



Predictors of species sensitivity to fragmentation

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Abstract. We reviewed empirical data and hypotheses derived from demographic, optimal foraging, life-history, community, and biogeographic theory for predicting the sensitivity of species to habitat fragmentation. We found 12 traits or trait groups that have been suggested as predictors of species sensitivity: population size; population fluctuation and storage effect; dispersal power; reproductive potential; annual survival; sociality; body size; trophic position; ecological specialisation, microhabitat and matrix use; disturbance and competition sensitive traits; rarity; and biogeographic position. For each trait we discuss the theoretical justification for its sensitivity to fragmentation and empirical evidence for and against the suitability of the trait as a predictor of fragmentation sensitivity. Where relevant, we also discuss experimental design problems for testing the underlying hypotheses. There is good empirical support for 6 of the 12 traits as sensitivity predictors: population size; population fluctuation and storage effects; traits associated with competitive ability and disturbance sensitivity in plants; microhabitat specialisation and matrix use; rarity in the form of low abundance within a habitat; and relative biogeographic position. Few clear patterns emerge for the remaining traits from empirical studies if examined in isolation. Consequently, interactions of species traits and environmental conditions must be considered if we want to be able to predict species sensitivity to fragmentation. We develop a classification of fragmentation sensitivity based on specific trait combinations and discuss the implications of the results for ecological theory.

Key words: Biogeographic traits, Demographic traits, Ecological traits, Empirical evidence, Extinction proneness, Habitat fragmentation, Sensitivity indicators, Testing, Theory

Introduction

The pressures for land use change have led to a steady loss of habitat and to the increasing isolation of habitat remnants throughout the world. Habitat

destruction and fragmentation are the most likely major causes of the increase in the rate of species extinctions in recent decades (Henle and Streit 1990; Groombridge 1992). As fragmentation proceeds, stochastic forces are added to the deterministic declines caused by a dwindling supply of habitat. Even when loss and fragmentation of habitats is halted, there may be a legacy of further species loss due to stochastic extinctions (Shaffer 1981; Belovsky 1987) and the relaxation of communities within the remnants (Diamond 1984; Wilcove et al. 1986; Terborgh et al. 1997). Nevertheless, mounting empirical evidence and intuition tells us that not all species decline towards extinction following habitat fragmentation (e.g., Margules et al. 1994; Jackel and Poschold 1996; Dooley and Bowers 1998; Davies et al. 2000). Some species are at greater risk in fragmented landscapes than others. A better understanding of these differential sensitivities has wide implications for ecological and evolutionary theory and for the setting of priorities and the identification of target species in applied conservation biology (Sieving and Karr 1997; Biedermann et al. 1999).

Theories about population extinction have advanced considerably within the last two decades (Henle et al. 2004 (this issue)). Likewise, an increasing number of controlled fragmentation experiments have now been running for lengthy periods of time (Margules 1996; Laurance and Bierregaard 1997; Debinski and Holt 2000; Laurance et al. 2002), data from uncontrolled land use driven fragmentation experiments become increasingly available (e.g., Soulé et al. 1988; Karr 1990; Laurance and Bierregaard 1997), and experimental additions of plant species in grasslands support a metapopulation-like perspective in the understanding of plant community composition (Tilman 1997). Along with these data a considerable number of hypotheses about the susceptibility of different habitat types to fragmentation and the differential extinction proneness of species have been proposed and related to biological characteristics of the species.

Why analyse species characteristics in relation to fragmentation and extinction and not simply concentrate on particular species? Species that display similar realised niches with respect to multiple environmental factors and similar traits are assumed to behave similarly in the face of environmental change. They can be assigned to 'Functional types' independent of the origin and taxonomy of species (Lavorel et al. 1997). Functional types may be a suitable abstraction to reduce the great diversity of plant and animal species to operational entities for prediction and modelling (Thompson et al. 1996). To tailor functional types to the process of fragmentation, it is necessary to know which traits are sensitive to fragmentation. The purpose of this paper is to review hypotheses on predictors of species sensitivity to fragmentation, their theoretical basis, and the empirical evidence.

Predictors of species sensitivity to fragmentation

For our review we made a search in BIOSIS with the key words ‘fragmentation’, ‘sensitivity’, and ‘ecological traits’ for the years 1999–2000. Starting from these references and our own fragmentation literature databases containing more than 1000 references, we traced back relevant literature cited. We found four groups of theories used for deriving predictive traits and 12 traits (trait groups) that have been suggested as predictors of species sensitivity to fragmentation (Table 1). Whereas theories for demographic traits are based directly on population extinction models, the linkage of other traits with extinction proneness is indirect via their association with demographic traits (Table 1). For each suggested trait we first outline the theoretical arguments, review the empirical evidence, and briefly discuss design problems for experimental testing.

Table 1. Summary of theories used for deriving predictors of species sensitivity to fragmentation and empirical evidence. +: Prediction supported; -: prediction not supported; in parentheses: rare results or rarely tested. For discussion and references see text.

Theory	Sensitivity indicators	Empirical support
Stochastic models of population extinction	Population size	+
	Population fluctuation and storage effects	+
	Dispersal power	+/-
	Reproductive potential/growth rate	+/-
	Annual survival	-
Central place foraging theory	Sociality	(+/-)
Life-history theories; community theories	Body size	+/-
	Trophic position	+/-
	Interaction of trophic position and body size	+/-
	Morphological and physiological traits rendering plants disturbance sensitive	+
	Ecological specialisation, microhabitat use, and matrix presence	+/(-)
Biogeographic theories and fragmentation history	Rarity	+/(-)
	Biome type and fragmentation history	+/-

*Demographic parameters and stochastic population models**Population size*

Theories of stochastic extinction of populations predict higher extinction rates for small compared to large populations because small populations are more vulnerable to the proximate causes of extinction: demographic and environmental stochasticity, genetic deterioration, and social dysfunction (e.g., Goodman 1987; Lande 1993; Pimm et al. 1993; Wissel et al. 1994; Henle et al. 2004 (this issue)). Furthermore, since large populations will have to pass through small size before extinction, this prediction should be very general, with species that exhibit chaotic dynamics being an exception (May and Oster 1976; Gabriel and Bürger 1992). Attempts to detect density dependence in natural populations strong enough to drive species to extinction simply by chaotic dynamics have usually failed (Hassell et al. 1976). The prediction may also fail if populations in habitats with different reproductive quality (Liu 1993) or carrying capacity (Henle et al. 2004 (this issue)) are compared.

Although occupancy patterns of habitat patches and islands of different size provide indirect empirical evidence for the increased survival of larger populations (reviewed by Diamond 1984; see also Sarre et al. 1996; Bolger et al. 1997; Warburton 1997), very few studies have tested this prediction directly. This is due to the fact that in the case of fragmentation driven by land use change and associated habitat clearing, we generally lack any information on population size prior to fragmentation. Likewise, fragmentation experiments usually have not collated information on population size before the start of the experiments (but see Margules 1996).

All but one of the studies directly testing the prediction reported positive results (Table 2). The only exception was an experimental introduction of lizards to islands. In this study persistence probability was independent of population size (Schoener and Schoener 1983). The very short observation time and the very low number of individuals involved make this study a test of the likelihood of individual establishment rather than population extinction, particularly given that the yearly survival rate of the species, if established, was up to 80%.

Design problems were also present in most other studies. In the experiment with the intertidal snail *N. emarginata* (Quinn et al. 1989) population size was confounded with patch size and the same may have been the case in most other studies listed in Table 2. Since theoretical models show that the extinction risk of populations of the same size in patches with different carrying capacity can differ (reviewed by Henle et al. 2004 (this issue)), this confounding is relevant. What is needed are experiments across a sufficient range of population sizes and organisms that control for patch size.

Table 2. Summary of tests of population size as a predictor of species sensitivity to fragmentation. +: Prediction supported; -: prediction not supported.

