-willow riparian woodlands (Horton, 1977). By the mid-1900s, several *Tamarix* species and their hybrids (Gaskin and Schaal, 2002) had invaded roughly 1 million ha of the western United States (Robinson, 1965; Everitt, 1998) and replaced these riparian woodlands, as well as other vegetation types such as mesquite bosque, riparian scrub, and saltgrass/halophytic scrublands, in part as a consequence of reduced water availability, soil salinization, and other degradation that reduced these ecosystems' capacity to sustain native vegetation (Busch and Smith, 1995). At this time, water managers also removed large areas of riparian vegetation

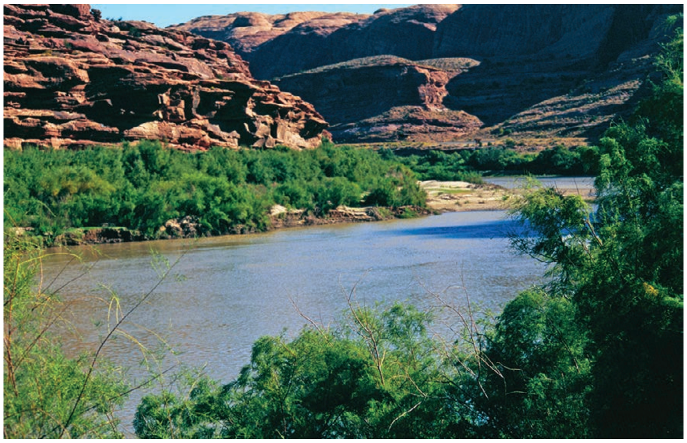

Figure 10-1. Several species of invasive saltcedars (*Tamarix* spp.) dominate riparian areas over much of the southwestern United States (Credit: Steve Dewey, Utah State University, bugwood.org)

for presumed water 'salvage' in places like the Gila River (Orr et al., 2014), which further facilitated *Tamarix*'s expansion in human-altered habitats due to its tolerance of degraded conditions and its capacity to outcompete native plants under such conditions (Sher and Marshall, 2003; Shafroth et al., 2005; Hultine and Dudley, 2013). *Tamarix* invasion, however, is also observed in many largely non-degraded systems where hydrology or fire regimes allow its expansion (Dudley et al., 2000; Whiteman, 2006; Mortenson and Weisberg, 2010).

Once *Tamarix* becomes a dominant element in a system, it causes several environmental and economic problems, including high evapotranspiration rates that deplete groundwater (Smith et al., 1998), inhibition of native plant recruitment as a consequence of depleted soil moisture and soil salinization by throughfall and deposition of salt-laden litter (Shafroth et al., 1995), and increased sedimentation and erosion where dense *Tamarix* stands slow water flow and re-direct water into narrower open areas that are scoured (Graf, 1978; Birken and Cooper, 2006). *Tamarix* offers poorer quality habitat to wildlife than native vegetation, in part by presenting a simplified vegetative structure and altering understory conditions for birds, reptiles, and other taxa (Ellis, 1995; Shafroth et al., 2005). Arthropods are also affected, which may reduce habitat suitability for insectivorous vertebrates (Durst et al., 2008; Longland and Dudley, 2008). Of special concern is a federally listed sub-species, the southwestern willow flycatcher (SWFL, *Empidonax traillii extimus* Phillips) (Figure 10-2), which has declined globally, in part due to the *Tamarix* invasion. However, the bird's use of *Tamarix* as a nesting substrate in a limited portion of its range (Sogge et al., 2003) led to legal actions to modify or halt measures, including biocontrol, to reduce *Tamarix* abundance (Dudley and DeLoach, 2004).

Figure 10-2. The endangered subspecies of willow flycatcher, *Empidonax traillii extimus*, in tamarisk in Tonto National Forest, Arizona (Credit: Andre Silva, USDA Forest Service)

Aquatic systems benefit from riparian litter, which forms the trophic base for many aquatic invertebrates, as well as the fish that then feed on these invertebrates, but *Tamarix* litter is relatively unsuitable for detritus-feeding organisms (Going and Dudley, 2008; Moline and Poff, 2008), with subsequent effects on fish (Kennedy et al., 2005). Salt marsh habitats are also affected by *Tamarix* invasion, with trophic assemblages being degraded by low nutritional quality of organic inputs (Whitcraft et al., 2008).

An increasingly serious impact of *Tamarix* invasion is the promotion of wildfire (Busch, 1995; Drus, 2013) (Figure 10-3). Fire is uncommon in native-dominated riparian vegetation in the invaded region, but *Tamarix* ignites readily and burns with high intensity whether foliage is senescent and dry, or green and healthy (Drus et al., 2013), thus turning riparian areas into promoters of wildfire spread, rather than acting as barriers (Lambert et al., 2010). Burn severity increases with *Tamarix* density, as does mortality of associated native woody plants such that fire drives a positive feedback that can lead to *Tamarix* monocultures (Drus, 2013). *Tamarix* is also poor quality forage for wildlife and livestock, albeit the nitrogen-rich flowering parts can be useful for livestock when present (Cliven Bundy, pers. comm.).

