Journal of Animal Ecology 2003
72, 484–490

Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed

ERICA FLEISHMAN*, NEIL MCDONAL†, RALPH MAC NALLY‡, DENNIS D. MURPHY§, JACK WALTERS¶ and TED FLOYD**††

**Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, USA; †1900 Klamath Falls Way, Las Vegas, NV 89128, USA; ‡Australian Centre for Biodiversity: Analysis, Policy and Management, School of Biological Sciences, Monash University 3800, Australia; §Department of Biology/314, University of Nevada, Reno, NV 89557–0015, USA; ¶2850 Airport Road # 1, Carson City, NV 89706, USA; and **Great Basin Bird Observatory, One East First Street Suite 500, Reno, NV 89501, USA*

Summary

1. In the deserts of the south-western United States of America, as in many ecoregions around the world, invasion of non-native plants is modifying the structure and composition of riparian vegetation.
2. Restoration of native plant species frequently proves to be ecologically and economically difficult. In the Muddy River drainage in the Mojave Desert (Nevada, USA), eradication of one the most aggressive invasive plants, *Tamarix ramosissima* (salt-cedar), often reduces the structural and compositional diversity of the remaining vegetation. This can have negative effects on native animals, including birds.
3. The objectives of our work were (i) to examine relationships between avian diversity and measures of vegetational diversity (species richness, dominance of non-native plants and vegetation structure [total vegetation volume]), (ii) to explore the extent to which avian community composition was associated with vegetation composition (floristics) or vegetation structure (physiognomy), and (iii) to consider the potential effects of alternative land management and ecological restoration strategies on the biodiversity of birds and other native fauna in watersheds in the arid south-western USA.
4. Species richness of all birds and of breeding birds was best modelled by total vegetation volume alone. Neither species richness of plants nor dominance of non-native plants had a statistically significant effect on species richness, abundance or evenness of birds.
5. Species composition of birds between sites was more similar when floristics was more similar, and vice versa. Species composition of birds was not correlated with physiognomy.
6. Species richness of native birds in the Muddy River drainage appears not to suffer from invasion of non-native plants, provided that the vegetational community retains sufficient structural diversity.
7. The composition of the bird community is closely related to floristics, and other taxonomic groups may exhibit different responses to vegetation structure and composition. Therefore, explicit strategies for landscape-scale management, restoration and maximization of native faunal diversity should consider how removal of invasive plants may affect physiognomy and floristics of the vegetational community as a whole.

Key-words: ecosystem function, functional redundancy, invasive species, restoration ecology, *Tamarix ramosissima* (salt-cedar).

Journal of Animal Ecology (2003) **72**, 484–490

© 2003 British Ecological Society

Correspondence: Erica Fleishman (tel. +1 650 725 9914, fax +1 650 723 5920, e-mail efleish@stanford.edu).
††Present address: American Birding Association, PO Box 7974, Boulder, CO 80306-7974, USA.

Introduction

The incidence of non-native invasive species is increasing around the world, affecting ecosystem function, species distributions and the population dynamics of native species (Higgins *et al*. 1999; Mooney & Hobbs 2000; Palumbi 2001). The preferred course of action might seem clear, albeit ecologically and economically difficult – eradicate the invaders and restore any native species that the invaders have displaced. Unfortunately, it is rarely simple and sometimes is virtually impossible to reestablish native species. Reestablishment of some native species may require reinstating large-scale disturbance regimes, including fire (Covington *et al*. 1997; Fulé & Covington 1999) and flooding (Lake 1995; Smith 1998; Meretsky, Wegner & Stevens 2000; Richter & Richter 2000). Restoration of historic disturbance cycles can be prohibitively expensive and politically contentious. Moreover, while actions taken to return 'natural' disturbance processes to an ecosystem have considerable biological benefits, it is unclear how successful those actions will be in terms of reestablishing target species (Sher, Marshall & Gilbert 2000; Walters *et al*. 2000; Swengel 2001; Gabbe, Robinson & Brawn 2002). Therefore, while we continue exploring mechanisms to minimize the further geographical expansion of non-native species, it is critical to understand whether invasive species can provide any ecological services in their own right.

