Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

OPINION ARTICLE

Building Taxon Substitution Guidelines on a Biological Control Foundation

Clare E. Aslan,[1,2] Austin Aslan,[3] Don Croll,[4] Bernie Tershy,[4] and Erika Zavaleta[5]

Abstract

When a species becomes extinct, its ecological functions are lost as well. Taxon substitution is a controversial approach to restoring such functions via introduction of non-native species known to serve similar functions elsewhere. Due to the possibility of nontarget effects from such introductions, taxon substitution has been proposed and implemented in only a few systems, but these attempts have successfully restored functions. As a conservation tool, taxon substitution bears similarity to biological control, wherein species are also introduced for their ecological function with consideration of potential nontarget effects. To improve both the safety and efficacy of taxon substitution, regulatory bodies that currently issue guidelines for biological control can do the same for taxon substitution. Indeed, many biological control guidelines would apply well to taxon substitution. We examine the standard practices followed by biological control programs and propose corresponding taxon substitution guidelines. Integration of taxon substitution into the existing national and international environmental management conversation will improve the tool and has the potential to enhance conservation efforts across a wide diversity of systems if appropriate and stringent precautions are taken.

Key words: **controlled release, ecological analogue, ecosystem function, regulatory framework, species introduction.**

Introduction

Extinction disrupts interspecific interactions (Thompson 1997). Lost species can include mutualists, predators, prey, parasites, substrate providers, nutrient cyclers, and decomposers. In the absence of these species, ecosystems can lose important functions, particularly where extinctions have been widespread or functional redundancy is low (Larsen et al. 2005).

Functional losses from ecosystems are of particular concern because their effects ripple across the system, potentially affecting a wide diversity of species (Ehrlich & Ehrlich 1982). The loss of functional groups represents a particular threat to ecosystem services and potential source of broad-scale breakdown of ecological communities (Petchey & Gaston 2002; Fontaine et al. 2005; Worm et al. 2006). Functional loss also complicates conservation and restoration. In the absence of key native species, ecosystem managers face the prospect that some highly disturbed systems will require endless ecological manipulation (such as hand-pollination, tilling, controlled burning, etc.) in order to prevent further species losses (Scott et al. 2010).

[1]Conservation Education and Science Department, Arizona-Sonora Desert Museum, Tucson, AZ 85743, U.S.A.
[2]Address correspondence to C. E. Aslan, email caslan@desertmuseum.org
[3]Geography Department, University of Arizona, Tucson, AZ 85721, U.S.A.
[4]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, U.S.A.
[5]Department of Environmental Studies, University of California, Santa Cruz, CA 95064, U.S.A.

doi: 10.1111/rec.12096

As an alternative to such resource-intensive tactics, taxon substitution has been proposed as a means to restore ecological functions (Atkinson 1988). Under this strategy, a non-native taxon is introduced to a focal region to restore an ecological function lost through extinction of a native taxon (Atkinson 2001). Taxon substitutions are already underway (Table 1). On Ile aux Aigrettes off the coast of Mauritius, giant tortoises, *Aldabrachelys gigantea*, have been introduced following the extinction of native *Cylindraspis* tortoises (Griffiths et al. 2011). Seed dispersal and germination of the endangered plant *Diospyros egrettarum* have increased as a result of frugivory by the introduced tortoises (Griffiths et al. 2011). A similar taxon substitution in the Galapagos is currently in an earlier stage: national park personnel have introduced to sterilized Isabela Island, Santa Cruz Island, and Pinta Island a variety of giant tortoises in an effort to restore lost seed dispersal and nutrient cycling regimes (Hunter et al. 2013). Subspecies substitutes were included in the introduction of North Island kokako to a South Island site in New Zealand (Parker et al. 2010). Taxon substitution may be particularly useful on oceanic islands (Hansen et al. 2010). Because islands have reduced functional redundancy and simplified interaction networks, loss of all species providing a particular ecological service is more likely on islands than in mainland ecosystems (Aslan et al. 2013).

Notably, most taxon substitutions that are identified as such involve the introduction of fauna. However, introduction of non-native flora to restore functions (e.g. nitrogen enrichment, soil stabilization, etc.) (Parrotta 1992; D'Antonio & Meyerson 2002) is also possible. Many of the guidelines explored here

Table 1. Examples of past intentional taxon substitutions.