Figure 10-3. In absence of biocontrol, native cottonwood trees, *Populus fremontii*, were killed by *Tamarix*-fueled wildfire at the San Pedro River, Arizona (Credit: G. Drus)

WERE OTHER CONTROLS FEASIBLE?

Western U.S. land managers have long attempted to reduce *Tamarix* densities by one means or another, primarily to save water that otherwise would be lost to the atmosphere through *Tamarix* transpiration (Cleverly et al., 2002), as well as for fuel reduction and habitat or range improvement. Control measures have included herbicide treatments to wood or foliage using hand, ground rig, or aerial application methods, particularly with triclopyr formulations. Other methods have been use of prescribed fire and direct mechanical removal with handtools, bulldozers, or other tools (Taylor and McDaniel, 1998; Kaufmann, 2005; Shafroth et al., 2005). These methods can be effective under many circumstances, but control is hard to sustain because chemical applications generally require repeated follow-up treatments, and re-sprouting following fire or mechanical clearing is typical.

Substrate disturbance associated with mechanical treatments also tends to promote secondary invasion of disturbance-associated weeds such as Russian thistles (*Salsola* spp.), knapweeds (*Centaurea* spp., *Rhaponticum* [*Acroptilon*] *repens* [L.] Hidalgo), and pepperweeds (*Lepidium* spp.), which are also management concerns (Bay and Sher, 2008; Ostoja et al., 2014). Also, *Tamarix*-infested sites tend to be of marginal economic value and benefits rarely justify the exorbitant costs of conventional treatments, while collateral damage to the landscape and remnant native vegetation are not readily mitigated (Dudley and Brooks, 2011). Furthermore, the anticipated water conservation believed to follow *Tamarix* removal has been largely unattained. This difficulty is in part due to the ambiguities inherent in measuring water yields under arid conditions and in part because groundwater retained in one river reach by *Tamarix* clearing can be negated by increased uptake and transpiration further downstream (Shafroth et al., 2005).

WHAT AGENTS WERE RELEASED AND WERE THEY SAFE?

Since there are no native species of Tamaricaceae (to which *Tamarix* belongs) in the New World, and *Tamarix* species in North America are of little economic or ecological value (other than the evergreen athel, *Tamarix aphylla* [L.] Karst., which is used as a shade tree in warm, arid regions), this group of invasive shrubs seemed an appropriate target for biological control. A biocontrol program against *Tamarix* was started by the USDA-ARS in the 1960s by Lloyd Andres and subsequently led by Jack DeLoach, who with many overseas cooperators identified over 300 specialist herbivores with potential for suppressing this invasive plant in North America (Pemberton and Hoover, 1980; DeLoach et al., 1996). At this phase, the U.S. Fish & Wildlife Service was an active participant in the biocontrol program (Stenquist, 2000). Of candidates tested for specificity and efficacy, by 1996 three were approved by the USDA-APHIS TAG (Technical Advisory Group on the Biological Control Agents of Weeds) review process as safe for open release (DeLoach et al., 2004). These three were a mealybug (*Trabutina mannipara* [Hemprich & Ehrenberg]), a foliage-feeding weevil (*Coniatus tamarisci* F.), and a leaf beetle (originally referred to as *Diorhabda elongata deserticola* Chen, and subsequently reconsidered as *D. carinulata* [Desbrochers] within a complex of *Tamarix*-feeding *Diorhabda* species) (Tracy and Robbins, 2009).

Four of the *Diorhabda* species (*D. carinulata, D. elongata* Chen, *D. carinata* [Faldermann], and *D. sublineata* [Lucas]) and various geographic ecotypes of these species eventually underwent quarantine testing in USDA quarantine facilities in Albany, California or Temple, Texas (Lewis et al., 2003; Milbrath and DeLoach, 2006). Additional taxa have received attention in overseas or U.S. quarantine studies (DeLoach et al., 1996), but these additional species have not yet been submitted to APHIS for TAG consideration. On the other hand, several unintentionally introduced *Tamarix* specialists, including a leafhopper (*Opsius*