Species	Type of test	Population size range	Observation period	Result	References
British marine island bird species	Natural populations of known size	1–18 pairs	29–66 years	+	Pimm et al. (1988, 1993); Rosenzweig and Clark (1994)
Big horn sheep (<i>Ovis canadensis</i>)	Natural mountain top populations of known size	Classes of 1–5 to ≥ 100 individuals	10(?)–70 years	+	Berger (1990); Wehausen (1999)
Three lycaenid butterfly species in regularly mown grasslands	Natural subpopulations of known size	25–1500	5 years	+	Settele (1998, unpublished)
Seven species of Bahamian island orb spiders	Natural populations of known size	1– ≤ 1024	6–9 years	+	Schoener and Spiller (1987, 1992)
Bellflower (<i>Campanula cervicaria</i>)	Natural populations of known size	1–240 fertile individuals	8 years	+	Eisto et al. (2000)
Field cow-wheat (<i>Melampyrum arvense</i>)	Natural populations of known size	10–>1000	6 years	+	Matthies (1991)
Eight rare plant species in northern Germany	Natural populations of known size	1 – <3000 (<i>Lepidium campestre</i> , <i>Gentianella germanica</i>); ? for remaining species	10 years	+(7 out of 8 species)	Bräuer et al. (1999)

Table 2. (continued)

Species	Type of test	Population size range	Observation period	Result	References
Bank vole (<i>Clethrionomys glareolus</i>)	Experimental introductions to small islands	2–20	91–113 days	+	Ebenhard (1989)
Rodents (<i>Clethrionomys gapperi</i> , <i>Peromyscus maniculatus</i>)	Experimental introductions to small islands	2–16	2–3 years	+	Crowell (1973)
Lizards (<i>Anolis sagrei</i> ; <i>Leiocephalus punctatus</i>)	Experimental introductions to small islands	5–10	5 years	–	Schoener and Schoener (1983)
Brown algae (<i>Postelsia palmaeformis</i>)	Experimentally seeded populations	1–>120	1 year	+	Paine (1988)
Intertidal snails (<i>Nucella emarginata</i>)	Populations established on different sized plots	2–128	17 months	+	Quinn et al. (1989)
<i>Drosophila hydei</i> , <i>D. pseudoobscura</i>	Experimental laboratory populations	25, 50	18 weeks	+	Forney and Gilpin (1989)
Bean beetles (<i>Callosobruchus maculatus</i>)	Experimental laboratory populations	2–20	Not given	+	Vucetich et al. (2000)

Population fluctuations and storage effects

Theoretical models of population viability generally predict that species unable to maintain stable populations in the face of environmental vagaries (species with high population fluctuations) may be prone to local extinction (e.g., Leigh 1981; Lande and Orzack 1988; Wissel et al. 1994; see also Henle et al. 2004 (this issue)). Whereas a number of studies implicated population fluctuations as a predictor of sensitivity without separating it from other potential factors (e.g., Forney and Gilpin 1989; Pollard and Yates 1992; Thomas et al. 1994), few studies have directly tested this prediction (Table 3). These tests have yielded variable, controversial results. The hypothesis was supported by a study controlling variability experimentally and by a study that measured population variability for the same length of time for extant and extinct species. For another study, the British island bird populations, controversy about statistical procedures and the interpretation of results exists (Pimm et al. 1988; Tracy and George 1992; Rosenweig and Clark 1994). However, a reanalysis of the data with the Cox proportional hazard model by Vucetich et al. (2000) did provide support for a positive relationship.

The animal studies that did not support the hypothesis compared the standard deviation or the coefficient of variation of population size between extant and extinct populations. However, this approach can yield statistical artefacts, including negative relationships, because population viability tends to be underestimated for populations with short persistence times (Vucetich et al. 2000). Simulation studies showed that the probability of these artefacts dramatically increased as the extinction risk threshold for data inclusion decreased. For an extinction risk threshold of less than one extinction within 6 years, the power of the test for a positive relationship approached an asymptotic maximum (Vucetich et al. 2000).

Vucetich et al. (2000) regarded a significant relationship in extant populations between an arbitrary quasi-extinction level and population fluctuation as further support for the hypothesis. However, such a conclusion is problematic because of the strong interactions between extinction sensitivity, quasi-extinction levels, and type and strength of density regulation (Henle et al. 2004 (this issue)).

In plants, the storage of reproductive potential across generations can promote persistence even if variance in the recruitment rate is high (Higgins et al. 2000). Storage effects (Warner and Chesson 1985) relate to life history features such as long life span and iteroparity or clonal propagation and nutrient recycling in plants. These traits may cause population inertia, that is, enable organisms to build up remnant population systems in which local populations persist over long periods of unfavourable environmental conditions and low recruitment rates (Eriksson 1996). If storage of reproductive potential across

Table 3. Summary of test results reported for the relationship of population variability and extinction risk. +: Positive relationship; 0: no significant relationship; -: negative relationship; CV: coefficient of variation; SD: standard deviation.

Organisms	Type of comparison	Results	References
Experimental laboratory populations of bean beetles (<i>Callosobruchus maculatus</i>)	Experimental variation of mortality risk in laboratory populations	+	Vucetich et al. (2000)
Birds on Barro Colorado Island (BCI)	Comparison of CV in capture rate at nearby sites on the mainland for species extinct and extant on BCI	+	Karr (1982a)
British marine island bird species	Cox regression model of time to extinction as dependent and CV in number of pairs as independent variable	+, 0, controversy	Pimm et al. (1988); Tracey and George (1992); Vucetich et al. (2000)
Five Neotropical small mammal species	Relationship of extinction rate and SD of size of subpopulations	-	Lima et al. (1996)
Four orb spiders on Bahamian islets	Relationship of extinction rate and SD/CV of population size	-, 0 (+ when zero counts were included)	Schoener and Spiller (1992)
Experimental populations of <i>Daphnia</i>	CV of population size in extant versus extinct populations	+, 0	Bengtsson (1989); Bengtsson and Milbrink (1995)

generations is possible, the rate of increase of a population is influenced more by favourable periods than by periods with no recruitment. In declining populations, storage effects may drastically extend the time to extinction. On the other hand, if no storage is possible, populations may be prone to extinction if a sequence of years with no recruitment occurs. In this case, the unfavourable periods control population dynamics (Higgins et al. 2000).

A prolongation of unfavourable periods between successional stages suitable for recruitment by land use change has been called fragmentation in time (Poschlod et al. 1998). Examples are mowing regimes in grassland that are interrupted by set aside periods (Kieffer and Poschlod 1996). Farmers have used extensive crop rotations to prevent weeds from germinating, i.e. they created extended temporal windows with unsuitable growing conditions for weeds associated with a certain crop. Seed bank longevity creates storage effects, as it allows plants to overcome long periods with unsuitable conditions for germination. Comparisons of vegetation samples of 1950 and 1985 in Switzerland revealed that plants with a persistent seed bank had lower extinction rates in remnants of dry grasslands (Stöcklin and Fischer 1997). Dormancy applies also to other classes of organisms. Species inhabiting ephemeral pools such as some Crustacea are known to remain dormant in the sediments until seasonal rains fill the basins (Hildrew 1985). The relative extinction proneness of animal species with and without such storage effects remains to be studied under increased anthropogenic isolation of habitats.

Dispersal power

In classic metapopulation theory, subpopulations living on isolated patches periodically go extinct and patches are recolonised by individuals migrating from other patches (Levins 1970). The risk of extinction of a metapopulation increases with the correlation of environmental fluctuations of the subpopulations and decreases with dispersal power (e.g., Frank et al. 1994; Settele 1998). Furthermore, the rescue effect may save populations from extinction (Brown and Kodric-Brown 1977) and dispersal power also increases the persistence chance of spatially structured populations of territorial species (Lande 1987). Individual based models of spatially structured populations of territorial species also predict that extinction proneness should decrease with dispersal power (reviewed by Henle et al. 2004 (this issue)). Thus, species with high dispersal power, enabling them to rescue or recolonise distant patches beyond the distance of correlated environmental fluctuations, should have a lower extinction risk in highly fragmented habitats. Since metapopulation survival is optimal if habitat patches are as close as possible but still outside the range of correlated environmental fluctuations (Frank et al. 1994), dispersal power as a predictor of fragmentation sensitivity should be scale-dependent.

