Kevin J. Gaston

Biodiversity and Macroecology Group, Dept of Animal and Plant Sciences, University of Sheffield, Sheffield UK S10 2TN (k.j.gaston@sheffield.ac.uk)

References

- 1 Rosenzweig, M.L. (1995) Species Diversity in Space and Time, Cambridge University Press
- Gaston, K.J. *et al.* (1998) Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* 13, 70–74
 Gaston, K.J. and Chown, S.L. (1999) Why Rapoport's rule does not generalise. *Oikos* 84,
- 309–312 4 Chown, S.L. and Gaston, K.J. (2000) Areas,
- cradles and museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.* 15, 311–315
 5 Rohde, K. (1998) Latitudinal gradients in
- 5 Konde, K. (1998) Latitudinal gradients in species diversity. Area matters, but how much? *Oikos* 82, 184–190
- 6 Chown, S.L. and Gaston, K.J. (1999) Patterns in procellariiform diversity as a test of speciesenergy theory in marine systems. *Evol. Ecol. Res.* 1, 365–373
- 7 Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in Neotropical birds. *Am. Nat.* 149, 875–902

Eradication of exotic species

In their recent *TREE* review, Myers *et al.*¹ thoroughly discuss the pros and cons of eradication programs of invasive exotic species. Although these authors acknowledge the importance of evaluating possible ecological side effects when implementing such eradication programs, they do not explicitly consider the situation in which certain invasive exotic species become keystones for the survival of local endemics.

This is well illustrated by two proposed plant eradication programs in island archipelagos in the northern Atlantic, such as the Azores and Madeira. Most of the native and endemic laurel-juniper forest vegetation on these islands has been replaced or severely altered by several introduced exotic plants (the area of origin is shown in parentheses), such as Clethra arborea (Europe), Cryptomeria japonica (Japan), Hedychium gardneranum (Himalayas), Hydrangea macrophylla (Japan) and Pittosporum undulatum (Australia). Therefore, the restoration of the native vegetation would require the eradication of these exotics and, in particular, of the extremely fast-growing rhizomatous perennial herb H. gardneranum²⁻⁴. However, some of these exotic plants provide a good microecological environment (e.g. water-balance and hiding places) for several unique endemic land snail species, such as Actinella, Columella, Drouetia, Hydrocena, Leptaxis, 'Napaeus' (this genus is currently under revision, thus we use this name provisionally) and Insulivitrina. Today, many of these endemic snails more commonly live in association with the introduced exotic plants than with the native (endemic) vegetation⁵⁻¹⁰. Hence, the eradication of the exotic plants

would inevitably provoke severe population bottlenecks, if not (local) extinction, for several of the endemic snails. Also, on the island of Mauritius in the Indian Ocean, experimental studies showed that the weeding of exotic plants was detrimental to most native species of land snails¹¹.

Similarly, the eradication of *C. arborea* in the Azores would be detrimental for the endemic bullfinch (*Pyrrhula murian*) because *C. arborea* provides the best food source during winter³. Hence, eradicating exotic plants (and the concomitant re-establishment of the original vegetation) might be detrimental for local endemics, particularly if these endemics have established beneficial relationships with the alien species. Therefore, we believe that this issue should not be overlooked when implementing eradication programs in areas with high endemicity.

Acknowledgement

P.V.R. holds an IWT scholarship.

Patrick Van Riel

Kurt Jordaens

Dept of Biology, University of Antwerp (RUCA), Groenenborgerlaan 171, B-2020 Antwerp, Belgium (vanriel@ruca.ua.ac.be; jordaens@ruca.ua.ac.be)

Antonio M. Frias Martins

Depto de Biologia, Universidade dos Açores, Rua de Mãe de Deus 58, Apartado 1422, 9501-801 Ponta Delgada, S. Miguel, Açores, Portugal (frias@alf.uac.pt)

Thierry Backeljau

Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium (tbackeljau@kbinirsnb.be).