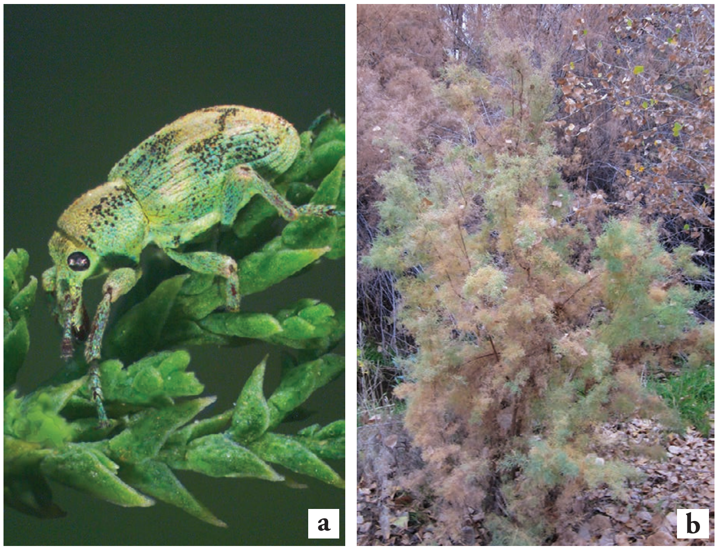

Figure 10-4. The tamarisk weevil, *Coniatus splendidulus* (a), is a self-introduced herbivore affecting *Tamarix* in the United States, which may damage *Tamarix ramosissima*, as seen here on the Bill Williams River in Arizona (b) (Credits: a Z. Ozsoy; b Tom Dudley)

stactogalus Fieber) and two diaspidid scales in *Chionaspis* are present in North America (Wiesenborn, 2005) and can interact with agents intended for release (Louden, 2010). Finally, the weevil *Coniatus splendidulus* F. (Figure 10-4a,b), of unknown origin, was recently detected in Arizona and quickly spread to surrounding states (Eckberg and Foster, 2011; Dudley and Bean, 2012), and this species is similar ecologically to one approved previously by TAG (Sohbian et al. 1998) but not released.

In the 1990s, the *Tamarix* biocontrol program came under increased scrutiny when it was found that the SWFL was nesting in *Tamarix* in some regions, particularly in Arizona and New Mexico (Sogge et al., 2003). Informal consultation with the US Fish & Wildlife Service delayed releases until 1998 when a compromise was reached between USFWS and USDA under which one agent, *Diorhabda* sp., could proceed to open release, but with the limitation that releases would be made at least 200 miles from known locations where SWFL was known to use *Tamarix* for nesting (Kaufman, 2005). Thus, in 1999, *D. carinulata* (formerly known as *D. elongata deserticola*) from northwestern China and Kazakhstan was released into secure cages in seven western states to evaluate its growth and survival, while avoiding the southwestern region where SWFL was present (Dudley et al., 2001). Where overwintering of the beetle was successful, beetles were released into the open in 2001, and evidence of substantial defoliation of ca 2 ha was first observed in the Humboldt River drainage of northern Nevada in late 2002 associated with high densities of larvae (Figure 10-5a-c) (DeLoach et al., 2004). In subsequent years, the area of defoliation expanded by several orders of magnitude, and establishment was also documented in other locations (e.g., the lower stretches of the Walker River, Nevada, the Sevier River, Utah, and the Dolores and

Figure 10-5. *Diorhabda carinulata*: (a) adults scraping *Tamarix* photosynthetic stem tissue; (b) larvae on *Tamarix*; (c) larvae reaching high densities that defoliate saltcedar (Credits: a A. Abela; b Dan Bean, Colorado Department of Agriculture; c Tom Dudley)

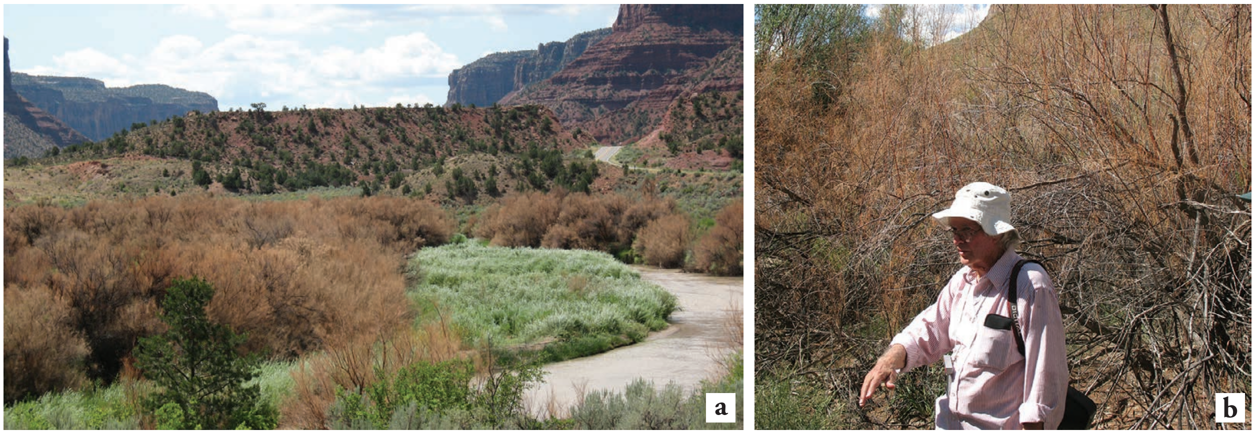

Figure 10-6. (a) *Tamarix* defoliation and native plant recovery in 2008, Dolores River, Colorado; (b) C. J. DeLoach, USDA-ARS, lead scientist for the *Tamarix* biocontrol program, in front of defoliated *Tamarix ramosissima* on the Rio Grande in Texas (Credits: a,b Dan Bean, Colorado Department of Agriculture)

Colorado Rivers in the Colorado/Utah border region, while another form, *D. sublineata*, established along the Rio Grande in Texas and New Mexico) (Figures 10-6a,b). Here, the focus is on the Colorado River Basin and Great Basin where most of Dudley's work has taken place.