Beneficial effects of dispersal power may be negated because mobile species tend to have larger individual home ranges (Mühlenberg et al. 1991). In this case, the same amount of remaining habitat will support fewer individuals. The smaller population size in turn should increase extinction risk (see above). Tilman et al. (1997), Huxel and Hastings (1998), and Vos et al. (2001) considered these interactions between natural abundance and dispersal in theoretical models but reached different conclusions. Whereas Huxel and Hastings (1998) found that the combination of abundance and dispersal ability was important, the models of Tilman et al. (1997) and Vos et al. (2001) suggested that dispersal ability, respectively, population size alone were overriding. The conclusions of these models depend on specific assumptions, for the former two models in particular that the community is structured by a trade-off between dispersal and competitive abilities (see also section *disturbance related traits, competitive ability, and fragmentation sensitivity*). In the model of Vos et al. (2001) patches supported at least 50 reproductive units of the species with low individual area requirements but only 1–16 units of species with large individual area requirements. In such small subpopulations extinction rates are high, so that colonisation potential is low even if dispersal power is high (Frank et al. 1994).

Empirical studies show a lack of correlation between dispersal power and fragmentation sensitivity or scale-dependent effects (Table 4). Most deviations from theory can be explained by interactions with other traits or scale effects. A large set of the sensitive migratory North American bird species depend on the forest interior and have low reproductive rates, whereas most non-migratory species are not restricted to the forest interior and show higher reproductive rates (Lynch 1987; Whitcomb 1987). In the case of the grassland snails and butterflies the scale of habitat fragmentation was too coarse or too fine to be perceived as fragmentation by these organisms (Bahl et al. 1999), confirming the prediction of a spatially explicit simulation model of Fahrig (1998) that predicted that fragmentation effects should be low for species with low or high dispersal power and maximum at intermediate dispersal power.

A problem not as yet accounted for in deriving and testing dispersal power as a predictor of fragmentation sensitivity is that the dispersal process is not only influenced by dispersal power but also by the dispersal rate (sometimes confused with dispersal power) and colonisation probability once a patch is reached. Dispersal power may or may not be related to these other components of the dispersal process and theoretical models show that in strongly fragmented habitats an increased dispersal rate reduces persistence chances of metapopulations if dispersal power is limited and dispersal mortality occurs (Casagrandi and Gatto 1999). A further problem in empirical

Table 4. Summary of tests of dispersal power as a predictor of species sensitivity to fragmentation. +: Prediction supported; -: prediction not supported.

Organisms	Type of comparison	Sensitivity	References
Australian rainforest birds	Six classes of movement patterns from sedentary to migratory	–	Warburton (1997)
British marine island birds	Migratory versus non-migratory species	–	Pimm et al. (1988, 1993)
North American forest birds	Migratory versus non-migratory species	–	Lynch (1987); Whitcomb (1987)
Temperate grassland invertebrates	Three different mobility classes (incidence data and simulation models)	– (snails and butterflies); + (species of intermediate mobility)	Bahl et al. (1996, 1999); Samietz et al. (1996)
Temperate grassland plants	Small seeded versus large seeded species in experimental fragments	+	Robinson and Quinn (1988)
Temperate grassland plants	Clonal versus non-clonal species in small experimental patches	Clonal species persisted better and, in contrast to non-clonal species, showed sensitivity to patch size	Robinson et al. (1992)
Tropical tree species	Zoochorous versus barochorous species	+ (interaction of dispersal power and scale of landscape structure)	Metzger (2000)

studies is the use of the observed presence in the matrix as a surrogate for dispersal power, since this surrogate potentially confounds dispersal power with habitat specialisation. Therefore, the use of this surrogate parameter is discouraged unless it can be ascertained that only migrating individuals are present in the matrix (but see the chapter *microhabitat specialisation and matrix use*).

In addition, for plants on the scale of real landscapes, dispersal power depends on their dispersal agents (e.g., wind, animals, man; Bonn and Poschlod 1998). In a landscape of fragmented habitats, transport agents of plant dispersal may become extinct or change the targeting of new and suitable habitats, and effects of fragmentation on the transport agents will be carried onto the dependent plant species. Several studies showed that the loss of traditional land use practices resulted in the loss of seed dispersal processes in landscapes (Fischer et al. 1996; Strykstra et al. 1997). In effect, loss of dispersal agents leads to increasing fragmentation even if the spatial configuration and quantity of suitable habitats remain unchanged. Likewise, vertebrate dispersed rain forest plants are more sensitive to fragmentation than species with other dispersal modes (Laurance and Bierregaard 1997; Tabarelli et al. 1999). Transport of seeds relates to several plant traits such as dispersal unit morphology, mass, size, and shape; releasing height and terminal velocity of the dispersal unit; attachment, digestion survival, and floating capacity (see Poschlod et al. (2000) for details on these traits). Wind-dispersed seeds are at a high risk of falling on unsuitable patches (Salisbury 1976).

Reproductive potential and annual survival/longevity

Reproductive potential and annual survival/longevity are tightly linked life-history traits (Stearns 1976; Roff 1992) and there is at least a threefold influence of reproductive potential on the extinction proneness of species. High reproductive potential may increase the number of emigrants, it may enhance the chance of successful colonisation by facilitating a fast increase to a save population size, and, depending on other traits, it may decrease or increase population fluctuations.

Reproductive potential or/and annual survival have been suggested as predictors of habitat sensitivity by Karr (1990), Noon and McKelvey (1996), and Sieving and Karr (1997). Noon and McKelvey (1996) argued that, besides low vagility, species with low reproductive potential should be particularly sensitive to fragmentation, implicitly assuming that the number of successful colonisations is a function of fecundity. In contrast, Karr (1990) and Sieving and Karr (1997) postulated that species with low annual survival should be more sensitive to fragmentation than species exhibiting high

survival. Since species with a low annual survival must have a high reproductive potential, this implies that species with high reproductive potential should be more extinction prone than species with low reproductive potential. As a causative mechanism Sieving and Karr (1997) assumed that species with low annual survival should be particularly sensitive to additional mortality that is likely to occur in fragments due to the release of medium-sized predators from the effects of large predators (Terborgh 1974; but see below under the traits *body size, trophic position, and their interactions*). They further argued that a higher fecundity is required to balance increased mortality in fragments due to nest predation or inbreeding. They did not test their hypothesis with a theoretical model and to our knowledge no theoretical comparisons of the relative effect of increased mortality on persistence for populations that differ in annual mortality have been published. However, it is well known that populations of long-lived species with low adult mortality are particularly sensitive to slight changes in adult mortality (e.g., Jonsson and Ebenman 2001; Wiegand et al. 2001). Therefore, we might expect the opposite relationship than the one assumed by Karr (1990) and Sieving and Karr (1997).

Both hypotheses and their assumptions have received only limited attention. Evidence in support of the hypothesis and assumption of Noon and McKelvey (1996) is available from a plant study, but results from animal studies either do not conform with the prediction or with the assumed underlying mechanism (Table 5). For plants with passive dispersal, the probability of hitting a suitable habitat patch is higher the more propagules per mother are involved in the dispersal lottery. Propagule number relates to dispersal success all the more if transport agents, such as wind, are relatively unspecific with respect to the targeting of suitable habitats. In the animal studies supporting the prediction confounding or interactions with other parameters, such as habitat specialisation in the case of the North American bird species (compare Whitcomb 1987), cannot be excluded.

There is no support for annual survival as a predictor of fragmentation sensitivity, in spite of Karr (1990) reporting a statistical difference in mean annual survival measured on the mainland for those forest bird species that are not present on Barro Colorado Island. However, if those species that were never observed on Barro Colorado Island are excluded from his list of extinct species, mean annual survival is not statistically different for extant and extinct species (0.59 ± 0.02 , $n = 17$ and 0.53 ± 0.15 , $n = 5$, respectively; one-tailed t -test: $t = 1.58$; $\alpha > 0.05$). There is also no indication of a difference in annual survival for species that survived or became extinct on Barro Colorado Island in a more recent data set (Table 11.2 in Sieving and Karr 1997). Longevity also did not explain extinction proneness of reptiles on Aegean land-bridge islands (Foufopoulos and Ives 1999).

Table 5. Reproductive potential as a predictor of species sensitivity to fragmentation and its correlation with dispersal power. +: Prediction supported; -: prediction not supported.

