

Essay Review : recent perspectives in conservation biology of rare plants

Autor(en): **Holderegger, Rolf**

Objektyp: **Article**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **63 (1997)**

PDF erstellt am: **23.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-377811>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

ESSAY REVIEW

Recent perspectives in conservation biology of rare plants

ROLF HOLDEREGGER

*Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland,
email: holder@systbot.unizh.ch*

Summary

1 Recent trends in population ecology and population genetics are discussed with respect to conservation biology of rare plants. Special attention is given to dynamic concepts (e.g. metapopulations), to approaches which consider different time scales (e.g. “old rare species” vs “new rare species”), and to evolutionary processes.

2 The great value of genetic studies in evaluating population history is stressed. However, traditional natural history, including floristics and biogeography, remain important for a population-based conservation biology of rare plants, since they work on extensive temporal and spatial scales.

3 Biological invasions, subsequent hybridization, and gene introgression are considered as future threats to indigenous, rare and/or endangered plant species.

Keywords: genetic erosion, natural history, new rare species, old rare species, population dynamics, population genetics

Bulletin of the Geobotanical Institute ETH (1997), 63, 109–116

Introduction

Conservation biology as a scientific discipline is of recent origin (Soulé 1985). From its beginning about twenty years ago, it was closely related to both population ecology and population genetics. These two fields experienced a remarkable renewal in the last few years by influencing each other and by being stimulated by studies on conservation. While the population-based conservation biology is an esteemed academic science in English-speaking countries, it is still not entirely accepted in Central Europe (Cornelius 1991). This is rapidly changing now, although the more traditional geobotanical approach, of course having its own merits, still dominates the

studies on conservation of rare and/or endangered plants.

The purpose of the present review is to illustrate some recent, maybe fashionable, trends in the conservation biology of rare plants based on population biology. It summarizes and comments different approaches underlining the most important issues.

Population demography and genetics in conservation

In an influential essay, Lande (1988) asked whether demographic processes, including environmental stochasticity, are more important causes of extinction of small populations

than genetic processes. Although this author did not deny that genetic processes in populations like inbreeding depression, drift and/or impoverishment of genetic variation may be serious problems in some special cases, he concluded that demographic processes are by far more important for local extinction. According to Schemske *et al.* (1994), 95% of the empirical studies on rare and/or endangered plant species have taken either an ecological, mainly demographic, or a genetic approach. Only a few researchers tried to combine both disciplines in order to evaluate potential extinction threats (e.g. Colas *et al.* 1997).

Demographic studies revealed several important factors that influence the persistence of populations, e.g. intrapopulation age structure, the longevity of soil seed banks, which buffer fluctuations in population size produced by stochastic disturbances, or the degree of seed set and dispersal (Schmid & Matthies 1994; Oostermeijer *et al.* 1996b; Poschlod 1996). Eriksson (1996a) argued that generalizations in conservation biology with respect to management should take specific life histories into account. Other key factors of population extinction are (small) population size and its subsets, degree of isolation and fragmentation caused by human activities. Although the first issue received special attention (Gilpin & Soulé 1986), feasible rules of minimum viable population sizes have not been established and are unlikely to be established except for a small number of distinct cases (species or guilds). The general "magic numbers" given so far are little more than rules of thumb (Given 1994).

Many studies focused on the genetic variation of small populations of rare plants, probably promoted by the easy application of allozyme or PCR techniques. The genetic effects of small population size are summarized

