CLASSICAL BIOLOGICAL CONTROL OF ARTHROPODS IN THE 21ST CENTURY

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INTRODUCTION

The first attempt by man at classical biological control of an arthropod pest was a spectacular success. The cottony cushion scale (*Icerya purchasi* Maskell) program in California over the period 1877-1879 was the first scientifically and institutionally backed biological control program. Foreign exploration by Arthur Koebele, resulted in the importation and release of two natural enemies, the vedalia beetle (*Rodolia cardinalis* [Mulsant]) and a parasitic fly (*Cryptochaetum iceryae* [Williston]) from Australia for cottony cushion scale control in California. The combined impact of these two natural enemies drove cottony cushion scale densities to almost undetectable levels and by saving the young citrus industry from imminent destruction put California on an economic trajectory towards unprecedented wealth and prosperity. Biological control came to be viewed as a panacea for pest problems after this program and ladybirds as silver bullets for agricultural pests. The resulting "ladybird fantasy," "parasite craze" and "bug versus bug method" did not produce the impressive results that the vedalia beetle had achieved. The potential of biological control as a pest management tool had been greatly exaggerated by the technology's proponents (Sawyer, 1996).

The cottony cushion scale program illustrates important tenets of classical biological control that are still practiced today, although, in some instances greatly modified. These principles include: (1) adventive pest identification; (2) foreign exploration for specialized natural enemies in the pest's home range where densities are often orders of magnitudes lower than in the adventive range; (3) importation and mass rearing of natural enemies; (4) establishment, redistribution, and impact monitoring of imported biological control agents; and (5) frugality and pragmatism. These basic practices, although substantially refined (e.g., use of quarantine facilities and requirements for high levels of host specificity), still form the foundation upon which current biological control programs are built (Bellows and Fisher, 1999; DeBach, 1964; Sawyer, 1996; Van Driesche and Hoddle, 2000; Van Driesche and Bellows, 1993).

Despite many project failures, or only partial success in suppressing noxious arthropod pests, classical biological control will be increasingly practiced against organisms that cause intolerable damage to crops and wilderness areas, especially when orthodox pest control strategies that rely on chemicals are not feasible or economically or environmentally sustainable. Classical biological of arthropods in the 21st Century will make large strides as practitioners of the discipline grapple with new issues relating to host specificity and assessment of agent safety, and advances in community ecology theory facilitate greater understanding of niche accommodation and accompanying factors that affect environmental accommodation of invasive organisms (i.e., pests and their natural enemies).

INVASIVE SPECIES AND BIOLOGICAL CONTROL

The damage invasive organisms cause to natural and agricultural environments and the potential exotic threats that lurk outside state and country borders are well documented phenomena that are understood by scientists, politicians, economists, and the lay public. California acquires six new exotic species per year, while for Hawaii and Florida the rate of acquisition is much higher, being close to 15 species per year on average. As new problems continue to be identified the only the practical management option may be biological control.

Sources and introduction routes of invasive organisms are varied and can include the following pathways:

1. Transportation of people and goods
2. The aquarium trade
3. Nursery trade in popular "weedy" plants
4. Redistribution of novel plants
5. The pet trade
6. Redistribution of game and sport fish
7. Importation and release of biological control agents

Accidental introductions associated with transportation of people and goods have resulted in the frequent introductions of pestiferous weeds, arthropods, mollusks, and vertebrates into new areas. For example, the brown tree snake, *Boiga irregularis* (Merrem), was transported to Guam on military equipment moved from Indonesia and Papua New Guinea after World War II (Rodda et al., 1997). Zebra mussels, *Dreissena polymorpha* (Pallas), and the water flea *Cercopagis pengoi* (Ostroumov) were discharged into the Great Lakes with ballast water from Europe (Charlebois *et al*., 2001; Cox, 1999).

