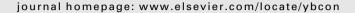


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Biological Control





Review

Classical biological control for the protection of natural ecosystems *

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ABSTRACT

Of the 70 cases of classical biological control for the protection of nature found in our review, there were fewer projects against insect targets (21) than against invasive plants (49), in part, because many insect biological control projects were carried out against agricultural pests, while nearly all projects against plants targeted invasive plants in natural ecosystems. Of 21 insect projects, 81% (17) provided benefits to protection of biodiversity, while 48% (10) protected products harvested from natural systems, and 5% (1) preserved ecosystem services, with many projects contributing to more than one goal. In contrast, of the 49 projects against invasive plants, 98% (48) provided benefits to protection of biodiversity, while 47% (23) protected products, and 25% (12) preserved ecosystem services, again with many projects contributing to several goals. We classified projects into complete control (pest generally no longer important), partial control (control in some areas but not others), and "in progress," for projects in development for which outcomes do not yet exist. For insects, of the 21 projects discussed, 62% (13) achieved complete control of the target pest, 19% (4) provided partial control, and 43% (9) are still in progress. By comparison, of the 49 invasive plant projects considered, 27% (13) achieved complete control, while 33% (16) provided partial control, and 49% (24) are still in progress. For both categories of pests, some projects' success ratings were scored twice when results varied by region. We found approximately twice as many projects directed against invasive plants than insects and that protection of biodiversity was the most frequent benefit of both insect and plant projects. Ecosystem service protection was provided in the fewest cases by either insect or plant biological control agents, but was more likely to be provided by projects directed against invasive plants, likely because of the strong effects plants exert on landscapes. Rates of complete success appeared to be higher for insect than plant targets (62% vs 27%), perhaps because most often herbivores gradually weaken, rather than outright kill, their hosts, which is not the case for natural enemies directed against pest insects. For both insect and plant biological control, nearly half of all projects reviewed were listed as currently in progress, suggesting that the use of biological control for the protection of wildlands is currently very active.

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1. Introduction

Natural ecosystems and their component species are experiencing catastrophic and rapid loss as habitat is destroyed for human use and invaded by species from other biogeographical areas (Simberloff et al., 1997; Cox, 1999; Lockwood et al., 2006), Political solutions may be devised to stop habitat loss, and restraints and economic incentives used to reduce human exploitation of natural habitats. However, damage from invasive species cannot easily be reversed. While better legislation and detection tools will be paramount in preventing new invasions, invaders - once established often persist indefinitely and spread to their ecological limits. Reducing damage in small areas with chemical or physical/ mechanical control is possible for some species if funds and staff are available. But at the landscape level, these tools work only if the infested area is small or sufficiently isolated to prevent quick re-infestation. However, on continents, most invasive plants and insects cannot easily be eradicated. For landscape-level suppression or prevention of emerging damage from an expanding invasion, classical biological control should be considered because if successful it brings about desired ecological change over large areas without repeated cost or treatment of the entire infested area (Van Driesche et al., 2008). Other management practices that can be effective at landscape scales against invasive plants (but rarely, insects) include changes in land use, grazing, or fire management, and manipulation of nutrients or hydrology. For successful control of invasive plants, it may be necessary to integrate one or more of these approaches with biological control.

Biological control efforts against plants and insects have different histories, with insect biological control being used for much of its first century largely against crop pests. Only in the1990s did insect biological control against environmental pests develop as an independent goal (Van Driesche, 1994). In contrast, biological control efforts were rarely focused on invasive plants infesting crops. Rather, invasive plants in forests, grasslands, and aquatic areas were targeted to preserve timber, forage, water, and navigation

(Huffaker, 1957). Over time, protection of native biodiversity and ecosystem function also became major goals of biological control of invasive plants (Van Driesche and Bellows, 1996).

Biological control projects have successfully contributed to the protection of the flora and fauna of many natural ecosystems, and are presently a component in many recovery plans (e.g., Causton, 2001 for Galápagos plants) and restoration efforts worldwide. Benefits of biological control in natural areas also include the preservation of wildlands as sources of renewable resources and recreational use. Finally, biological control programs have proven effective in the protection of some ecosystem services such as flood control, fire regulation, and maintenance of healthy soils.

Damage to natural ecosystems from biological control agents is also a potential outcome. For example, in North America the tachinid Compsilura concinnata, introduced for the control of the gypsy moth (Lymantria dispar) may be responsible for regional declines of several saturniids and other moths in the northeastern USA (Boettner et al., 2000; Schweitzer et al., 2010). The non-target effects of biocontrol agents on native insects on islands, and especially Hawaii, have received considerable attention (Howarth, 1991; Henneman and Memmott, 2001). Risks posed by biological control introductions have been the focus of several reviews, and we refer readers to these: Howarth (1991), Simberloff and Stiling (1996), Lynch and Thomas (2000), Pemberton (2000), Louda et al. (2003), and van Lenteren et al. (2006), among others. We do not review non-target impacts and important cases of such effects exist, particularly for projects directed against agricultural or pasture pests, which are outside the scope of this article. Limited mention is made here of such important impacts if they pertain to the species covered in this article.

Here we focus on the benefits of classical biological control as a tool for ecosystem preservation and restoration, especially given the fact that more biological control projects will needed in the future to correct damage from the increasing number of invasive plants and insects that are establishing in new communities worldwide. Over the course of coming decades, we foresee an expanding

need for carefully planned and professionally monitored biological control programs in wildlands that will require the joint efforts of biological control practitioners, invasion biologists, ecologists, taxonomists, policy makers, and conservation specialists.

2. Protecting biodiversity in natural ecosystems

Loss of native biodiversity is the most enduring consequence of alien species invasions; here we discuss the contribution of classical biological control to reversing such losses, in a variety of natural habitats (wetlands, forests, grasslands, deserts/shrublands, coastal/sand dune, and island communities). Effects of invasive species commonly cascade from the attacked species, upward or downward, affecting other members of the food web such as specialized herbivores, or their parasitoids and predators. The benefits of successful biological control also ramify through ecosystems, and where known these are also discussed.

2.1. Aquatic and wetland habitats

Invasive aquatic plants can cause radical changes in even pristine aquatic systems, either by physically altering the habitat or by strong plant–plant competition between the invader and native plants for resources. No examples were found of biological control of invasive insects in aquatic systems. Consequently, here we discuss only invasive plants, of which many species have been subject to biological control. These invasive plants are grouped as (1) floating/emergent species that can cover the surface of water bodies, (2) submerged plants that take resources from native macrophytes, and (3) other species that grow in wetlands but are not themselves aquatic species.

2.1.1. Floating or emergent species

Floating plants strongly affect the physical character of the habitats they invade (Toft et al., 2003), and therefore their effects on biodiversity have much in common across several invasive species. Layers of invasive plants cover the water surface, sequester nutrients, and block sunlight from reaching submersed native macrophytes. Light-deprived submerged plants photosynthesize at lower rates and thus produce less oxygen, which when combined with lower rates of physical aeration by wind and waves (due to damping by floating plant mats) leads to less dissolved oxygen (Ultsch, 1973), more CO₂ and H₂S, and lower pH (Mitchell, 1978; Thomas and Room, 1986a). These changes make the habitat less suitable for native invertebrates (Hansen et al., 1971) and fish. Death of native plants eliminates the foundation for the native food web, with cascading effects on herbivores and predators. Five floating invasive plants of major importance have been targets of successful biological control: Azolla filiculoides (Hill and McConnachie, 2009), Eichhornia crassipes (Coetzee et al., 2009), Salvinia molesta (Julien et al., 2009), Pistia stratiotes (Neuenschwander et al., 2009), and Alternanthera philoxeriodes (Buckingham, 2002).

Azolla filiculoides (red fern) infested much of South Africa by the 1990s (Hill, 1999), forming mats that affected biodiversity (Gratwicke and Marshall, 2001). It caused the near extinction of the rare fish Sandelia bainsii by altering its last remaining habitat (Cambray, Albany Museum, personal communication). The North American weevil Stenopelmus rufinasus was released in 1997. It established and dispersed widely, and very rapidly provided complete control of the weed wherever it occurred (McConnachie et al., 2004), allowing recovery of affected water bodies (Hill and McConnachie, 2009)

Eichhornia crassipes (waterhyacinth) infestations have altered the ecology of water bodies in the southern USA, Mexico, East and West Africa, India, and other warm regions. Weed mats reduce light reaching submerged plants and deplete oxygen, depressing

phytoplankton (McVea and Boyd, 1975) and microinvertebrates (Hansen et al., 1971). Benthic invertebrates beneath E. crassipes mats were less diverse than under open water in the New Year's Dam reservoir in South Africa (Midgley et al., 2006). Similarly, E. crassipes mats lowered diversity of littoral macroinvertebrates on Lake Victoria (Masifwa et al., 2001). Varying levels of biological control of waterhyacinth have been achieved with two species of Neochetina weevils on the Nile River in the Sudan (Beshir and Bennett, 1985), the southern USA (Center et al., 2002), South Africa, West Africa, Malawi, Lake Victoria, and Papua New Guinea (Coetzee et al., 2009). In Lake Victoria, biological control reduced waterhyacinth to about 5-10% of its peak levels (Wilson et al., 2007; Anonymous, 2000; Julien, personal communication). In Benin, following successful biological control of *E. crassipes*, fish populations (Citarhinus spp.) rebounded (Ajuonu et al., 2003; Neuenschwander, personal communication).

Salvinia molesta (giant salvinia), a South American floating fern, formed thick mats on lakes and river oxbows in Australia, Papua New Guinea, parts of the USA, and parts of Africa, especially the Congo basin. Its biological control has been successful in Australia (Room et al., 1981), Papua New Guinea (Thomas and Room, 1986a), the Congo (Mbati and Neuenschwander, 2005; Diop and Hill, 2009), and 14 other countries, through releases of the weevil *Cyrtobagous salviniae* (Julien et al., 2009).

Invasions of water lettuce (*P. stratiotes*) led to similar floating plant mats on lakes in Australia, the southern USA, and Congo. Water lettuce has been controlled in Papua New Guinea and Australia (Harley et al., 1990), several regions in Africa (Mbati and Neuenschwander, 2005; Ajuonu and Neuenschwander, 2003; Neuenschwander et al., 2009), and warm parts of North America (Dray and Center, 1992), most often with the weevil *Neohydronomus affinis*. Infested lakes, once matted over by water lettuce, are now open (e.g., Mbati and Neuenschwander, 2005). Elimination of water lettuce and giant salvinia mats reversed the physical and chemical habitat changes discussed above that are commonly produced by floating invasive plants.

Alternanthera philoxeriodes (alligator weed) is an emergent species that roots on shore or in shallow water and then produces recumbent stems that develop into floating mats. These mats restrict light and oxygen and lead to anaerobic conditions, which in turn affect native flora and fauna. Infestations also increase siltation and reduce flow (Coulson, 1977; Julien, 1995). In the southern USA, Australia, New Zealand, and China, the introduced flea beetle Agasicles hygrophila, either alone or with the crambid moth Arcola malloi, effectively destroyed floating alligator weed mats and prevented their regrowth (Coulson, 1977; Julien, 1981; Julien and Griffiths, 1998; Sainty et al., 1998). The weed is now restricted to banks and shallow margins, so impacts on aquatic biodiversity have largely been eliminated.

2.1.2. Submersed species

The principal submersed invasive species against which biological control has been attempted is *Hydrilla verticillata* (hydrilla). It is a disturbance specialist that rapidly colonizes areas and forms surface canopies that block out the light. It has a broad tolerance range and thrives in many habitats. It matures quickly and propagates and disperses by fragmentation. Hydrilla beds displace native plants and degrade infested habitats (Holm et al., 1997). Four natural enemies of hydrilla have been released in the USA (Balciunas et al., 2002). In Lake Seminole, Florida, damage to hydrilla by an introduced dipteran leafminer, *Hydrellia pakistanae*, was associated with an increase in the number of native plant species (Grodowitz et al., 2003) and a general decline in hydrilla competitiveness with other plants (Grodowitz, personal communication). However, hydrilla continues to be a serious problem in many areas and the introduction of additional agents will be needed, perhaps together with

reintroduction of propagules of native plants, to restore invaded communities.

2.1.3. Other invaders damaging to wetlands

Wetland communities have also been invaded by such non-aquatic plants as the tree *Melaleuca quinquenervia*, the climbing fern *Lygodium microphyllum*, the shrub *Mimosa pigra*, and the herbaceous perennials *Lythrum salicaria* and *Fallopia japonica*. Through a mixture of habitat change and competition, these plants strongly affect native biodiversity. Biological control of all five species is underway, or already achieved.

Melaleuca quinquenervia aggressively invades wetlands in Florida and the Caribbean, forming monospecific stands that displace native vegetation and degrade wildlife habitat (Rayamajhi et al., 2002). Melaleuca reduced biodiversity of freshwater marshes in south Florida by 60–80% (Austin, 1978). Introduced biological control agents (especially the weevil Oxyops vitiosa and the psyllid Boreioglycaspis melaleucae) have curtailed the tree's reproduction, greatly reducing its spread (Pratt et al., 2005; Tipping et al., 2008; Rayamajhi et al., 2008). Biological control agents have reduced seed production and seedling survival (Center et al., 2007; Rayamajhi et al., 2007; Tipping et al., 2009), killing 85% of seedlings, saplings, and suppressed understory trees. This has led to a corresponding decrease in melaleuca cover and a fourfold increase in plant biodiversity (Rayamajhi et al., 2009). Combined with cutting and chemical control, biological control is helping to suppress melaleuca in Florida (see Plate 1).

Old World climbing fern, *L. microphyllum*, also threatens the Everglades and other south Florida habitats, where it dominates Everglade hammocks, cypress swamps, and pine flatwoods (Pemberton and Ferriter, 1998). Two-thirds of southern Florida is susceptible to invasion by this weed (Volin et al., 2004). The pyralid moth *Neomusotima conspurcatalis* and the gall mite *Floracarus perrepae* have been introduced and become established (Boughton and Pemberton, 2009; Boughton and Pemberton, unpublished data). The moth has spread rapidly, defoliating the fern around release sites (Boughton and Pemberton, 2009), and some defoliated areas have already been repopulated by native plants (Boughton and Pemberton, 2009).

Mimosa pigra is an aggressive invader of tropical wetlands in Australia, Asia, and Africa. In Australia, it occurs particularly in wetland margins, lakes, and channels with a long period of inundation and disturbance by feral animals. It also spreads into open plains and swamps (Cook et al., 1996). It currently occupies 800 km² of northern Australian wetlands and threatens 40,000 km². Invasion converts several vegetation structural types into homogeneous mimosa shrublands with greatly reduced biodiversity (Braithwaite et al., 1989). Infestations threaten many vulnerable plant and animal species (Walden et al., 2004), as further discussed under "Ecosystem Services/Provision of habitat for vertebrate wildlife." Both of two fungal species and nine of 13 insect agents released in Australia have established. Although it has been difficult to separate their impacts, both the sesiid borer Carmenta mimosa and the leafmining gracillariid Neurostrota gunniella have reduced seed rain and seedling regeneration, lowered seed banks, and caused the retreat of mimosa at stand edges (Heard and Paynter, 2009). Seed banks are 90% below pre-biological control levels. The impacts of the more recently released agents have not been measured, but appear substantial.

Lythrum salicaria (purple loosestrife) is a Eurasian perennial that has extensively invaded wetlands across the northern USA and adjacent areas in Canada. Loosestrife monocultures damage populations of specialist wetland plants, birds, amphibians, and insects (Blossey et al., 2001b; Brown et al., 2006; Maerz et al., 2005a; Schooler et al., 2009). In Oregon, purple loosestrife infestations have lowered plant and insect diversity in tufted hairgrass (Deschampsia cespitosa) communities (Schooler et al., 2006) and affected insect

diversity in estuarine habitats important for juvenile salmon migration (Schooler et al., 2009). Four biological control agents - the leaffeeding beetles Galerucella calmariensis and Galerucella pusilla, the root-mining weevil Hylobius transversovittatus, and the flowerfeeding weevil Nanophyes marmoratus - were widely released (Blossey et al., 2001b). Stand defoliation occurred within 4 years at some release sites and later occurred more widely (Blossey et al., 2001b). Although impacts varied among sites (Denoth and Myers, 2005; Grevstad, 2006; Landis et al., 2003), these herbivores suppressed L. salicaria in many habitats. Assessments in Michigan found that G. calmariensis established, spread, and reduced plant height by 61-95% (Landis et al., 2003). Purple loosestrife abundance is best suppressed where both leaf beetles and the root weevil are present (Blossey, unpublished data). In many areas where loosestrife has been suppressed, native species have returned (Landis et al., 2003). However in others, invasive hybrid cattails (Typha × glauca). Phragmites australis (Type M), or reed canary grass (Phalaris arundinaceae) (Schooler, 1998) have expanded.