References

- Myers, J.H. et al. (2000) Eradication revisited: dealing with exotic species. Trends Ecol. Evol. 15, 316–320
- 2 Press, J.R. (1993) Introduced plants and their effects on the flora of Madeira. *Bol. Mus. Munic. Funchal* Suppl., 243–248
- 3 Pereira, M.J. et al. (1998) Conservation of natural vegetation in Azores Islands. Bol. Mus. Munic. Funchal 5, 299–305
- 4 Sjögren, E. (2000) Aspects on the biogeography of Macaronesia from a botanical point of view. *Arquipélago Life Mar. Sci.* 2 (Suppl. A), 1–9
- 5 Backhuys, W. (1975) Zoogeography and Taxonomy of the Land and Fresh-water Molluscs of the Azores, Backhuys & Meesters
- 6 Frias Martins, A.M. *et al.* (1989) Moluscos terrestres da Ilha Graciosa. Lista preliminar. *Relatórios e comunicações do Departemento de Biologia* 17, 41–47
- 7 Frias Martins, A.M. et al. (1990) Moluscos terrestres das Flores. Lista preliminar. Relatórios e comunicações do Departemento de Biologia 18, 39–45
- 8 Frias Martins, A.M. *et al.* (1991) Moluscos terrestres da Ilha de Santa Maria. Lista preliminar. *Relatórios e comunicações do Departemento de Biologia* 19, 53–59

CORRESPONDENCE

- 9 Frias Martins, A.M. et al. (1993) Moluscos terrestres da Ilha de São Jorge. Lista preliminar. Relatórios e comunicações do Departemento de Biologia 21, 55–60
- 10 Frias Martins, A.M. et al. (1994) Moluscos terrestres da Ilha do Faial. Lista preliminar. Relatórios e comunicações do Departemento de Biologia 22, 16–19
- 11 Florens, F.B.V. *et al.* (1998) The impact of controlling alien plants and animals on the snail fauna of forests on Mauritius. *J. Conch.* 2, 87–88

Reply from J. Myers, D. Simberloff, A. Kuris and J. Carey

Van Riel et al.1 provide several examples of exotic plant species apparently becoming 'keystone species' in island archipelagos, and providing habitats for snails and birds after displacing native plants. We could easily have provided other examples. The federally endangered giant kangaroo rat (Dipodomys ingens) in California depends on exotic Mediterranean annuals for its continued existence2. The well publicized, invasive, exotic saltcedars, Tamarix ramosissima and Tamarix parviflora, are the source of a major controversy in western USA (Refs 3,4). In riparian areas, dense stands of these species displace native plants and their associated animals, reduce the water table causing increased salination of the soil, dry up ponds, and narrow waterways. Saltcedars have been associated with the decline of 41 threatened or endangered species, especially birds and fish. However, because the endangered southwestern subspecies of the willow flycatcher (Empidonax traillii extimus) nests in saltcedars, the initial biological control proposal was rejected.

Successful biological control reduces the density of the target weed over several years, thus providing the potential for native species to re-establish. In addition, revegetation programs could facilitate the recovery of native species. Reconsideration of saltcedar impacts and the potential of native plant species to re-establish have led to a re-evaluation of the biological control proposal.

The decision to manage an exotic species must be made before holding discussions regarding the costs and the likelihood of success of any control technology, including eradication. We did not attempt to deal with this issue in our 'revisitation of eradication'5. our goal was to elucidate when eradication is a promising control technique, not when to attempt control. As pointed out in our review, eradication is one of several responses to introduced organisms and one that is likely to be successful in rather limited circumstances. Eradication would probably be neither successful nor appropriate in the situations described by Van Riel et al.1, but biological control might be used to reduce the density of exotics to allow some recovery of native plant species. Biological control is one approach to exotics and, if successful (as it is in only

PERSPECTIVES

15–20% of weed $programs^6$), can be expected to only reduce the weed populations, not to eradicate them.

Judith Myers

Dept of Zoology and Faculty of Agricultural Sciences, Centre for Biodiversity Research, University of British Columbia, 6270 University Blvd, Vancouver, BC, Canada V6T 1Z4 (myers@zoology.ubc.ca)

Daniel Simberloff

Dept of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA (dsimberloff@utk.edu)

Armand Kuris

Marine Science Institute and Dept of Ecology, Evolution and Marine Biology,

University of California, Santa Barbara, CA 93106, USA (kuris@lifesci.ucsb.edu)

James R. Carey

Dept of Entomology, University of California, Davis, CA 95616, USA (jrcarey@ucdavis.edu)