Substituted Taxon	Extinct Native Taxon	Function Replaced	Location	Ecological Function Successfully Replaced?	Undesired Consequences Detected	Sample Reference
Nycticorax violacea	*N. violacea gravirostris*	Crab predation	Bermuda	Yes	None	Wingate 1982
Ovibos moschatus	*Ovibos palantis*	Herbivory	Siberia	Yes	None	Zimov 2005; Neronov et al. 2008
Aldabrachelys gigantea, *Astrochelys radiata*	*Cylindraspis* spp.	Seed dispersal, grazing	Mauritius	Yes	Dispersal of non-native plant species	Waibel 2009; Griffiths et al. 2010, 2011
Callaeas cinerea wilsoni	*Callaeas cinerea cinerea*	Browsing	Secretary Island, New Zealand	Too early	None yet	Parker et al. 2010
Anostostomatidae (weta)	Anostostomatidae	Prey, seed dispersal	Minor islands, New Zealand	Yes	None	Watts et al. 2008
Coenocorypha huegeli	*Coenocorypha iredalei*	Trophic interactions	Putauhinu Island, New Zealand	Yes	None	Hansen 2010
Aldabrachelys gigantea	*Cylindraspis* spp.	Seed dispersal, grazing	Rodrigues	Yes	Dispersal of non-native plant species	Waibel et al. 2013
Apis mellifera	Bees and birds	Pollination	Various	Yes, at least partially	Transmission of pathogens to native species; possibly competition with native species	Potts et al. 2010 and references therein
Galapagos giant tortoise (genotype hybrid; taxonomy in flux); saddlebacked variety	*Chelonoidis abingdonii*	Grazing, seed dispersal	Pinta Island	Yes, preliminarily	Short-term decline in cactus populations may impact other cactus interactors	Hunter et al. 2013

apply equally well to flora and fauna, particularly the need to monitor frequently for potential spread.

There currently exist neither overarching guidelines for the practice of taxon substitution nor broad conversation about its utility, best practices, and limitations (Hansen et al. 2010; Parker et al. 2010). Discussion of relevant international rules that could be expanded to incorporate taxon substitution has centered around the International Union for the Conservation of Nature's (IUCN) translocation and reintroduction guidelines (www.iucn.org). IUCN translocation guidelines are intended to promote conservation of particular species by reestablishing or expanding populations (Parker et al. 2010) and are heavily single species-focused (Hansen et al. 2010).

There is another commonly performed, well-regulated, and widely accepted practice involving introduction of non-native species: biological control. In spite of some high-profile biological control disasters in the past (e.g. Phillips et al. 2007), biological control today occurs frequently and with little backlash, in part because established guidelines ensure that nontarget effects are avoided. As nontarget effects are the main concern with taxon substitution, it seems likely that biological control guidelines could be adapted for use with taxon substitutions.

Biological Control: History and Regulation

Biological control agents are introduced for their ecological function and have logged some notable successes. Two European beetles, *Chrysolina hyperici* and *Chrysolina quadrigemina*, were introduced in the 1940s to control Klamathweed (*Hypericum perforatum*) in California; the rangeland weed was subsequently reduced in density by 99% (Huffaker 1951). The myxoma virus was introduced to Australia in the 1930s to control invasive European rabbits, killing 50% of infected individuals (Fenner 2010). As a note of caution, many of the most problematic invasive species that currently threaten native ecosystems were also originally introduced for their ecological functions. Examples include the cane toad *Bufo marinus* (introduced to Australia to control beetles), the cactus moth *Cactoblastis cactorum* (introduced to the Lesser Antilles to control *Opuntia*), and mongoose *Herpestes javanicus* (introduced to Hawaii to control rats) (Loope et al. 1988; Simberloff 1992; Lampo & De Leo 1998).

Because of this history, introduction of biological control agents for conservation is performed with extreme care and carefully regulated by governmental agencies. In the United States, the import of all new biological control agents must be authorized by the U.S. Department of Agriculture's Animal and Plant Health Inspection Service, Plant Protection and Quarantine (Hough-Goldstein 2009). International organizations have established standards and general guidelines for conservation-targeted biological control (Tanaka & Larson 2006). The International Plant Protection Convention (IPPC) facilitated the development of International Standards for Phytosanitary Measures (ISPMs) (IPPC 2005). The guidelines identify responsible parties and establish documentation, inspection, quarantine, release, monitoring, and evaluation standards for biological control endeavors in the 178 signatory nations (IPPC 2005).