in the reviews of Barrett & Kohn (1991), Ellstrand & Elam (1993), and Schemske *et al.* (1994). Using theoretical and empirical data, these authors examined the influences of genetic drift and inbreeding on the fitness of small populations. Despite of the abundance of genetic studies, the practical value of population genetics in rare plant conservation remains unclear. Genetic variation within populations may be less critical than other determinants in the short term, but may play a decisive role for population persistence in the long run, because of its potential of adaptation to a changing environment (Lande & Shannon 1996). The evolutionary significance of genetic variation even within very small populations is also stressed by Frankham (1995) and Levin (1995a). However, genetic variability within populations is not an indicator of population viability *per se*. According to a meta-analysis, multilocus heterozygosity as revealed by allozymes seems to be only weakly correlated with individual fitness (Britten 1996), although a high correlation is proclaimed in theory (Mitton 1993), and for isolated, rare species (Oostermeijer *et al.* 1996a). Presently, there is no explanation for this obvious discrepancy in the valuation of heterozygosity but it clearly shows that farguing interpretations of empirical genetic studies (allozymes or RAPDs) should be taken with caution. Nevertheless, genetic studies on populations are powerful tools in detecting population history (e.g. bottle necks or colonization events), population substructuring, and prevailing breeding systems. For instance, as a rule of thumb, small numbers of polymorphic loci (P) and alleles (A) per locus are caused by genetic drift, while a deficit in heterozygotes (H_o) is due to inbreeding (Oostermeijer *et al.* 1996a). However, inbreeding also increases the probability that alleles will be lost to drift. Correlations be-

tween several life history traits, e.g. seed dispersal modes or timing of reproduction, and intra- and interpopulational genetic variation, are well established (Loveless & Hamrick 1984; Hamrick *et al.* 1991).

Rare species

An often used and still debated classification of species rarity is the one proposed by Rabinowitz *et al.* (1986). Their seven classes of rarity are based on geographic distribution, habitat specificity, and local population size. Species with narrow distributions, restricted habitat specificities, and generally small population sizes are thus regarded as heavily endangered, e.g. *Lloydia serotina* on the British Isles (Rabinowitz *et al.* 1986).

Recently, the significance of this classification was questioned, since it is largely based on a static, non-historical definition of species rarity. A more dynamic concept, which distinguishes between “new rare species” and “old rare species” (Huenneke 1991), was recently published. The former category contains species that were once abundant and common with a more or less continuous regional distribution, but which are now rare due to human impact. The latter category contains species with naturally isolated and/or small populations. They might or might not have been additionally fragmented by human activities.

The population genetics of some “new rare species” is well studied, particularly in the Netherlands. Formerly common species like *Scabiosa columbaria*, *Gentiana pneumonanthe*, and *Salvia pratensis* are nowadays restricted to small and often isolated habitat patches (Ouborg 1993). Dutch investigators found that several genetic factors may threaten local populations of these species (van Treuren *et al.* 1993a, 1993b; Ouborg & van Treuren 1994, 1995; Oostermeijer *et al.* 1995). The

most important factors are genetic drift, decrease in population fitness due to inbreeding depression, and loss of heterozygosity (reviewed in Young *et al.* 1996). Similar results were obtained for *Gentianella germanica* in Central Europe (Fischer & Matthies in press). In conclusion, there are several studies which indicate that “new rare species” may indeed be endangered by genetic factors, a process known as genetic erosion (van Treuren *et al.* 1993a).

In contrast, “old rare species” do actually not show genetic erosion. On the historical time scale, they have always been rare with naturally isolated and often small populations because of restricted habitat requirements. It is argued that these species, e.g. several fern species of rock habitats (Schneller & Holderegger 1996a), exhibit a life history well adapted to this kind of distribution. In the Swiss Plateau, local populations of *Asplenium ruta-muraria* and *A. septentrionale* (glacial relicts) do not exhibit inbreeding depression (Schneller & Holderegger 1996b). On the contrary, these ferns are usually capable of intragametophytic selfing, leading to completely homozygous offspring. These rock inhabiting fern species may thus colonize new habitat patches with single spores. They survive in very small, genetically uniform populations for at least two hundred years (Holderegger & Schneller 1994). Schneller (1996) argues that inbreeding is of such high adaptive value in *A. ruta-muraria* that selection led to fully fertile inbred lines. The crossing of two genetically different lines disturbs the genetic control of meiosis and thus causes outbreeding depression (Schneller 1996). Similar cases of genetically uniform, small and isolated populations are also known in flowering plants, e.g. *Iris lacustris* (Simonech & Morgan 1995). Lande’s (1988) opinion that demography is the more important cause of

local extinction than genetics is therefore likely to be true for "old rare species".