The aquarium trade has been responsible for importing noxious plants, algae, mollusks, crustaceans, vertebrates, and aquatic pathogens into new areas (Bright, 1998). One highly publicized aquarium escapee is the green marine alga *Caulerpa taxifolia* (Vahl) C. Agardh, a Caribbean native that occupies more than 6,000 acres of sea floor in the Mediterranean Sea (Meinesz, 1999). This aggressive Mediterranean-adapted strain of *C. taxifolia* recently invaded the coastal waters of California with wastewater discharged from commercial aquaria (Jousson *et al.*, 2000).

Plants with "weedy" characteristics are popular nursery plants because they are hardy and easy to grow, both attributes that promote escape from cultivation. *Clematis vitalba* L., euphemistically referred to as "old man's beard," is a vine of European origin that escaped from gardens in the 1930s to become one of New Zealand's worst forest weeds (Ogle *et al*., 2000).

The importation and redistribution of novel horticultural plants by nurseries and botanical gardens may also assist the spread of adventive insects, mites, slugs, and pathogens that attack or infest leaves and stems (Bright, 1998; Guy *et al.*, 1998). Exotic organisms can also spread in the soil of transported plants. The New Zealand flatworm *Artioposthia triangulata* (Dendy) has been associated with earthworm declines in Scotland and Ireland following its introduction in the 1950s in potting soil (Christensen and Mather, 1995).

The pet trade is another major biotic conduit for introducing exotic vertebrates (e.g., amphibians, birds, mammals, and reptiles) and invertebrates (e.g., spiders, cockroaches, millipedes, and scorpions) into areas outside of their natural range. Monk parakeets, *Myiopsitta monachus* (Boddeart), a South American native that became naturalized in New York City in 1967 (Todd, 2001), have now spread to 15 states and threaten to become agricultural pests (Cox, 1999). The wild bird trade is responsible for the introduction of at least nine species of exotic parrots that are now established in the U.S.A. (Cox, 1999).

Exotic game and sport fish have been intentionally imported, established, and redistributed by acclimatization societies and private individuals for recreational pursuits (i.e., hunting and fishing). Reproducing populations–some of which may be periodically augmented with mass-reared individuals (e.g., releases of hatchery raised fish)–of deer, goats, pigs, chamois, brush-tail possums, rabbits, tahr, wallabies, pheasants, quail, ducks, geese, trout, and bass can have profound detrimental impacts on native vegetation and compete with native animals for food and habitat (Cox, 1999; Hoddle, 1999; King, 1990a), and may inadvertently spread pathogens lethal to native wildlife (Kiesecker *et al*., 2001) and domesticated animals.

Some of the pest problems alluded to above may be amenable to effective regulation by host specific upper trophic level organisms that reduce pest densities to less damaging levels. The liberation of upper trophic level organisms, known as biological control agents, or natural enemies, is a deliberate importation and release practice that attempts to establish permanent exotic populations that alter community structure and reduce densities of target pest species. Introduction of a biological control agent either adds a guild that was previously lacking in the target community or enriches an existing guild. The introduction of an efficient natural enemy can substantially reduce pest densities and free resources for use by competing organisms (e.g., endemic wildlife) in the same or lower trophic levels (Bellows, 2001).

THE BENEFITS OF BIOLOGICAL CONTROL

A compelling motivation for adoption of biological control is reduced ongoing expenditure for pesticides, labor, specialized equipment, and – potentially – a permanent return to ecological conditions more similar to those seen before the arrival of the pest. Economic analyses indicate that benefit:cost ratios for successful biological control of arthropod pests are high, and can exceed 145:1 (Norgaard, 1988; Pickett et al., 1996; Jetter et al., 1997), and potential benefit:cost ratios overwhelmingly favor support for biological control programs as an option for pest control (Gutierrez *et al*., 1999). Estimates of economic benefits from successful biological control programs tend to be conservative and profits continue to accrue annually with little or no additional management of the system (Norgaard, 1988). Comparisons of costs for biological control programs indicate that benefits amassed from successful projects outweigh the combined costs of unsuccessful projects, even though failures are more numerous. For example, just 10% of arthropod biological control programs have provided full control of the target pest (Gurr *et al*., 2000), and for weed programs, less than 30% of projects have resulted in either total or partial control of the target (Syrett *et al*., 2000), although in some instances evaluations may have been conducted too early to determine final outcomes (McFadyen, 1998). Projects sponsored by the Australian Center for International Agricultural Research had a cost:benefit ratio of 13.4:1 for ten projects that spanned 1983-1996, even though just four of these projects were documented successes (Lubulwa and McMeniman, 1998).