Fallopia japonica (Japanese knotweed) invades riparian areas in Europe and the northern USA, damaging native flora and associated fauna, especially amphibians (Maerz et al., 2005b; Gerber et al., 2008). The Japanese psyllid *Aphalara itadori* is host-specific (Shaw et al., 2009) and its release for biological control of Japanese knotweed is anticipated in the UK in 2010, which will be the first classical weed biological control introduction in Europe.

2.2. Boreal and temperate forests

Natural forest ecosystems have been strongly affected by both invasive insects that kill native trees and invasive plants that compete with native plants.

2.2.1. Invasive insects

Biological control projects against invasive forest insects were initiated in North America to protect threatened lumber sources. Classical biological control of forest pests was rare in Europe due to a lack of important invaders and rare in the Southern Hemisphere because forestry, and hence associated biological control, was largely based in plantations of exotic trees. North American projects to protect lumber supplies also protected forest biodiversity, which had been eroded by invasions of tree-killing insects and pathogens (Campbell and Schlarbaum, 1994, 2002). However, few efforts were made during this period to document impacts of invasive species on forest biodiversity or improvements following biological control of the invasive pests, except for effects on the attacked tree species.

2.2.1.1. Tree-killing borers. Beginning in the 1980s, increased shipment of containerized goods from Asia to the USA facilitated the establishment of several wood boring beetles that were transported as larvae or pupae in wooden crates and pallets. The most damaging species was the ash-feeding buprestid Agrilus planipennis (emerald ash borer), discovered in Michigan in 2002. Ecological damage from this invasion includes >80% mortality of several species of ash at many locations, including rare species such as pumpkin ash (Fraxinus profunda) (Bauher, personal communication). Ash is a dominant or co-dominant in many forest communities, particularly in mesic woodlands and riparian areas (MacFarlane and Meyer, 2005), and many of these habitats have been severely affected. Six ash species were attacked in the central USA by 2009, while several others in western North America are threatened. Twenty-one species of moths are monophagous on Fraxinus (Wagner, 2007), of which five sphingids - Ceratomia undulosa, Manduca jasminearum, Sphinx canadensis, Sphinx chersis, Sphinx franckii - are particularly vulnerable to extinction due to tree death from emerald ash borer. Three parasitoids (Oobius agrili, Tetrastichus plani-

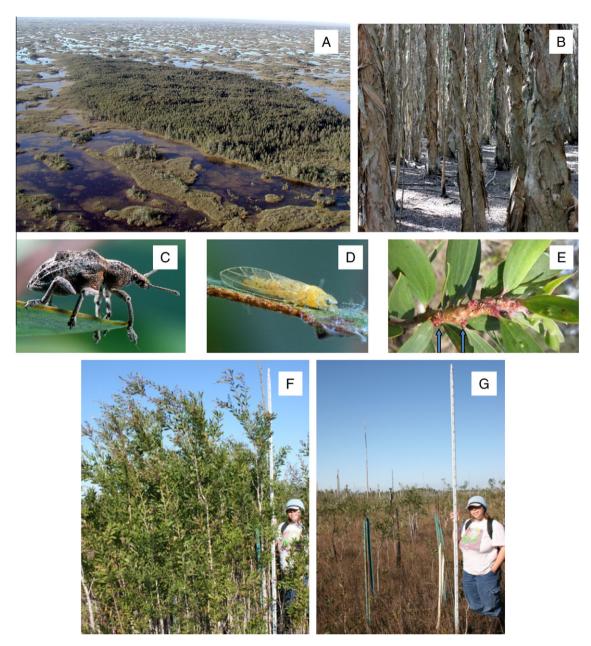


Plate 1. The Australian tree Melaleuca quinquenervia invades wetlands of the Florida Everglades (A), where trees displace native species. Melaleuca monocultures lack native understory plants (B). Three species have been introduced to help suppress melaleuca: the weevil Oxyops vitiosa (C), the psyllid Boreioglycaspis melaleucae (D), and the stem galling midge Lophodiplosis trifida (E). Herbivory from these insects has greatly reduced flowering, seedling recruitment, and growth, as demonstrated by an insecticide exclusion trial in Florida after the establishment of these insects. Trees treated with insecticides to exclude these agents (F) grew rapidly from 2003 to 2008, but untreated trees exposed to the effects of herbivory were markedly stunted (G). Photo credits: Fraçoise Laroche, South Florida Water Management District (A); Paul Pratt, USDA/ARS (B and E); and Steve Asmus, USDA/ARS (C and D); Phil Tipping, USDA/ARS (F and G).

pennisi, and *Spathius agrili*) from China that attack this borer were collected, screened for host-specificity, released, and recovered (Bauer et al., 2007; Duan et al., unpublished data) and their impact is presently being evaluated.

A second invasive tree-killing invasive beetle, the great spruce bark beetle (*Dendroctonus micans*), is a Siberian species that has spread west to the UK and south to Turkey since the 19th century. As the beetle expanded its range, it apparently outpaced the spread of its specialized natural enemies, leading to serious outbreaks in Western Europe and the Caucasus region, causing widespread mortality of spruce (*Picea* spp.) (Grégoire, 1988). In Western Europe damage occurred most often in plantations, but in Georgia and northeastern Turkey the beetle seriously affected natural stands of oriental spruce (*Picea orientalis*), a tree of high regional

ecological significance that stabilizes steep slopes (Kobachidze, 1967; Grégoire, 1988). A host-specific predatory beetle, *Rhizophagus grandis*, associated with low, stable populations of *D. micans* in Siberia was released in Georgia, Turkey, and Western Europe, and significantly lowered spruce beetle populations and tree mortality in most locations (Fielding and Evans, 1997).

2.2.1.2. Sucking insects. High densities of invasive Hemiptera can devitalize and even kill their hosts. In temperate forests, an invasive adelgid and a cypress aphid have had such effects. Hemlock woolly adelgid (Adelges tsugae) spread in the USA from its point of invasion in 1951 in Virginia south to Georgia and north to Maine. South of Massachusetts, it caused high levels of mortality of eastern hemlock (Tsuga canadensis) and Carolina hemlock (Tsuga caro-

liniana) and affected hemlock-dependent organisms in the Appalachian Mts. (Evans, 2002), where eastern hemlock is the only species whose canopy produces dense shade. In the Delaware River Basin, hemlock deaths affected stream insects (Snyder et al., 2002), brook trout (Ross et al., 2003), and various understory plants (Eschtruth et al., 2006), with species requiring cooler temperatures being replaced by ones adapted to warmer habitats. Because native predators were unable to prevent adelgid outbreaks (Montgomery and Lyon, 1996), predators were sought in the adelgid's native range, including coccinellids from China and Japan, and Laricobius (Derodontidae) beetles from western North America, China, and Japan. The coccinellids Sasajiscymnus tsugae, Scymnus ningshanensis, and Scymnus sinuanodulus and the derodontid Laricobius nigrinus have been introduced to the eastern USA (Cheah and McClure, 1998: McClure et al., 2000: Lu and Montgomery, 2001: Montgomery et al., 2002; Zilahi-Balogh et al., 2002, 2003). Laricobius nigrinus established well at 13 of 22 release sites (Mausel, unpublished data) and spread in the Appalachian Mts. Biological control investigations continue on this invasive insect.

In Africa, the invasive cypress aphid (*Cinara cupressivora*) spread rapidly from Malawi in 1986 into neighboring countries and attacked native Cupressaceae trees, causing dieback (Watson et al., 1999; Day, R., et al., 2003). Heavy infestations killed mature trees and, in Malawi, threatened the endemic, endangered Mulanje cedar, *Widdringtonia whytei*, on the Mt. Mulanje massif (Baylis et al., 2007). In Kenya, it attacked *Juniperus procera*, an important native tree in many watersheds. By 2003, the aphid invaded Colombia, Brazil, Bolivia, and Chile, attacking various Cupressaceae, including the Cordilleran cypress *Austrocedrus chilensis* (Baldini et al., 2007). Release of the braconid *Pauesia juniperorum* in Africa began in 1994 and its establishment was confirmed in Malawi and Kenya by 1996 (Day, R., et al., 2003). Aphid densities declined in the mid 1990s in Africa, and this decline was associated at least in part with this parasitoid (Kairo, personal communication).

2.2.1.3. Defoliating sawflies and moths. From the last decades of the 19th century to the early 20th century, a series of European sawflies and moths invaded North American forests. The invasive sawflies especially affected pine and spruce. White pine (*Pinus strobus*), abundant in many northeastern forests, was commonly defoliated after 1910 by *Diprion similis*. Spruce (*Picea* spp.) forests in eastern Canada and Maine were extensively defoliated in the 1930s by *Gilpinia hercyniae* (Van Driesche et al., 1996). Biological control programs suppressed both species, *D. similis* being controlled by introduced parasitoids (especially *Monodontomerus dentipes*) (McGugan and Coppel, 1962) and *G. hercyniae* by a highly specific nucleopolyhedrovirus probably introduced accidentally along with European parasitoids (Magasi and Syme, 1984).

During this same period, several invasive European moths invaded North American forests, affecting especially larch and oak. Larch forests were defoliated by the coleophorid *Coleophora laricella*, which first infested eastern larch (*Larix laricina*) (1886–1950s) and later western larch (*Larix occidentalis*) (1957–1980s). Better records of impact exist for the western infestation. There, defoliation was principally of new growth (Ryan, 1990). Repeated, intense infestations reduced terminal and radial growth, and caused some tree mortality. Biodiversity impacts on species other than larch were not studied. Two introduced parasitoids, the braconid *Agathis pumila* and the eulophid *Chrysocharis laricinellae*, controlled the pest in both eastern (Webb and Quednau, 1971) and western North America (Ryan, 1990), and subsequent outbreaks have been small, brief, and infrequent. In Oregon, larval densities declined >98% following biological control introductions (Ryan, 1990).

Also in this era, oaks (*Quercus* spp.) were affected by the geometrid *Operophtera brumata* (winter moth) and the lymantriid *L. dispar* (gypsy moth). Winter moth was first reported in 1949 in

Nova Scotia, but later invaded British Columbia and then Massachusetts. Winter moth outbreaks defoliated oaks repeatedly, causing up to 50% mortality. Winter moth's populations were suppressed in both Nova Scotia (Embree, 1971) and British Columbia (Embree and Otvos, 1984) by introduced parasitoids, mainly the tachinid fly *Cyzenis albicans*. In Nova Scotia, outbreaks collapsed within 3 years once *C. albicans* parasitism reached 10% (Embree, 1971). Moth densities dropped from >1000/tree in 1954 to <1/tree in 1963.

In Massachusetts by the late 1800s, the gypsy moth began defoliating oaks and other hardwoods over an ever increasing area (McManus and McIntyre, 1981) - stripping 10.7 million ha of forest in the USA in the outbreak of 1980-1982 and 5.8 million ha in the outbreak of 1989-1991 (USDA Forest Service website). In many areas, oak mortality caused stand composition to shift toward sweet birch, black gum, red maple, and tulip poplar (Muzika and Gottschalk, 1995). Control programs directed against gypsy moth with aerial forest pesticide applications (1950-1980) endangered more than a dozen species of rare eastern butterflies and moths (Schweitzer et al., 2010). Many natural enemies were introduced against gypsy moth starting in 1905 (Doane and McManus, 1981) and continuing to 2000 (Ertle, personal communication). These efforts achieved widespread establishment of one predator and six parasitoids (Van Driesche et al., 1996), and the accidental establishment of one fungus, Entomophaga maimaiga. Apart from the periphery of the infested area, no large-scale pesticide applications have been necessary to control gypsy moth since 1989, likely due to fungal epizootics (Webb et al., 1999) and the introduced parasitoids. One introduced generalist parasitoid, the tachinid C. concinnata, attacks many native moths and is held to be a threat to native silkmoths (Boettner et al., 2000) and a variety of other native lepidopterans (Schweitzer et al., 2010).

2.2.1.4. Gall makers. Gall insects are generally not considered important as determinants of plant density but an appreciation of the strength of their impacts is developing based on their successful use as biological control agents (Muniappan and McFadyen, 2005) and the damage that some invasive gall makers have caused to native plants (e.g., Gramling, 2005). In temperate forests, the invasive chestnut gall wasp (Dryocosmus kuriphilus) damaged native trees in Asia, North America, and Europe. This Chinese species invaded Japan (1940s), Korea (1950s), the USA (1970s), and Italy (Quacchia et al., 2008). In all invaded regions, it caused significant damage to native Castanea species, galling shoots, reducing tree vigor, preventing flowering, and killing trees (Kato and Hijii, 1997; Cooper and Rieske, 2007). In Japan and southern Europe, Castanea species are an important component of native forests, providing food for wildlife, bee forage, soil improvement, and slope stabilization in mountains (Howes, 1979; Thomas et al., 1992; Quacchia et al., 2008). In the USA, D. kuriphilus threatened to retard the recovery program for American chestnut (Castanea dentata) in Appalachian and New England forests (where chestnut was previously devastated by the introduced fungus Cryphonectria parasitica [Cooper and Rieske, 2007]). The Chinese parasitoid Torymus sinensis reduced galling to non-pest levels in Japan (Moriya et al., 2003) and the USA (Cooper and Rieske, 2007). Its release in Italy (Quacchia et al., 2008) is too recent to evaluate.

2.2.2. Invasive plants

Many weeds have invaded temperate forests and their number, area of infestation, and importance are increasing. However, only a few have been targets for biological control. Here we discuss four projects (a vine, an herb, and two trees) that are under way in North America but have not yet controlled their targets. Assessing the value to native biodiversity of such projects is limited by the general lack of pre-release studies on damage to native flora and

fauna from invasive plants (Morin et al., 2009), in part, because such effects develop slowly over long periods of time.

2.2.2.1. Mile-a-minute weed. Persicaria perfoliata, a spiny annual vine of Asian origin, developed extensive monocultures in disturbed open areas in the mid-Atlantic region of the USA after its invasion into Pennsylvania in the1930s (Hough-Goldstein et al., 2008). It inhibited both commercial reforestation and natural forest regeneration and interfered with the recreational use of natural areas. It reduced the quality of wildlife habitat and out-competed native plants, presumably due to its early germination, rapid growth, and ability to climb over other plants (Wu et al., 2002). A host-specific Asian weevil, Rhinoncomimus latipes, was released and established at sites throughout the range of mile-a-minute weed (Hough-Goldstein et al., 2009). At release sites, spring densities of the plant declined by 75% within 2–3 years, compared to no change at control sites. Benefits to native biodiversity, as mile-a-minute weed densities continue to decline, are being monitored.

2.2.2.2. Tree of heaven. The Chinese tree Ailanthus alitissima has invaded 41 of the contiguous 48 US states, where it often out-competes native pioneer plants due to its ability to survive harsh conditions, sprout from cut stumps, and produce large number of seeds. It also affects vegetation through the release of allelochemicals (Voigt and Mergen, 1962). Significant funding was allocated annually to control the weed in national and state parks, but these efforts had limited effect. A classical biological control program against tree of heaven was initiated in 2004 with the weevil Eucryptorrhynchus brandti, which causes mortality of A. altissima in China (Ding et al., 2006). Of 28 plant species examined in nochoice feeding tests in quarantine, adult feeding occurred only on corkwood (Leitneria floridiana) and choice tests demonstrated a strong preference for A. altissima (Kok et al., 2008). Tests assessing development of immature stages and egg maturation by adults are underway.

2.2.2.3. Garlic mustard. Alliaria petiolata is a cool-season, shade-tolerant, obligate biennial herb that invades forests. First detected in New York in 1868 (Nuzzo, 1993), it has since spread across the northern USA (Blossey et al., 2001a). Dense garlic mustard stands can displace native herbaceous plants and may harm insects, ground-nesting birds, reptiles, amphibians, and rodents (Blossey et al., 2001a). It is an oviposition sink for one native butterfly, Pieris virginiensis (Porter, 1994), whose larvae are unable to complete development on garlic mustard (Courant et al., 1994) and is a partial egg sink for a second species, Pieris oleracea, which shows variation in its ability to develop successfully on the plant (Keeler and Chew, 2008). Garlic mustard also damages the mycorrhizal associations essential to many native plants (Callaway et al., 2008). Surveys of its associated insects in Europe identified four weevils as potential biological control agents (Blossey et al., 2001a). Demographic modeling (Davis et al., 2006) suggested that the root-feeding weevil Ceutorhynchus scrobicollis is the most promising species, but that stem-mining or seed-feeding weevils may also be needed. Advanced host-specificity testing is underway for C. scrobicollis and preliminary work is in progress for the three other species.