More broadly, losses of native species have led ecologists to question the relative importance of species richness and ecological function. There is considerable debate about the extent to which the number of species *per se* affects the magnitude, stability and maintenance of ecosystem processes, such as primary productivity and nutrient cycling (Pimm 1991; Tilman 1999; Waide *et al*. 1999; Loreau 2000; Mittelbach *et al*. 2001). Some authors have proposed that many species are functionally redundant – that they serve the same purpose with respect to ecosystem processes (e.g. Walker 1992). If so, species richness may provide evolutionary 'insurance' in the event of long-term environmental change (Yachi & Loreau 1999; Tilman 2000; Loreau *et al*. 2001). In the short term, however, the number of species may be less critical than the role that each species performs (Tilman *et al*. 2001). These issues have meaningful ramifications for development of effective strategies for restoring or maintaining native biodiversity, ecological functions and ecological services at both local and landscape scales.

The practical implications of such matters are illustrated throughout the arid western United States of America, where invasion of non-native plants – compounded and in some cases exacerbated by dryland and irrigated agriculture and urbanization – is modifying the structure and composition of vegetation in riparian zones. Along the Muddy River in the Mojave Desert (Clark County, Nevada), as in many south-western drainages (Sher *et al*. 2000), introduced *Tamarix ramosissima* (salt-cedar) has displaced native tree species including *Populus fremontii* (cottonwood), *Salix* spp. (willow) and *Prosopis* spp. (mesquite). In many areas, *T. ramosissima* now overwhelmingly dominates the vegetational overstorey. However, many species of native birds, including the endangered and federally protected *Empidonax traillii extimus* (south-western willow flycatcher), are able to exploit *T. ramosissima* for shelter and nesting, especially when some native trees remain. Aggressive campaigns to remove *T. ramosissima* frequently eradicate thousands of individual trees along several kilometre stretches of riparian corridors, but such areas may be left without either a woody overstorey or a diverse understorey of shrubs, forbs and grasses. Unless native riparian vegetation can be restored in the near term, removal of *T. ramosissima* may not benefit native biota that require a mature vegetational community, and may threaten the local persistence of some of these species.

Our contemporary efforts to understand interactions between vegetation composition, vegetation structure and the requirements of native fauna echo a long-standing ecological debate: the role of floristics vs. physiognomy in avian community composition (MacArthur & MacArthur 1961; Robinson & Holmes 1984; Rotenberry 1985; Mac Nally 1990). This core ecological question may not be novel in and of itself. However, the issue bears reexamining in light of its ramifications for relatively new areas of research and management emphasis, such as development of effective strategies for restoration and reconstruction of vegetation at landscape scales. The traditional view is that avian composition is more closely associated with vegetation structure (physiognomy) than with vegetation composition (floristics) (e.g. MacArthur, Recher & Cody 1966; Anderson & Shugart 1974; Rotenberry & Wiens 1980), but empirical evidence also supports the alternative hypothesis (e.g. Tomoff 1974; Power 1975; Wiens & Rotenberry 1981). It has been suggested that as spatial grain and extent increases, floristics becomes less important and physiognomy becomes more important with respect to bird community composition (Rotenberry 1985; Wiens, Rotenberry & Horne 1987), although, at regional scales, strong correlations may exist between floristic similarities and structural similarities (Mac Nally *et al*. 2002).

Our work in the Muddy River drainage allowed us to address three major issues of ecological and conservation relevance. First, we examined relationships between avian biodiversity, species richness of the vegetation, dominance of non-native plants and vegetation structure (using structure as a crude indicator of ecological 'function'). Second, we explored the extent to which avian community composition was associated with floristics or physiognomy at the 'local' scale of our study (*c*. 25 km^2). Third, we considered the potential effects of alternative land management and restoration strategies on native faunal biodiversity in the Muddy River drainage and similar watersheds in the south-western USA and other arid landscapes.

© 2003 British Ecological Society,

Methods

We established 33 study sites along the Muddy River drainage (36°–69′ N, 114°–64′ W). Species richness, composition and structure of the vegetation varied considerably among sites, ranging from near-monocultures of non-native *Tamarix ramosissima*, to fairly open sites dominated by native halophytic plants such as *Atriplex* and *Distichlis*, to sites in which *T. ramosissima* was interspersed with native trees including *Salix exigua* (coyote willow), *Prosopis* spp. and *Populus fremontii*.