Biological control of agricultural pests can indirectly benefit native wildlife through the reduction of pesticides released into the environment because of natural enemy suppression of economically important targets. The acute impact of insecticides on wildlife because of aerosol drift from agricultural areas, run off into waterways, food chain accumulation, or indiscriminant application was first brought to public attention by Rachel Carson (1962). An insidious, chronic side effect from pesticide use that has been recently postulated is the potential ability of synthetic chemical pollutants in the environment to accumulate in the bodies of vertebrates, and for these sequestered compounds to mimic or block the actions of endogenous hormones (Colborn *et al*., 1997). The environmental endocrine hypothesis has been used as a unifying theory linking wildlife declines, reproductive ailments, behavioral abnormalities (e.g., reproductive and anti-predator), and gross physical deformities with agricultural pesticides, pharmaceuticals, and other industrial chemicals that mimic or obstruct hormonal activity in animals (Pelley, 1997; Ankley *et al*., 1998; Krimsky, 2000; Souder, 2000; Nagler *et al*., 2001; Park *et al*., 2001; Releyea and Mills, 2001;) and humans (Schettler *et al*., 1999).

ROGUE BIOLOGICAL CONTROL AGENTS

Biological control, when practiced correctly, is a carefully orchestrated scientific endeavor that alters community structure through the deliberate manipulation of upper trophic level organisms that use the targeted pest as a resource. Therefore, the practice of classical biological control (i.e., the importation of specialized natural enemies from the pest's home range) intimately links this pest management strategy to the science of population ecology and supports the paradigm of top down regulation by host-specific biological control agents. Consequently, high levels of host specificity ensure strong links and maximal impact by natural enemies on the target, while ensuring weak links and minimal impacts to non-targets. Theoretical community assembly studies indicate risks to non-targets are increased if moderately effective natural enemies are established as they maintain high numbers while not substantially reducing pest densities, and ultimately causing their own population decline. Consequently, susceptible native species are subject to constant attack by these mediocre natural enemies that maintain moderate densities on the target pest. Additionally, if exotic natural enemies provide an abundant resource for generalist resident predators or parasites thereby promoting an increase in their density, attacks on preferred native prey may occur more frequently as a consequence (Holt and Hochberg, 2001).

When biological control projects stray from this fundamental ecological principle of high natural enemy host specificity or the technology is applied without ecological justification to poorly chosen pest targets (e.g., neoclassical biological control of native pests [see Hokkanen and Pimental, 1989]), undesired outcomes such as non-target impacts and lack of control are more likely to occur. This risk of unintended consequences is further amplified with releases of generalist natural enemies, these being biological control agents that are polyphagous and can attack many hosts. Generalist natural enemies, which by definition lack high levels of host and habitat specificity, are frequently cited as examples of the inherent and unpredictable risks associated with releasing biological control agents because of their adverse effects on native organisms and lack of impact on the pestiferous target (Howarth, 1983, 1991; Elliot *et al*., 1996; Simberloff and Stiling, 1996; Stiling and Simberloff, 2000; Henneman and Memmott, 2001). Biological control introductions have also been criticized for diluting endemic biodiversity and contributing to homogenization of global biota. In New Zealand, 13% of this country's insects are exotic. Of these exotic species, only 2.5% have been intentionally introduced for biological control, just 0.35% of New Zealand's total insect fauna. Intentional natural enemy introductions are negligible in comparison to the numbers of adventive insect pests and weeds that have established in New Zealand and biological control agents are not considered a major source of biological pollution diluting native biodiversity (Emberson, 2000).