2.2.2.4. Chinese tallow tree. Triadica sebifera is a tree native to China that is invading warm temperate forests and meadows of the southeastern USA (Richard et al., 2004; Pattison and Mack, 2007). Its seeds are readily dispersed by birds and it has the potential to spread throughout most of eastern North America. A biological control program against Chinese tallow tree has been initiated to evaluate the impacts of seed-feeding herbivore insects, with the goal of restricting dispersal. A leaf-rolling weevil, Hetera-poderopsis bicallosicollis, was found to be host-specific to the plant

(Wang et al., 2009) and has been imported from China into quarantine for evaluation.

2.3. Subtropical and tropical forests

2.3.1. Invasive insects

Tropical or subtropical forests have greater biodiversity than temperate area forests and thus more species potentially at risk from invasive insects. However, effects of invasions may go unrecognized because inventories of tropical biotas are more preliminary than those of temperature communities. We discuss nine examples.

2.3.1.1. Bromeliad weevil. Metamasius callizona is native to Mexico and Guatemala. Its larvae mine meristematic tissue of bromeliads and kill plants. Importation of infested bromeliads from Veracruz, Mexico brought this weevil to Florida around 1989 (Frank and Thomas, 1994), where it now severely damages eight of Florida's native epiphytic bromeliads in their natural habitats and is a risk factor for four other rare bromeliads. Most of these are state-listed endangered or threatened taxa, two of which (Tillandsia fasciculata and *T. utriculata*) are listed expressly because of the threats posed by this weevil. One bromeliad (Tillandsia simulata) is endemic to Florida. Also at risk are at least 14 invertebrates that live in pools of water impounded in leaf axils of these bromeliads and might disappear if their hosts were lost (Frank and Fish, 2008). Biological control of this weevil has been started with the discovery and release of a specialized tachinid (Lixadmontia franki) (Frank and Cave, 2005; Cave, 2008). Evaluations of establishment of the fly are in progress.

2.3.1.2. Lobate lac scale in the Florida everglades. Paratachardina pseudolobata, an invasive Asian scale found in Florida and the Bahamas, attacks 95 of 155 native south Florida woody plants and 67 of 107 woody plants from the Bahamas. It caused death in 12 species (Pemberton, unpublished data). Scale infestations on four rare plant species, monitored for 2 years in Florida, remained high and caused progressive branch die back on Eugenia confusa and Payonia paludicola, but declined on Amorpha herbaceae var. crenulata and Dalea carthagenensis (Liu and Pemberton, unpublished data). Comparison of naturally infested wild Psychotria nervosa with plants from which scales were excluded, showed that scales reduced fruit set (Liu and Pemberton, unpublished data). Surveys for natural enemies in India and Sri Lanka, the scale's presumed native range (Pemberton, 2003), found two Indian parasitoids that oviposited in Floridian lac scales, but eggs were unable to complete development because of encapsulation by the host (Schroer and Pemberton, 2007). Subsequently, molecular analysis of the lac scales in Florida showed the Floridian populations of lac scales are a distinct, undescribed species (Schroer et al., 2008), most likely native to Malaysia (Pemberton, unpublished data). Parasitoid collections from this region are planned.

2.3.1.3. Invasive scales affecting Australian forests. In Australia, several exotic scales attacking crops also damaged forest plants, but this impact was largely overlooked. These invasive coccids weakened native plants and their honeydew benefitted invasive ants, compromising native butterfly/ant mutualisms. Biological control of these coccids for crop protection benefitted native forest species. Examples below are drawn from Waterhouse and Sands (2001) and personal observations (Sands, unpublished data)

White wax scale (*Ceroplastes destructor*) from South Africa invaded Australia before 1893 (Zeck, 1932) and became a pest of fruit crops and ornamentals (Snowball, 1969). It also damaged native plants along roads, in woodlands, rainforests, and other natural ecosystems in temperate and subtropical eastern Australia. Principal hosts along roadsides were *Bursaria spinosa* and *Dodonaea*

triquetra; in woodlands, Pittosporum undulatum; and in rainforests, Auranticarpa rhombifolia, Syzigium spp. (Waterhouse and Sands, 2001), Hymenosporum flavum, Syzigium australe, and Acmena smithii. Heavy infestations produced copious honeydew, which nourished invasive tramp ants and sooty molds. Two relatively hostspecific encyrtid parasitoids of white wax scale, Anicetus communis and A. nyasicus, were collected from South Africa (Snowball, 1969) and provided complete biological control (Sands et al., 1986). Since the 1970s, C. destructor has been uncommon in natural plant communities. Infested native plants in the national parks of southeastern Queensland regained vigor and the abundance of honeydew and sooty mold declined. Exotic ants (e.g., Pheiodole megacephala) declined in abundance on native plants formerly infested with wax scales. As a consequence, several native ants have reappeared on plants from which they were formerly excluded. This has benefitted some native, ant-tended lycaenids, such as Hypochrysops miskini and Pseudodipsas cephenes, which require the ant Anonychomyma gilberti, a species now more abundant following biological control of white wax scale. Similarly, in some eucalypt woodlands, the indigenous ant Papyrius nitidus, which attends larvae and pupae of the lycaenid Hypochrysops ignitus, was displaced by exotic ants foraging on the butterfly's scale-infested host plants. However, very few P. nitidus have returned to these plants following biological control of white wax scale, and both the butterfly and its attendant ant continue to be scarce.

Pink wax scale, *Ceroplastes rubens*, of African origin (Quin and Gullan, 1998), became a pest of citrus and ornamentals in Australia, but also fed on rainforest plants such as *Ficus* spp., *Syzygium* spp., *Shefflera actinophylla*, *Pittosporum* spp. (Smith et al., 1997), *Waterhousea floribunda*, and *Drypetes deplanchei*. It is most abundant in exposed locations. The introduced encyrtid *Anicetus beneficus* controlled the scale on citrus and on some of its native hosts (e.g., *S. actinophylla*), but not on others (e.g., *Syzygium* spp.). Heavy infestations in natural settings are now rare, except in forest regeneration plantings. Densities on forest plants no longer attract numerous exotic ants, and thus no longer affect indigenous rainforest species in eastern Australia or Norfolk Island (another formerly infested area).

2.3.2. Invasive plants

Invasive plants have been highly damaging in subtropical and tropical forest areas, although as with temperate forest pests, long-term monitoring and careful study of actual damage to native flora have been sporadic. Some examples of invasive plants with developing or completed biological control projects and their benefits follow. Examples occurring on islands (e.g., *Miconia calvescens* in Tahiti) are treated in another section ("Ocean Island Communities").

2.3.2.1. Mist flower in New Zealand. Ageratina riparia, native to Central America and Mexico, became a significant weed in northern New Zealand by the 1990s. Damage was greatest in river corridors and disturbed areas in native forests, but the weed also infested wetlands and forest margins (Anonymous, 1999). Mist flower was controlled biologically in Hawaii in the 1980s (Trujillo, 2005), and studies suggested the program could be transferred to New Zealand (Morin et al., 1997). The white smut fungus Entyloma ageratinae and the gall fly Procecidochares alani were released in New Zealand in 1998 and 2001, respectively, and the fungus in particular established and spread rapidly. Results were monitored from 1998 to 2008 (Barton et al., 2007; Landcare Research, unpublished data). The percentage of live leaves infected with fungus reached 60% within 2 years, maximum plant height declined significantly, and in heavy infestations the mean percentage cover of mist flower declined from 81% to 1.5%. By 2008, the gall fly reached a mean density of 0.6 galls/stem and the fungus remained abundant (averaging 55% leaf infection) despite mist flower cover remaining below 1%. As mist flower declined, the species richness and the mean percentage cover of native plants at forest sites increased, with no increase in other invasive plants, except a weak response by African club moss (*Selaginella kraussiana*). Many plants colonizing plots were native mid- or late-successional shrubs or trees. Concurrent with mist flower reduction, the number of reports of threats to rare endemic plants from mist flower decreased, indicating substantial benefit to native forests (Barton et al., 2007).

2.3.2.2. Cat's claw creeper in Australia. Macfadyena unguis-cati, native to South America, is an environmental weed of the Australian subtropical eastern seaboard, the southeastern USA, South Africa, India, Mauritius, and New Zealand (Downey and Turnbull, 2007). In forested riparian areas, this vine kills mature trees, causes bank destabilization, and is an intense root competitor with native plants (Downey and Turnbull, 2007). Ground-level vines smother low vegetation and prevent recruitment of native plants (Floyd, 1989). Biological control is under way in both South Africa and Australia. In Australia, the tingid Carvalhotingis visenda and the pyralid Hypocosmia pyrochroma have been released (Dhileepan et al., 2007a,b) and impacts are being monitored.

2.3.2.3. Brazilian peppertree in Florida. Schinus terebinthifolius is an invasive South American woody plant that rapidly colonizes both disturbed areas and intact natural habitats in over 20 countries in subtropical regions (Cuda et al., 2006). In Florida, this plant displaced populations of the rare or threatened plants Jacquemontia reclinata (Convolvulaceae) and Remirea maritima (Cyperaceae) (Austin, personal observations, in Langeland et al., 2008) and invaded the nesting habitat of the Florida state-listed gopher tortoise (Gopherus polyphemus). Insects attacking this plant in South America and Florida have been studied as potential biological control agents (Cuda et al., 2006; McKay et al., 2009). Field impact studies in Brazil and host-specificity testing in Brazil and Florida confirmed that a stem-feeding thrips, Pseudophilothrips ichini sensu lato, is a specialist on Brazilian peppertree and the Peruvian peppertree (Schinus molle) (Manrique et al., 2008; Cuda et al., 2009). In 2007. P. ichini sensu lato was recommended for field release, but thrips from different source populations were found to be genetically distinct, and more work is required to confirm population-level specificity before release.

2.3.2.4. Air potato in the southeastern USA. Dioscorea bulbifera is an herbaceous vine native to Old World tropics, which is now established along the Gulf of Mexico from Florida to Texas (Wheeler et al., 2007), where it climbs on and out-competes native vegetation for limited resources (Gordon et al., 1999; Wheeler et al., 2007). It occurred in 12 of 48 habitats surveyed in southern Florida (Gann et al., 2001), where it aggressively exploits disturbed sites, such as forest canopies damaged by hurricanes, and impedes the reestablishment of native species (Gordon et al., 1999). A potential biological control agent, the Nepalese leaf beetle *Lilioceris* nr. *impressa*, was found to be both damaging to the target weed and safe to native plants. A petition for its release has recently been approved (Pemberton, 2009).

2.3.2.5. Madeira vine in Australia. The South American plant Anredera cordifolia is a serious environmental weed in coastal areas of eastern Australia, Hawaii, New Zealand, and South Africa (Vivian-Smith et al., 2007). In Australia, Madeira vine threatens several endangered communities (Vivian-Smith et al., 2007) and is detrimental to riparian vegetation, tall open forest, and damp sclerophyll forests (Floyd, 1989). Its prolific growth and ability to climb 40 m into tree canopies has caused mature trees to collapse under the weight of its vines. Australia and South Africa are coordinating

biological control efforts. The leaf beetles *Plectonycha correntina* (Cagnotti et al., 2007) and *Phenrica* sp. (van der Westhuizen, 2006) have narrow host ranges, but neither insect has yet been released in either country. Further exploration in South America to find additional agents is planned.

2.4. Grasslands

As a biome, grasslands of the world have been extensively altered by people for farming and grazing, and a lower percentage of this biome has been conserved than of forests or wetlands. In many areas, grazing by livestock has changed plant competition in favor of invasive, grazing-tolerant exotic species, which themselves have often affected the fire regime, further promoting invasion (Brooks et al., 2004). Only in recent decades have the rich biotas of grasslands been identified as important subjects for conservation and restoration. Invasive plants, including both accidental introductions and grasses sown to increase forage on wildlands, have affected native grassland biodiversity worldwide. While introduced forage species have not been selected by governments for biological control, many invasive forbs have been, particularly in the USA, Canada, Chile, and Australia.

2.4.1. American grasslands

Biological control of invasive species affecting US grasslands was begun in order to restore productivity of rangelands infested with European forbs. At least 14 species were targeted for biological control (Nechols et al., 1995; Julien and Griffiths, 1998; Van Driesche et al., 2002), including knapweeds (Centaurea spp.), yellow starthistle (Centaurea solstitialis), tansy ragwort (Senecio jacobaea), St. Johnswort (Hypericum perforatum), spurges (Euphorbia spp.), and thistles (especially Cirsium arvense). The first successful weed biological control project in the USA was in the 1950s against St. Johnswort, an invader in natural grasslands in California. Its successful biological control (Huffaker and Kennett, 1959; McCaffrey et al., 1995) reduced St. Johnswort density by 99% in open areas, with the plant only persisting is shaded areas. The subsequent recovery of other vegetation was monitored in detail and showed that native grasses such as California oatgrass (Danthonia californica) and blue wild rye (Elymus glaucus) increased in abundance (Huffaker and Kennett, 1959). California oatgrass is used in restoration of degraded California coastal prairies (Buisson et al., 2006).

Another early project resulted in successful biological control of tansy ragwort, reducing the infestation by 93% in many areas (McEvoy et al., 1991; Turner and McEvoy, 1995; Coombs et al., 1996). In coastal prairies in Oregon, biological control of tansy ragwort led to a 40% increase of the rare hairy stemmed-checkered mallow (Sidalcea hirtipes) (Gruber and Whytemare, 1997). In California, biological control of tansy ragwort allowed the return of natural plants in coastal prairies, such as California poppy (Eschscholzia californica), beach strawberry (Fragaria chiloensis), Alameda County thistle (Cirsium quercetorum), coyote mint (Monardella villosa), and coyotebrush (Baccharis pilularis) (Pemberton and Turner, 1990). The recent release of one of the two tansy ragwort control agents, the arctiid Tyria jacobaeae in Montana, USA (Markin and Littlefield, 2008) raised concerns of potential non-target effects to Senecio triangularis (McEvoy et al., 2008).

Successful biological control is developing for yellow starthistle (Gutierrez et al., 2005; Pitcairn et al., 2005; Smith, 2007; Woods et al., 2009), leafy spurge (*Euphorbia esula*) (Cornett et al., 2006; Cline et al., 2008; Samuel et al., 2008), and diffuse (*Centaurea diffusa*) and spotted (*Centaurea stoebe*) knapweeds (Smith, 2004; Story et al., 2000, 2006, 2008; Seastedt et al., 2007; Myers et al., 2009). The value of these programs to the native biota of invaded grasslands requires further documentation. Harris (1988) noted that use of herbicides to suppress leafy spurge threatened popula-

tions of the western prairie fringed orchid (*Plantathera praeclara*) in North Dakota. Introduction of *Aphthona* flea beetles as biological control agents, plus targeted sheep or goat grazing, reduced leafy spurge to acceptable levels in parts of Montana and North Dakota and allowed native forage species to increase (Lym, 2005; Cline et al., 2008; Samuel et al., 2008). Integration of biological control agents with herbicide applications allowed recovery of the threatened orchid (Lym, 2005). A related native *Euphorbia* species (*E. robusta*), predicted to be within the host range of one of the leafy spurge control agents (*Aphthona nigriscutis*), was attacked in the field. However, this plant's population increased in the presence of this agent because of lowered competition pressure from leafy spurge, which declined due to biological control (Baker and Webber, 2008).

Solanum viarum (tropical soda apple), native to South America, has invaded 400,000 ha of grasslands and other natural habitats in Florida since 1988 (Medal et al., 2008). Surveys for biocontrol agents in South America started in 1994 and a leaf beetle, *Gratiana boliviana*, was released in Florida, Georgia, Alabama, and Texas in 2003–2008 (Diaz et al., 2008; Medal, unpublished data). The beetle established at most release sites in Florida, and caused 30–100% defoliation and reduced fruiting to virtually zero. Beetles dispersed 1.6–16.0 km/year and non-target effects were not observed during 6 years of monitoring (Medal et al., 2008). Petitions for release in the USA of three additional agents (the weevil *Anthonomus tenebrosus* and the leaf beetles *Metriona elatior* and *Gratiana graminea*) are under review.

Gorse (Ulex europaeus) is an invasive shrub that invades grasslands and other communities in the USA (Markin et al., 1995), New Zealand (Hill and Gourlay, 2002), Australia (Ireson et al., 2003), and Chile (Norambuena et al., 2007), where it forms dense stands that compete with native plants. In the USA, gorse replaced desirable vegetation in salt spray meadows (Coombs et al., 2004). In coastal areas in Oregon, gorse reduced habitat for the plant Lycopodium inundatum and the butterfly Speyeria zerene var. hippolyta (Pratt et al., 2003), and threatened the rare plant Phaceila argentea (Coombs, personal communication). In Chile, mechanical removal of gorse caused damage to Berberis negeriana plants (Norambuena. personal communication) in the Yani Hills (37°S), which is one of few areas still supporting this endemic barberry (Gomez et al., 2008). Gorse biological control is currently being attempted with ten agents in six countries or islands (Julien and Griffiths, 1998; Hill et al., 2008). The spider mite Tetranychus lintearius reduced gorse dry matter 36% in Tasmania (Davies et al., 2007), and shoot size and flowering 37% and 82%, respectively, in Hawaii (Hill et al., 2008; Markin, unpublished data). In Chile, late summer mite outbreaks reduced regrowth and flowering (Norambuena et al., 2007), and the seed weevil Exapion ulicis reduced seed production and seedling establishment (Norambuena, 1995; Norambuena and Piper, 2000).