Population dynamics in conservation biology

Hanski (1982) established the concept of core and satellite species in the early 1980s. It is based on species characteristics like abundance, habitat type, regional distribution, dispersal ability, as well as on the ratio of occupied to unoccupied suitable habitat patches. The recognition of precise dispersal characteristics and of habitat patch dynamics opened up a new understanding of species rarity. Söderström (1989) found two additional types of species behaviour in space and time (urban and rural species) testing the core and satellite species concept on bryophytes. It is clear that in each of these different types of species abundance is coupled with distinct forms of regional population dynamics. While it was the merit of the core and satellite species concept to stress the importance of dispersal abilities and modes, it is nowadays only rarely used. Nevertheless, its basic assumptions were important for the development of the metapopulation concept.

Gilpin & Hanski (1991) directed research in conservation biology towards dynamic population processes, thus, replacing the more static attitude. "Populations linked by significant flow of individuals, these are generally seeds in the case of plants, constitute a metapopulation, or a population of local populations" (Silvertown & Lovett-Doust 1993: 107). Unfortunately, the discrimination of populations in the common sense of population biology (Harper 1977) and of metapopulations is often not feasible in plants, because direct estimates of dispersal between habitat patches are difficult to obtain (Poschlod 1996). The evolutionary significance of metapopulation structure is still un-

der debate. On one side, Harrison & Hastings (1996) stressed that evolution in metapopulations is unlikely to be promoted by selection since relatively frequent dispersal will break down local adaptive processes. On the other side, Levin (1995b) stated that metapopulations may persist longer than single populations of similar size. The former may therefore retain genetic variation more readily. It may also offer more opportunities for genomic reorganizations due to colonization events and genetic drift. The practical difficulties to recognize metapopulations as well as the lack of direct empirical data lead to a still uncertain validity of the metapopulation concept in conservation biology of rare plants (Reich & Grimm 1996), although it clearly underlines the detrimental effects of fragmentation (Hanski *et al.* 1996). Vegetation scientists realize more and more that dispersal pathways and thus connectivity are vital landscape structures, also in the case of rare species populations (Taylor *et al.* 1993; Brand & Parker 1995).

A classical study, done by Menges (1990) on the North American river-valley plant *Pedicularis furbishae*, shows how important the incorporation of population dynamics into conservation management can be. Observed rates of natural disturbances dominated the population viability estimates in this species. Menges (1990) concluded that the metapopulation dynamics exhibited extinction rates greater than recolonization rates in *P. furbishae*. In other cases, only landscape dynamics, i.e. frequent erosion, can warrant the survival of a species within a river valley or a ravine, e.g. in the prealpine *Saxifraga mutata* (Holderegger 1996, 1997).

Recently, Eriksson (1996b) asked for the ecological background against which data on metapopulations, including source-sink systems, might be tested. He stated that little is

known about fluctuations in remnant populations, especially in the case of long-lived plants. Remnant populations are difficult to study because their dynamics occur over extended time scales. Therefore, circumstantial evidence like site history or spatial structure of habitat patches are necessary for the delimitation of remnant populations (Eriksson 1996b).

Hybridization: a new threat to rare plants?

Hybridization and gene introgression may threaten local populations of rare plant species (Whitham *et al.* 1991; Ellstrand & Elam 1993). Two major processes are distinguished: genetic assimilation of a rare species by an abundant, sympatric congener and demographic swamping (Levin *et al.* 1996; Rhymer & Simberloff 1996; Thompson 1996). Demographic swamping is the out-competing of a local population of a rare parental species by a hybrid, while genetic assimilation means that a native population becomes genetically absorbed by a hybrid.

An impressive example for extinction caused by hybridization is illustrated in Rieseberg *et al.* (1989). The world's only remaining population of *Cercocarpus transkiae*, a tree species endemic to St. Catalina Island (California), is threatened by hybridization with *C. betuloides*, which genetically assimilates the former. Allozyme and RAPD analyses showed that the removal of all hybrids between the two species and of all introgressed individuals would also remove a substantial proportion of the total remaining genetic variation of *C. transkiae* (Rieseberg & Gerber 1995).