Organisms	Correlation with dispersal power	Sensitivity	References
Two common and two rare dry grassland plant species	Positive correlation of clonal and sexual reproductive potential with probability of occurrence in potential habitats	+	Jackel and Poschlod (1996)
North American forest birds	Reproductive potential negatively correlated with migratory power	+	Whitcomb (1987)
Australian rainforest avifauna	Not given	+	Warburton (1997)
Terrestrial insectivorous birds on Barro Colorado Island, Panama	All included species have low dispersal power	+? (not tested statistically due to low number of species)	Sieving and Karr (1997)
Australian subtropical forest mammals	The problematic surrogate 'presence in the matrix and in corridors' not correlated to fecundity	-	Bentley et al. (2000)

Sociality and central place foraging theory

Recher et al. (1987) postulated that social or gregarious species should be particularly sensitive to fragmentation and Reed (1999) assumed that lek mating and social facilitation makes birds extinction prone. Recher et al. (1987) derived their hypothesis from the concept of central place foraging, which is a part of optimal foraging theory. Central place theory predicts that the greater the number of individuals occupying the same central place, the greater the area required for supplying food for the group. Recher et al. (1987) assumed that this requirement would translate into increased sensitivity to fragmentation. Neither Recher et al. (1987) nor Reed (1999) provided a theoretical justification for their assumptions. Implicitly, they may have assumed that gregarious species require a larger minimum area of contiguous habitat than solitary species. However, stochastic population models show that small populations consisting of very few solitary individuals have a very high extinction risk unless they form part of a patchy but large population or are replenished regularly from a source population (Goodman 1987; Wissel et al. 1994). Gregariousness does have different underlying causes, such as limited dispersal in sessile organisms, reproductive facilitation, or predator avoidance (Allee et al. 1949; Hawkins 1994; Tullberg and Hunter 1996; but see Hoffmeister and Rohlf 2001). These factors may lead to demographic differences between gregarious and solitary species, for example, differences in density regulation and population fluctuation, that may carry different extinction risks, but such relationships have not been explored as yet.

Recher et al. (1987) supported their argument with the greater sensitivity of the social yellow-bellied glider (*Petaurus australis*) to forest fragmentation compared to the solitary greater glider (*Petauroides volans*). Unfortunately, the analysis was not extended to the other arboreal marsupials present in the study region. However, the social Leadbeater's possum (*Gymnobelideus leadbeateri*) is also more sensitive to fragmentation than the solitary mountain brush tail possum (*Trichosurus caninus*) (Lindenmayer and Lacy 1995a,b). In contrast to the social marsupials, gregarious trap-door spiders (Mygalomorphae) species persist better in habitat fragments in the Western Australian wheatbelt than solitary species (Main 1987). Likewise, the gregarious spider *Eresus cinnaberinus* is less affected by fragmentation of dry grassland habitats in Germany than many, but not all, non-gregarious arthropod species (Biedermann et al. 1999). In a stochastic population model, social structure influenced persistence probability for monk seals (*Monachus monachus*), but not for roan antelopes (*Hippotragus equinus*) or gorillas (*Gorilla gorilla*) (Durant and Mace 1994). Thus, no clear relationship of sociality

and fragmentation sensitivity emerges from the limited number of available studies.

Ecological traits and extinction theories

Four different ecological traits or trait groups (body size, trophic position, disturbance sensitive traits, specialisation) and various interactions between them have been suggested as predictors of species sensitivity to fragmentation. All of these traits have been linked indirectly to extinction proneness based on their (assumed) relationship with one or several demographic parameters that have been shown to influence extinction risks in stochastic population models. Some of these ideas have been expanded into theories that relate life-history traits to extinction proneness and community structure following fragmentation: the mesopredator release hypothesis and the hypothesis of edge effects and parasitism. Since these theories, as well as body size, community structure, and trophic position are tightly interrelated, we discuss them together in this section.

Body size, trophic position, and their interactions

It has often been claimed that large-bodied species are at a greater risk of extinction than small-bodied species (Belovsky 1987; Gaston and Blackburn 1996a). However, theoretical arguments can also be made for a reduced risk, or for the lowest extinction risk, for species of intermediate size (Johst and Brandl 1997). Species at the top end of food chains are often large in body size. Therefore, and because species at higher trophic levels are usually the taxa with lower population densities, they are regarded as more extinction prone than those at lower levels (Gard 1984). Some authors further assume that species at the top end of the food chain tend to have more unstable population dynamics and therefore should be less likely to persist in a fluctuating environment (Pimm and Lawton 1977; Lawton 1995; Holt 1996). These ideas have been expanded into two related hypotheses on the effects of life-history traits on community structure in fragmented habitats. For tropical forest fragments, Terborgh (1974) hypothesised a loss of top-predators that will lead to increased population sizes of medium-sized predators ('mesopredator release') that in turn will cause a demise of predation sensitive bird species. Along similar lines it has been argued that forest fragmentation, especially edge effects, will favour medium-sized generalist predators and nest parasites and lead to the demise of predation and host sensitive bird species of the forest interior (Lynch 1987; Rosenberg et al. 1999). Extending these ideas, one can hypothesise that predator sensitive species with traits rendering them insensitive to habitat fragmentation should survive better in

smaller than in medium-sized remnants because predators should be absent in small fragments – unless they are broad habitat generalists.

The theories above do not link body size and trophic position to extinction risk directly. The link is indirect via correlations with three demographic variables, abundance, population fluctuations, and population growth rate, which in turn are correlated with extinction risk. However, the relationships between body size and trophic position with these parameters are variable. First, the relationship between body size and abundance has received much attention without a clear pattern emerging (Blackburn et al. 1992, 1993, 1994; Cotgreave 1993; Blackburn and Gaston 1994; Gaston and Blackburn 1995, 1996a,c,d; Cyr et al. 1997). Recent evidence suggests that the spatial scale of the study may be crucial. Studies at local spatial scales rarely find a relationship between body size and abundance, whereas studies at regional scales often find negative linear relationships (Blackburn and Gaston 1997). Second, opinions about body size and population fluctuations are contentious (Johst and Brandl 1997). Some theories assume that populations of large-bodied animals fluctuate less than populations of small-bodied animals and therefore predict that large species are less likely to fluctuate to extinction [reviewed by Pimm (1991) and Cook and Hanski (1995)]. Others argue that neither empirical evidence nor logic support this prediction (Schoener and Spiller 1992; Tracy and George 1992) and that fluctuations are only likely to lead to extinction when populations are uncharacteristically small (Chesson 1991; but see Wissel et al. 1994). Third, because small species recover faster from low numbers than large species, they could be at lower risk of extinction (Wissel et al. 1994). On the other hand, large body size is also associated with longevity, which, like a storage effect, could also lower extinction risk (Pimm et al. 1988).

The action of these variables in combination probably contributes to the fuzziness of the body size versus population decline relationship (Lawton 1994). That is, the positive correlation between body size and extinction risk, due to population abundance and rate of recovery (Cotgreave 1993; Lawton 1994), is offset by the negative correlation between body size and extinction risk, due to population fluctuation (Pimm 1991). In addition, the presence of both environmental stochasticity, causing population fluctuations that are correlated to body size, and catastrophes that reduce the population size by a fixed relative amount independent of population size have been predicted to favour the persistence of species of intermediate size (Johst and Brandl 1997).

Empirical studies focused on correlative analyses of body size and extinction risk in mammal or bird communities. They report a range of findings including positive, negative, and no relationships between extinction risk and body size (e.g., Terborgh and Winter 1980; Pimm et al. 1988;

Soulé et al. 1988; Burbidge and McKenzie 1989; Laurance 1991; Kattan et al. 1994; Rosenzweig and Clark 1994; Angermeier 1995; Gaston and Blackburn 1996b; Bentley et al. 2000; for reviews see Gaston and Blackburn 1996a; Foufopoulos and Ives 1999). In one of the only studies to examine the effect of body size on extinction risk in an experimental setting, Davies et al. (2000) found no relationship between beetle body size and population decline in forest fragments compared to control populations in continuous forest.

Recently, it became apparent that the relationship of body size and extinction risk can also depend on the time-scale considered. In the pre-war period 1923–1949, extant Singapore forest bird species were significantly smaller than species that had gone extinct. No significant difference was found for the post-war period 1949–1998 or the whole period 1923–1998 (Castelletta et al. 2000). This observation suggests that large-bodied species are particularly sensitive in the early stages of habitat loss, but that the effects are more evenly distributed in more advanced stages of habitat loss. This hypothesis is supported by a significant relationship between body size and relative time to local extinction in North American sage scrub birds (Crooks et al. 2001).