Also in Chile, invasive blackberries (*Rubus* spp.) infested 5 million ha of arable or grazing land (Oehrens, 1977). The rust *Phragmidium violaceum*, was introduced for its control, became widely established within 3 years, and reduced the size and competitiveness of *Rubus*. Partial control of blackberry allowed an increase in the native pioneer shrub *Aristotelia chilensis*, a species important in limiting erosion (Oehrens, 1977; Oehrens and Gonzalez, 1977).

In the eastern USA, grasslands have been invaded by several weeds, some of which are the same as discussed above. Invaders unique to this area include two species of European swallow-worts, *Vincetoxicum nigrum* and *Vincetoxicum rossicum*, which are lethal oviposition sinks for monarch butterflies (*Danaus plexippus*) (Casagrande and Dacey, 2007). At high densities, they also lower site quality for nesting grasslands birds (DiTomaso et al., 2005). In Vermont, black swallow-wort (*V. nigrum*) threatens the endangered Jessop's milkvetch, *Astragalus robbinsii* (DiTomaso et al., 2005).

Surveys in Europe identified several potential biological control agents, which were collected for further study in US quarantine.

2.4.2. Australian grasslands

Grasslands constitute a high proportion of the Australian landscape. Consequently, plants invasive in this biome are of special importance, and many exotic plants are of concern across several regions of the country, including dry and wet tropical savannahs in Queensland and the Northern Territory. Lantana, Lantana camara (Verbenaceae), is perhaps the oldest target for biocontrol in Australia (Day, M.D., et al., 2003). It is found along the east coast and the Great Dividing Range from Cape York to southern New South Wales. Where abundant, lantana blocks plant succession, displaces native species, changes structure and floristics of natural communities, and decreases species richness (Dav. M.D., et al., 2003; Dav. and Zalucki, 2009). It has also proven an extremely difficult biological control target because of its high genetic diversity caused by multiple (horticultural) introductions and subsequent hybridization (Swarbrick et al., 1995; Day, M.D., et al., 2003). Thirty biocontrol agents have been released in Australia over nearly a century. Several agents are effective in some areas (Day and Zalucki, 2009), but the plant remains at pest levels in most locations.

In the dry tropics of Queensland, rubber vine (*Cryptostegia grandiflora*) from Madagascar invaded forested areas along rivers and later spread into adjacent grasslands and savanna (Tomley, 1995). In riparian areas, dense stands killed eucalyptus trees and reduced native biodiversity. Successful biological control in drought-prone areas has been achieved by the rust *Maravalia cryptostegiae* (Evans and Tomley, 1994; Vogler and Lindsay, 2002) and, to a lesser extent, the pyralid moth *Euclasta whalleyi* (Mo et al., 2000), allowing increased growth of local grass species.

In central Queensland, *Parthenium hysterophorus* has invaded large areas and displaced native perennial grasses. Its domination of seedbanks suggests it has substantial impact on native plant communities (Navie et al., 2004). While nine biological control agents failed to establish or were ineffective, two species, the leaf-feeding beetle *Zygogramma bicolorata* and the stem-galling moth *Epiblema strenuana*, have controlled the plant in some areas (Dhileepan, 2003).

2.5. Deserts and arid shrublands

Several invaders of deserts and arid shrublands have been targets of weed biological control, including cacti (especially *Opuntia* spp.), saltcedars (*Tamarix* spp.), tumbleweeds (*Salsola* spp.), mesquite (*Prosopis* spp.), and hakea (*Hakea sericea*).

Opuntia cacti (native to the Neotropics), became widely invasive in dry regions of the Old World, especially Australia and South Africa, where native cacti do not occur. Invasive Opuntia cacti were successfully suppressed with biological control in both of these areas (Dodd, 1940; Zimmermann et al., 2009), but projects either were organized to restore rangeland productivity or remove cacti from parks, and effects on biodiversity were rarely investigated. Nevertheless, dense stands of cacti that dominated large regions in countries such as South Africa certainly caused declines in abundance of native species (Hoffmann, personal communication). Introduction of the Opuntia-feeding pyralid moth Cactoblastis cactorum into the Caribbean region in the 1950s for pasture enhancement, however, damaged - but did not extirpate - some native cacti species on Nevis and St. Kitts (Pemberton and Liu, 2007). This introduction added this pyralid moth into a region near the center of Opuntia biodiversity where it had not formerly occurred, without a non-target risk assessment.

Saltcedars (*Tamarix ramosissima*, other *Tamarix* species, and hybrids) infest about 650,000 ha in western North America, primarily along desert rivers where they displace native willow (*Salix* spp.)

and cottonwood (Populus spp.) (Zavaleta, 2000). Fifty rare or endangered species of amphibians, arthropods, birds, fish, reptiles, or plants occur in saltcedar-infested areas (DeLoach and Tracv. 1997). Saltcedar has degraded their habitats through displacement of native vegetation (Lovich et al., 1998), change to physical conditions (Busch and Smith, 1993), loss of food resources (Kennedy and Hobbie, 2004), effects on aquatic invertebrates (Bailey et al., 2001), and water depletion (Davenport et al., 1982). Effects on endangered fish include the loss of shallow sandbar habitat for the Rio Grande silvery minnow (Hybognathus amarus), loss of low velocity nursery habitat for the Colorado pikeminnow (Ptychocheilus lucius), and reduction in water levels in springs supporting desert pupfish (Cyprinodon macularius). In some areas, rare fish were found for the first time only after saltcedar was removed (DeLoach et al., 2000: Kennedy et al., 2005). Introduced leaf-feeding beetles (Diorhabda spp.) have defoliated hundreds of thousands of hectares, and are beginning to kill saltcedar trees (Hudgeons et al., 2007; Carruthers et al., 2008; Deloach et al., 2008; Tracy and Robbins, 2009). If saltcedar tree deaths from biological control agents become widespread, this should significantly improve wildlife habitat, as physical removal of saltcedar is documented to benefit native plants (Lovich and Bainbridge, 1999), reptiles (Bateman et al., 2008), fishes (Kennedy et al., 2005), and birds (Longland and Dudley, 2008). Field assessments of potential non-target risk to native Frankenia species, the taxon identified as potentially at risk from Diorhabda feeding, found no significant impacts under field "worst case" conditions (Dudley and Kazmer, 2005).

Drought and disturbance promote invasion of tumbleweeds (*Salsola* spp.) in western North American, causing competition with desirable vegetation (Allen, 1982; Brandt and Rickard, 1994; Hrusa and Gaskin, 2008). Tumbleweeds infest large areas in the Carrizo Plain National Monument in southern California (Smith, personal communication). In Death Valley National Park, USA, *Salsola paulsenii* competes with endangered Eureka Dunes evening primrose (*Oenothera californica* ssp. *eurekensis*) and Eureka Valley dune grass (*Swallenia alexandrae*) (Smith, personal communication). A mite (*Aceria salsolae*) specific to the genus *Salsola* has been discovered that reduces plant size by 80% (Smith et al., 2009) and permission for its release has been requested (Smith, 2005).

In Australia,invasive mesquite shrubs (*Prosopis* spp.) form extensive, dense groves in some arid and semi-arid rangelands, excluding ground cover, especially in the more mesic areas (van Klinken et al., 2006). In the Pilbara region, the spread of mesquite has been reduced through biological control with a leaf-tying moth (a gelechiid, *Evippe* sp. #1) (van Klinken and Campbell, 2009; van Klinken, unpublished data).

In South Africa, the Australian shrub hakea invaded the Southwestern Cape and displaced fynbos (a floristic kingdom with 8700 plant species, 68% endemic) over large areas (Richardson et al., 1997; Holmes et al., 2000). The introduction of five herbivorous insects attacking the flowers, fruits, and stems (Gordon, 1999; Gordon, personal communication), together with the pathogen *Colletotrichum gloeosporioides*, caused considerable damage and mortality to *H. sericea*. This complemented mechanical control, resulting in substantial decline of hakea in invaded areas (Esler et al., 2010), benefiting fynbos communities.

2.6. Coastal areas and sand dunes

Dunes, coastal shrublands and tidal wetlands are fragile ecosystems that are under threat from invasive plants in many countries. In some instances, exotic plant species were deliberately introduced or extensively planted to stabilize and limit movement of wind-blown sand. The negative consequences of these invasive plants for native biodiversity were eventually recognized and triggered the implementation of biological control programs in several

countries. Here we discuss four plants and one insect that have seriously affected these early successional habitats: *Chrysanthemoides monilifera* ssp. rotundata, Asparagus asparagoides, Spartina alterniflora, Acacia cyclops, and the insect Jamella australiae.

Chrysanthemoides monilifera ssp. rotundata (bitou bush), a woody shrub native to South Africa, has invaded over 80% of the coastline of New South Wales, Australia, in the past century (Thomas and Leys, 2002). Dense stands dominate sand dunes, coastal grasslands, heath, woodlands, and rainforests and drastically alter these communities. Bitou bush out-competes native plants, particularly at the seedling stage (Ens and French, 2008), by exuding allelochemicals (Ens et al., 2009). Its invasion severely alters vegetation structure and richness (Mason and French, 2008) and produces a darker, cooler, moister environment that changes invertebrate assemblages (Lindsay and French, 2006). Bitou bush is the dominant threat to 150 native plant species in 24 coastal plant communities in New South Wales (DEC, 2006). A biological control program initiated in 1987 has established four insect species (Downey et al., 2007), of which the geometrid tip moth Comostolopsis germana and the seed fly Mesoclanis polana are widespread and significantly suppress flowering and seed production (Holtkamp, 2002; Edwards et al., 2009). Modeling suggests, however, that the introduction of foliage-feeding agents will be needed for complete control of the weed (Kriticos et al., 2004).

Asparagus asparagoides (bridal creeper) from South Africa is a major invader of coastal vegetation in temperate Australia (Morin et al., 2006a). It also occurs in inland shrublands, woodlands, and forests. It smothers areas of natural vegetation and severely limits growth of many native plants. In Western Australia, bridal creeperinfested areas had only half as many native plant species as nearby non-invaded areas (Turner et al., 2008a). It is also a threat to four endangered ecological communities in New South Wales - littoral rainforest, river-flat eucalypt forest on coastal floodplains, swampoak floodplain forest, and subtropical coastal floodplain forest (Downey, 2006) and to many native plants, including the orchid Pterostylis arenicola (Sorensen and Jusaitis, 1995) and the shrub Pimelea spicata (Willis et al., 2003). Three biological control agents have been released against bridal creeper in Australia: an undescribed leafhopper (previously referred to as *Zygina* sp.), the rust fungus Puccinia myrsiphylli, and the leaf beetle Crioceris sp. (Morin and Edwards, 2006; Morin et al., 2006b). The leafhopper and rust fungus have established widely across temperate Australia; the rust appears to be the more effective agent (Morin et al., unpublished data; Turner et al., 2008b). However, dead but persistent rhizomes and tubers in the soil after effective biological control remain an impediment to quick recolonization by native plants (Turner et al., 2006).

Spartina alterniflora (and the foliosa × alterniflora hybrid), S. anglica, S. patens, and S. densiflora (collectively, "cordgrasses") have invaded intertidal wetlands on the Pacific coast of the USA (Ayres et al., 2004), transforming mudflats into salt marshes and eliminating critical habitat for birds, fish and shellfish. Cordgrasses also outcompete native salt marsh plants in the upper intertidal zone (Daehler and Strong, 1996). In Oregon, cordgrasses invaded native stands of D. cespitosa and Scirpus maritimus (Callaway and Josselyn, 1992). In San Francisco Bay, invasion by a Spartina foliosa × alterniflora hybrid reduced macrofaunal species richness and increased dominance of subsurface detritus feeders (Neira et al., 2007). In 2000, the planthopper *Prokelisia marginata* (a common herbivore of S. alterniflora in its eastern USA native range) was introduced to Willapa Bay, Washington, to complement chemical and mechanical control (Grevstad et al., 2003). There, the planthopper reduced above-ground biomass of S. alterniflora by 50% soon after release (Grevstad et al., 2003). One S. alterniflora genotype, however, is tolerant to planthopper feeding and may gradually increase as vulnerable genotypes are suppressed (Garcia-Rossi et al., 2003).

A meta-analysis of effectiveness of cordgrass management techniques concluded that the planthopper was highly effective against *S. anglica* (causing 92.5% reduction in density), but was less so against *S. alterniflora* (18.4% reduction in density) (Roberts and Pullin, 2008).

Acacia cyclops (rooikrans) is an Australian species invasive in coastal dune systems of South Africa, where it forms impenetrable stands in the lowlands fynbos of the Eastern and Western Cape Provinces (Richardson et al., 1996). Rooikrans is among three invasive species that are most threatening to native plant biodiversity in the Cape Peninsula (Higgins et al., 1999). However, because the plant is valued in some contexts, biological control agents were selected that attack plant reproduction, rather than cause death. The introduced seed-feeding weevil Melanterius cf servulus damages up to 90% of the seeds (Impson et al., 2004) but has been slow to increase and disperse. The flower-galling midge Dasineura dielsi more rapidly increased in density and spread (Adair, 2005; Impson et al., 2008), but its impact has been more variable between sites and years.

The flatid insect *J. australiae*, native to north Queensland, invaded south Queensland, where it killed native *Pandanus tectorius* trees, an ecologically important coastal species. An egg parasitoid, *Aphanomerus* sp., moved from north to south Queensland, brought the pest under control (Smith and Smith, 2000).

2.7. Oceanic island communities

Island biodiversity is not high, but often consists of endemic species derived from mainland immigrants. Many plants imported to islands for human use have escaped cultivation and become damaging environmental pests. Accidental insect introductions to islands frequently occur because of agriculture, movement of plants, trade, and tourism. About 20 exotic arthropod species invade the Hawaii Islands each year, and many of these become serious pests on native vegetation (Messing and Wright, 2006). Several human-assisted invasions have been linked to the species extinctions (Elton, 1958). Here we discuss the role of biological control in conserving the endemic biodiversity of islands.

2.7.1. Invasive insects attacking native plants

Invasive herbivorous insects are frequently transported to islands on introduced ornamentals or crop plants or they may hitch-hike unnoticed on cargo. Invasive insects can be highly damaging to native plants as well as to native invertebrate and vertebrate species that depend of them for refuge or food. Biological control of exotic insects attacking native flora is an extension of the use of biological control against arthropod pests of crops and ornamental plants, and its use is increasing.

2.7.1.1. Scales. A large number of scales, especially in the Diaspididae and Coccidae, have been moved around the world through the transportation of plants. Small founding population size frequently results in key parasitoids of invading scales being unrepresented in the material transported to new locations, allowing scale population explosions. Examples of the biodiversity impacts of invasive scales on tropical forests were discussed above for Australia. The same processes also occur on islands.

In 1991, the South American scale *Orthezia insignis* was recorded on St. Helena in the south Atlantic (Fowler, 2004). By 1992, the scale was killing endangered, endemic gumwood trees (*Commidendrum robustum*) (Fowler, 2004). The lady beetle *Hyperaspis pantherina* was released in 1993 (Booth et al., 1995; Fowler, 2004) and by 1995 scale density had decreased by 97% and tree death due to scale infestations no longer occurred (Fowler, 2004). Biological control of *O. insignis* saved the remnant gumwood stands, and removed the scale's threat to the three other *Commidendrum* spp. (Fowler,

2004), a genus which comprises a significant part of St. Helena's remaining native trees (Cronk, 1989). Additional conservation benefits included prevention of damage to the newly restored Millenium Forest (St. Helena National Trust, 2009), prevention of harm to natural regeneration of *Commidendrum rugosum* on 50% of St. Helena (Fowler, 2004; Anonymous, 2009; Joint Nature Conservation Committee, 2009), and the preservation of several endemic weevils (e.g., *Nesiotes* spp.) associated with gumwoods (Pearce-Kelly, personal communication in Booth et al., 1995; Joint Nature Conservation Committee, 2009).