Examination of the commonly cited "rogue" biological control agents presented in Table 1 clearly demonstrates that these biological control projects were ill-conceived, not necessarily because the pests were unsuitable targets, but primarily because the natural enemies selected had very broad host ranges and substantial non-target impacts should have been predictable. In some instances, agricultural interest groups (e.g., sugar cane growers and farmers) carried out the projects listed in Table 1 with little or no scientific grounding, and government oversight was lax either because of non-involvement, or there was no regulatory infrastructure (i.e., governing legislation) by which to identify suitable targets and to assess the safety of imported natural enemies before release or their subsequent redistribution following establishment.

SAFEGUARDS TO PREVENT BIOLOGICAL CONTROL ACCIDENTS

The increasing demand for greater use of biological control for suppressing invasive species, coupled with recent criticisms by reputable biologists that biological control may not always be a safe alternative to pesticides has resulted in the development of evaluation protocols and legislation to regulate

Table 1. Generalist biological control agents, target pests, country and year of first introduction and unintended impacts on non-target wildlife.

Biological Control Agent	Target Pest	Country and Year of First Introduction	Non-Target Impacts	Reference
European red fox, *Vulpes vulpes* L. (Native range: Palaearctic regions)	Rabbits, *Oryctolagus cuniculus* L.	Australia, 1871	Foxes eat native marsupials and birds, and lambs.	Saunders et al., 1995.
Stoat, *Mustela erminea* L. (Native range: Eurasia and North America)	Rabbits	New Zealand, 1884	Stoats eat native birds, insects, and lizards.	King, 1990b.
Ferret, *Mustela furo* L. (Native range: Central Europe and the Mediterranean).	Rabbits	New Zealand, 1879	Ferrets eat native birds.	Lavers and Clapperton, 1990.
Weasel, *Mustela nivalis vulgaris* Erxleben (Native range: Eurasia and North America).	Rabbits	New Zealand, 1884	Weasels eat native birds, insects, and lizards.	King, 1990c.
Small Indian mongoose, *Herpestes javanicus* (Saint-Hilaire), (= *auropunctatus* [Hodgson]) (Native range: Iraq to the Malay Peninsula)	Rats, *Rattus* spp.	Trinidad 1870; Jamaica, 1872; Cuba, 1886; Puerto Rico, 1877; Barbados, 1877; Hispaniola, 1895; St Croix, 1884; Surinam, 1900; Hawaii, 1883	Mongoose eats native birds and reptiles.	Hinton and Dunn, 1967; Loope et al., 1988.
Cane toad, *Bufo marinus* L. (Native range: Northwestern Mexico through southern Brazil)	White grubs, *Phyllophaga* sp.; sweet potato hawk moth, *Agrius convolvuli* L.; Grey backed cane beetle, *Dermolepida albohirtum* (Waterhouse)	Jamaica, 1844; Bermuda 1855; Puerto Rico 1920; Hawaii, 1932; Australia, 1935; Fiji, 1936; Guam, 1937; New Guinea, 1937; Phillipines; 1934.	Cane toads eat native insects, amphibians, and reptiles. Toads are toxic to native wildlife that consume it, and *B. marinus* out-competes native amphibians for shelter and breeding sites.	Easteal, 1981; Freeland, 1985.
Mosquito fish, *Gambusia affinis* (Baird and Girard) (Native range: eastern U.S.A. and Mexico)	World-wide dissemination of *G. affinis* for control of mosquito larvae promoted by the World Health Organization until 1982.	Intensive releases began worldwide around 1900 and approximately 70 countries now have permanent *G. affinis* populations including: Afghanistan, Australia, Canada, China, Ethiopia, Grand Cayman Island, Greece, Hawaii, Iran, Korea, New Zealand, Somalia, Turkey, Ukraine.	Substantial non-target attacks on native aquatic invertebrates and vertebrates outside its native range.	Diamond, 1996; Gamradt and Kats, 1996; Legner, 1996; Meisch, 1985; Rupp 1996; Walton and Mulla, 1991.

Table 1. Generalist biological control agents, target pests, country and year of first introduction and unintended impacts on non-target wildlife (cont.).