The results from studies linking extinction risk and trophic level are also mixed. In laboratory microcosms of protozoa and bacteria, prey went extinct more often than predators (Lawler 1993). Likewise, predatory beetle species were less sensitive to fragmentation than detritivores in the Amazonian rainforest fragmentation experiment (Didham et al. 1989). The opposite was the case in a temperate forest fragmentation experiment in Australia; and herbivores also declined significantly less than predators (Davies et al. 2000). When the effects of fragment size and edges were considered, predators declined most at small fragment edges and least in large fragment interiors (Davies et al. 2001). In boreal forest fragments, the proportion of predatory species of small mammals also declined with decreasing species richness, the proportion of insectivores remained constant, and the proportion of herbivores increased (Patterson 1984). Similar relationships were obtained for extant mammals in fragmented tropical rainforests in Australia (Laurance 1991). In contrast, in a study incorporating data from five different surveys of vertebrates and plants, there was no tendency for species in any trophic group to go extinct more often than any other (Mikkelsen 1993). Similarly, Warburton (1997) did not find any relationship of trophic position and sensitivity to fragmentation in an Australian rainforest avifauna, and results were also inconsistent across different taxonomic groups in the Amazonian rainforest fragmentation experiment (Laurance et al. 2002).

In line with the fuzzy relationships between trophic position, body size, and extinction proneness is the evidence for the mesopredator release and related hypotheses, rendering the issue still generally controversial [compare

Terborgh (1999) with Schwartzman et al. (2000)]. For example, Crooks and Soulé (1999) showed a decline in activity of the top predator coyote (*Canis latrans*) in small sage-scrub fragments close to urban areas and a release (increased activity) of human tolerant mesopredators (especially domestic cats and non-native opossums). However, when larger control sites more distant to urban areas were included, several native mesopredator species were more fragmentation sensitive than the coyote (Crooks 2002). Though nest predation is higher on Barro Colorado Island than on the neighbouring mainland, contributing to the high sensitivity of terrestrial ground nesting birds to fragmentation, data on mesopredator release are inconclusive (Sieving and Karr 1997). In contrast, in an Australian rainforest avifauna, vulnerability of nests to predation was not significantly related with sensitivity to fragmentation (Warburton 1997). A review and meta-analysis of avian nest predation in temperate habitat fragments showed complex relationships. Predator effects were more prevalent in tests conducted at the landscape than at the local scale, in agricultural landscapes than in predominantly forested landscapes, and for avian predators than for mammalian predators (Chalfoun et al. 2002). Also, predator response to fragmentation was not consistent across geographic regions.

Sensitivity to brood parasitism also has been related frequently to avian fragmentation sensitivity. For example, Lynch (1987) reported that in North American bird species nest parasitism declined with increasing distance from forest edges and that it was virtually non-existent in the interior of very large forest tracks. However, as for mesopredators, there is amounting evidence that brood parasitism is highly variable across regions even when the degree of fragmentation is similar (e.g., Rosenberg et al. 1999).

The hypothesis that species with traits rendering them fragmentation insensitive should survive better in smaller than in larger forest fragments because of an absence of predators has not been addressed thoroughly in empirical studies, but native forest snails and wild pigs in New Zealand may corroborate this idea. Snails are insensitive to fragmentation (Bahl et al. 1996), wild pigs occur in most large but in few small forest patches, and the survival of the large land snail *Paryphanta busbyi* appears to be more assured in small than in large remnants (Ogle 1987).

The failure of a clear pattern to emerge from the empirical literature is perhaps not surprising given the complexity of the relationship between extinction risk, body size, and trophic position. For future studies, we recommend that data on body size, trophic position, abundance, population growth rate, and population fluctuations as well as data on the spatial and temporal scale of habitat loss should be collected and analysed simultaneously. Otherwise, it is unlikely that a clearer pattern and understanding will emerge.

*Disturbance related traits, competitive ability,
and fragmentation sensitivity*

Fragmentation of habitats often causes drastic changes in resource dynamics and disturbance regimes (Saunders et al. 1991; Kleyer et al. 1996; Cadenasso et al. 1997; Laurance et al. 2002), and the competitive ability of plants is tightly linked to the resource dynamics of their habitats (Goldberg 1996; Kleyer 1999). Competitive ability is a major function for both exclusion risk and recolonisation chance, and disturbances can impede the enforcement of competitive hierarchies by temporarily breaking dominance. In her meta-analysis of 21 multi-species competition experiments, Goldberg (1996) found that competitive hierarchies are consistent among different competitors. Increasing disturbance intensity can lead to local extinction if regeneration is no longer possible (Huston 1979).

Since competitive ability and response to disturbance are two main factors associated with the persistence of plants, traits related to disturbance sensitivity and competitive ability should also be suitable indicators for plant species' sensitivity to fragmentation. In recent theoretical work, Tilman et al. (1997) assumed that abundant species are good competitors but poor dispersers because of larger seeds. They predicted that they are most at risk of extinction in a fragmented landscape. Although a trade-off between dispersal power and seed size promoting local competitive advantage exists in many plants (Stykstra et al. 1997; Eriksson and Jakobsson 1999), this relationship does not hold generally. In dry grassland some abundant plant species are also better dispersers than rare species (Jackel and Poschlod 1996). Moreover, the relationship between dispersal power and seed size is only valid for wind dispersal. Other dispersal vectors such as animal transport or transport by man should not be sensitive to seed size. Likewise, several butterflies, such as *Maculinea nausithous* (Settele 1998) or the migratory species *Vanessa cardui*, *Vanessa io*, or *Aporia crataegi* (Eitschberger et al. 1991), are more common and have better dispersal power than less common sympatric species. Tilman et al. (1997) introduced the assumption of a negative relationship between abundance and dispersal power to allow co-existence of competitors in metapopulations. However, Iwasa and Roughgarden (1986) showed that co-existence is also possible if there is a source habitat in which each species outcompetes all others. Furthermore, McCarthy et al. (1997) showed that the model of Tilman et al. (1997) is valid only when patches are destroyed at random and the remaining patches remain unaltered. This is an unlikely scenario for real landscapes. They also compiled evidence that competitively inferior bird and mammal species were more fragmentation sensitive than dominant species.

Studies on tropical trees in forest fragments (e.g., Benitez-Malvido 1998; Laurance et al. 1998, 2002; Tabarelli et al. 1999; Metzger 2000) fit well with the idea that traits related to disturbance sensitivity and competitive inferiority should also be suitable indicators of fragmentation sensitivity. These studies showed that shade-tolerant species are fragmentation sensitive because an increased mortality, lower growth rate, and lower dispersal capability compared to edge species lead to a competitive disadvantage under the modified light and increased disturbance regimes that dominate a larger percentage of the area in small compared to large fragments. For plants in other habitats, and for animal communities in general, the hypothesis remains to be systematically tested. Notwithstanding, Leach and Givnish (1996) showed that plant species characterised by traits (small-seeded, short, and nitrogen fixing) making them competitively inferior in the absence of disturbance by fire, are most sensitive to the fragmentation of prairies.

The association of traits with the competitive ability of plants has been analysed in a large body of observational and experimental studies (e.g., Troll 1937–1943; Ellenberg 1950; Grime 1973; Goldberg 1996; Kleyer 1999). The competitive effect depends mainly on the lateral and vertical expansion of the mature canopy, the rate at which the canopy is formed, and its seasonal duration (reviewed by Goldberg 1996). These general traits encompass a range of different, yet often correlated, characters of plant morphology, life history, and physiology (Grime et al. 1988; Kleyer 1999; see Poschlod et al. (2000) for a compilation). Traits associated with competitive response are more diverse depending on the productivity of the environment. Under productive conditions high foliar concentrations of mineral nutrients and attributes of the vertical expansion in time and space were strongly correlated with the capacity for rapid growth for 43 species in the Sheffield region (Grime et al. 1997).

A checklist of traits related to disturbance sensitivity of plants is given in McIntyre et al. (1999). In temperate environments mainly annuals will survive if disturbance impacts reach deeply below the soil surface several times a year. With disturbance intensity declining, perennial plants may survive by means of vegetative regeneration.