Icerya scales (Margarodidae) have invaded various islands - the Galápagos, the Seychelles, Ascension, and various parts of Micronesia – and attacked native plants. The best known Icerya species is the polyphagous cottony cushion scale, Icerya purchasi, which in addition to being a major citrus pest (Hale, 1970; Ben-Dov et al., 2009), damages many native island plants, often ones with restricted distributions (Cronk, 1980; Causton, 2001; Causton et al., 2006). The scale also indirectly threatens rare insects that depend on these plants for food or shelter (e.g., Roque-Albelo, 2003). It has been repeatedly controlled by the specialized predatory coccinellid Rodolia cardinalis (Caltagirone and Doutt, 1989), which develops exclusively on monophlebine (Hemiptera: Margarodidae) scales, principally Icerya species (Causton, 2001; Causton et al., 2004). On the Galápagos, I. purchasi attacked 16 threatened plant species, as well as many other native plants (Causton, 2001, 2003). Scale-induced mortality of one rare plant, Darwiniothamnus tenuifolius, was linked to local population extirpations of three moths (Roque-Albelo, 2003). Important mangrove habitats were damaged by heavy scale infestations (Causton, 2003). Rodolia cardinalis was released on ten Galápagos islands in 2002 to protect threatened native plants (Causton et al., 2006; Causton, unpublished data). Exclusion experiments and post-introduction monitoring were conducted on heavily infested stands of white mangrove (Laguncularia racemosa) in Puerto Ayora, Santa Cruz Island, and data showed a marked decrease in scale density within 12 weeks of liberating R. cardinalis (Calderon Alvarez, 2002). More extensive evaluations of the impacts of this predator were begun in 2009. In the South Atlantic, R. cardinalis was released on Ascension Island in 1976 to control cottony cushion scale on ornamental plants (Cronk, 1980). The beetle also provided protection for the rare endemic spurge Euphorbia origanoides, which was suffering population decline due to scale attack (Cronk, 1980; Fowler, 2004). By 1995 scale density on the island was low, and the scale was completely absent on sampled E. origanoides populations, including one population specifically examined by Cronk (1980) (Fowler, unpublished data). Icerya purchasi was also absent on E. origanoides when the plant was re-surveyed in 1997 (Ashmole and Ashmole, 1997) (see Plate 2).

Other species of *Icerya* have threatened island plants, including Icerya seychellarum in the Seychelles and Icerya aegyptiaca on various coral atolls in the western Pacific (Waterhouse, 1993). Icerya seychellarum invaded Aldabra in the Seychelles around 1968 and quickly became damaging (Hill and Newbery, 1980). By the 1980s, native plant species such as Avicennia marina, Euphorbia pyrifolia, Ficus lutea, Scaevola sericea, and the endemic Sideroxylon inerme ssp. cryptophlebium were heavily damaged (Newbery and Hill, 1985; Newbery, 1988; Gery, 1991). The rare native species Maillardia montana and Psychotria pervillei were on the point of extinction from I. sevchellarum and other stresses (Friedmann. 1994). Rodolia chermesina was released on Aldabra in 1989 to control I. seychellarum (Gery, 1991). Monitoring for 5 years following the release of R. chermesina showed reduced scale density and recuperation of the affected plant species (Johnson and Threadgold, 1999; Beaver, personal communication). In the western Pacific, destructive populations of I. aegyptiaca developed on various coral atolls including Kiribati, Federated States of Micronesia, the Mariannas, and Marshall and Wake Islands (Beardsley, 1955; Waterhouse, 1993). Native plants attacked included *Casuarina* equisetifolia, *Calophyllum inophyllum*, and the sand dune plants *Scaevola koenigii* and *Scaevola frutescens* (Manser, 1974; Maddison, 1976). From 1994 to 1999, CSIRO in Australia introduced *Rodolia limbata* into infested western Pacific atolls and within 2 years, control was achieved on atolls of the Federated States of Micronesia, Kiribati and Marshall Islands (Brancatini and Sands, 1997; Sands et al., 1999).

On Guam, an invasive cycad-attacking diaspidid scale, Aulacaspis vasumatsui, destroyed much of the island's native cycad forests. The scale is native to Thailand where it is a minor pest kept at low densities by parasitoids (Tang et al., 1997). In 2003, the scale was detected on ornamental cycads at two of Guam's hotels. It quickly spread into wild populations of Micronesia's endemic cycad. Cycas micronesica, which is the dominant tree-sized plant in Guam's limestone forests and a keystone species of the community. This scale, in combination with two other cycad-feeding invasive species (the lycaenid Chilades pandava and the tineid leafmining moth Erechthias sp. [Moore et al., 2005; Marler and Muniappan, 2006]), caused cycad death rates to reach 60-90% in some areas in 2004-2008. This high mortality led conservationists to place C. micronesica on the IUCN Red List (Marler, 2006). Biological control began after surveys in Guam found no attack of the scale by local parasitoids or predators. The aphelinid parasitoid Coccobius fulvus was introduced in 2005 from Florida (where it had suppressed the target scale) (Weise et al., 2005), but it failed to establish. The coccinellid R. lophanthae was introduced from Hawaii, established widely, and suppressed the scale on mature cycads. It 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, which continued to die at elevated rates. Further biological control introductions, likely of parasitoids, are needed to protect seedlings and secure the future of Guam's cycad limestone forests.

2.7.1.2. Gall wasps. Like scales, galling insects are tightly associated with plants and may be moved with their hosts to new regions. where they may spread to native plants. The plant genus Erythrina has 112 species in tropical or warm temperate regions (Neill, 1988), several of which are on the IUCN Endangered Species List and are threatened by invasion of the gall wasp Quadrastichus erythrinae. In Hawaii, this eulophid wasp devastated stands of the wiliwili tree (Erythrina sandwicensis), causing severe tissue distortion, defoliation, and death (Kim et al., 2004; Yang et al., 2004). The wiliwili tree is an endemic keystone species in lowland Hawaiian forest, one of the most endangered ecosystems in the world (http:// www.hear.org). The invader's area of origin is not certain (Gramling, 2005; Messing et al., 2009), but natural enemies surveys were conducted in Africa, where the parasitoid Eurytoma erythrinae was found attacking Quadrastichus spp. (Gates and Delvare, 2008). This parasitoid was evaluated in quarantine and released in Hawaii. Initial observations showed ready establishment, rapid spread, and high impact of E. erythrinae. A second parasitoid (Aprostocetus sp.) is also under study.

2.7.1.3. Vectors of plant pathogens. Certain invasive insects, especially leafhoppers and aphids, have the potential to introduce or more efficiently vector plant pathogens to native plants. The cicadellid leafhopper Homalodisca vitripennis (glassy-winged sharpshooter) is a polyphagous xylem feeder that vectors the plant pathogenic bacterium Xylella fastidiosa. Native to parts of the USA and Mexico, this leafhopper invaded French Polynesia (in 1999), Hawaii (2004), Easter Island (2005), and the Cook Islands (2007), most likely via the movement of ornamental plants. In the absence of the mymarid egg parasitoid Gonatocerus ashmeadi, dense leafhopper populations developed and retarded plant growth and fruit

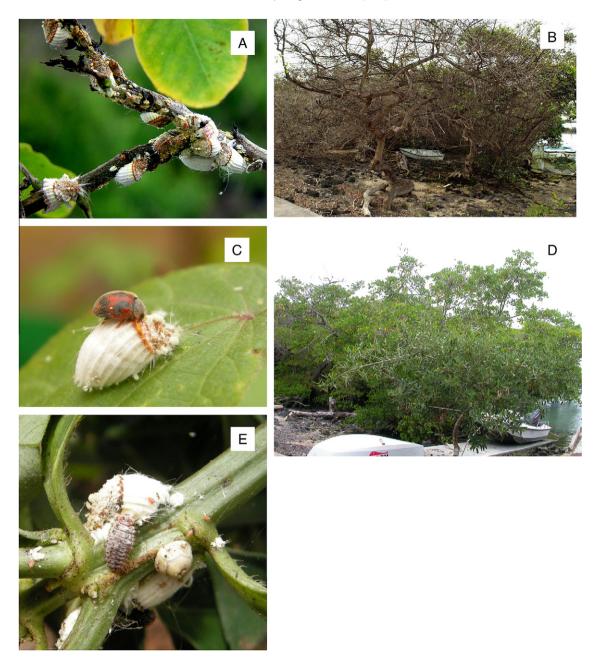


Plate 2. The invasion of the Galápagos National Park by the cottony cushion scale (*Icerya purchasi* Maskell) was highly damaging to a variety of native plants. Prior to the successful biological control of this scale, dense populations developed on white mangrove (*Laguncularia racemosa*) (A), a keystone species in the marine littoral habitat. By 2001, stands of white mangrove along the coast in Puerto Ayora on Santa Cruz island (background of photo B) had been heavily damaged by the scale. The biological control agent *Rodolia cardinalis* (adult – C; larva – E), introduced in 2002, suppressed scale density, allowing for full recovery of affected mangrove stands by 2005, as seen in a subsequent photo (D) of the same location. Photos courtesy of Helmuth Rogg, Charles Darwin Foundation (A), Mark Hoddle, University of California (C and E), Heidi Snell, Visual Escapes.smugmug.com (B), and Charlotte Causton, Charles Darwin Foundation (D).

yields, and produced copious watery excreta (Grandgirard et al., 2006). Nymphs and adult leafhoppers were toxic to some generalist predators, in particular native spiders (Suttle and Hoddle, 2006). Following risk assessment studies (Grandgirard et al., 2007), *G. ashmeadi* was released into French Polynesia and suppressed the leafhopper in all archipelagos within 7–10 months (Grandgirard et al., 2008; Petit et al., 2009). Suppression of leafhopper density protected native spiders and reduced the likelihood of infection of native plants with *X. fastidiosa*.

2.7.2. Invasive plants

Islands have been extensively invaded by introduced plants. Some of these have been subject to weed biological control, especially in Hawaii and New Zealand. Examples from small islands include miconia and gorse.

Miconia calvescens, a small, broad-leafed tree from Central and South America, escaped cultivation and established widely on Pacific islands, including Hawaii and Tahiti. It invaded natural forests and formed dense monospecific stands that were damaging to native vegetation (Meyer and Florence, 1996; Medeiros et al., 1997; Meyer, 1998). The fungus Colletotrichum gloeosporioides forma specialis miconiae from Brazil is specific to M. calvescens (Killgore et al., 1999). It was released in Tahiti in 2000, where it established from sea level to 1400 m and caused partial defoliation of miconia canopy trees in mesic and wet forests. Defoliation reached 47% and this allowed increases in cover and diversity of native vegetation

(Meyer et al., 2008, 2009). The fungus was also introduced into Hawaii, but had little impact, apparently due to higher temperatures. Additional agents, particularly insects, are under investigation (e.g., Seixas et al., 2004; Badenes-Perez et al., 2007).

Gorse is a thorny European shrub introduced into several countries, including Chile, where in the archipelago of Chiloé it became invasive on at least 10 islands (Norambuena et al., 2007). On Chiloé (and associated islands) releases have been made of the seed-feeding brentid *E. ulicis* and the spider mite *T. lintearius*, both of which established on three islands (Norambuena, unpublished data).

3. Protecting resources obtained from natural ecosystems

Many early biological control projects were started to protect resources harvested from wildlands, especially wood, forage, and water. Others were begun to protect the use of rivers for hydroelectric power generation, navigation, or fishing. Most of the species reviewed in the following section were previously discussed in regard to their impacts on biodiversity and here we elaborate further on the economic losses of natural resources caused by these invasive species. Details of their biological control, presented in the previous section, are summarized in Table 1 (insects) or Table 2 (plants). Values given below are in United States dollars.

3.1. Wood products from native forests

Damaging insects can reduce the ability of native forests to yield wood products. Some forest pests are native species, and as such are outside the scope of this article. Also, some invasive insects are serious pests in forest plantations, which are also not covered here, even though many have been successful targets of classical biological control. We restrict our review to invasive species that have reduced the productivity of native forests or increased mortality of key timber species. Most of the examples discussed are from North America, which has both extensive native forests and many invasive forest pests. Other regions have either been less often invaded by pests of native forests, or rely heavily on plantation forestry, whose biological control projects are outside the scope of this article. In North America, five species introduced pine sawfly (D. similis), European spruce sawfly (G. hercyniae), larch casebearer (C. laricella), winter moth (O. brumata), and gypsy moth (L. dispar) – have been wholly or partly controlled with biological control. Two other important biological control projects targeted at emerald ash borer (A. planipennis) and hemlock woolly adelgid (A. tsugae) are in progress (Table 1).

3.1.1. Introduced sawflies and moths

All of the species discussed in this section have been successfully suppressed with biological control in all or part of the invaded range (Table 1). The introduced pine sawfly and European spruce sawfly invaded North America about 1914–1922 (Coppel et al., 1974; Drooz, 1985) and spread widely, attacking pines and spruce, respectively. By 1981, the introduced pine sawfly defoliated 2.2 million ha of pine forests in Virginia and North Carolina (Drooz et al., 1979; Ghent et al., 1982), but caused little tree death. In 1935, European spruce sawfly defoliated 1.5 million ha spruce in the Gaspé Peninsula, New Brunswick, Canada, with high tree mortality in some stands. At its peak, the European spruce sawfly infested 363,000 km² of forest (see Van Driesche et al., 1996).

Larch casebearer invaded Massachusetts about 1886 and spread into the Canadian maritime provinces and west to British Columbia (Drooz, 1985), tracking larch distributions. In eastern North America, outbreaks occurred from the early 1900s (Felt and Bromely, 1932) through the 1950s (Webb and Quednau, 1971), eventually ceasing due to introduced parasitoids. Outbreaks in Idaho and Ore-

gon occurred from 1957 until larch casebearer was suppressed by natural enemies (Ryan, 1990). Before its biological control, this moth was among the top two pests of western larch (Schmidt et al., 1976). Repeated defoliation of larch in northern Idaho reduced tree growth by 80%, but growth returned to normal after successful biological control (Long, 1988).

Winter moth invaded the Canadian Maritimes in the 1930s and later British Columbia and Massachusetts. This polyphagous species feeds on a great range of deciduous trees, and repeated defoliation causes thin tops, dead branches, and tree death (Drooz, 1985). In Nova Scotia in a 1950s outbreak, damage to Q. rubra was greatest on trees with early bud break (due to better synchrony with the caterpillars), and in the most defoliated plots 40% of oaks died over several years (Embree, 1967). The infestation in eastern Canada peaked in 1954-1956 when it covered 60% of Nova Scotia, killing up to 100% of oaks in areas with greatest defoliation (Cuming, 1961). In 1977, a separate infestation in British Columbia covered 120 km² (Gillespie et al., 1978). A third infestation - in Massachusetts - defoliated 60,325 ha in 2003 (Anonymous, 2004). Damage from winter moth includes loss of oak lumber due to tree death, and loss of quality white pine regeneration in the absence of over story shade (i.e., increased forking from more oviposition by Pissodes strobi) (Embree, 1965).

Gypsy moth was imported to Massachusetts by an amateur entomologist in 1869 and escaped. It established and spread throughout many oak-dominated forests of the northeastern USA, eventually reaching Ontario, Michigan, and Virginia. The most intense defoliation occurred in 1911–1922 in New England (Houston, 1981) and the largest outbreaks were in 1980–1982 and 1989–1991 (10.7 and 5.8 million ha defoliated, respectively) (USDA Forest Service website). Depending on tree health and site conditions, defoliated oaks suffered varying degrees of mortality. In 1911–1931 in eastern New England, 35% of oaks in poor condition died from a single defoliation, while 7% of trees in good condition did so (Campbell and Sloan, 1977). Deaths occurred up to several years after defoliation.

3.1.2. Tree-killing borers and adelgids

Biological control projects against the two species discussed here are in progress (Table 1). By 2009, the emerald ash borer (Coleop.: Buprestidae) infested eleven US states and several Canadian provinces (http://www.emeraldashborer.info/). Infestations are currently expanding annually by 16-32 km due to adult flight, and new infestations are being created by long distance movement of fire wood or live infested trees. In Michigan, where 18.2 million cubic meters (7.7 billion board feet) of ash timber are harvested annually (USDA APHIS, 2007), more than 30 million ash (Fraxinus spp.) trees had been killed (Poland and McCullough, 2006; EAB, 2009). The loss to date in Michigan is estimated at 42.5 million cubic meters of wood (18 million board feet) valued at \$4-9 million (Michigan Department of Natural Resources website). Many Michigan stands have lost up to 100% of their large ash trees. Nationally, US timberlands contain an estimated 8 billion ash trees, 7.5% by volume of all hardwoods. Thus future losses, given spread to the pest's ecological limits, could increase greatly (see www. aphis.usda.gov/plantpest/emerald_ash_borer).

Hemlock woolly adelgid invaded the USA from Japan (Havill et al., 2006) and has widely degraded eastern hemlock forests. Lumbering of eastern hemlock is modest due to its lower wood quality compared to other softwoods, but about 1.2 million cubic meters of wood (500 million board feet) are harvested annually (Brisbin et al., 1970; Howard et al., 2000). Hemlock bark is used for mulch (Howard et al., 2000) and its wood for log home construction, pulpwood, and composite materials (Winn and Araman, 2005). Since the 1950s, hemlock woolly adelgid has spread over 20–30% of eastern hemlock's range. In New Jersey in 1984 (before hemlock woolly

Table 1 Status of classical biological control programs for invasive insects mentioned in the text.