Biological Control Agent	Target Pest	Country and Year of First Introduction	Non-Target Impacts	Reference
Predatory snail, *Euglandina rosea* (Ferrusac) (Native range: southeastern USA).	Giant African snail, *Achatina fulica* Bowdich	Hawaii, 1955; Tahiti, 1974; Moorea, 1977; New Caledonia, 1978; Guam; 1957; Vanuatu, 1973; Papua New Guinea, 1952; Japan, 1958; Taiwan, 1960; Madagascar, 1962; Seychelles, 1960; Mauritius, 1961; Reunion, 1966; India, 1968; Bermuda, 1958.	Predation of native snails (e.g., native *Achatinella* spp. and *Partula* spp.), probably leading to extinction of some native species.	Clarke et al., 1984; Davis and Butler, 1964; Griffiths et al., 1993; Kinzie, 1992. Murray et al., 1988; Simmonds and Hughes, 1963
Tachinid fly, *Compsilura concinata* Meigen (Native range: Europe).	Gypsy moth, *Lymantria dispar* (L.) and other lepidopteran pests.	USA, 1906	Regional declines of native saturniid moths because of heavy parasitism of larvae.	Boettner et al., 2000.
Tachinid fly, *Bessa* (=Ptychomyia) *remota* (Aldrich) (Native range Indo-Malay archipelago)	Coconut moth, *Levuana iridescens* Bethune-Baker,	Fiji, 1925	Possible extirpation of the native Fijian zygaenid *Heteropan dolens* and reduction in abundance of other native zygaenids.	Howarth 1991, Robinson 1975, Sands 1997, Tothill et al., 1930.
Seven spotted lady beetle, *Coccinella septempunctata* L. (Native range: Palearctic regions)	Species of pest aphids	USA, 1957	Competitive displacement of native aphidophagous coccinellids in agricultural crops, and non-target predation of native lepidopterans.	Elliot et al., 1996; Obrycki et al., 2000.
Cactus moth, *Cactoblastis cactorum* (Bergroth) (Native range: Northern Argentina, Uruguay, Paraguay, and southern Brazil)	*Opuntia* spp. of cacti	Australia, 1925; Caribbean, 1957; Hawaii, 1950; Mauritius, 1950; South Africa, 1932; accidental introduction into the USA in 1989.	Invaded mainland USA from the Caribbean in 1989 and attacks native Opuntia spp. thereby threatening the survival of endangered native species	Bennett and Habeck, 1992; Holloway, 1964; Pemberton, 1995.
The flowerhead weevil, *Rhinocyllus conicus* Fröelick (native to Eurasia).	*Carduus* spp. thistles.	USA, 1968	Attacks on seed heads of native *Cirsium* spp. thistles potentially limiting regeneration of plants, and displacing native thistle head feeders.	Louda et al., 1997; Strong, 1997. Louda, 2000; Gassmann and Louda, 2001;

the importation and release of exotic natural enemies. Laws governing biological control vary by country, or they may not exist at all.

In the United States, the U.S. Department of Agriculture and the U.S. Department of Interior are required by Invasive Species Executive Order 11987 (1977) to restrict the introduction of exotic species into natural ecosystems unless it had been shown that there would be no adverse effects (Follett *et al.,* 2000). Biological control in the United States has been facilitated by the 1999 Invasive Species Executive Order 13112, which established a Cabinet-level Invasive Species Council to provide guidance on rational and cost effective control measures of exotic pests. The Animal and Plant Heath Inspection Service (APHIS) (an arm of the USDA) is charged to examine the potential environmental impacts of introduced biological control agents before authorizing their release in order to comply with statutes such as the National Environmental Policy Act (1969) and the Endangered Species Act (1973). Despite these regulations, the United States does not have an encompassing "biological control law" and no legal mandate or agency to explicitly oversee the importation and release of exotic organisms (Howarth, 2000). This is in stark contrast with current legislation enacted in New Zealand and Australia (see below). Interestingly, the importation of candidate biological control agents by scientists into the United States is regulated, and highly secure quarantine facilities are used to screen and test natural enemies prior to release, and Federal and State level clearances are needed to move organisms from quarantine facilities. However, such procedures are generally not required for the importation of exotic and potentially invasive aquatic, terrestrial, and arboreal species that are sold by the pet, nursery, and aquarium trades in the United States (Van Driesche and Van Driesche, 2000), although State laws may make such requirements (e.g., Florida, Hawaii). Strong and Pemberton (2001) suggest that native invertebrates are inadequately protected from biological control agents under current U.S. legislation, and recommend that a review process similar to the one currently in place for biological control of weeds be applied to invertebrate targets to reduce the risks of collateral damage to non-target species. Host specificity testing protocols are being developed and evaluated for arthropod biological control agents, and current protocols are following systems developed for determining the host specificity of weed biological control agents (see Withers *et al*., 1999; Van Driesche *et al*., 1999).