Biological Control Regulatory Framework as a Model for Taxon Substitution

Here, we examine each step of biological control and use this assessment to craft proposed taxon substitution steps. We work with the California Department of Agriculture's guidelines (CDFA 2013) because they are similar to but more succinct than other national and international guidelines (Fisher et al. 1999; Balciunas & Coombs 2004). To emphasize the translatable nature of biological control guidelines, we have retained the original wording of these as closely as possible in our suggested taxon substitution analogs:

> *Biological control step 1*: Accurate identification of the pest species and confirmation of the pest as a target for biological control. (CDFA 2013)
>
> *Taxon substitution step 1*: Careful, scientific evaluation of the target species or function of concern, to determine whether functional disruption has indeed occurred.

Taxon substitution may replace an ecological function directly affecting a wide range of species or a more narrow set. Careful study must ensure that the desired ecological function is not carried out by any extant species in the region of interest.

> *Biological control step 2*: Surveys for natural enemies (generally insects, mites, nematodes, and diseases) are conducted in the area of origin of the pest (usually overseas). (CDFA 2013)
>
> *Taxon substitution step 2*: A global search for potential taxon substitutes is conducted. Species sharing key traits (relevant to the focal ecological function) with the extinct taxon should be identified and examined.

Researchers should strive for a substitution occupying as similar a multidimensional niche as possible to the extinct species. Translocation of any species will require coordination with the government of both the country of origin and the country of destination of the species (Legner & Bellows 1999). Conversations with these entities should begin at this stage.

> *Biological control step 3*: Determine host-specificity of potential control organisms to assess impact on targets and nontargets and environmental safety. (CDFA 2013)
>
> *Taxon substitution step 3*: Nontarget effects of the candidate taxon substitute should be assessed via analysis of the candidate's full diet, behavior, reproductive rate, and natural enemies.

Nontarget effects are the dominant concern for both taxon substitution and biological control (Louda et al. 2003). Research in the region of origin of any candidate species is essential prior to taxon substitution. The full dietary breadth of the species as well as its habitat needs and behavior should be documented and examined. Additionally, the possibility that the taxon substitute could pass pathogens to native species must be considered (Woolhouse et al. 2005). A thorough assessment of regional at-risk species in light of these potential community-level nontarget effects is essential.

> *Biological control step 4*: Following approval from federal and state regulatory officials, biological control agents are shipped to a domestic quarantine facility where they are examined to confirm species identity and to determine whether they are free of parasites and diseases. (CDFA 2013)
>
> *Taxon substitution step 4*: Following approval from federal and state regulatory officials, taxon substitutes are shipped to a domestic quarantine facility where they are examined to confirm species identity and to determine whether they are free from parasites and diseases.

At this step, taxon substitution mirrors biological control exceptionally well. In both cases, candidate species have been prescreened, in their regions of origin, and are imported to a quarantine facility in the target conservation area (Fisher & Andres 1999).

> *Biological control step 5*: These agents are tested in field plots to determine that the agents do reduce densities of the target pest and do not have adverse effects on nontargets. Once this small-scale testing is completed, appropriate natural enemies can be mass-reared to high numbers and released at field sites established by county biologists. (CDFA 2013)
>
> *Taxon substitution step 5*: The imported taxon substitutes are tested in controlled field plots to determine that they do perform the ecological function for which they were introduced and do not have adverse effects on nontargets. Once this small-scale testing is completed, appropriate taxon substitutes can be reared and released at field sites established by biologists.

Taxon substitutes can be evaluated in controlled conditions, where their ecological functions can be assessed. Scale becomes important here. Many biological control agents are insects, fungus, pathogens, etc. (Gurr et al. 2000). To date, proposed taxon substitutes have been vertebrates, which can have larger ranges (Atkinson 1988; Parker et al. 2010). One potentially useful strategy is to sterilize and radio-track trial individuals (Hunter et al. 2013) so that the initial release group remains amenable to removal if negative effects are observed.

> *Biological control step 6*: Once released, each biological control agent is evaluated for establishment, spread, impact on the target species, and impact on nontarget species. Careful, long-term evaluation studies provide scientific data that are used to improve current and future programs. Additional releases may be made in an augmentative manner in systems where long-term stability of the natural enemies is not feasible. (CDFA 2013)

Taxon substitution step 6: Once released, each taxon substitute is evaluated for establishment, spread, impact on the target species, and impact on nontarget species. Careful, long-term evaluation studies provide scientific data used to improve current and future programs. Additional releases may be made in an augmentative manner in systems where long-term stability of the taxon substitutes is not feasible.