	Target species	Host plant	Nature of Impacts (X) ^a			Outcome (∕′) ^b		/ ∕/) ^b	Location/comments	References
			Biodiv.	Prod.	Eco. Sv.	С	P	IP		
1	Adelges tsugae Annand (hemlock woolly adelgid)	Hemlock	X	X	X			100	Eastern USA	Evans (2002), Cheah and McClure (1998), McClure et al. (2000), Lu and Montgomery (2001), Montgomery et al. (2002), Zilahi-Balogh et al. (2002, 2003)
2	Agrilus planipennis (emerald ash borer)	Ash	X	Χ				~	Agents confirmed established and impact being evaluated	Bauer et al. (2007)
3	Aulacaspis yasumatsui (cycad scale)	Cycads	X				~		Guam; control effective only on mature plants, not seedlings	Ross Miller and Aubrey Moore (personal communication)
4	Cinara cupressivora (cypress aphid)	Cupressaceae	X	X			∠ 1		East/South Africa 1 – control due to several factors	,
5	Ceroplastes destructor (white wax scale)	Diverse plants	X			_			Queensland, Australia	Sands et al. (1986)
6	Ceroplastes rubens (pink wax scale)	Diverse plants	X				1		Queensland, Australia 1 – controlled on some native hosts but not others	Waterhouse and Sands (2001)
7	Coleophora laricella (larch case bearer)	Larch		X		1			North America	Webb and Quednau (1971), Ryan (1990), Long (1988)
8	Dendroctonus micans (spruce beetle)	Spruce	X1	X2		1			1 – Caucasus region 2 – Western Europe and Caucasus region	Grégoire (1988), Fielding and Evans (1997)
9	Diprion similis (pine sawfly)	Pine		X		1			North America	McGugan and Coppel (1962)
10	Dryocosmus kuriphilus (chestnut gall wasp)	Chestnut	X	X		1		1 2	1 – Japan, USA 2 – Europe	Moriya et al. (2003), Cooper and Rieske (2007), Quacchia et al. (2008)
11	Gilpinia hercyniae (European spruce sawfly)	Spruce		Χ					North America	Magasi and Syme (1984)
12	Homalodisca vitripennis (glassy-winged sharpshooter)	Diverse plants	X			1		1 2	1 - complete control in Tahiti2 - project in progress in California,but control developing slowly	Grandgirard et al. (2008), Petit et al. (2009)
13	Icerya aegyptiaca	Diverse plants	X			1			Kiribati, Federated States of Micronesia, the Mariannas, Marshall, and Wake Islands	Brancatini and Sands (1997), Sands et al. (1999)
14	Icerya purchasi (cottony cushion scale)	Diverse plants	X			1		1 2	 1 - control complete on Ascension Island 2 - control being evaluated in Galapagos, but appears effective 	Causton et al. (2006), Causton (unpublished data), Calderon Alvarez (2002), Fowler (unpublished data), Ashmole and Ashmole (1997)
15	Icerya seychellarum	Diverse plants	X			1			Seychelles	Johnson and Threadgold (1999), Beaver (personal communication)
16	Jamella australiae	Pandanus tectorius	X			1			Southern Queensland, Australia	Smith and Smith (2000)
17	Lymantria dispar (gypsy moth)	Oak	X	X			~		Successful control in the core infested area of New England	Van Driesche et al. (1996, see pp. 85–88), Webb et al. (1999), Gillock and Hain (2001)
18	Metamasius callizona (bromeliad weevil)	bromeliads	X					1	Florida (USA)	Frank and Cave (2005), Cave (2008)
19	Operophtera brumata (winter moth)	Oak		X		1		1 2	1 – Nova Scotia, British Columbia 2 – Massachusetts	Embree (1971), Embree and Otvos (1984)
20	Paratachardina pseudolobata (lobate lac scale)	Diverse plants	X					~	Florida (USA)	Pemberton (2003), Schroer et al. (2008)
21	Quadrastichus erythrinae (erythrina gall wasp)	Erythrina spp.	X					1	Hawaii; agents being evaluated; one released and established	Gates and Delvare (2008)

 ^a Biodiv. (effects on biodiversity), Prod. (loss of products produced by natural ecosystems), Eco. Sv. (loss of ecosystem services).
 ^b Degree of control achieved: C – complete control, P – partial control, IP – in progress.

Table 2Invasive plants status of classical biological control programs for invasive plants mentioned in the text.

	Target species Nature of impa		mpacts Outcome ((∠) ^b	Location/comments	References	
		Biodiv.	Prod.	Eco. Sv.	С	P	IP		
1	Acacia cyclops (rooikrans)	Χ					1	Coastal dunes of South Africa; 90% seed damage	Impson et al. (2004)
2	Acacia longifolia (long leafed wattle)	X	X	X				South Africa, especially the fynbos region	Dennill et al. (1999), Moran et al. (2005)
3	Acacia nilotica subsp. indica (prickly acacia)	X	X	X			1	Australia, especially Mitchell grass downs	Radford et al. (2001), Palmer et al. (2007)
4	Acacia pycnantha (golden wattle)	X	X	X	1			South Africa, especially the fynbos region	Moran et al. (2005)
5	Acacia saligna (Port Jackson willow)	X	X	X				South Africa, especially the fynbos region	Moran et al. (2005)
6	Ageratina riparia (mist flower)	X			1			Hawaii and New Zealand	Trujillo (2005), Barton et al. (2007), Landcare Research (unpublished data)
7	Ailanthus alitissima (tree of heaven)	X						Eastern USA	Ding et al. (2006), Kok et al. (2008)
8	Alliaria petiolate (garlic mustard)	X					_	Northeast and north central USA; agents under evaluation	Blossey et al. (2001a)
9	Alternanthera philoxeriodes (alligator weed)	X	X		~	~		USA, Australia, New Zealand, and China; floating infestations generally controlled but terrestrial populations on edges of water bodies still a problem	Coulson (1977), Julien (1981), Julien and Griffiths (1998), Sainty et al. (1998)
10	Arundo donax (giant reed)	X	X	Χ			1	Southwestern USA, especially Texas; first agents (gall wasp and armored scale) released in 2009	Tracey and DeLoach (1998); Goolsby (personal communication)
11	Asparagus asparagoides (bridal creeper)	Χ					~	Coastal areas of temperate Australia; little control to date	Morin et al. (unpublished data), Turner et al. (2008b)
12	Anredera cordifolia (Madeira vine)	Χ					1	Coastal eastern Australia, South Africa; agent surveys underway	Cagnotti et al. (2007), van der Westhuizen (2006)
13	* '	X			1			South Africa	McConnachie et al. (2004)
14	Centaurea diffusa and C. stoebe (diffuse and spotted knapweeds)	Χ	Χ			~		Western North America	Smith (2004), Story et al. (2000, 2006, 2008), Seastedt et al. (2007), Myers et al. (2009)
15	Centaurea solstitialis (yellow starthistle)	X	X				~	Western North America; plant densities have not yet been reduced in most locations, but declines have occurred in Oregon and California	Gutierrez et al. (2005), Smith (2007), Pitcairn et al. (2005)
16	Chromolaena odorata (Siam weed)		X	X		1	~ 2	1 – significant control in Papua New Guinea and East Timor of one biotype 2 – no control yet of second biotype in South Africa	Day and Bofeng (2007), Zachariades et al. (2009), Day (personal communication)
17	Chrysanthemoides monilifera ssp. Rotundata (bitou bush)	Χ				"		Coastline of New South Wales, Australia; flowering and seed production widely suppressed	Holtkamp (2002), Edwards et al. (2009)
18	Cryptostegia grandiflora (rubber vine)	X	Χ			~		Dry tropics of Australia; control achieved in droughty areas	Evans and Tomley (1994), Mo et al. (2000), Vogler and Lindsay (2002)
19	Dioscorea bulbifera (air potato)	Χ					1	Florida, USA; petition for agent release approved	Pemberton (2009)
20		Х	X		1	~		Southern USA, Mexico, East and West Africa, India, and other warm regions; complete control in many tropical areas; partial control in cooler regions	Beshir and Bennett (1985), Center et al. (2002), Coetzee et al. (2009)
21	Euphorbia esula (leafy spurge)	Χ	X			~		Northern prairies of North America; complete control in many areas	Cornett et al. (2006), Cline et al. (2008), Samuel et al. (2008)
22	Fallopia japonica (Japanese knotweed)	X					1	United States and United Kingdom; first agent approved for release	Shaw et al. (2009)
23	Hakea sericea (hakea)	X			~			South Africa (fybos of Cape region); control achieved in combination with mechanical control	Gordon (1999), Gordon (personal communication), Esler et al. (2010)
24	Hydrilla verticillata (hydrilla)	Χ				~	~	Southern USA; partial control in a few areas	Balciunas et al. (2002), Grodowitz (personal communication)

(continued on next page)

Table 2 (continued)

	Target species Nature of impacts $(X)^a$		cts	Outcome (✓) ^b			Location/comments	References	
		Biodiv.	Prod.	Eco. Sv.	С	P	IP		
25	Hypericum perforatum (St. Johnswort)	X	Х		1	1 2		Western USA, Australia; 1 – compete control in the USA 2 – partial control in Australia	Huffaker and Kennett (1959), McCaffrey et al. (1995), Briese (1997)
26	Lantana camara (lantana)	X	X	X				Northern and eastern Australia; limited success in a few areas	Day and Zalucki (2009)
27	Lygodium microphyllum (Old World climbing fern)	X		X			/	Southern Florida, USA; control is developing at release sites	Boughton and Pemberton (2009)
28	Lythrum salicaria (purple loosestrife)	X				/		Northern USA and adjacent areas of Canada; control in some areas	Blossey et al. (2001b), Landis et al. (2003), Denoth and Myers (2005), Grevstad (2006)
29	Macfadyena unguis-cati (cats claw)	X						South Africa, Australia	Dhileepan et al. (2007a,b)
30	Melaleuca quinquenervia (melaleuca)	X		X				Southern Florida, USA; control very effective in combination with mechanical and chemical control of mature plants	Pratt et al. (2005), Center et al. (2007), Rayamajhi et al. (2007, 2008, 2009), Tipping et al. (2008, 2009)
31	Miconia calvescens (miconia)	X		X		1	∠ 2	1 – partial control in Tahiti 2 – no control yet in Hawaii	Meyer et al. (2008, 2009), Seixas et al. (2004), Badenes- Perez et al. (2007)
32	Mimosa pigra (mimosa)	X				/		Northern Australian wetlands; seed production reduced and stands retreating at edges	Heard and Paynter (2009)
33	Opuntia stricta (prickly pear cactus)	X	X					Australia, South Africa	Dodd (1940)
34	Parthenium hysterophorus (parthenium weed)	X	X					Central Queensland, Australia; control achieved in some areas	Dhileepan (2003)
35	Persicaria perfoliate (mile-a-minute weed)	X					_	Eastern USA	Hough-Goldstein et al. (2009)
36	Pistia stratiotes (water lettuce)	X	X		1			Papua New Guinea, Australia; several regions in Africa; and warm parts of North America	Harley et al. (1990), Mbati and Neuenschwander (2005); Ajuonu and Neuenschwander (2003), Neuenschwander et al. (2009), Dray and Center (1992)
37	Prosopis spp. (mesquite)	X	X			1		arid parts of Australia; control achieved in the Pilbara region	van Klinken and Campbell (2009), van Klinken (unpublished data)
38	Rubus spp. (blackberries)	X						Chile; reduction in size and competitiveness of plants	Oehrens (1977), Oehrens and Gonzalez (1977)
39	Salsola spp. (tumble weeds)	X	X					Western USA, especially California	Smith et al. (2009), Smith (2005)
40	Salvinia molesta (giant salvinia)	X	Х					Australia, Papua New Guinea, parts of the USA, and parts of Africa, especially the Congo basin	Room et al. (1981), Thomas and Room (1986a), Mbati and Neuenschwander (2005), Diop and Hill (2009), Julien et al. (2009)
41	Schinus terebinthifolius (Brazilian peppertree)	X					/	Florida, USA; agents under evaluation	Manrique et al. (2008), Cuda et al. (2009)
42		X	Χ		1			Western USA	McEvoy et al. (1991), Turner and McEvoy (1995), Coombs et al. (1996), Pemberton and Turner (1990)
43	Sesbania punicea (sesbania)	X	X		1			South Africa, especially the fynbos region	Hoffmann and Moran (1998)
44	Solanum viarum (tropical soda apple)	X						South eastern USA; control achieved at release sites; agent spreading	Medal et al. (2008)
45	Spartina alterniflora (cordgrass)	X				~		Esturaries of Washington state, USA; widespread reduction of biomass by 50%	Grevstad et al. (2003), Roberts and Pullin (2008)
46	Tamarix ramosissima (saltcedar)	X		X			/	Western USA; control developing around release sites	Hudgeons et al. (2007), Carruthers et al. (2008), Deloach et al. (2008), Tracy and Robbins (2009)
47	Triadica sebifera (Chinese tallow tree)							South eastern USA; agents under evaluation	Wang et al. (2009)
48	Ulex europaeus (gorse)	X	Х	X				Chile, Oregon (USA), Tasmania, Hawaii, New Zealand; some impact in Chile, Hawaii and Tasmania	Norambuena (1995), Norambuena and Piper (2000), Davies et al. (2007), Norambuena et al. (2007), Hill et al. (2008)
49	Vincetoxicum nigrum; Vincetoxicum rossicum	X					-	Northeastern USA; surveys for agents in progress	,

a Biodiv. (effects on biodiversity), Prod. (loss of products produced by natural ecosystems), Eco. Sv. (loss of ecosystem services).
 b Degree of control achieved: C – complete control, P – partial control, IP – in progress.

adelgid), hemlock was the dominant tree on nearly 8000 ha, but in 1994 (after adelgid invasion), 44% of these trees had experienced moderate to severe defoliation, and 9% were dead (Royle and Lathrop, 1997). In Connecticut in 1998, all hemlocks in 7 of 8 stands were infested and over 90% suffered at least 50% foliar loss (Orwig and Foster, 1998).

3.2. Forage from natural grasslands

Invasive plants can reduce the "carrying capacity" (stock supported per ha) of natural grasslands by (1) lowering the quantity or quality of forage, (2) plant toxicity or repellency, or (3) conversion of grasslands to other vegetation.

3.2.1. Reduction of forage production

Desirable forage species in native grasslands may be displaced by less palatable invasive plants, especially when grasslands are over-grazed. Grasslands of the western USA have been extensively invaded by toxic or thorny forbs from Europe. More than 300 invasive plants on US rangelands collectively cause an estimated \$2 billion in annual losses (DiTomaso, 2000). Many of the most important of these are exotic forbs that have been targets of classical biological control (Skinner et al., 2000), such as yellow starthistle, spotted knapweed, leafy spurge, and Russian knapweed (*Acroptilon repens*). Before biological control-induced change, these plants infested, respectively, 8, 3, 1.0, and 0.6 million ha in the USA (Lajeunesse et al., 1999; Duncan, 2001).

In California, moderate infestations of yellow starthistle (20-31% total vegetation) reduced carrying capacity for cattle 10-15%, and heavier infestations reduced forage up to 50% (Connor, 2003). Although ruminants can digest immature plants, spines on flower heads deter late season grazing (Sheley et al., 1999). In western Montana, spotted knapweed infestations reduced production of the dominant native forage (Pseudoroegneria spicata) up to 88% (Watson and Renney, 1974), while diffuse knapweed infestations in British Columbia reduced forage up to 90% (Harris and Cranston, 1979: Strang et al., 1979). Annual losses from both knapweeds were \$600,000 in Oregon and \$0.9-2.9 million in Idaho (Maddox. 1979; Roché and Roché, 1988). In Montana, the Dakotas, and Wyoming, leafy spurge caused annual losses of \$40.5 million from reduced forage and control costs (Leitch et al., 1994). Successful biological control of leafy spurge produced direct economic benefits of \$19.1 million annually, and total benefits of \$58.4 million (Bangsund et al., 1999). In California in the late 1940s, St. Johnswort infested 900,000 ha, displacing forage and poisoning cattle. Its successful biological control brought about increases of species with forage value (Huffaker and Kennett, 1959; Goeden, 1978). Economic benefits of St. Johnswort's biological control in the USA were not estimated, but annual benefits in Australia, where control was only partial (McCaffrey et al., 1995; Briese, 1997) exceed \$20.6 million (Paige and Lacey, 2006). In Oregon, biological control of a 1.2 million ha tansy ragwort infestation ended \$5 million in annual losses from reduced pasture productivity and herbicide costs (Coombs et al., 1999).