BIRDS

We surveyed birds using fixed-radius point counts during the breeding season. Eight points had a radius of 125 m; all other points had a radius of 100 m. Each site was visited at least seven times between 2 May and 29 June 2001. During each visit, we recorded all birds seen or heard during 30 min at each point. We classified bird species as either locally breeding (including both year-round residents and species that winter well to the south) or non-breeding (see Fleishman *et al*. 2002).

For each site, we calculated species richness (number of species), abundance and species evenness, the extent to which individual birds in each site were equally partitioned among species (Pielou 1975). Species richness, abundance and evenness were calculated separately for the 'all species' and 'breeding species' classifications. Because some individual birds may have been recorded on more than one site visit, we calculated abundance as the mean number of individual birds per site per visit. We quantified evenness using the diversity index E (Hayek & Buzas 1997). E is calculated as $E = e^H/S$. In this formula, $H = -\Sigma p_i \ln(p_i)$, where p_i is the proportion of individuals found in the ith species, and S is the number of species in the site (Hayek & Buzas 1997). E ranges from 0 to 1, approaching 1 when individuals are partitioned equally among species.

VEGETATION

At three randomly selected locations in each site, we extended a 6·1-m (20-foot) pole vertically through the vegetation. The taxonomic identity of all vegetation contacts in each 30-cm (1-foot) interval was recorded (Rotenberry 1985; Mills, Dunning & Bates 1991). We calculated total vegetation volume (TVV, Mills *et al*. 1991) at each sampling location as $h/10p$, where h = the total number of 'hits' (intervals that contained vegetation) and p = the number of points at which vegetation volumes were measured (21 in this case). Total vegetation volume for each site was estimated as the mean TVV of the three sampling locations. For each site, we also calculated species richness of plants and the proportion of plant species that were native to the Muddy River drainage.

ANALYSES

Because the distribution of our species-richness values for birds was non-normal, and suggestive of a Poisson distribution, we tested the effects of vegetation on species richness by using generalized linear models. The procedure involved an exhaustive search of all possible 2^K (K predictor variables) models of species richness using 'criteria' (Mac Nally 2000). In our case, $K = 3$, so $2^K = 8$ models. Richness was modelled on the log scale (the appropriate link function in a generalized linear model for a Poisson distribution, McCullagh & Nelder 1989). The selected model is the one minimizing a Bayesian information criterion (BIC; Schwarz 1978), which represents the most efficient model with respect to the minimum prediction error (or 'fit') balanced against the model complexity (i.e. number of terms). Selection of the 'best' model by using criteria avoids the problem of compromised Type I error rates associated with sequential searching protocols (e.g. stepwise model selection) because no explicit statistical tests are conducted; one merely accepts the most 'efficient' model based on the minimum BIC criterion.

We calculated similarity (Canberra distances) of species composition of all birds, species composition of breeding birds, species composition of vegetation (floristics) and vegetation structure (physiognomy) between all pairs of sites. For these analyses, physiognomy was considered to be similar between sites if the same intervals above ground contained vegetation (see description of TVV calculations). We used Mantel tests (Mantel 1967; Douglas & Endler 1982) to evaluate whether species composition of birds and breeding birds tended to be more similar in sites with similar floristics or physiognomy, and to evaluate whether similarity of species composition, floristics or physiognomy was a function of distance between sites. The Mantel procedure circumvents the lack of independence among data values associated with traditional matrix correlations between all pairs of sites (Douglas & Endler 1982). Partial Mantel statistics, which measure the partial linear correlation of two variables after controlling for the linear effect of a third variable, also were computed. We tested whether species composition of all birds and species composition of breeding birds was correlated with floristics after controlling for physiognomy, and whether species composition of birds was correlated with physiognomy after controlling for floristics. In addition, we tested whether species composition of all birds and species composition of breeding birds was correlated with floristics or physiognomy after controlling for distance between sites. Canberra distances and Mantel tests were calculated using the *R* Package (Casgrain & Legendre 2001).

Results

A total of 125 species of birds, 76 of which are believed to breed in the Muddy River drainage, were recorded

© 2003 British Ecological Society,

Table 1. Summary data values for diversity measures of birds in 33 sites in the Muddy River drainage. Averages are presented as mean (SD)

	Minimum	Maximum	Average
Species richness			
All species	17	59	34·1 (11·9)
Breeding species	15	45	28·4 (8·5)
Abundance			
All species	11	61	25·4 (11·0)
Breeding species	10	60	24·3 (10·7)
Evenness			
All species	0·334	0·837	0·695 (0·116)
Breeding species	0·340	0·845	0·706 (0·116)

from our 33 study sites (Fleishman et al. 2002). Summary values for species richness, abundance and evenness of birds are presented in Table 1.