Given the extent of naturally occurring plant hybrids (Ellstrand *et al.* 1996) and the still increasing magnitude of biological invasions (Baskin 1996), it has to be concluded

that hybridization may become a serious and important cause of extinction (Rhymer & Simberloff 1996).

Conclusions

Experimental and demographic studies have proven to be of great value in the study of rare and/or endangered plant species. Nevertheless, for a sound interpretation of the results, information on the history of the investigated populations or metapopulations is needed but often hard to work out or to find in the literature. For this purpose, population genetics has great potential. For instance, hypotheses on realized mating systems, on colonization events, or on past bottle necks can be tested using allozyme electrophoresis. The results of both demography and population genetics have to be evaluated in space and time, and the history of populations has to be explicitly considered in conservation studies.

In this context, the traditional Central European approach to conservation biology which is based on phytosociology, vegetation science, floristics, and biogeography is of great potential value. In my opinion, the last two disciplines may stimulate significant new perspectives in conservation biology. In the Central European, mainly German literature lies dormant a bulk of information waiting for analysis with modern statistical techniques and for incorporation into studies of population history. For instance, Ouborg (1993) and Fischer & Stöcklin (in press) compared phytosociological relevés from calcareous grasslands made in the 1950's and repeated in the 1980's at the same locations in order to evaluate multispecies population dynamics.

An example may illustrate the use of floristics in this context. It is well known that there are suitable, potentially primary habitats of "new rare species" in Central Europe (Däniker 1939). Small, isolated populations

of, e.g. *Gentianella germanica* or *Aster amellus* grow on erosion slopes in river valleys or on patches of sparse vegetation along steep slopes of low mountains. If these locations were indeed natural habitats of “new rare species”, one might argue that they should have adapted to a distribution with isolated habitat patches and, therefore, behave like “old rare species”, i.e. show no genetic erosion. I am not aware of any test of this idea.

Weiner (1995: 156) also voted for the importance of natural history in empirical studies of plant ecology: “I would like to advance the historical hypothesis that most of the major advances in ecology have been made by scientists with either an extensive background in field natural history or at least a very large treasure of biological knowledge in their heads”. I think, the same is true in conservation biology.

Acknowledgements

I thank C.D.K. Cook, F. Gugerli, J.J. Schneller, R. Rutishauser, the journal's editor and two anonymous reviewers for valuable comments and improvement of the manuscript.

References

- Barrett, S.C.H. & Kohn, J.R. (1991) Genetic and evolutionary consequences of small population size in plants: implications for conservation. *Genetics and Conservation of Rare Plants* (eds. D.A. Falk & K.E. Holsinger), pp. 3–30. Oxford University Press, Oxford.
- Baskin, Y. (1996) Curbing undesirable invaders. *BioScience*, **46**, 732–736.
- Brand, T. & Parker, V.T. (1995) Scale and general laws of vegetation dynamics. *Oikos*, **73**, 375–380.
- Britten, H.B. (1996) Meta-analysis of the association between multilocus heterozygosity and fitness. *Evolution*, **50**, 2158–2164.
- Colas, B., Olivieri I. & Riba, M. (1997) *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: a demographic and genetic study. *Proceedings of the National Academy of Sciences USA*, **94**, 3471–3476.
- Cornelius, R. (1991) Zur Bedeutung populationsbiologischer Forschung für den Naturschutz. *Populationsbiologie der Pflanzen* (eds. B. Schmid & J. Stöcklin), pp. 298–310. Birkhäuser, Basel.
- Däniker, A.U. (1939) Die Pflanzengesellschaft, ihre Struktur und ihr Standort. *Berichte der Schweizerischen Botanischen Gesellschaft*, **49**, 522–540.
- Ellstrand, N.C. & Elam, D.R. (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217–242.
- Ellstrand, N.C., Whitkus, R. & Rieseberg, L.H. (1996) Distribution of spontaneous plant hybrids. *Proceedings of the National Academy of Sciences USA*, **93**, 5090–5093.
- Eriksson, O. (1996a) Population ecology and conservation – some theoretical considerations with examples from the Nordic flora. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses*, **31**, 159–167.
- Eriksson, O. (1996b) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.
- Fischer, M. & Matthies, D. (in press) Mating structure, inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany*.
- Fischer, M. & Stöcklin, J. (in press) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*.
- Frankham, R. (1995). Conservation genetics. *Annual Review of Genetics*, **29**, 305–327.
- Gilpin, M. & Soulé, M.E. (1986) Minimum viable populations: processes of species extinction. *Conservation Biology. The Science of Scarcity and Diversity* (ed. M.E. Soulé), pp. 19–34. Sinauer, Sunderland.
- Gilpin, M. & Hanski, I. (eds.) (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London.
- Given, D.R. (1994) *Principles and Practice of Plant Conservation*. Chapman & Hall, London.
- Hamrick, J.L., Godt, M.J.W., Murawski, D.A. & Loveless, M.D. (1991) Correlations between species traits and allozyme diversity: implications for conservation biology. *Genetics and Conservation of Rare Plants* (eds. D.A. Falk & K.E.