Monitoring is an essential component of environmental management (Vos et al. 2000). Careful monitoring can determine whether nontarget effects are appearing as well as whether the desired ecological function is occurring.

Can Taxon Substitution Become a Viable Tool?

Regulatory and best practices entities exist to place taxon substitution in the same cautious and transparent framework surrounding biological control. Indeed, deliberate adoption of taxon substitution guidelines would likely not only stimulate important international conversation about taxon substitution (Hansen et al. 2010), but would also help to protect against injudicious introductions in the name of taxon substitution. Because the structure and protocols necessary for regulating biological control are already in place at such regulatory bodies, these agencies at all levels (state/provincial, national, and international) may be well-positioned to extend their regulations to encompass taxon substitution. However, conservation of biodiversity is not necessarily a primary goal of such entities. Conservation and land management agencies will prioritize conservation and may therefore seek more readily to employ taxon substitution as a tool. With these considerations in mind, we suggest that conservation and land management agencies be responsible for issuing taxon substitution guidelines, and that they seek to do so in consultation with biological control regulatory agencies. Such guidelines will make taxon substitution safer and more effective.

Implications for Practice

- Taxon substitution has the potential to be as effective at restoring ecological functions as biological control, but requires acceptance by and involvement of regulatory agencies.
- Conservation and land management organizations can consult with biological control regulatory agencies to develop taxon substitution regulation guidelines that may offer long-lasting and wide-reaching functional replacement options at minimal risk.

LITERATURE CITED

Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. PLoS ONE **8:**e66993.

Atkinson, I. A. E. 1988. Presidential address: opportunities for ecological restoration. New Zealand Journal of Ecology **11:**1–12.

Atkinson, I. A. E. 2001. Introduced mammals and models for restoration. Biological Conservation **99:**81–96.

Balciunas, J. K., and E. M. Coombs. 2004. International code of best practices for classical biological control of weeds. Pages 130–136 in E. M. Coombs, editor. Biological control of invasive plants in the United States. Oregon State University Press, Corvallis.

CDFA. 2013. Biocontrol. California Department of Food and Agriculture, Plant Health and Pest Prevention Services, Integrated Pest Control Branch (available from http://www.cdfa.ca.gov/plant/ipc/biocontrol/bc_whoweare.htm).

D'Antonio, C., and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology **10:**703–713.

Ehrlich, P. R., and A. H. Ehrlich. 1982. Extinction: the causes and consequences of the disappearance of species. Gollancz, London, United Kingdom.

Fenner, F. 2010. Deliberate introduction of the European rabbit, *Oryctolagus cuniculus*, into Australia. Revue Scientifique et Technique **29:**103–111.

Fisher, T. W., and L. A. Andres. 1999. Quarantine concepts, facilities and procedures. Pages 103–124 in T. S. Bellows and T. W. Fisher, editors. Handbook of biological control. Academic Press, San Diego, California.

Fisher, T. W., T. S. Bellows, L. E. Caltagirone, D. L. Dahlsten, C. B. Huffaker, and G. Gordh. 1999. Handbook of biological control: principles and applications of biological control. Academic Press, San Diego, California.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2005. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. PLoS Biology **4:**e1.

Griffiths, C. J., C. G. Jones, D. M. Hansen, M. Puttoo, R. V. Tatayah, C. B. Müller, and S. Harris. 2010. The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. Restoration Ecology **18:**1–7.

Griffiths, C. J., D. M. Hansen, C. G. Jones, N. Zuël, and S. Harris. 2011. Resurrecting extinct interactions with extant substitutes. Current Biology **21:**762–765.

Gurr, G. M., N. D. Barlow, J. Memmott, S. D. Wratten, and D. J. Greathead. 2000. A history of methodological, theoretical and empirical approaches to biological control. Pages 3–37 in G. Gurr, S. D. Wratten and J. Waage, editors. Biological control: measures of success. Springer, New York.

Hansen, D. M., C. J. Donlan, C. J. Griffiths, and K. J. Campbell. 2010. Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. Ecography **33:**272–284.

Hough-Goldstein, J. 2009. Biology and biological control of mile-a-minute weed. USDA, US Forest Service, Forest Health Technology Enterprise Team, Morgantown, West Virginia.

Huffaker, C. B. 1951. The return of native perennial bunchgrass following the removal of Klamath weed (*Hypericum perforatum* L.) by imported beetles. Ecology **32:**443–458.