Australian grasslands have also experienced numerous plant invasions. *Opuntia stricta* infested 25 million ha in the 1920s and 1930s and the infestation was expanding 0.5 million ha/year when the pyralid moth *C. cactorum* was released. Infested land had no economic use (Walton, 2005) until a successful biological control project returned land to productivity due to feeding of the larvae of *C. cactorum*, which facilitated attack by local pathogens in damaged tissues. In the 1980s, Patterson's curse (*Echium plantagineum*), which is not grazed by cows or horses, infested 5.2 million ha in Australia (Briese et al., 2004). Its biological control provided benefits of \$1.2 billion (from 1972 to 2005) (Paige and Lacey, 2006). In 1996, musk thistle (*Carduus nutans*) infested 1.1 million ha of Aus-

tralian grassland (Paige and Lacey, 2006). Its subsequent biological control provided \$81.3 million in benefits (Paige and Lacey, 2006). Biological control of a 2.8 million ha Scotch thistle (*Onopordum* spp.) infestation provided \$18 million in benefits (Paige and Lacey, 2006). For a discussion of the non-target impacts in North America of biological control agents released against thistles that are pests in pastures, see Louda and Potvin (1995), Louda et al. (1997, 2003), Louda (1998), and Rose et al. (2005).

3.2.2. Toxicity or repellency to livestock

Many invasive plants have toxins or structures that directly harm livestock or deter their grazing. Spotted and diffuse knapweeds, yellow starthistle, leafy spurge, Russian knapweed, houndstongue (Cynoglossum officinale), tansy ragwort, and St. Johnswort are all toxic or repellent to livestock (Kingsbury, 1964; DiTomaso, 2000). Leafy spurge latex contains ingenols and macrocyclic diterpenes that are toxic and irritating to cattle, which avoid feeding near leafy spurge (Lym and Kirby, 1987; Hohmann et al., 1997). In Montana, cattle avoided grazing in areas with ten percent or greater leafy spurge cover (Hein and Miller, 1992). Russian knapweed and yellow starthistle contain repin, a sesquiterpene lactone that causes mouth ulcers and brain lesions in horses (Cordy, 1978; Robles et al., 1997). St. Johnswort contains hypericin, which causes symptoms ranging from severe dermatitis to hyperthermia when ingested by sheep or cattle (Bourke and White, 2004). Tansy ragwort and houndstongue contain pyrrolizidine alkaloids poisonous to cattle (Baker et al., 1991). In the 1970s along the Oregon coast, dairy herds suffered 2-10% annual losses due to tansy ragwort poisoning (Coombs et al., 1999). Successful biological control of tansy ragwort has reduced associated animal poisonings (Turner and McEvoy, 1995; Coombs et al., 1999).

3.2.3. Conversion of grasslands to other vegetation

Woody invasive species reduce forage production by converting grasslands to shrublands. For example, prickly acacia (*Acacia nilotica* subsp. *indica*) was introduced into grasslands in western Queensland for livestock shade and as reserve forage in droughts. It now infests 6 million ha (Mackey, 1997), displacing native grass species and causing soil erosion (Johnson, 2004). In areas that are heavily infested, it is often uneconomical to reclaim the land, other than by biological control. Several agents have been introduced, including the moth *Chiasmia assimilis*, which is causing large scale defoliation in coastal areas (Palmer et al., 2007), and the bruchid beetle *Bruchidius sahlbergi*, which is widespread and attacks up to 65% of developing seeds (Radford et al., 2001). However, the problem is not yet resolved and further exploration for agents is occurring in India.

3.3. Water from rivers

In drier areas of the world, invasive plants can be a major threat to water supplies from rivers. Among the species contributing most to water loss are invasive riparian plants such as Australian Acacia and Eucalyptus, northern hemisphere Pinus, Asian Tamarix (saltcedar) (Nagler et al., 2008; van Wilgen et al., 2008), and European Arundo donax (giant reed) (Seawright et al., 2009). Such plants reduce water flow by clogging channels and increase water loses from evapotranspiration. Although the amount of water being lost is debated (Shafroth et al., 2005), Zavaleta (2000) estimated that losses in the western USA from effects of saltcedar on irrigation water, municipal water, hydropower, and flood control were \$133–285 million/year. Similarly, Seawright et al. (2009) estimated that \$4.75 million worth of water could potentially be saved annually through biological control of giant reed in the lower Rio Grande Valley of Texas. In South Africa, plant invasion models showed that up to 58% of the nation's water could be lost if invasive plant populations went uncontrolled (van Wilgen et al., 2008), and a massive campaign ('Working for Water') was created to remove invasive trees from water courses. Other management programs to suppress invasive riparian plants exist in North America, Australia, and the Middle East, principally against giant reed and saltcedar (Bell, 1997; Kelly et al., 1998; Csurhes and Edwards, 1998; Williams and West, 2000).

Although cutting, burning, and herbicide applications are commonly used for immediate removal of invasive woody plants, biological control is a key element for effective programs, to slow spread and prevent re-infestation. This is often achieved by releasing agents that lower seed production and/or seedling survival. In some cases, mature plants may be directly affected by biological control agents, as for example defoliation of *Tamarix* spp. by *Diorhabda* chrysomelids in the USA (Carruthers et al., 2008).

South Africa's struggle to protect its water supplies from invasive woody plants is the clearest example of the threat from such invasive plants and the potential role of biological control. Particularly in the mountains of the Western Cape, invasive Pinus, Acacia, Hakea, and Sesbania have greatly increased the total plant biomass compared to that of the native vegetation, thus increasing water use. This has led to localized reductions of river outflow of 30-80% (van Wilgen et al., 1992; Le Maitre et al., 1996). These invasive trees were imported mainly for use as timber or ornamentals. In most cases, the public wants these uses to continue. Therefore, biological control agents could not be used to kill mature plants. The goal, rather, was to reduce spread outside of cities and forestry plantations by limiting seed production and/or lowering seedling survival. These effects, combined with mechanical removal of mature trees, allowed plant populations to be suppressed in desired areas, without threatening economic and aesthetic uses of these trees in other areas. To date, no success has been achieved against Eucalyptus or Pinus. Biological control, however, has been effective against species of Acacia and Sesbania (Moran et al., 2005), with best success against Acacia longifolia, Acacia saligna, Acacia pycnantha, and Sesbania punicea (Hoffmann and Moran, 1998; Dennill et al., 1999). Before its biological control, A. longifolia was a topranked South African weed. Two biological control agents, the flower-galling pteromalid wasp Trichilogaster acaciaelongifoliae and the seed weevil Melanterius ventralis, reduced seed production of A. longifolia by >95% (Dennill et al., 1999). As existing stands were killed by fires, lack of seed prevented their replacement. Acacia longifolia is concentrated along water courses and in the absence of its biological control, this species would have continued to deplete water resources in many catchments.

Sesbania punicea is a leguminous tree from South America that forms dense bands 20–30 m wide along South African rivers. The impact of the tree on water flow was never quantified but it grows where water is plentiful, suggesting strong demand and high transpiration rates. Three beetle species were introduced for its biological control in the 1970s: *Trichapion lativentre*, a bud feeding apionid; *Rhyssomatus marginatus*, a seed-feeding weevil; and *Neodiplogrammus quadrivittatus*, a stem boring weevil (Hoffmann and Moran, 1991). Collectively they curtailed *S. punicea* reproduction and destroyed existing plants. Plant density declined by >95% in most areas and current levels are not problematic (Hoffmann and Moran, 1998). In many regions, stretches of rivers once clogged with *S. punicea* are again open and free flowing (Hoffmann, personal observations).

3.4. Electricity generation

Production of hydroelectric power depends on reliable water flow. Blockage by invasive plants such as waterhyacinth, water lettuce, and giant salvinia, can create flow shortages (Holm et al., 1969; Rørslett, 2006; Liabunya, 2007). Invasive aquatic plants

can also increase siltation and detritus build-up, reducing the life of reservoirs (Moorhead et al., 1988; Liabunya, 2007). The Jebel Aulia Dam on the White Nile in Sudan, for example, became clogged by waterhyacinth within 10 years of its invasion (Holm et al., 1969; Beshir and Bennett, 1985). A power station on the Waikato River in New Zealand had to be shut down due to a massive infestation by the invasive submersed plant Ceratophyllum demersum (Chapman et al., 1974). Operations of power stations on the Shire River in Malawi were disrupted in the 1990s by floating islands of waterhyacinth, giant salvinia, and water lettuce, which choked intake screens and caused silt build-up at intake ponds. The resulting interruptions in the electrical power supply affected the economy by reducing industrial production (Liabunya, 2007). Similar problems occurred at stations on the Kafue River in Zambia (Chola, 2001) and at Owen Falls in Uganda (Appelgren et al., 2000). Biological control of waterhyacinth, water lettuce, and giant salvinia the weeds most disruptive to electrical power generation in warm regions – has been achieved in many locations (Table 2) and details of the biological control of these species are presented in the previous section on biodiversity.

3.5. Commercial, recreational, or subsistence fishing or hunting

Wildlands are widely used for harvesting wild fish or game species for commerce, recreation, or subsistence consumption. Invasive species, especially plants, can lower the quality of fish or game habitat, reducing this form of human use of wildlands.

3.5.1. Fishing

Damaging effects of invasive plants on commercial or subsistence fishing are well documented. In Benin (Africa), waterhyacinth infestations interfered with the use of nets and destroyed fish breeding grounds, causing annual losses of \$84 million/year (De Groote et al., 2003). After suppression of this invasive plant with biological control, fishing resumed (Ajuonu et al., 2003), and fishermen incomes increased \$30.5 million/year (De Groote et al., 2003). In Kenya, the Lake Victoria fishery in the Winam Gulf, with a net worth of \$83 billion that supports 15 million people (Opande et al., 2004), was reduced when waterhyacinth blocked fish landing spots, destroyed fishing gear, and interfered with water transportation of the catch (Opande et al., 2004). Biological control of waterhyacinth on Lake Victoria restored economic viability to the fishing industry. In Papua New Guinea, infestations of salvinia prevented fishermen from setting fish nets and fouled nets set in open water (Mitchell, 1981). By 1978, salted fish production from infested areas dropped 30%. Biological control of salvinia cleared plant mats (Thomas and Room, 1986a), permitting fishing to return to normal levels. In the Congo, fishing ceased in salvinia- or water lettuce-infested areas, but resumed after there plants were suppressed by biological control (Mbati and Neuenschwander, 2005).

3.5.2. Hunting

Invasive plants affect game hunting in wild areas by changing forage levels and habitat features. In Idaho, areas infested by yellow starthistle were used 33% less than uninfested areas by chukars (*Alectoris chukar*), a popular game bird (Lindbloom et al., 2004). In the western USA, elk (*Cervus elaphus*) hunting is a popular sport carried out in natural habitats that are now widely invaded by plants such as Russian knapweed, St. Johnswort, leafy spurge, yellow starthistle, and knapweeds (Stalling, 1998). In western Montana, areas dominated by spotted knapweed are not used as major feeding areas by elk, which prefer grasses (Kufeld, 1973). Spotted knapweed-infested areas received only 2% as much elk use as areas with bluebunch wheatgrass (*P. spicata*) (Hakim, 1979). Infestation of elk winter range in Montana by spotted knapweed caused an estimated loss of 220 elk (Spoon et al., 1983). At

\$1063 value per animal (Fried et al., 1995), this is an annual loss of \$234,000. Similarly, infestation of rangeland with leafy spurge reduced use from bison (*Bison bison*) 83% and from deer by 70% (Trammell and Butler, 1995). Leafy spurge reduced browsing by big game animals in green ash (*Fraxinus pennsylvanica*)-chokecherry (*Prunus virginiana*) habitat by 32% (Trammell and Butler, 1995). Tansy ragwort has very low palatability to black-tailed deer (*Odocoileus hemionus*) (Dean and Winward, 1974). Biological control projects against spotted knapweed, leafy spurge, and tansy ragwort have been successful in many areas (Table 2).

3.6. Water transport

Aquatic invasive plants infesting navigable waterways can impede boat traffic. Waterhyacinth blocked steamboat traffic on the St. John's River in Florida in the late 1800s (Buker, 1982). During this period, steamboats and other craft were unable to reach docks or pass through navigable channels beneath bridges because of waterhyacinth (Zeiger, 1962). Waterhyacinth also interfered with use of seaplanes in the 1940s (Zeiger, 1962). In developing countries where roads may be non-existent, and local people may depend on small boats for their livelihood, trade, or for access to critical services, such blockages of rivers or lakes can be life-threatening. Salvinia infestations have fouled the propellers of small boats (Abbasi and Nipaney, 1986) and damaged their engines (Mitchell, 1980). On the Sepik River in Papua New Guinea, blockages caused by salvinia and waterhyacinth cut off many people's access to villages, schools, market places, as well as to fishing, hunting and gardening grounds, and to locations of administrative and health services. Some people subsisted on dried coconuts because they could not reach fishing areas, or obtain sago palm, or trade for food. Some villages were abandoned (Thomas and Room, 1986b) but were re-occupied after successful biological control of salvinia (Room and Thomas, 1985). Similarly, villages were abandoned in the Congo when waterways were blocked by waterhyacinth (Mbati and Neuenschwander, 2005). In the 1980s, waterhyacinth prevented navigation on the River Niger (Farri and Boroffice, 1999) and in the 1990s, prevented movement of ferries in and out of the port at Mwanza, Tanzania (Mallya, 1999). From 1995 to 1997, police boats based in Kisumu, Kenya could not operate because waterhyacinth infestations blocked their access to the lake. In this same period, waterhyacinth prevented large vessels that transported goods and people between Kenya, Uganda, and Tanzania from docking at the Kisumu Railway Pier, resulting in substantial economic losses (Mailu et al., 1999). Weed clearance to maintain ship passage for docking at Port Bell, Uganda cost US \$3-5 million from 1994 to 1997 (Mailu, 2001).

3.7. Recreational land use

Invasive plants can impede outdoor recreation. In Nevada (USA), economic costs of invasive plants on wildlife-related recreation were estimated as \$6-12 million/year (Eiswerth et al., 2005). The US National Park Service funds a team in California whose sole function is to remove invasive plants in National Parks. Yellow starthistle, which is toxic to horses (Cordy, 1978), increases the cost of keeping horses for recreation because of the need to keep the weed out of pastures and forage fed to horses. In South Africa, O. stricta invaded a large portion of Kruger National Park, used for game viewing. To remove the aesthetic blemish of dense invasive cacti in an otherwise pristine area, substantial funds were spent on an herbicide program, which ultimately failed (Hoffmann et al., 1998). Subsequently, two introduced biological control agents, the pyralid moth C. cactorum and the cochineal insect Dactylopius opuntiae, reduced the opuntia biomass in the park by >90% (Hoffmann and Moran, 2008).

4. Protecting valuable ecosystem services

In addition to being sources of raw materials for human societies, natural ecosystems perform ecosystem services supporting environmental conditions that are beneficial and sustainable for many species, including humans. Some services are to provide habitat for vertebrate wildlife, protect soils, maintain hydrological, biogeochemical, or fire cycles, and preserve air quality. Some invasive species diminish these services and such changes are often permanent because affected areas are too large or remote for use of pest control approaches other than biological control. Biological control projects against the species discussed below have either been successful or are in progress as discussed above (see also Table 2).

4.1. Maintenance of soils

Invasive species can affect soil attributes, including erosion rate, moisture, salinity, pH, nitrogen availability, tilth, and leaf litter depth. Of these, impacts on erosion, moisture, salinity, and nitrogen levels have been reduced in some instances through biological control of invasive plants and are discussed here.

4.1.1. Soil erosion

Increased rates of soil erosion, often from agriculture or other human use of land, have long been of concern. In general, any change in vegetative cover has potential to change erosion rates. Some accidentally introduced plants accelerate erosion by reducing ground cover, as is the case when grasslands are invaded by shrubs, vines, or forbs. Examples include knapweeds (Lacey et al., 1989; Wilcox et al., 1996) in Montana, and prickly acacia (Mackey, 1997) and rubber vine in Australia (Vogler and Lindsay, 2002). In extreme cases, invasive plants may increase landslides, as does miconia, a shallow rooted tree that replaced native forests on steep slopes in Tahiti (Meyer and Florence, 1996). Conversely, some reductions in soil erosion rates may be biologically undesirable, such as the use of exotic plants to "stabilize" dune systems (e.g., Reckendorf et al., 1985; see also earlier discussions under "Coastal Areas and Sand Dunes"), which harms the unique native biota associated with these high disturbance environments. Restoration of normal erosion rates depends on a return of the habitat to a vegetation cover level similar to that before invasion. Biological control projects are currently making significant progress against knapweeds, rubber vine, and miconia (Table 2).