The released beetle caused no significant impacts to non-target plants. The potential for feeding by the biocontrol agent on native species of *Frankenia* (Tamaricales: Frankeniaceae) was evaluated in the field because *Frankenia* species were fed on to a limited extent in quarantine studies (Lewis et al., 2003; Herr et al., 2009; Moran et al., 2009). At two field sites where *Diorhabda* beetle densities were high and host plants were defoliated, larvae left plants in search of food but still caused insignificant damage to *F. salina* experimentally planted adjacent to the infested *Tamarix* stands (Dudley and Kazmer, 2005).

Furthermore, this central Asian beetle selectively oviposited on forms of *Tamarix* from central Asia but did not recognize the Mediterranean *Tamarix* species (*Tamarix parviflora* DC., *T. aphylla*) (Figure 10-7) as suitable oviposition hosts, while middle eastern or Mediterranean *Diorhabda* species, presumed to be

Figure 10-7. Defoliation of *Tamarix ramosissima* next to *Tamarix parviflora*, which is largely unaffected by *Diorhabda* feeding, in 2011 on the Virgin River in Arizona (Credit: Tom Dudley)

Figure 10-8. Traps baited with aggregation pheromone are used for detection of *Diorhabda* colonization, showing beetles caught on trap (Credit: Tom Dudley)

sympatric in origin with these plants, did oviposit on them (Dudley et al., 2012; Moran et al., 2009). When herbivore densities were at epidemic levels causing complete defoliation of *T. ramosissima*/*T. chinensis* Lour. forms, some spillover onto *T. aphylla* occurred and was a concern to landowners, especially in northern Mexico. But affected trees readily recovered and little impact was observed in subsequent years when insect densities were more moderate (DeLoach et al., 2012). This specificity within the genus *Tamarix* was a strong indication that non-target effects outside this taxon are unlikely.

WERE THERE UNANTICIPATED SYSTEM RESPONSES?

In the Herbivore-Plant System

Initial expectations were that *Tamarix* biocontrol would be gradual, and thus the rapid insect population growth and expansion of the area of defoliation at key locations (Bean et al., 2013; Pattison et al., 2011) was unexpected (Hultine et al. 2010), although this should reasonably be considered a positive sign of pending biocontrol success. At the same time, however, releases of *Diorhabda* beetles did not lead to establishment in most locations, for reasons that were unclear at the time (Dudley et al., 2012). It was later found out that these failures were due to factors such as release on the wrong species of *Tamarix*, consumption by generalist predators (Knutson et al., 2012, Strudley and Dalin, 2013), and, most importantly, a mismatch between the beetle's diapause induction requirements and the local day length patterns (Bean et al., 2007). Thus, at latitudes south of ca 38ºN (the area used by SWFL), adult insects entered diapause too early (in mid-summer), resulting in mortality because metabolic reserves were exhausted before the following spring (Dalin et al., 2010). Other genotypes of *Diorhabda* were introduced that were more effective at lower latitudes, particularly in Texas (Knutson et al., 2012; Michels et al., 2013) or against *T. parviflora* (Tracy and Robbins, 2009). Sentinel traps baited with an aggregation pheromone were used to detect populations before defoliation occurs (Figure 10-8), followed by long-term monitoring to determine impacts on *Tamarix* plants (Figure 10-9a,b).