References

- 1 Van Riel, P. *et al.* (2000) Eradication of exotic species. *Trends Ecol. Evol.* 15, 515
- 2 Schiffman, P.M. (1994) Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland. *Biodiv. Conserv.* 3, 524–537
- 3 DeLoach, C.J. (1996) Biological control programme against saltcedar (Tamarix spp.) in the United States of America: progress and problems. In Proceedings of the IX International Symposium of the Biological Control of Weeds

(Moran, V.C. and Hoffman, J.H., eds), pp. 253–260, University of Capetown

- DeLoach, C.J. and Lewis, P. (2000) Petition to release into the field the weevil Coniatus tamarisci from France for biological control of saltcedars, Tamarix ramosissima and T. parviflora weeds of riparian areas of the western United States and northern Mexico. Technical Advisory Group for Biological Control Agents of Weeds, USDA-APHIS
- 5 Myers, J.H. et al. (2000) Eradication revisited: dealing with exotic species. Trends Ecol. Evol. 15, 316–320
- 6 Myers, J.H. et al. (1988) The ability of plants to compensate for insect attack: why biological control of weeds with insects is so difficult. In Proceedings of the VII International Symposium of the Biological Control of Weeds (Delfosse, E., ed.), pp. 67–73, Instituto Sperimentale per la Patologia Vegetale

Predicting extinction risks for plants: environmental stochasticity can save declining populations

Steven I. Higgins, Steward T.A. Pickett and William J. Bond

An emerging generalization from theoretical and empirical studies on conservation biology is that high levels of environmental stochasticity increase the likelihood of population extinction. However, coexistence theory has illustrated that there are circumstances under which environmental stochasticity can increase the chance of population persistence. These theoretical studies have shown that the sign of the effect of environmental stochasticity on population persistence is determined by interactions between life history and environmental stochasticity. These interactions mean that the stochastic and deterministic rates of population growth might differ fundamentally. Although difficult to demonstrate in real systems, observed life histories and variance in the vital rates of populations suggest that this phenomenon is likely to be common, and is therefore of much relevance to conservation biologists.

Steven Higgins is at the UFZ Centre for Environmental Research Leipzig-Halle, Dept of Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany (higgins@oesa.ufz.de); Steward Pickett is at the Institute for Ecosystem Studies, Box AB, Millbrook, NY 12545-0129, USA (picketts@ecostudies.org); William Bond is at the Dept of Botany, University of Cape Town, Private Bag Rondebosch 7701, South Africa (bond@botzoo.uct.ac.za).

Conservation biology is a science that aims to develop the understanding and collect the information, needed to promote and maintain biodiversity at a time when we are witnessing radical reductions in biodiversity. An important part of conservation biology is the population-viability analysis (PVA; Ref. 1). PVA aims to use field data and models to forecast the likelihood of population persistence, and to propose remedial actions as necessary. PVA includes a range of approaches, most of which involve developing and parameterizing a model of population behavior, and then exploring the sensitivity of this model to environmental variance and to management interventions. The emerging view from case studies and theory is that environmental variance increases the likelihood of population extinction^{2–4}. However, other branches of ecological theory seem to contradict this view.

Theoretical studies of coexistence have demonstrated that variance in recruitment rates can allow the coexistence of strongly competing organisms, provided that some life history mechanism allows the storage of reproductive potential across generations and that variance in the recruitment rates of the competing species are asynchronous⁵. Although this theoretical mechanism of coexistence, called the storage effect, is now an accepted concept of coexistence theory⁶, its potential implications have been ignored by conservation biologists. This seems peculiar because the fate of rare populations is the central business of conservation biology and the storage effect is a mechanism that allows populations to increase when rare. The aims of this article are to argue that the domain of the storage effect includes PVA and to explore the consequences of the storage effect for PVA. We do this by demonstrating why the storage effect contradicts generalizations currently found in the conservation biology literature and by arguing that many real populations are likely to be influenced by the storage effect. Recognition of the storage effect could help redefine priorities for plant conservation and we conclude by discussing some of the challenges involved in applying these ideas.

What is the storage effect?

The storage effect emerges from a recognition that population growth is a function of both recruitment and the storage of reproductive potential over generations (survivorship). In a general sense, the dynamics of such a population can be presented as:

$$N_{t+1} = N_t(r_t + s_t) \tag{1}$$

where r_t is the recruitment rate in year t, s_t is the survival rate in year t and N is the population number⁷. It should be emphasized that the storage effect operates in many model formulations, provided the model is capable of describing the interaction between variance in recruitment and life history where reproductive potential