Ecological specialisation, microhabitat use, and matrix presence

As for other ecological traits, specialisation, microhabitat use, and matrix presence are not directly linked to extinction proneness but they are linked to two other variables, population abundance and variability, which in turn are related to extinction risk. Terborgh and Winter (1980) and Patterson (1987) suggested that species dependent on resources likely to be variable and/or

patchy in their distribution are prone to extinction. Tracking of those resources in space results in a locally variable population size for such species. Theory predicts that species that are unable to maintain stable populations under environmental vagaries are more extinction prone (see above). However, species depending on naturally patchily distributed resources should also have evolved strong dispersal powers and theory predicts that such species should have lower extinction risks than species with limited dispersal power (see above) and both forces may balance each other.

Specialists are likely to have a more discontinuous distribution than generalists. Therefore, they should have a higher extinction risk because the chance that they and their niche are represented in the remaining fragments should be smaller than for generalists. In addition, populations sampled by (non-homogeneous) fragments should be smaller for specialists than for common species (Sarre et al. 1996; Andr n et al. 1997). Furthermore, habitat fragmentation leads to abiotic changes (Saunders et al. 1991; Cadenasso et al. 1997) that in turn may affect habitats more strongly for specialists than for generalists.

Empirical evidence for the influence of ecological specialisation and microhabitat use on extinction proneness is mainly based on forest fragmentation studies. Most of these studies support the hypothesis that these traits are linked to extinction proneness, though the mechanisms vary and are not always clear (see e.g., Laurance et al. 2002). Several studies showed sensitivity of microhabitat specialists to fragmentation due to the effects of habitat sampling by small fragments and/or structural habitat changes in small remnants and corridors (Table 6). Unwillingness or inability to cross even small forest gaps can be a further mechanism, for example, for understory birds and for strictly arboreal non-flying species. For North American forest interior species increased parasitism and predation are the main causative mechanisms implied, but this issue remains controversial (see above). Also, studies on single highly endangered species such as the red-cockaded woodpecker (*Picoides borealis*) (Haig et al. 1993) or the spotted owl (McKelvey et al. 1993) have shown that the absence of suitable microhabitat and limited dispersal may be main factors determining their sensitivity to forest fragmentation. The absence of suitable habitat may be a generally relevant factor for the fragmentation sensitivity of North American forest interior species. Studies on reptiles also support the hypothesis of an increased extinction sensitivity of specialists (Sarre et al. 1996; Foufopoulos and Ives 1999).

For other guilds observations are inconsistent. Monodiet guilds and especially insectivorous bird species were more extinction prone than multidiet guilds in Singapore rainforests (Castellatta et al. 2000). In contrast, the distribution of species extinct on Barro Colorado Island across food guilds did not

Table 6. Summary of fragmentation-sensitive ecological guilds/specialists.

Organisms analysed	Sensitive species/guilds	Mechanism	References
Mammals and birds of eastern Australian forests	Habitat specialists, especially species depending on old-growth forests with large hollow trees	Essential microhabitat rarely present in small fragments, corridors, and the matrix	Recher et al. (1987); Lindenmayer et al. (1990); Bentley et al. (2000)
Tropical forest trees	Shade tolerant species	Physical habitat change leading to competitive exclusion; increased disturbance and mortality towards edges	Benitez-Malvido (1998); Laurance et al. (1998, 2002); Tabarelli et al. (1999); Metzger (2000)
Arboreal geckos in forest remnants in Australia	The habitat specialist <i>Oedura reticulata</i>	Preferred trees less frequently present in small fragments, absence of stepping stones in the matrix, and (presumably) lower dispersal rates	Sarre et al. (1995)

Table 6. (continued)

Organisms analysed	Sensitive species/guilds	Mechanism	References
Tropical forest birds	Terrestrial (understory) species	Unwillingness to cross even small forest gaps	Kattan et al. (1994); Stouffer and Bierregaard (1995); Sieving and Karr (1997); Castellatta et al. (2000); Laurance et al. (2002)
Tropical forest birds and insects	Large canopy frugivores; obligatory ant-followers; euglossine bees	Habitat specificity and dependence on keystone resources assumed	Willis (1979); Kattan (1992); Restrepo et al. (1997); Laurance et al. (2002)
North American forest bird species	Forest interior species, especially Neotropical migratory species	Parasitism and predation (but see text)	Lynch (1987); Whitcomb (1987)

differ from the distribution expected based on the species composition on the adjacent mainland (Karr 1982b).

In many empirical studies the importance of matrix use as a predictor of fragmentation sensitivity is pointed out and it is suggested that specialists have a low tolerance for the modified habitat matrix surrounding remnants (e.g., Whitcomb 1987; Klein 1989; Laurance 1991; several authors in Laurance and Bierregaard 1997; Gascon et al. 1999; Bentley et al. 2000). There are at least two problems with this assumption. First, the absence of a species in the matrix does not mean that these species are more specialised than those present in the matrix, unless a sufficient number of different types of matrices have been studied. Species may perceive landscapes differently than humans and habitats are not fragmented for those species that reproduce in the matrix. Such species may still be fragmentation sensitive if land use alters the matrix in such a way that their habitat becomes fragmented. Second, though absence in the matrix can be used as an *a posteriori* explanation of fragmentation sensitivity, it cannot be used to predict and identify *a priori* which species will be fragmentation sensitive before the fragmentation has taken place. Therefore, a key issue is measuring the degree of specialisation that avoids these problems. Sarre et al. (1996) suggested the use of the number of occupied (micro-)habitats and the variance of density across (micro-)habitats in non-fragmented landscapes as such a measure. Mac Nally and Bennett (1997) argued for a similar alternative: to combine maximum density within a habitat and an index of habitat similarity into an index of ubiquity. These approaches, together with quantitative habitat models, should allow a better separation of the effects of sampling and environmental modifications occurring in habitat fragments on the relationship between specialisation and extinction proneness, independent of a specific type of matrix.

In addition, testing with empirical data the hypothesis that specialists depending on patchily distributed resources should fluctuate more than generalists and therefore are more extinction prone, runs into problems of scale (McArdle and Gaston 1993). Whereas it is likely that such species fluctuate strongly on a local scale, they may be fairly stable on a broader scale. Most empirical studies are carried out on a local scale and thus are likely to suggest strong fluctuations, whereas in reality the populations analysed may be quite stable. For these reasons, it is not surprising that patterns of extinction and indicators of sensitivity to fragmentation are scale-dependent (e.g., Metzger 2000).

Biogeography and fragmentation history

It is widely believed that biogeographical factors are associated with the vulnerability of species and communities to fragmentation. The biogeographical

range of a species plays a direct decisive role if its extent coincides with the history of human occupation and large-scale land use changes. For instance, EU agricultural policies lead to similar land use changes across the total European Union. Species dependent on semi-natural grasslands with a range confined to the European Union are at risk of extinction because abandonment of semi-natural grasslands has taken place from northern Sweden to Sicily. Globally, habitats on fertile soils are those that have suffered greatest loss and fragmentation (e.g., Usher 1987; Whitcomb 1987). North American prairie fragments in the most productive environments showed higher species loss than fragments in less productive environments (Leach and Givnish 1996).

Biogeographic factors are also thought to be suitable as predictors of community sensitivity to fragmentation because of the linkage of species distributions and rarity with dispersal power and specialisation. In the following, we review hypotheses about the effects of rarity, biogeographical position, and fragmentation history on fragmentation sensitivity.

Rarity

Rarity takes several forms (Rabinowitz et al. 1986; Fiedler and Ahaus 1992) but these distinctions are not always made clear when examining the suitability of rarity as a predictor of the extinction proneness of species. In this section we discuss the most frequently used form of rarity: species that are rare because of their low abundance within a habitat. Rarity due to habitat specialisation and rarity because of a restricted geographical distribution are discussed in the sections *ecological specialisation*, *microhabitat use*, and *matrix presence* and *biomes and fragmentation history*, respectively.

Theory predicts that small populations are at greater risk of extinction than large populations (see section *population size*). Consequently, species that occur naturally at low abundance should be more extinction-prone than those that occur at high abundance (e.g., Diamond et al. 1987; Robinson and Quinn 1988) because, when isolated on fragments, their populations become smaller than those of co-occurring species with higher abundance.