We recorded 28 plant taxa from our 33 study sites (Table 2). Four taxa could not be identified beyond the morphospecies level; we were unable to determine whether those taxa were native or non-native. Of the remaining taxa, 18 were native to the Muddy River drainage and six were not (Table 2). Physiognomically, the plant taxa included 3 trees, 9 shrubs, 10 herbs and 6 grasses (Table 2).

Tamarix ramosissima was recorded in more sites than any other plant taxon (13 of 33, Table 2). Mean species richness of plants was slightly greater in sites with *T. ramosissima* than in sites without *T. ramosissima* (3·08 vs. 2·00, $F_{1,32} = 7·67$, $P < 0·01$), but the mean proportion of native plants in sites with and without *T. ramosissima* was not significantly different at the 0·05 level (0·47 vs. 0·69, $F_{1,32} = 3·35$, $P = 0·08$).

Summary values for species richness of plants, proportion of native species of plants, and total vegetation volume (TVV) are presented in Table 3. Minimum species richness and TVV values of 0 reflect the fact that one site was mowed after our surveys began but before vegetation measurements were taken. As a result, we could not identify the plant taxa present in the site, and TVV at the three randomly selected locations in the site was negligible. Discounting this latter site, minimum species richness was 1 and minimum total vegetation volume was 0·016.

In all cases, analyses of all species of birds and analyses of breeding birds produced qualitatively identical results. Therefore, we present data for breeding birds only. Data for all species of birds are available from the corresponding author. Species richness of breeding birds (ln S) was best modelled by total vegetation volume (TVV) alone (Fig. 1), with the BIC minimized for just this variable (BIC = −84, root-mean-square prediction error [log-scale] = 0·266). Poisson regression yielded similar results. Only when total vegetation volume alone was in the model was the regression coefficient of any term significant (β[TVV] = 2·15 ± 0·70, $P \sim 0·004$). No combination of

Table 2. Plant taxa recorded in 33 study sites in the Muddy River drainage, residency status, growth form and occurrence rate (proportion of sites in which the taxon was present)

Species	Status	Growth form	Occurrence
Acroptilon repens	Non-native	Herb	0·12
Allenrolfea occidentalis	Native	Shrub	0·06
Anemopsis californica	Native	Herb	0·12
Annual composite	Non-native	Herb	0·03
Arceuthobium sp.	Native	Herb	0·03
Artemesia tridentata	Native	Shrub	0·03
Atriplex elegans var. *elegans*	Native	Shrub	0·03
Atriplex sp.	Unknown	Shrub	0·09
Atriplex torreyi	Native	Shrub	0·24
Carex sp.	Native	Grass	0·06
Chenopodium species a	Non-native	Herb	0·12
Chenopodium species b	Non-native	Herb	0·06
Eriogonum sp.	Native	Herb	0·03
Grass species a	Unknown	Grass	0·30
Grass species b	Unknown	Grass	0·03
Happlopappus acradenius	Native	Shrub	0·09
Heliotrope curusaviccum	Native	Herb	0·06
Lycium torreyi	Native	Shrub	0·03
Phragmites australis	Native	Grass	0·06
Pluchea sevicea	Native	Shrub	0·09
Prosopis glandulosa	Native	Tree	0·12
Prosopis pubescens	Native	Tree	0·06
Reed species a	Native	Grass	0·03
Shrub species a	Unknown	Shrub	0·03
Sporobolus airoides	Native	Grass	0·06
Tamarix ramosissima	Non-native	Tree	0·39
Tidestromia oblongifolia	Native	Herb	0·03
Vitis sp.	Non-native	Herb	0·03

© 2003 British Ecological Society,

Table 3. Summary data values for measures of plant species richness, composition and structure in 33 sites in the Muddy River drainage. Values for proportion of native species include only those taxa that could be identified to species. Averages are presented as mean (SD)

	Minimum	Maximum	Average
Species richness	0	6	2·4 (1·2)
Proportion of native species	0·00	1·00	0·61 (0·35)
Total vegetation volume	0·000	0·270	0·091 (0·063)