Hunter, E. A., J. P. Gibbs, L. J. Cayot, and W. Tapia. 2013. Equivalency of Galápagos giant tortoises used as ecological replacement species to restore ecosystem functions. Conservation Biology **27:**701–709.

IPPC. 2005. ISPM No. 3: Guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms. International Plant Protection Convention.

Lampo, M., and G. A. De Leo. 1998. The invasion ecology of the toad *Bufo marinus* from South America to Australia. Ecological Applications **8:**388–396.

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters **8:**538–547.

Legner, E. F., and T. S. Bellows. 1999. Exploration for natural enemies. Pages 87–101 in T. S. Bellows and T. W. Fisher, editors. Handbook of biological control. Academic Press, San Diego, California.

Loope, L. L., O. Hamann, and C. P. Stone. 1988. Comparative conservation biology of oceanic archipelagoes: Hawaii and the Galapagos. Bioscience **38:**272–282.

Louda, S. M., R. W. Pemberton, M. T. Johnson, and P. A. Follett. 2003. Nontarget effects-the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology **48:**365–396.

Neronov, V. M., L. A. Khlyap, V. V. Bobrov, and A. Warshavsky. 2008. Alien species of mammals and their impact on natural ecosystems in the biosphere reserves of Russia. Integrative Zoology **3:**83–94.

Parker, K. A., M. Seabrook-Davison, and J. G. Ewen. 2010. Opportunities for nonnative ecological replacements in ecosystem restoration. Restoration Ecology **18:**269–273.

Parrotta, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agricultural Ecosystems and Environment **41:** 115–133.

Petchey, O. L., and K. J. Gaston. 2002. Extinction and the loss of functional diversity. Proceedings of the Royal Society of London, Series B: Biological Sciences **269:**1721–1727.

Phillips, B. L., G. P. Brown, M. Greenlees, J. K. Webb, and R. Shine. 2007. Rapid expansion of the cane toad (*Bufo marinus*) invasion front in tropical Australia. Austral Ecology **32:**169–176.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25:**345–353.

Scott, J. M., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel. 2010. Conservation-reliant species and the future of conservation. Conservation Letters **3:**91–97.

Simberloff, D. 1992. Conservation of pristine habitats and unintended effects of biological control. Pages 103–117 in W. C. Kauffman and J. E. Nechols, editors. Selection criteria and ecological consequences of importing natural enemies. Entomological Society of America, Lanham, Maryland.

Tanaka, H., and B. Larson. 2006. The role of the International Plant Protection Convention in the prevention and management of invasive alien species. Pages 56–62 in F. Koike, M. N. Clout, M. Kawamichi, M. de Poorter and K. Iwatsuki, editors. Assessment and control of biological invasion risks. IUCN, Gland, Switzerland.

Thompson, J. N. 1997. Conserving interaction biodiversity. Pages 285–293 in S. Pickett, R. S. Ostfeld, M. Shachak and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Springer, New York.

Vos, P., E. Meelis, and W. J. Ter Keurs. 2000. A framework for the design of ecological monitoring programs as a tool for environmental and nature management. Environmental Monitoring and Assessment **61:**317–344.

Waibel, E. A. 2009. Mixed effects of ingestion by the Aldabran giant tortoise (*Aldabrachelys gigantea*) on the germination of alien plant species on the Mascarene Islands. M.S. thesis. University of Zürich, Zürich, Switzerland.

Waibel, E. A., C. Griffiths, N. Zuël, B. Schmid, and M. Albrecht. 2013. Does a giant tortoise taxon substitute enhance seed germination of exotic fleshy-fruited plants? Journal of Plant Ecology **6:**57–63.

Watts, C., I. Stringer, G. Sherley, G. Gibbs, and C. Green. 2008. History of weta (Orthoptera: Anostostomatidae) translocation in New Zealand: lessons learned, islands as sanctuaries and the future. Journal of Insect Conservation **12:**359–370.

Wingate, D. B. 1982. Successful reintroduction of the yellow-crowned night-heron as a nesting resident on Bermuda. Colonial Waterbirds **5:**104–115.

Woolhouse, M. E., D. T. Haydon, and R. Antia. 2005. Emerging pathogens: the epidemiology and evolution of species jumps. Trends in Ecology and Evolution **20:**238–244.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. Jackson, H. K. Lotze, F. Micheli, and S. R. Palumbi. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314:**787–790.

Zimov, S. A. 2005. Pleistocene park: return of the mammoth's ecosystem. Science **308:**796–798.