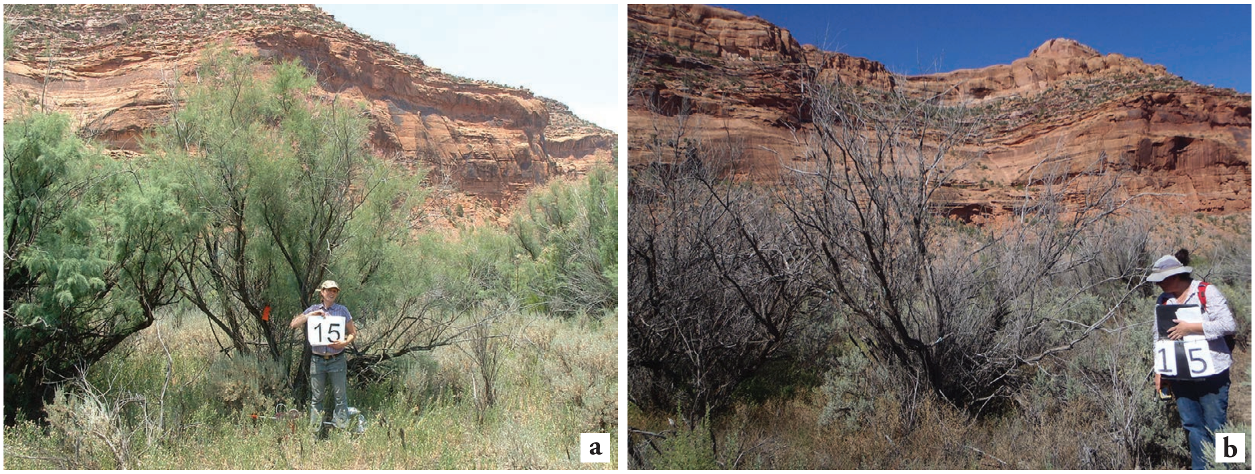

Figure 10-9. Monitoring the progress of the *Tamarix* biocontrol program at Bedrock Creek, in Colorado, showing the impact of *Diorhabda carinulata* on *Tamarix ramosissima* between 2010 (a) and 2014 (b) (Credits: a,b Colorado Department of Agriculture)

Subsequently, *D. carinulata* was observed to have become established south of the former latitudinal limit along the Virgin River in southern Utah downstream to the lower Colorado River (Hultine et al., 2015a). Growth chamber studies with beetles collected from these field sites showed that in only 4-5 years natural selection for delayed diapause induction had enabled this southern expansion (Bean et al., 2012). By late 2016, beetles had become established through the lower Colorado River Basin, south to almost 34ºN (unpub. data). It is likely these beetles will continue to expand southward to the Mexican border and into the Colorado Delta where *Tamarix* is also of conservation concern (Nagler et al., 2009).

On the other hand, we have typically observed that the initial epidemic levels of *Diorhabda* population increase and defoliation were followed a few years later by unanticipated population declines, the mechanism for which is not clear. This decline probably involves a combination of reductions in the host plant biomass (necessarily supporting fewer herbivores) and the impacts of generalist predators (arthropods as well as vertebrates), which respond positively to this new prey resource (Longland and Dudley, 2008; Bateman et al., 2010; Bean et al., 2013; Strudley and Dalin, 2013).

Ecosystem Responses

Major alteration of any dominant vegetation type must be assumed to have secondary or interactive effects, many of which can only be anticipated in general terms (Denslow and D'Antonio, 2005). Indeed, such indirect secondary effects as competitive release of associated flora, improvements in litter and soil traits or water relations, and increased use of native vegetation by wildlife are primary objectives of 'conservation biocontrol,' although some short-term negative effects may occur. Some positive responses occurred immediately; for instance, over 2,500 acre-feet of water were estimated to have been conserved annually in groundwater due to reduced evapotranspiration after defoliation of *Tamarix* (Pattison et al., 2011). But given the diverse objectives of *Tamarix* biocontrol, none of the responses in affected ecosystems were unanticipated, even if their magnitudes were unknown.

The consequences of *Tamarix* biocontrol for vertebrate wildlife are unclear (Bateman et al., 2013), but early projections of major mortality of nesting birds from defoliation (Sogge et al., 2008) have not been borne out. Inferential data (Paxton et al., 2011) suggest that biocontrol was implicated in some nesting failures. Certainly, *Tamarix* dieback reduced habitat quality for some taxa in the short term (Bateman et al., 2013). While long-term outcomes are still not known, emerging data in defoliated areas indicate that as riparian systems trend back toward native plant composition (Figure 10-10) due to the biocontrol program, reptiles and amphibians increase in diversity and abundance, but in heavily altered systems some measure of active restoration may be needed to accelerate this response (Mosher and Bateman, 2016). Wildlife benefits from substantial native vegetation cover (> ca 30%) within mixed *Tamarix* stands (van Riper et al., 2008), so the key question is whether a given system has capacity for recovery in a timeframe that sustains wildlife.

WAS INVADER SUPPRESSION SUFFICIENT FOR RESTORATION?

The initial few years of *Tamarix* suppression by *Diorhabda* was impressive, and reduction in aerial cover of this competitive invader was associated with measureable increases in native or desired vegetation in several locations (N. Louden, unpub. data). Mortality of 60% or more was noted in some areas (Bean et al., 2012; Hultine et al., 2015a) due to gradual depletion of stored metabolites by repeated defoliation that prevented the plants from replenishing their carbohydrates (Hudgeons et al., 2007).

Figure 10-10. *Tamarix* defoliation and mortality, with recovery of native willow, *Salix gooddingii*, and cottonwood, *Populus fremontii,* in 2010 at the Virgin River, Arizona (Credit: Tom Dudley)

Whether this suppression was sufficient to promote ecosystem recovery is a more complex question. In systems where native woody plant abundance is moderately high and environmental conditions (moisture, soil salinity, etc.) are not excessively degraded, such as the Dolores River near Moab, Utah or the Walker River in central Nevada, we find that recovery may be slow but is taking place without major intervention. Recovery of important natural resource features is likely to be the case in many other systems where ecosystem processes still favor growth of native woody plants (Shafroth et al., 2007), but recovery will be slower where degradation levels are high or multiple stress factors inhibit regeneration. It is important to note that SWFL is absent and other sensitive riparian species rare under such degraded conditions (Dudley and DeLoach, 2004).