However, there are also theoretical reasons why rare species may be less at risk of extinction when isolated on fragments. First, rare species may do better when isolated on fragments because they are preadapted to life as small, isolated populations, in contrast with species that were once widespread and abundant (Kunin and Gaston 1993; Lawton 1994). This hypothesis follows from evidence that abundance and range size are persistent, rather than labile, characteristics of species in evolutionary time (Jablonski 1987; Ricklefs and Latham 1992). Second, in recent theoretical work, Tilman et al. (1997) assumed that abundant species are good competitors but poor dispersers and predicted that therefore, they are most at risk of extinction in a fragmented

landscape (but see section *disturbance related traits, competitive ability, and fragmentation sensitivity*).

Most experimental and empirical evidence confirms the theoretical predictions that small populations and species that are rare within a habitat are at greatest risk of extinction (Table 2). In addition, there is indirect empirical evidence for this prediction (see section *population size*).

Biogeographic position and fragmentation history

Fragmentation history is not uniform geographically. Major habitat loss had already occurred a millennium ago in parts of Europe (Wilcove et al. 1986), the Middle East, the Mediterranean, and North Africa (Oedekoven 1992), and larger animals have gone extinct a long time ago. Habitat loss is more recent in other regions of the world, such as the wheatbelt in Western Australia (Saunders 1996) and many tropical regions (McDade et al. 1994; Laurance and Bierregaard 1997). High extinction rates of species have been observed in many tropical and (non-European) mediterranean habitats (e.g., Soulé et al. 1988; Kattan et al. 1994; McDade et al. 1994; Saunders 1996; Laurance and Bierregaard 1997) but not in temperate forest bird communities of the Northern Hemisphere (Lynch 1987). Therefore, it is widely believed that tropical and mediterranean communities are more vulnerable to the effects of habitat loss and fragmentation than temperate ones. Several, not mutually exclusive, explanations for a differential sensitivity of biomes have been suggested (Henle et al. 1996).

One hypothesis contends that the effects of habitat fragmentation seem to be less severe in the Temperate Zone of the Northern Hemisphere because habitat loss and (forest) fragmentation in Europe and, to a lesser degree, in North America (Wilcove et al. 1986; Lynch 1987) have occurred long before people became aware of it as an ecological problem, whereas it is more recent in tropical forests and (some) mediterranean systems, such as the Australian wheatbelt and southern USA (e.g., Soulé et al. 1988; Saunders 1996; Laurance and Bierregaard 1997; Metzger 2000). High extinction rates early in the fragmentation process can be expected theoretically, as persistence time increases rapidly with population size at low numbers (Wissel et al. 1994), and because natural communities are generally characterised by numerous rare and few abundant species (Preston 1949). Empirical evidence supports this expectation (e.g., Diamond 1984; Soulé et al. 1988; Davies and Margules 2000; Laurance et al. 2002).

As an alternative hypothesis, biomes are thought to be predictors of community sensitivity to fragmentation because of demographic and distributional characteristics of the component species. Wilcove et al. (1986) contend that temperate species tend to occur at higher densities, to be more

widely distributed, and to have better dispersal powers than their tropical counterparts. This assumed generality of latitudinal trends in range extent, known as Rapoport's rule, has been challenged recently (Gaston et al. 1998). Their review showed inconsistent results of studies, with some taxonomic groups following the rule but not others. Notwithstanding, most tropical species are locally rare (Laurance et al. 2002), and tropical forests and many mediterranean scrub habitats are characterised by high species diversity (α -diversity) and high rates of geographic replacement of species within a habitat type (γ -diversity) (Cody 1986; Gentry 1990; Metzger 2000). These factors imply narrow distributions and limited dispersal power. Soulé et al. (1988) showed that endemic bird species in mediterranean scrub of the southern USA indeed have low vagility. (See Gaston (1994) for a review of studies reporting similar relationships.) Theory predicts that all these characteristics should predispose mediterranean scrub and tropical communities to higher rates of local extinction. The high sensitivity of endemic birds in temperate forests of New Zealand with their narrow distribution and limited dispersal power (Ogle 1987) corroborates the idea that the causative factor is not the biogeographic position per se. Rather, different characteristic life-histories are responsible for the differential sensitivity of biomes to fragmentation.

Sarre et al. (1996) used similar lines of reasoning to suggest that species of relict biota with narrow habitat requirements and distributions should be particularly sensitive to habitat loss and fragmentation. In contrast, species of expanding habitats with broad habitat requirements and distributions should be relatively insensitive. Henle et al. (1996) extended these arguments and hypothesised that young and expanding biotas should be composed of a sample of species biased towards species with higher dispersal powers, particularly when natural barriers such as the Alpes in Europe come into play as well. They further argued that the same should apply to species, which colonise habitats that always had a patchy distribution. They list studies from the Temperate Zone that provide evidence for the latter idea. For rain forests Laurance and Bierregaard (1997) advanced similar ideas and evidence. They suggested that regions that have been unstable over geological or ecological time scales should be intrinsically more resilient to fragmentation because the most extinction prone species will already have disappeared.

Unfortunately, a test of these, not mutually exclusive, explanations for a differential sensitivity of the communities of different biomes with existing data is rendered very difficult because of non-standardised data recording and analyses. This applies particularly to dispersal power and distribution, if these data are presented at all. Likewise, for the most popular model group, birds,

different authors use different criteria to select the set of species they include in their analyses (e.g., compare different authors in Laurance and Bierregaard 1997).

Relative biogeographic position also may cause differential sensitivity to habitat loss and fragmentation among species within a community. Kattan et al. (1994) suggested two reasons for a greater vulnerability. First, species may be at their ecological limits and therefore may have low population densities and narrow habitat requirements. Thus, they are less likely to be sampled by the remnants and have low abundance, both factors that theoretically should contribute to higher extinction risk. Second, fragmentation inhibits altitudinal movement and thus disrupts migration and recolonisation. Since recolonisation can occur from fewer directions for species at their altitudinal limit than for species in the centre of their altitudinal range, rescue effects (Brown and Kodric-Brown 1977) should be lower and thus make such species more extinction prone. A similar effect can be expected if habitats are linearly arranged, contrary to habitats integrated into networks (Roland et al. 2000). For birds there is good empirical support for relative biogeographic position as a predictor of fragmentation sensitivity (Terborgh and Winter 1980; Temple and Carey 1988; Kattan et al. 1994).

Interactions of traits

The theories and empirical evidence discussed above show that single ecological traits usually are not sufficient as predictors of species sensitivity to fragmentation. Several authors have analysed the combined effects of traits on fragmentation sensitivity with experimental or empirical data. Traits can reinforce or replace each other in determining extinction proneness. In an experimentally fragmented forest the combined effects of being rare and specialised were synergistic in beetles so that species with both traits had a greater reduction in their growth rates in fragments, compared to continuous forest, than the sum of the reductions in growth rates attributable to these traits (Davies et al. in press). Predators also declined, but the effect of being predatory was additive. In tropical rainforest mammals in Australia almost half of the traits showed significant correlations and therefore could replace each other in predicting fragmentation sensitivity (Laurance 1991). When traits were analysed in isolation, abundance in the matrix and dietary specialisation (herbivores, insectivores, frugivores, and predators on vertebrates) were significantly correlated with extinction proneness. In a principal component analysis, natural rarity, trophic level, longevity, fecundity, and body size were all significantly associated with axes that were significant for explaining extinction proneness. However, when matrix effects

were removed, no other trait remained significant. Notwithstanding, longevity, fecundity, and body size again explained extinction proneness when restricting the analyses to species that avoided or very rarely used modified habitats.

Environmental characteristics also interact with the sensitivity of traits to fragmentation. In birds of British marine islands, island area and type (oceanic vs. channel) interacted with migratory status and body size, respectively (Tracy and George 1992). Sieving and Karr (1997) compiled evidence that terrestrial insectivorous bird species of tropical rainforests, a group widely regarded as an extinction prone guild, are sensitive to fragmentation because of increased nest predation in fragments. However, whether a particular species will be sensitive or not will depend on the type of nest used and the ability of the species to compensate for high nest loss by repeated nesting and high fecundity. Metzger (2000) showed that persistence of tree species in tropical forest fragments depended on a complex interaction of dispersal traits, connectivity, landscape structure, and scale of analysis. Whereas zoochorous species (mainly bird dispersed) were sensitive to connectivity and boundary complexity on a coarse scale, they were insensitive to connectivity on a fine scale. In contrast, species with low dispersal capacity (barochorous species) were sensitive to isolation and boundary complexity on a fine but not on a coarse scale.