In Australia, the importation of exotic organisms is controlled by two legislative Acts, the Quarantine Act (1985) designed to prevent the introduction of agricultural pests as well as diseases of humans, and the Wildlife Protection Act (1982) intended to control trade in endangered wildlife (McFadyen, 1997). The purpose of the Biological Control Act (1984) was to resolve conflicts of interest that arise when a biological control target is classified both as a pest and a beneficial organism. For example, vast monotypic stands of invasive weeds that provide nectar and pollen for commercially managed bees are seen as beneficial by bee keepers but not by conservationists or rangelands managers (Cullen and Delfosse, 1985). Permits for the importation and release of biological control agents are granted by the Australian Quarantine Inspection Service (AQIS), and involve wide consultation with interested parties within Australia before a consensus on the outcome of the application for release is achieved.

New Zealand has one of the most stringent legislative requirements for importation of potential biological control agents. The Hazardous Substances and New Organisms Act 1996 (HSNO) has greatly increased the obligations incumbent on proponents of new biological control agents, requiring them to provide adequate data on which approvals for importation and release can be based (Fowler et al., 2000). This legislation (i.e., HSNO) provides a solid framework within which risks and benefits of proposed natural enemy introductions can be weighed, and decisions can be made in accordance with presented data. The Environmental Risk Management Authority (ERMA) administers the review process for the importation and release of biological control agents in New Zealand.

International agreements designed to safeguard the process of introducing biological control agents against causing economic and environmental damage may lead to increased restrictions on the release of biological control agents in other parts of the world. The Food and Agriculture Organization (FAO) International Code for the Import and Release of Exotic Biological Control Agents was approved by all member states in 1995, and these guidelines should be adopted worldwide. Under these guidelines, not only must approval for the introduction be gained from the government of the importing country, but other countries in the region must also be consulted as natural enemies may cross international boundaries. The host range of the proposed biological control agent must be adequately measured before it is released, and an evaluation of the impact of the organism must be made following its establishment (Anon., 1997; Food and Agriculture Organization, 1996; McFadyen, 1997).

Despite the best-intentioned laws, flagrant disregard of legislation by shareholders who feel disenfranchised by the regulatory bureaucracy can result in the illegal importation of biological control agents. The rabbit calicivirus disease (RCD) was probably smuggled into the South Island of New Zealand from Australia by high country farmers in August 1997 for the control of rabbits. The virus was illegally disseminated by feeding rabbits carrots and oats saturated with contaminated liquefied livers extracted from rabbits that died from RCD. A network of cooperators spread the virus over large areas of the South Island and its subsequent spread (human assisted through the movement of carcasses, baiting, and insect vectors) made containment and eradication of the disease impossible. Such actions by farmers clearly violated New Zealand's Biosecurity Act (1994) that was enacted in part to protect agriculture and this country's unique flora and fauna from unwanted introductions of pests. A small group of New Zealand farmers justified their actions because they felt New Zealand Government was not moving rapidly enough on the importation of biological control agents for rabbits (the myxoma virus, that causes the lethal rabbit disease myxomatosis is not present in New Zealand). The New Zealand government has now sanctioned controlled virus releases into new areas, and the short term impact of RCD on New Zealand rabbit populations has resulted in 47-66% mortality in central Otago, and large-scale long-term field studies of RCD on rabbits are planned. Fortunately, native New Zealand birds and mammals, groups identified to be at high risk from RCD, do not appear to be affected by this virus (Buddle *et al.,* 1997).