The Virgin River is an interesting case, in that it largely retains the hydrologic integrity (flood/drought sequences) that normally favors native species over *Tamarix*, and indeed where active restoration measures were implemented in areas along this river that had been affected by *Tamarix* biocontrol, recovery of native vegetation appears to be good (Leverich et al., 2014; Mosher and Bateman, 2016). But in this system, we have observed that periodic wildfires, promoted by *Tamarix*, have nearly eliminated native trees (Fremont cottonwood, *Populus fremontii* S. Watson and Goodding's willow, *Salix gooddingii* C.R. Ball) from much of the system such that propagules are lacking that could regenerate native riparian woodlands (Dudley and Brooks, 2011). That is, recruitment limitation circumvents the process by which natural flooding creates scoured substrates that facilitate germination and establishment of these native taxa (Stella et al., 2006; Merritt and Poff, 2010). In such cases, a restoration strategy is to re-introduce native trees (manual seeding, container-stock outplanting, pole cuttings etc.) in patches distributed at intervals across the floodplain. These 'propagule islands' serve as seed sources so that in the future when hydrological conditions favor recruitment, there will be sufficient reproductive plants to broadly disperse seed across the floodplain. This approach can be done with relatively low investment, while enhancing riparian recovery because natural recruitment tends to yield better plant growth and survival than in large-scale active re-vegetation (Dudley and Bean, 2012, Leverich et al., 2014). In addition, because biocontrol reduces *Tamarix* fuel loads, it also can improve native plant survival by reducing the frequency, extent, and severity of wildfires (Drus, 2013).

In other cases, the same environmentally damaging processes that facilitated conversion from native woodlands to *Tamarix* stands (water diversion, salinization, livestock grazing, etc.) must be mitigated along with *Tamarix* suppression if recovery is to take place. At the Humboldt River, Nevada, diversion and salinization are intense and grazing ubiquitous, so that cottonwood-willow recovery has low probability of success, although some native taxa that tolerate such conditions (e.g., *Atriplex*, *Sarcobatus*, *Distichlis*) may still be able to increase with *Tamarix* suppression, but so do various other secondary weeds. Likewise, the lower Colorado River and many of its tributaries such as the Gila River have been so altered, particularly in curtailing natural flooding, that *Tamarix* suppression alone will not lead to passive recovery of riparian vegetation (Shafroth et al., 2007). Except for narrow bands immediately adjacent to the water's edge, restoration in such areas will likely require active re-vegetation to compensate for the loss of factors that promote native tree recruitment under more natural hydrologic regimes. A useful approach to improve recovery potential is manipulation of flow regimes to mimic natural processes (Konrad et al., 2011), which has been implemented at another Colorado River tributary, the Bill Williams River, where simulated flow fluctuations from the Alamo Reservoir were successful in sustaining diverse native woodlands despite presence of *Tamarix* (Shafroth et al., 2010). *Diorhabda* beetles established along the Bill Williams River in 2016; however, it is expected that there will be little or no need for active measures during the incremental decline of *Tamarix* because flow conditions and native propagules at the sites appear suitable for natural vegetation recovery.

For systems in which sufficient ecosystem function exists to support native vegetation, the probability for recovery can be improved by a strategic approach to restoration which integrates hydrology and fluvial geomorphology, soils, and current vegetation condition and wildlife status, a process termed "Ecohydrological Assessment." These factors are used along with historical and current aerial imagery and remote sensing to direct effort where it will be most productive, at relatively low cost, for improving the chances of riparian recovery (Leverich et al., 2014). This is being applied in several western streams, and in the context of *Tamarix* suppression by biocontrol, we are implementing restoration in the Virgin River (Nevada) and upper Gila River (eastern Arizona) based on these principles (Orr et al., 2014; Stillwater Sciences, 2014).

While it is too early to claim success, native vegetation is establishing well at Virgin River sites where SWFL populations had previously declined. Once *Diorhabda* beetles are established in a location, the resulting *Tamarix* defoliation occurs early in the season, before SWFL migrants return from their over-wintering grounds in Central America. Returning birds have been observed to pass over defoliated *Tamarix* and occupy the remaining patches of native willows (BOR, unpub data). The time frame for vegetation recovery at a site necessarily requires several years, but cottonwood-willow replacement of *Tamarix* in other systems, e.g., at Elephant Butte Reservoir on the Rio Grande (NM), was associated with dramatic increases of this endangered bird over a period of ca 10 years (Ahlers and Moore, 2009). Riparian plants are effectively native weedy species, dependent on natural disturbance to promote regrowth, and the SWFL and other sensitive riparian-associated species such as Bell's vireo (*Vireo bellii* Audobon) and yellow warbler (*Setophaga petechia* [L.]) are associated with early phases of riparian succession (Ellis, 1995; Shafroth et al., 2005), so it is unsurprising that they would respond positively to enhancement of native vegetation, essentially a "build it and they will come" relationship (Dudley and Bean, 2012).