- Holsinger), pp. 75–86. Oxford University Press, Oxford.
- Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, **38**, 210–221.
- Hanski, I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable metapopulation size. *American Naturalist*, **147**, 527–541.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Harrison, S. & Hastings, A. (1996) Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology and Evolution*, **11**, 180–183.
- Holderegger, R. (1996) Reproduction of the rare monocarpic species *Saxifraga mutata* L. *Botanical Journal of the Linnean Society*, **122**, 301–313.
- Holderegger, R. (1997) Intrapopulational size structure of the monocarpic species *Saxifraga mutata* and its relationship to succession. *Flora*, **192**, 151–156.
- Holderegger, R. & Schneller, J.J. (1994) Are small isolated populations of *Asplenium septentrionale* variable? *Biological Journal of the Linnean Society*, **51**, 377–385.
- Hueneke, L.F. (1991) Ecological implications of genetic variation in plant populations. *Genetics and Conservation of Rare Plants* (eds D.A. Falk & K.E. Holsinger), pp. 31–44. Oxford University Press, Oxford.
- Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.
- Lande, R. & Shannon, S. (1996) The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, **50**, 434–437.
- Levin, D.A. (1995a) Plant outliers: an ecogenetic perspective. *American Naturalist*, **145**, 109–118.
- Levin, D.A. (1995b) Metapopulations: an area for local speciation. *Journal of Evolutionary Biology*, **8**, 635–644.
- Levin, D.A., Francisco-Ortega, J. & Jansen, R.K. (1996) Hybridization and the extinction of rare plant species. *Conservation Biology*, **10**, 10–16.
- Loveless, M.D. & Hamrick J.L. (1984) Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics*, **15**, 65–95.
- Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.
- Mitton, J.B. (1993) Theory and data pertinent to the relationship between heterozygosity and fitness. *The Natural History of Inbreeding and Outbreeding* (ed. N.M. Thornhill), pp. 17–41. University of Chicago Press, Chicago.
- Oostermeijer, J.G.B., Berholz, A. & Poschlod, P. (1996a) Genetical aspects of fragmented plant populations. *Species Survival in Fragmented Landscapes* (eds J. Settele, C.R. Margules, P. Poschlod & K. Henle), pp. 93–101. Kluwer, Dordrecht.
- Oostermeijer, J.G.B., Brugman, M.L., de Boer, E.R. & den Nijs, H.C.M. (1996b) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology*, **84**, 153–166.
- Oostermeijer, J.G.B., Eijck, M.W., van Leeuwen, N.C. & des Nijs, H.C.M. (1995) Analysis of the relationship between allozyme heterozygosity and fitness in the rare *Gentiana pneumonanthe* L. *Journal of Evolutionary Biology*, **8**, 739–759.
- Ouborg, N.J. (1993) Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine system. *Oikos*, **66**, 298–308.
- Ouborg, N.J. & van Treuren, R.V. (1994) The significance of genetic erosion in the process of extinction. IV. Inbreeding load and heterosis in relation to population size in the mint *Salvia pratensis*. *Evolution*, **48**, 996–1008.
- Ouborg, N.J. & van Treuren, R. (1995) Variation in fitness-related characters among small and large populations of *Salvia pratensis*. *Journal of Ecology*, **83**, 369–380.
- Poschlod, P. (1996) Das Metapopulationskonzept – eine Betrachtung aus pflanzenökologischer Sicht. *Zeitschrift für Ökologie und Naturschutz*, **5**, 161–185.
- Rabinowitz, D., Cairns, S. & Dillon, Th. (1986) Seven forms of rarity and their frequency in the flora of the British Isles. *Conservation Biology. The Science of Scarcity and Diversity* (ed. M.E. Soulé), pp. 182–204. Sinauer, Sunderland.
- Reich, M. & Grimm, V. (1996) Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandesaufnahme. *Zeitschrift für Ökologie und Naturschutz*, **5**, 123–139.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.
- Rieseberg, L.H. & Gerber, D. (1995) Hybridization in the Catalina Island mountain mahogany