Table 4. Correlations (Mantel's *r* statistics) between species composition of breeding birds, species composition of vegetation (floristics), vegetation structure (physiognomy) and distance between sites

Variable 1	Variable 2	Covariate	Mantel's *r*	*P*
Breeding birds	Floristics	–	0·31	0·002
Breeding birds	Physiognomy	–	0·10	NS
Breeding birds	Distance	–	0·72	0·001
Floristics	Distance	–	0·36	0·001
Physiognomy	Distance	–	0·19	0·025
Breeding birds	Floristics	Physiognomy	0·29	0·001
Breeding birds	Physiognomy	Floristics	0·04	NS
Breeding birds	Floristics	Distance	0·07	NS
Breeding birds	Physiognomy	Distance	–0·05	NS

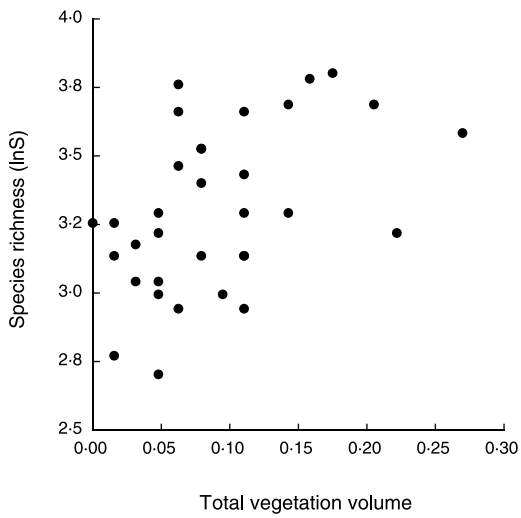

Fig. 1. Relationship between species richness of breeding birds and vegetation structure (total vegetation volume).

the vegetation composition variables we measured explained significant amounts of deviance (the Poisson-regression equivalent of variance) in abundance or evenness of birds.

Species composition of breeding birds between sites was significantly more similar when floristics was more similar, and vice versa (Table 4). Correlations between species composition of birds and physiognomy were not statistically significant. Similarity of species composition of birds, floristics and physiognomy all increased as distance between sites decreased (Table 4). Partial Mantel tests yielded a similar pattern (Table 4). There were statistically significant correlations between species composition of birds and floristics after controlling for physiognomy, but not after controlling for distance. Correlations between species composition of birds and physiognomy after controlling for floristics and after controlling for distance were not statistically significant.

Discussion

Species richness and composition of birds in the Muddy River drainage appeared to be closely related to several measures of vegetational diversity. Species richness of birds was best predicted by total vegetation volume, and species composition of birds was strongly associated with floristics. We acknowledge that much of the avifaunal similarity as a function of floristic similarity may have resulted from spatial proximity. However, the relationship between species composition of birds and physiognomy remained non-significant after controlling for distance. Thus, the correlation between similarity of birds and floristics can be represented as a conjoint autocorrelation pattern in which species composition of birds and vegetation – but not structure of vegetation – tends to covary in space. These patterns suggest that species composition of birds and plants exhibit similar responses to abiotic environmental gradients (Hawkins & Porter 2003).

There are at least four explanations (not mutually exclusive) as to why species richness of birds was primarily affected by vegetation structure as opposed to species richness of the vegetation or dominance of non-native plants. First, an increase in vegetation volume may be associated with an increase in both the number of feeding strategies that can be supported and the total volume of food (e.g. insects) available. Second, from the perspective of birds, there may be functional redundancy within the vegetational community with

© 2003 British Ecological Society,

respect to structure. For example, many birds may not have a strong preference for the species of tree in which they nest. In the latter context, a non-native *Tamarix ramosissima* may be functionally equivalent to a native *Salix*. Third, some birds may be using a relatively small proportion of the plant species present in their habitat – richness of understorey vegetation, for instance, may not be critical to the many insectivorous species that are arboreal nesters and mainly gather prey from tree foliage. Fourth, variation in species richness and dominance of non-native plants (including *T. ramosissima*) among sites, while representative of variation in the Muddy River drainage, may not have been sufficient to affect species richness of birds.