FUTURE OF SYSTEM

There are many *Tamarix*-affected ecosystems where biocontrol would provide a useful 'tool' for resource management, and in California an Alliance supported by the state EPA was recently formed to work with regional stakeholders to consider if and how biocontrol implementation would help meet their resource management goals. Implementation should consider how experiences to-date allow us to objectively evaluate the costs, benefits, and risks of *Tamarix* biocontrol, with the realization that to-date, neither the dire predictions of endangered species managers nor the early hopes of biocontrol practitioners have come to pass. With respect to wildlife, riparian areas are dynamic ecosystems and the biota, even including federally listed taxa, are adapted to periodic disturbances, so it is important to put short-term alteration of *Tamarix* vegetation into the context of shifting faunal populations as suitable habitat is transitive and routinely lost, whether

Figure 10-11. Defoliated *Tamarix* on Colorado River near Moab, Utah in 2008, following release of *Diorhabda carinulata* beetles, with patches of remnant native willow stands in the far background (Credit: Tom Dudley)

from biocontrol, wildfire, or community maturation into a less suitable state. At the same time, we would be naïve to ignore the landscape-level implications of both large-scale *Tamarix* decline (Figure 10-11) or of its continued domination (Mortenson and Weisberg, 2010), particularly in the context of the anticipated effects of climate change in western North America (Hultine et al., 2015b). That debate will continue, but recent discussion among federal agencies suggests that at least the legal situation that has constrained the *Tamarix* biocontrol program and even the monitoring of its consequences may soon be resolved.

Such resolution would allow the program to be re-initiated, and the mixed results of the current situation can be addressed in a more constructive manner. That would include evaluation of new agents given the moderate level of suppression and plateauing of host mortality from the *Diorhabda* beetle introduction alone. A potential agent is the already approved mealybug *T. mannipara*, considered appropriate for high temperature regions, while evaluation of the naturally established weevil *C. splendidulus* may ultimately provide the same benefit as that anticipated earlier from the related, TAG-approved related weevil *C. tamarisci,* which has not been introduced. Overseas cooperators have identified and tested other organisms that could be used to affect other plant parts, such as stem-feeding *Psectrosema* spp. (Cecidomyiidae), the gall-forming weevil *C. tamarisci*, a defoliating moth *Agdistis tamaricis* (Zeller) (Pterophoridae) and several other *Tamarix* specialists (Sohbian et al., 1998) if pre-release evaluation concludes that multiple agents will be synergistic rather than agonistic.

ACKNOWLEDGMENTS

The Tamarix Biological Control Program has involved many researchers and specialists over its 25+ year lifespan, too many to name but particular appreciation is given for the commitment to this program by long term colleagues, including Li Baoping (Nanjing Agricultural University), Roman Jashenko and ID Mityaev (Al-Farabi Kazakh National University), Rouhollah Sobhian (USDA-EBCL), from USDA-ARS & APHIS - James Tracy, John Gaskin, Bob Bartelt, Allard Cossé, Earl Andress, Phil Lewis, R. Carruthers and Julie Gould, Debra Eberts and Ken Lair (Bureau of Reclamation), Allen Knutson and Jerry Michels (Texas A&M University), David Thompson (New Mexico State University), Zeynep Ozsoy (Colorado Mesa University), Nina Louden (Colorado Department of Agriculture), Richard Reardon and Elizabeth Hebertson (USFS Forest Health Protection), Bruce Orr and Glen Leverich (Stillwater Sciences), Jeff Knight (Nevada Department of Agriculture), Gail Drus (St. Francis University), Tim Higgs (Grand County, Utah) and Mike Pitcairn (California Department of Food & Agriculture). Sorely missed but not forgotten are David Kazmer, Brian Cardall, and from USFWS, Scott Stenquist and John Taylor. Support has been from USDA-NIFA, Clark County, Nevada Desert Conservation Program, USFS Forest Health Protection, USDA-APHIS, and other sundry sources.

CHAPTER 11. FUTURE TRENDS IN USE OF NATURAL-AREA BIOCONTROL

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CONCLUSION FROM THE CASE STUDIES

Finally, for the *Tamarix* case and the other examples discussed above, we need to upgrade our collective perception of biological control and differentiate the conceptual framework of conservation biocontrol (against pests of natural areas) from agricultural biocontrol, with its simpler objective to suppress or eliminate pest organisms (Van Driesche et al., 2016a). Conservation biocontrol is a holistic approach to re-assembling a weed's or insect's co-evolved mosaic of species, based on what existed in the pest's area of origin so that this group of species functions in a more complex and less damaging manner than when the pest occurs in invaded areas without such associates. Post-biocontrol, the former pest exists in the invaded ecosystem, restrained by many such trophic links and becomes just another point in the local foodweb, with various feedbacks within the biotic assemblage, in place of acting as a source of biotic stress for the system.