4.1.2. Increased dryness and salinity

In the southwestern USA, removal of water for irrigation and loss of pulse flooding over river banks (due to dams) have made riparian areas drier and more saline (Glenn and Nagler, 2005). These conditions have been worsened by saltcedar infestations, which are more tolerant of increased groundwater salinity than many local native trees. As local species such as Populus fremontii declined (Pataki et al., 2005; Cleverly et al., 1997), saltcedars expanded their ecological dominance in riparian areas in the region. Saltcedar's high water use further increased groundwater salinity (at sites not immediately adjacent to rivers) (Nagler et al., 2008) and depressed native plant recruitment (Sher et al., 2002). Dryness of soil surfaces under saltcedar increased fires, leading to even higher levels of aridity and salinity (Busch and Smith, 1993). Reversing these outcomes will require substantial reductions in saltcedar coverage. Biological control of saltcedar is emerging, with widespread defoliation occurring at sites where agents have been released (Table 2).

In another case, infestation of yellow starthistle have made soils in some California annual grasslands drier, both to a greater depth and longer in the year, than uninfested areas (Enloe et al., 2004).

Reversal of this condition will also depend on the biological control of the invasive plant. Biological control of yellow starthistle is developing and has been successful in some areas (Table 2).

4.1.3. Changes in fertility

Habitats with low soil fertility, such as the fynbos of South Africa, have experienced increased fertility when invaded by nitrogen-fixing plants. Change in soil fertility may facilitate additional invasions and depress native plant growth. In the fynbos, invasion of several Acacia species has enhanced soil organic matter and nitrogen levels (Stock et al., 1995). In the Riverlands Nature Reserve in the Western Cape, A. saligna stands produced four times the litter fall of pristine fynbos, and acacia litter had twice as much nitrogen per gram as fynbos litter. Levels of nitrogen returned to the soil by the above-ground biomass were 10-fold higher under acacia than fynbos plants (Yelenik et al., 2004). Nitrogen inputs stimulated the growth of invasive native grasses such as Erharta calycina (Yelenik et al., 2004) and promoted invasion by exotic grasses (Holmes and Cowling, 1997). Growth of some fynbos species is reduced under elevated nitrogen (Lamb and Klaussner, 1988). In response to threats posed by A. saligna to fynbos biodiversity and water outflows from infested catchments, A. saligna was controlled with an introduced fungus, Uromycladium tepperianum (Saccado), which lowered tree density 87-98% (Wood and Morris, 2007). Five other invasive Acacia species have also been targets of biological control in South Africa, with considerable success (Moran et al., 2005), especially against A. longifolia and A. pycnantha.

4.2. Maintenance of historical hydrological conditions

Some invasive plants have the capacity to alter hydrological conditions, increasing flood crests or diminishing river outflows. Flooding, while damaging at times to human interests, is necessary to create and maintain natural flood-adapted communities along riparian corridors (e.g., Stromberg et al., 1997). As with fire, flood regimes become ecologically problematic if they depart from historical norms. In this regard, the major factor driving change is physical modification of rivers (channelization, bank stabilization, and damming). However, invasive species may also alter flood regimes. Dense stands of giant reed can increase flooding by several mechanisms, including increased stream sedimentation during non-flood periods in rivers and floodway channels, which can decrease channel depth by more than 1 m (Frandsen and Jackson, 1994). Secondly, flood heights can be increased by reduction in flood water velocity as floods push through dense reed stands. Lower velocity can increase sedimentation during floods, further narrowing and clogging channels (Graf, 1980). Thirdly, piles of loose reeds, lodged against bridges and other structures, can increase over-bank flooding (Frandsen and Jackson, 1994). Similar problems are caused by saltcedar in the southwestern USA, where riparian infestations reduce channel width and depth, increasing frequency and severity of flooding (Graf, 1978, 1980; Blackburn et al., 1982). Biological control against giant reed has been initiated (Tracey and DeLoach, 1998), with a gall wasp and an armored scale first released in the Rio Grande River valley in Texas in 2009 (Goolsby, personal communication).

Another effect of invasive plants in dry areas is to reduce discharge volumes of rivers by using more water than the displaced native vegetation. In South Africa's Western Cape, native *Protea* shrubs were displaced by invasive woody trees. These trees increased plant biomass in the mountain fynbos up to 10-fold (Versfeld and van Wilgen, 1986), decreasing river discharge volumes 30-80% (van Wilgen et al., 1992; Le Maitre et al., 1996). This problem has been reduced through successful biological control of several of the most important invasive species (Moran et al., 2005), in combination with manual clearance.

4.3. Conservation of normal fire regimes

Many plant communities have characteristic fire regimes (seasonality, frequency and intensity) that structure community composition and interspecific interactions. Such fire-mediated relationships can be disrupted if invasive plants change the nature of the available fuels, including quantity, spatial distribution, and ignitability (Brooks et al., 2004). Altered fire regimes can in turn dramatically change community structure, composition, or function. Some invasive plants gain a competitive advantage over native plants by their extreme fire tolerance or quick regrowth after fire, creating a positive feedback between invasion and fire. Biological control can help restore fire regimes to historical norms favorable to native plants and insects. Grasses are the invasive plant group that has most changed fire regimes (Brooks and Pyke, 2001), but they have rarely been biological control targets because many invasive grasses are valued as forage, set abundant seed, and regrow quickly after defoliation. Also, many grass-feeding insects are generalists that could pose non-target risks. However, some specialized insects and plant pathogens of grasses are known and with study more will be discovered. Therefore, it is likely that in the future some of the projects against invasive grasses that have been suggested will be carried out. Currently only a few species of grass (e.g., A. donax and Panicum maximum in the USA and Nassella spp. in Australia) are targets of on-going biocontrol projects (Goolsby and Moran, 2009). Here we discuss four fire-altering invasive plants - Chromolaena odorata, melaleuca, Old World climbing fern, and gorse - that are targets of biological control projects (Table 2).

Chromolaena odorata is a Neotropical shrub that has become widely invasive in the Old World. In areas with a distinct dry season, *C. odorata* increases the fire hazard because its dry pithy stems and leaves contain oils and increase fuel loads (McFadyen, 2004). In South Africa, the plant grows along forest margins, replacing vegetation of low flammability, and allows fires to penetrate the forest. Two biotypes of *C. odorata* have invaded different countries. The biotype in Asia has been substantially controlled in Papua New Guinea (Day and Bofeng, 2007) and East Timor (Zachariades et al., 2009; Day, personal communication) by the gall fly *Cecidochares connexa*. Natural enemy releases in South African against another biotype have resulted in establishment, but control has not yet occurred (Zachariades et al., 2009).

Melaleuca has invaded swamp and marsh habitats in southern Florida. Dense stands increase fuel loads and fire intensity. In pine and cypress habitats, melaleuca litter and standing trees can change ground fires into canopy fires that kill native pines and cypress (Wade, 1981). Loss of these dominant native tree species, coupled with high survival of older melaleuca and intense post-fire melaleuca seeding (Hofstetter, 1991), produces melaleuca monocultures. Similarly, the slower decomposition of melaleuca litter (compared to grass) raises fuel loads in sawgrass marshes, increasing fire intensity (Flowers, 1991). Increased fire, coupled with structural and vegetative conversion, has greatly changed these native plant communities (Serbesoff-King, 2003). Biological control agents, together with cutting and use of herbicides, have controlled melaleuca in Florida, as discussed earlier in the biodiversity section (see also Table 2).

Old World climbing fern is invasive in many habitats in south Florida, where it forms thick skirts of dead fronds around tree trunks. These flammable skirts can carry ground fires into tree canopies. Trees that could withstand ground fires (normal to the region) are killed by such canopy fires. The wet soils of cypress sloughs naturally cause ground fires to die out at slough margins. But fern-coated trees draw fire into cypress stands when burning debris kites from tree to tree, bringing fire effects into new communities (Pemberton and Ferriter, 1998). Biological control of this fern is developing (Boughton and Pemberton, 2009) (Table 2).

Gorse is a spiny European shrub that is a major invasive plant in Australia, western North America, Hawaii, New Zealand, and Chile, forming flammable thickets. Gorse quickly regrows after fire (Reyes et al., 2009), and seeds germinate from a long-lived seed bank. In Chile, gorse fires now occur in areas where fires were rarely started naturally by lightning and are most common between 36°S and 42 °S latitude (Maldonado, 2006), a world biodiversity 'hotspot' (Arroyo et al., 2004).

4.4. Air pollution reduction

In dry-land cropping areas, invasive plants in fallow fields can increase the need for tillage, which produces wind-blown soil. Tumbleweeds (*Salsola* spp.) have this effect in the wheat areas of eastern Washington (USA) and surrounding states (Young, 2006). The fine soil particles (<10 µm) produced are considered an air pollutant by the US-EPA (Sharratt and Lauer, 2006; Sharratt et al., 2007). Similar problems from *Salsola* occur in the San Joaquin Valley, California (http://www.arb.ca.gov/research/aaqs/pm/pm.htm). Biological control of *Salsola* is in progress (Smith, 2005; Smith et al., 2009; see also Table 2).

Air quality can also be lowered by allergenic pollens of invasive plants. Parthenium weed is a potent allergen (McFadyen, 1995). Although contact dermatitis is the greater problem, wind-borne parthenium pollen causes allergic rhinitis or nasobronchial allergy (Towers and Subba Rao, 1992; Agarwal and D'Souza, 2009). Biological control in Australia and India has succeeded in lowering flowering 40–82% at two study locations (Dhileepan, 2001; Dhileepan and Strathie, 2009).

4.5. Provision of habitat for vertebrate wildlife

Native plants provide essential food and habitat for native vertebrates, and invasive plants may displace essential species. While invasive plants sometimes are used by native wildlife, more often they lower wildlife habitat quality. Invasive insects may greatly reduce densities of particular plants. If these are foundation or keystone species, their loss may affect dependent wildlife.

4.5.1. Loss of food

Reduction in availability of wildlife food is a common effect of many invasive plants because they convert diverse plant communities into weed monocultures. The effects of spotted knapweed, leafy spurge, and tansy ragwort on ungulates in western North America were discussed previously. In Queensland, dense infestations of rubber vine along rivers are largely empty of native birds (Bengsen and Pearson, 2006), and rubber vine leaf litter is avoided by native lizards in preference to litter of native trees (Valentine et al., 2007). In North American wetlands, purple loosestrife has reduced food availability for amphibians (Brown et al., 2006). When cattails (Typha spp.) are replaced by loosestrife, tannin (which reduces digestibility) concentration in detritus increases, and algae found on submerged macrophyte stems shift from green algae (e.g., Spirogyra) toward less palatable blue green groups (e.g., Oscillatoria). In combination, these effects reduce performance of native amphibians such as the toad Bufo americanus (Brown et al., 2006).

4.5.2. Lower habitat quality

When invasive plants cause physical restructuring of communities or large vegetative changes, wildlife habitat quality is likely to decline. Invasion of subtropical riparian forests in Texas and southern California by giant reed caused a shift in structure from open forests to dense cane stands of little value to wildlife. In southern California, giant reed invasion affected birds most strongly, including the federally endangered bird *Vireo bellii pusillus* (Bell, 1997). Giant reed has the potential to dry up small desert rivers and its

invasion of the Cuatro Ciénegas basin in northern Mexico threatens both the endemic darter *Etheostoma segrex* (Hendrickson and McGaugh, 2005) and rare freshwater microbial stromatolites (Garcia-Pichel et al., 2004).

In northern Australia, the invasion of *M. pigra* caused widespread loss of sedgelands, paperbark forests, lakes, and channels. In place of a floristic mosaic of structurally diverse habitats, *M. pigra* created a uniform shrubland of low biodiversity. Birds and lizards declined in response to this habitat change (Braithwaite et al., 1989). Loss of sedgelands affected the magpie goose (*Anseranas semipalmata*) and the brolga (*Grus rubicunda*). Loss of wet forests affected sacred ibis (*Threskiornis aethiopicus*), royal spoonbill (*Platalea regia*), and the rufous owl (*Ninox rufa*).

In South Africa, invasion by *C. odorata* around Lake St. Lucia (a World Heritage Site) lowered the temperature of soils used for nesting by Nile crocodiles (*Crocodylus niloticus*), unbalancing hatchling sex-ratio and threatening the species' persistence at the site (Leslie and Spotila, 2001).

In Chile, gorse invasions of native rainforests and grasslands have caused habitat loss for Darwin's fox, *Pseudalopex fulvipes*, one of the world's most endangered canids and for "Monito del monte" (*Dromiciops gliroides*), the only living representative of the marsupial order Microbiotheria, found in *Nothofagus* rainforest and *Chusquea* bamboo (CONAMA, 2009).

4.5.3. Effects of invasive insects

Insect invasions, unlike plant invasions that add a new dominant species, typically remove or degrade one or several native plants. The largest impacts of invasive insects are usually on their host plant and its monospecific herbivorous insects. Effects on vertebrates, however, may sometimes occur if the affected plants are keystone species with no functional substitute available. For example, loss of hemlock in the Appalachian Mts. (USA) due to hemlock woolly adelgid reduced native brook trout (Salvelinus fontinalis) density by as much 67% in parts of the Delaware Water Gap (Ross et al., 2003). In some instances, invasive insects may affect native vertebrates via mechanisms other than killing native plants. In New Zealand, invasive wasps (Vespula spp.) consumed honeydew deposits of native scales on southern beech (Nothofagus sp.), which formerly were an important food for bell birds, tuis and stichbirds (Beggs, 2001). Sphecophaga vesparum, a parasitoid of yellow jacket brood, was introduced but did not lower yellow jacket density (Beggs et al., 2008).

5. Integration of biological control into comprehensive wildland invasive species management

As illustrated by the case studies reviewed here, classical biological control is a powerful tool that can potentially resolve many invasive plant and insect problems in natural ecosystems. However, not all invasive species problems will be amenable to biological control, and the use of natural enemies should not be viewed as a panacea for unwanted exotic species. In some cases, effective agents may not be available, or agents may lack adequate specificity, especially if the targeted invasive species has many native congeneric relatives in the invaded area. In such cases, non-target risks may be too great to warrant the release of additional exotic species

Several other factors affect biological control's use in management plans. In some instances, several invasive species may all require control, such as groups of similar invasive plants. In such cases, biological control of one invader by itself may be insufficient to achieve a community's ecological restoration because a different resident weed may increase as the targeted species declines. In aquatic systems for example, waterhyacinth, water lettuce and giant salvinia may all be present in the same region. Biological control of just one member of the invasive floating-plant guild may

lead to eruption of another invader that was formerly out-competed for control of space or resources by the dominant invader.

In other cases, a target plant may have uses society wishes to retain. Invasive wattles, acacias, and pines in South Africa are desired for their timber, beauty and shade, and biological control can only target their flowers and seeds in order to reduce their spread into natural ecosystems. In such cases, combining a biological control program against reproductive structures and seedlings with mechanical elimination of mature plants (by cutting and application of herbicides) may be necessary to suppress the invasive plant in wildlands.

More complex cases may arise if basic ecological processes have been damaged or terminated in ways that reduce the competitive abilities of native plants in the community. In dam-controlled desert river systems, loss of pulse flooding through controlled water releases may greatly reduce seedling establishment of native plants such as cottonwoods and willows that are needed as competitors in order to reduce invaders such as saltcedar. In such cases, biological control of saltcedar by itself may be inadequate for ecosystem restoration, and altered water management to allow floods and deliberate planting of native trees may be needed to recreate riparian able to sustain native biodiversity. Such programs may combine habitat management, biological control, and mechanical or chemical control.

6. Conclusions

Classical biological control is a powerful tool for suppression of invasive plants and insects in natural ecosystems. It will play an increasingly important part in ecological restoration because it provides a means to permanently suppress invaders over large landscapes without long-term resource commitments and hence is sustainable. As such, it merits use against many invasive plants and insects that are environmental pests in sensitive landscapes. Biological control efforts that are part of ecological restoration projects should set goals in concert with conservation biologists and ecologists and define the changes sought in the damaged native community. These goals should be unambiguous, peer-reviewed, and published in the public domain. As biological control projects unfold, monitoring of changes in pest density, together with responses of native species, particularly the non-target taxa identified as potentially at risk, should be carried out to quantify and document the program's effects (Morin et al., 2009). There should be a clear commitment to measure if and to what degree the target pest's density or range changes, and if native biodiversity is improved as a direct result of a given biological control project. Since population changes and community responses induced by biological control programs often require long periods (5-20 years) to reach stable end points, governments and other participating groups must be advised accordingly and projects must be planned and funded to cover such time periods. When carried out in this comprehensive manner, biological control of invasive plants and insects holds great promise for safeguarding biodiversity and wildlands, preserving and restoring ecosystem services and protecting valued natural resources.

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