Although some plant species (both native and non-native) may serve similar functions with respect to vegetation structure, the effect of vegetation composition on the avian community cannot be dismissed. In addition, plant composition undoubtedly influences the distributions of other faunal assemblages, including butterflies (Nelson & Andersen 1994; Blair & Launer 1997; Fleishman *et al*. 1999). Avian community composition in our study system was more closely associated with floristics than with physiognomy. This contradicts a widely held general view that vegetation structure is more important to the distribution of birds than vegetation composition (MacArthur *et al*. 1966; Anderson & Shugart 1974; Rotenberry & Wiens 1980), but supports the suggestion that floristics may have the greatest potential to influence avian community composition at relatively local scales (Rotenberry 1985; Wiens *et al*. 1987).

Ideally, we would prefer to eradicate all non-native species from ecosystems around the world and reestablish any native species that may have been displaced by the invaders. Unfortunately, there are few conceptual and empirical guidelines for determining whether and how native species can be restored, particularly at large spatial scales (Lake 2001). The extent to which native riparian floras can be reintroduced to drainages that are currently dominated by non-native *T. ramosissima* in the south-western USA is unclear; even if such efforts prove biologically feasible, they may be unworkable for economic reasons. Given these ecological and fiscal constraints, it is important to determine which aspects of the vegetational community have the strongest influence on native faunas. Many native animals – even some endangered species – can remain viable in the face of considerable habitat modification.

We offer two related suggestions for maximizing diversity of native birds while continuing efforts to eliminate non-native *T. ramosissima* or similar woody species of plants or to restore native vegetation. First, if possible, eradication strategies should avoid 'clear-cutting' extensive stands of non-native trees. Native animals that require some degree of structural complexity may suffer less disturbance if managers can remove non-native plants incrementally, in a spatially intermittent pattern. Second, it may be possible to give native trees a competitive advantage by selectively removing non-native trees while simultaneously attempting to re-establish at least some native taxa.

While these recommendations may seem intuitive to some ecologists, we believe they need reiterating in light of contemporary efforts to maintain and restore ecosystems at large spatial scales. Time and money for exploring the ecological effects of alternative management strategies inevitably is limited. Without robust data and associated scientific inferences, decision-makers and managers are under considerable pressure to implement the fastest and cheapest alternative. If clear-cutting appears to be an easy and effective way to meet the objective of removing non-native *T. ramosissima*, for instance, the additional expense of cutting smaller patches or thinning trees selectively must be justified in terms of other ecological goals using empirical data. Thus, demonstrating that conservation principles are not academic platitudes but instead have a compelling practical application greatly increases the probability that management strategies will be designed accordingly.

Acknowledgements

Thanks to Karen McDonal for field assistance, to Bruce Lund for assistance with vegetation identification, site access and field logistics, to the Great Basin Bird Observatory for assistance with logistics and site access, to Robert Reimer and Mary Savage for assistance with vegetation sampling, and to two anonymous referees for helpful comments on the manuscript. Support for this research was provided by the Nevada Biodiversity Research and Conservation Initiative and the Great Basin Bird Observatory. R.M. also acknowledges support of the Australian Research Council.

References

Anderson, S.H. & Shugart, H.H. (1974) Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology*, **55**, 828–837.

Blair, R.B. & Launer, A.E. (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. *Biological Conservation*, **80**, 113–125.

Casgrain, P. & Legendre, P. (2001) *The R Package for Multivariate and Spatial Analysis*, Version 4.0 d5. Département de sciences biologiques, Université de Montréal. http://www.fas.umontreal.ca/BIOL/legendre/.

Covington, W.W., Fulé P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S. & Wagner, M.R. (1997) Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry*, **95**, 23–29.

Douglas, M.E. & Endler, J.A. (1982) Quantitative matrix comparisons in ecological and evolutionary investigations. *Journal of Theoretical Biology*, **99**, 777–795.

Fleishman, E., Austin, G.T., Brussard, P.F. & Murphy, D.D. (1999) A comparison of butterfly communities in native and agricultural riparian habitats in the Great Basin. *Biological Conservation*, **89**, 209–218.

Fleishman, E., Murphy, D.D., Floyd, T., McDonal, N. & Walters, J. (2002) Characterization of riparian bird

© 2003 British Ecological Society,

communities in a Mojave Desert watershed. *Great Basin Birds*, **5**, 38–44.

Fulé, P.Z. & Covington, W.W. (1999) Fire regime changes in La Michilía Biosphere Reserve, Durango, Mexico. *Conservation Biology*, **13**, 640–652.