CHALLENGES AHEAD

Future use of biological control as an emerging tool for conservation biology (Van Driesche et al., 2016a) will depend on how well several currently visible problems are dealt with, including the following:

Funding and Scientist-power Going Down, While Need Goes Up

The costs of natural enemy discovery, assessment of safety, petitioning for release, mass rearing and release, and post-release efficacy and safety assessments all must be paid for by government, or these activities do not happen. Since the 1970s, there have been strong swings in the willingness of governments in the major biocontrol-conducting countries to pay such bills. Because many insect and even some weed biocontrol projects are done to provide economic benefits to grazers, farmers, or other private groups, the view has arisen, particularly in Australia and New Zealand, that those groups should pay these bills. That has worked relatively badly because the finer points of good biological control practice – taxonomic revisions, nontarget impact studies, post-release evaluations, development of new techniques, etc – may either be unknown to these groups or be little valued. Also, the projects of great need for protection of natural systems may be of only moderate economic importance and vice versa, mis-aligning selection of projects with ecological need. The need for strong governmental support, with private supplemental funds, remains – and when not provided, outputs decline. Similarly, continuity of biocontrol/natural enemy knowledge is critical, with new scientists learning much from the previous generation before they retire. Bottlenecking human resources in this science, by periodic steep reductions in hiring in the face of continued retirements of older scientists, degrades institutional capabilities, with loss of scientific competency. Furthermore, while the trend in funding and human resources for biocontrol in most of the major practicing countries is negative or neutral at best, the extent of invasive pest problems in natural areas continues to increase. Only in South Africa does an absolute increase in funding – via the Working for Water Program – seem to have occurred over the last several decades (see Moran et al. [2005] for comments on Working for Water Program).

Lingering Distrust of Biocontrol by Conservation Biologists

While some degree of improved understanding between conservation biologists and biological control scientists may be underway in the United States (Van Driesche et al., 2016a), much disagreement remains. This will likely take a full generation to alter. As such, this factor certainly will affect the choice of projects, speed of their adoption, and wide understanding of their consequences in the United States for the foreseeable future. This problem seems smaller or non-existence in other countries (e.g., South Africa).

Failure to Distinguish Use from Population-level Impacts

Conservation biologists focus on the welfare of *populations* of the species of concern. Animal-welfare groups (such as PETA), in contrast, focus on suffering or health of *individual animals*. This pits the two groups against each other in ways that may be unresolvable. For example, groups concerned with vegetation destruction due to overgrazing by introduced ungulates or equines, may be prevented from reducing such populations by animal right groups that demand no harm to any individual animals, despite them being the source of important ecological damage and suffering by native animals. For biological control, a similar difference exists between those focused on risks to non-target species populations versus others for whom the death of some individuals of non-target insects or plants is unacceptable.

Demands by Regulators to Identify Food Web-based Risks

Previously, the standard that new biological control agents had to meet was to demonstrate low risk of directly attacking native species at population-damaging levels. However, recently the US Department of Interior (responsible for protection of wildlife) has expanded this standard to require consideration of possible indirect, food web-mediated effects. While doing so has some potential benefits, two points need to be considered. First, introductions for no other purpose other than biocontrol are required to meet such a standard – not introductions made of horticultural plants, pets, species used in aquaculture, or other groups. Second, while host ranges of biocontrol agents are susceptible to being estimated by following an understandable and predictable set of tests, the same is not true of indirect effects. Indirect effects, rather, have no common thread and can only be sought and tested for one by one and only if the type of interaction can be imagined. That said, there are some categories of indirect effects that might be reasonable to test for, including potential toxicity of the agent to native species that might eat it. This risk, for example was considered in the case of the introduction of *Rodolia cardinalis* (Mulsant) to the Galápagos to ensure safety to native land birds, should they prey on the agent (Lincango et al., 2011). More comprehensive evaluation of indirect effects may be so unending as to be not a standard but a total barrier to agent introduction, depending on the inclination of the reviewing agency.

New Players with Old Values

A further complication likely to affect whether and how well biological control will be used for the protection of nature is that the group of countries practicing biocontrol introductions may increase in the future, bringing new regulatory systems (or countries with no system at all) and values (either highly conservative or rather careless) into play. Countries facing threats to food supplies that are only marginally secure or threats of important economic losses can be expected to weigh those things heavily, perhaps not being as concerned about potential for non-target effects.

REQUIRED ACTIONS

To enhance the frequency and quality of biocontrol projects in natural areas, several actions would be useful, including the following:

- Use high quality taxonomy to characterize the agent correctly BEFORE its release.

- When several agents are known at the same time, release them, if possible, in order of their likely impact.

- Expect some non-target host use, but work to avoid population-level impacts.

- Develop on-line summaries of relevant information on natural enemy releases.

- Plan biological control projects jointly with conservation partners.

- Conduct post-release studies of agents on the target and on non-target species believed to potentially be attacked or plausible negative indirect effect.

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