ECOLOGICAL AND ECONOMIC BENEFITS OF BIOLOGICAL CONTROL - EMPHASIZING THE POSITIVE

The reaction of the biological control community to evidence of non-target impacts by biological control agents and subsequent criticism of the use of this technology by reputable biologists has been largely defensive. Two recent books *Nontarget Effects of Biological Control* (eds. Follet and Duan) and *Evaluating Indirect Ecological Effects of Biological Control* (eds. Wajnberg, Scott, and Quimby) advocate improved host specificity testing procedures, more rigorous field assessments of potentially rogue agents with food web analyses, greater legislative guidance, more use of theoretical community assemblage studies, and ownership of past mistakes with a vision to strive towards improved safety and greater efficacy. Retrospective analyses of data sets that have well quantified non-target impacts may be invaluable in guiding studies and legislation that aim to improve the safety of biological control programs (Louda et al., 2003). A major publication by respected biological control scientists that compiles and documents the positive ecological and economic benefits derived from classical biological control programs is needed to temper some of the current criticism directed at the use of natural enemies for pest suppression. These case studies need not be limited to terrestrial arthropods and weeds and the scope should be expanded to include new projects focusing on the biological control of "non-traditional" targets. New targets being evaluated for biological control include marine algae, green crabs, zebra mussels, brown tree snakes, and vertebrates with sterilizing viruses.

CONCLUSIONS

Invasive species of agricultural and conservation importance are going to provide continual targets for biological control programs. Due to this chronic problem and greater public awareness of a need for sustainable control practices, biological control will probably be considered and used more frequently as part of a management program. If humans are to be good stewards of this planet then active management of valued ecosystems is essential. The "hands off" approach to management of wilderness areas will not preserve them from invasive species, and biological control will be the least disruptive technology available to help preserve valued areas.

Biological control projects should be carefully selected and conducted by trained professionals. Host specific natural enemies should be used, neo-classical biological control programs should be regarded warily and subjected to close scrutiny, and the legal or illegal movement of generalist natural enemies by individuals seeking quick fixes for environmental and agricultural problems must not be condoned. Furthermore, the "shotgun approach" which releases large numbers of different species of natural enemies increases the risks of generalists establishing as "environmental winnowing" will most likely select polyphagous agents that do not exhibit high host and habitat fidelity. These kinds of projects are seen as reckless and bring biological control into disrepute with ecologists and conservationists who should be considered supporters of biological control and proponents of the careful use natural enemies. Consequently, greater regulatory guidelines will probably be developed to mitigate adverse effects of biological control agents of arthropods and to provide criteria for selecting "safe" natural enemies for release.

Applied biological control research continues to provide enormous and valuable datasets for the development of theory in population ecology and invasion biology. Our predecessors laid down the foundations of many of the theoretical concepts and experimental techniques that are still in use. Prof. Harry S. Smith an entomologist from Riverside, California, coined the phrase "biological control" (Smith, 1919), and later formally developed the concepts of density dependent and density independent mortality (Smith, 1935). Smith's work influenced Nicholson who developed population dynamics models with Bailey, both of whom visited the University of California, Riverside Campus. G.C. Varley who spent a year in Smith's lab as post-doctoral research developed the concept of delayed density dependence after leaving Riverside (Sawyer, 1996). Paul DeBach, a student of Smith's made major experimental contributions towards evaluating natural enemy impact on target pest populations. Most notably DeBach used pesticide exclusion (i.e., removal of natural enemies with insecticides to demonstrate their regulatory effect), physical exclusion (i.e., the use of field cages to exclude natural enemy access to pest populations), and biological exclusion (i.e., the removal of ants to allow natural enemies access to honeydew producing pests). Current research efforts use similar experimental techniques and use refined theoretical concepts to build upon this historical foundation.

Biological control is unreservedly an ally of agriculture and conservation in its attempts to reduce pesticide use, as a habitat management tool, and biological control presents itself as the only sustainable and cost effective technology for pest management when the risks from the "do nothing" approach are unacceptably high.

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