Gabbe, A.P., Robinson, S.K. & Brawn, J.D. (2002) Tree-species preferences of foraging insectivorous birds: implications for floodplain restoration. *Conservation Biology*, **16**, 462–470.

Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist*, **161**, 40–49.

Hayek, L.C. & Buzas, M.A. (1997) *Surveying Natural Populations*. Columbia University Press, New York.

Higgins, S.I., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T.H. (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303–313.

Lake, P.S. (1995) Of floods and droughts: river and stream ecosystems of Australia. *River and Stream Ecosystems*, 22 (eds C.E. Cushing, K.W. Cummins & G.W. Minshall), pp. 659–690. Elsevier, Amsterdam, Netherlands.

Lake, P.S. (2001) On the maturing of restoration: linking ecological research and restoration. *Ecological Management and Restoration*, **2**, 110–115.

Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, **91**, 3–17.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.

MacArthur, R.W. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

MacArthur, R.W., Recher, H. & Cody, M.L. (1966) On the relation between habitat selection and species diversity. *American Naturalist*, **100**, 319–332.

Mac Nally, R.C. (1990) The roles of floristics and physionomy in avian community composition. *Australian Journal of Ecology*, **15**, 321–327.

Mac Nally, R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. *Biodiversity and Conservation*, **9**, 655–671.

Mac Nally, R., Bennett, A.F., Brown, G.W., Lumsden, L.F., Yen, A., Hinkley, S., Lillywhite, P. & Ward, D. (2002) How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications*, **12**, 900–912.

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, London.

Meretsky, V.J., Wegner, D.L. & Stevens, L.E. (2000) Balancing endangered species and ecosystems: a case study of adaptive management in Grand Canyon. *Environmental Management*, **25**, 579–586.

Mills, G.S., Dunning, J.B. & Bates, J.M. (1991) The relationship between breeding bird density and vegetation volume. *Wilson Bulletin*, **103**, 468–479.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough. L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.

Mooney, H.A. & Hobbs, R.J. (2000) *Invasive Species in a Changing World*. Island Press, Washington, D.C.

Nelson, S.M. & Andersen, D.C. (1994) An assessment of riparian environmental quality by using butterflies and disturbance susceptibility scores. *Southwestern Naturalist*, **39**, *137–142*.

Palumbi, S.R. (2001) Humans as the world's greatest evolutionary force. *Science*, **293**, 1786–1790.

Pielou, E.C. (1975) *Ecological Diversity*. Wiley, New York.

Pimm, S.L. (1991) *The Balance of Nature?* University of Chicago Press, Chicago.

Power, D.M. (1975) Similarity among avifaunas of the Galapagos Islands. *Ecology*, **56**, 616–626.

Richter, B.D. & Richter, H.E. (2000) Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. *Conservation Biology*, **14**, 1467–1478.

Robinson, S.K. & Holmes, R.T. (1984) Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk*, **101**, 672–684.

Rotenberry, J.T. (1985) The role of habitat in avian community composition: physiognomy or floristics? *Oecologia*, **67**, 213–217.

Rotenberry, J. & Wiens, J.A. (1980) Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate approach. *Ecology*, **61**, 1228–1250.

Schwartz, G. (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.

Sher, A.A., Marshall, D.L. & Gilbert, S.A. (2000) Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conservation Biology*, **14**, 1744–1754.

Smith, D.I. (1998) *Water in Australia. Resources and Management*. Oxford University Press, Oxford.

Swengel, A.B. (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, **10**, 1141–1169.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.

Tilman, D. (2000) Causes, consequences and ethics of biodiversity. *Nature*, **405**, 208–211.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843–845.

Tomoff, C.S. (1974) Avian species diversity in desert scrub. *Ecology*, **55**, 396–403.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.

Walker, B. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Walters, C., Korman, J., Stevens, L.E. & Gold, B. (2000) Ecosystem modeling for evaluation of adaptive management policies in the Grand Canyon. *Conservation Ecology*, **4** (2), online (http://www.consecol.org/Journal/).

Wiens, J.A. & Rotenberry, J.T. (1981) Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs*, **51**, 21–41.

Wiens, J.A., Rotenberry, J.T. & Van Horne, B. (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos*, **48**, 132–147.

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctutating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)*, **96**, 1463–1468.

Received 15 October 2002; accepted 20 February 2003

© 2003 British Ecological Society,