- (*Cercocarpus transkiae*): RAPD evidence. *Conservation Biology*, **9**, 199–203.
- Rieseberg, L.H., Zona, S., Abernomb, L. & Martin, T.D. (1989) Hybridization in the island endemic, *Catalina mahagony*. *Conservation Biology*, **3**, 52–58.
- Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M. & Bishop, J.P. (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, **75**, 584–606.
- Schmid, B. & Matthies, D. (1994) Seltenheit und Gefährdung – populationsbiologische Grundlagen des Artenschutzes. *Naturwissenschaften*, **81**, 283–292.
- Schneller, J.J. (1996) Outbreeding depression in the fern *Asplenium ruta-muraria* L.: evidence from enzyme electrophoresis, meiotic irregularities and reduced spore viability. *Biological Journal of the Linnean Society*, **59**, 281–295.
- Schneller, J.J. & Holderegger, R. (1996a) Genetic variation in small isolated fern populations. *Journal of Vegetation Science*, **7**, 113–120.
- Schneller, J.J. & Holderegger, R. (1996b) Colonisation events and genetic variability in populations of *Asplenium ruta-muraria* L. *Pteridology in Perspective* (eds J. Camus, M. Gibby & R.J. Johns), pp. 571–580. Royal Botanic Gardens, Kew.
- Silvertown, J.W. & Lovett-Doust, J.L. (1993) *Introduction to Plant Population Biology*. Blackwell, London.
- Simonech, M.T. & Morgan, M.D. (1995) Allozymic uniformity in *Iris lacustris* (dwarf lake Iris) in Wisconsin. *Canadian Journal of Botany*, **72**, 1720–1722.
- Söderström, L. (1989) Regional distribution patterns of bryophyte species on spruce logs in Northern Sweden. *Bryologist*, **92**, 349–355.
- Soulé, M.E. (1985) What is conservation biology? *BioScience*, **35**, 727–734.
- Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571–573.
- Thompson, J.N. (1996) Evolutionary ecology and the conservation of biodiversity. *Trends in Ecology and Evolution*, **11**, 300–303.
- Van Treuren, R., Bijlsma, R., Ouborg, N.J. & van Delden, W. (1993a) The effects of population size and plant density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution*, **47**, 1094–1104.
- Van Treuren, R., Bijlsma, R., Ouborg, N.J. & van Delden, W. (1993b) The significance of genetic erosion in the process of extinction. IV. Inbreeding depression and heterosis effects caused by selfing and outcrossing in *Scabiosa columbaria*. *Evolution*, **47**, 1669–1680.
- Weiner, J. (1995) On the practice of ecology? *Journal of Ecology*, **83**, 153–158.
- Whitham, T.G., Morrow, P.A. & Potts, B.M. (1991) Conservation of hybrid plants. *Science*, **254**, 779–780.
- Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution*, **11**, 413–418.

Received 19 February 1997

revised version accepted 8 May 1997