In summary, single traits alone have limited predictive powers for extinction proneness to fragmentation. In general, two or more traits contribute to extinction sensitivity and their importance will change with the environment. Unless we consider these interactions, the correlation of the traits with each other, the relevance of traits for population processes, and the scale of the study, we will have difficulties in understanding contrasting effects of fragmentation.

Discussion

Are ideas about the sensitivity and the reaction of plants and animals to fragmentation similar?

Current theories on the effects of fragmentation on species are well developed for a certain class of organisms (i.e., animals), but may lack validity for other types of organisms. Theories of stochastic extinction of populations have been developed mostly for animals. When transferring such theories from animal to plant ecology, some caveats should be kept in mind. The underlying concepts of demographic stochasticity and genetic deterioration were developed

mainly for unitary sexual species. Modular sessile species, such as plants, display various reproductive pathways, not only sexuality, that result in a different relevance of various factors associated with the fragmentation process. In clonal plant species vegetative multiplication is a regular feature and demographic and genetic stochasticity most likely play a different role than in non-clonal plant and animal species. Clonal plant individuals theoretically can be immortal, and populations consisting of a single or few individuals of some species are known to have existed for considerable periods of time (e.g., Cook 1985). Therefore, botanists often regard fragmentation as less important than zoologists do. Indeed, empirical studies suggest that plants in fragmented rainforests seem to be less extinction prone than vertebrates (Corlett and Turner 1997) but these studies are highly biased against short-lived plant species. The few available population viability analyses for short-lived plant species (e.g., Menges 1990; Nantel et al. 1996) do show that fragmentation and stochastic modelling are highly relevant to understand their extinction proneness.

Whereas stochastic modelling of population extinction is highly biased towards animal taxa, only botanists recognised the importance of temporal isolation for extinction processes (Poschlod et al. 1998). Temporal isolation is a prolongation of unfavourable periods between times when conditions are suitable for recruitment. The ability to build up persistent seed banks reduces the extinction proneness of plants in such cyclically changing habitats. Longevity may provide a similar storage effect particularly for woody plants and perhaps for long-lived vertebrates.

Notwithstanding, this review has shown that sensitivity to fragmentation is caused by similar traits in plants and animals, though the extent of variation of traits and the biases in selecting model groups with particular traits differ. For example, dormant stages with a long survival capacity are also known from animal taxa, though these have not yet been explicitly studied in relation to human caused habitat fragmentation and temporal isolation. Similarly, as sessile organisms, plant species often exhibit low dispersal power and seem to be particularly endangered by isolation when their habitats undergo rapid successions and loss of local habitats requires dispersal to new suitable locations (Poschlod et al. 1998; Oostermeier 2000). However, they share this sensitivity with animal taxa that exhibit low dispersal power such as terrestrial snails. Like plants, such animal taxa are insensitive to fragmentation when fragmentation is not associated with changes in habitat quality. These contrasting ideas and hypothesised similarities should cross-fertilise animal and plant fragmentation ecology and open up wider perspectives for future comparative theoretical and empirical studies of plant and animal extinction in fragmented habitats.

Vulnerability classification for applied conservation

Many authors identified fragmentation sensitive guilds for specific ecosystems (Table 6). Some authors also attempted to develop a more general classification for the fragmentation sensitivity of species based on the combination of several demographics traits. For plants Ehrlén and van Groenendael (1998) described the traits that most likely contribute to the vulnerability to fragmentation. Correlations among traits such as morphological dispersal characteristics of seeds and fruits may lead to 'emergent groups' (Lavorel et al. 1997) with respect to fragmentation sensitivity. Bonn and Poschlod (1998) list species with similar dispersal attributes (functional types) and discuss their sensitivity to fragmentation.

For animal taxa, several classification schemes for fragmentation vulnerability have been suggested. Settele and Poethke (1996) combined population size and its fluctuation in time, vagility, and colonisation ability to identify the sensitivity of butterfly species to fragmentation. Köhler (1996) used body size/wing formation, reproductive potential, instar numbers, and microhabitat use for grasshoppers and bush crickets. Köhler divided these traits into advantageous (value 1.0), intermediate (0.5), and unfavourable (0). The total yields a number called resistance value, which represents the lifetime susceptibility/sensitivity to sources of increased mortality. Fagan et al. (1999) suggested that species with low intrinsic growth rates should be sensitive to area loss whereas species with high intrinsic growth rates should survive best in fragmented or variable habitats with uncorrelated fluctuations of the environment. Vos et al. (2001) combined individual area requirement and dispersal power to identify ecological profiles for the fragmentation sensitivity of animal species. In their simulation models individual area requirement, which directly translated into population size, was of overriding importance for persistence. Species with high individual area requirements and low dispersal power showed the highest fragmentation sensitivity, whereas species with small individual area requirements and high dispersal power were least sensitive. This is not surprising given the very small patch size used in the simulations that supported only 1–16 reproductive units of species with large individual area requirement, whereas they supported at least 50 reproductive units for the small individual area requirement profile. Biedermann et al. (1999) also combined individual area requirement/population size with dispersal power into a classification scheme that additionally considered generation time. They distinguished species sensitive to the spatial effects of fragmentation from species insensitive to the spatial effects of fragmentation but sensitive to habitat deterioration that may follow fragmentation. Like Vos et al. (2001) they also identified a fragmentation insensitive group.

Below, we will merge, expand, and slightly modify the classification schemes of Biedermann et al. (1999) and Vos et al. (2001) based on the results of this review. Species combining several of the following traits should be particularly sensitive to fragmentation: low natural abundance/high individual area requirement, high population fluctuations, low reproductive potential, low storage effects, intermediate or low dispersal power, and specialised habitat requirements. The most fragmentation sensitive species should be those with high individual area requirements (low natural abundance) but low dispersal power, since fragmentation will lead to very small isolated populations with high risk of extinction and almost no chance of recolonisation (Vos et al. 2001). However, it is questionable whether species with such a trait combination exist. Least vulnerable should be generalist species that build large population sizes with high densities, low area requirements, high mobility, and short generation times, since they survive well in isolated fragments and have good colonisation ability ('Ideal-type' of Biedermann et al. 1999; least fragmentation sensitive profile of Vos et al. 2001). Such species have not received much attention in the fragmentation literature, most likely because they indeed are not affected by habitat fragmentation.

High fragmentation sensitivity should be shown by species with large individual area requirements, low population growth rate, and moderate dispersal power. Among these, most vulnerable should be specialists, species at the border of their geographic range, and species most prone to increased environmental fluctuations that may follow the fragmentation process. This sensitivity profile has not been identified in previous classifications. A high to intermediate fragmentation sensitivity should be shown by species characterised by low population size and density, large area requirements, and high mobility. Such species should have difficulties surviving even under moderate habitat loss, when fragments show little contagion (compare With and King 1999) but should cope comparably well if the remaining habitat is concentrated in a few more distant but larger remnants [unless there is high mortality when moving among fragments (Woodroffe and Ginsberg 1998)]. Likewise, generalist mobile species that are matrix tolerant and can integrate several fragments into a home range are less sensitive to moderate habitat loss than mobile species that are unable to do this. Biedermann et al. (1999) did not distinguish the above subgroups and combined them into their fragmentation sensitive 'Mobility-type'.

Species characterised by low to moderate dispersal but high density and low population fluctuations should be relatively insensitive to the spatial effects of fragmentation but may be sensitive to abiotic, structural, and successional changes associated with the fragmentation process. Particularly sensitive to changes in habitat quality should be specialist species and species

showing very stable population sizes in optimum habitat, medium densities, low to medium area requirements, low to medium mobility, and long generation times (modified 'Stability-type' of Biedermann et al. 1999). Of intermediate sensitivity should be species that reach high population sizes and densities, have low to medium area requirements, and medium mobility (modified 'Quantity-type' of Biedermann et al. 1999). These trait combinations allow long-term survival without or with low immigration in moderately fragmented habitats, provided the quality of the habitat does not deteriorate.

Future directions?

This review suggests several future approaches that should provide a fertile ground for an improved understanding of the differential sensitivity of species to fragmentation and its use in applied conservation. Beyond the suggestions made in the previous chapters we advocate the intelligent integration of results from field experiments and observational studies on 'natural' experiments, incorporation of both the temporal and spatial scales and the control of confounding factors. To allow more thorough comparative analyses of different studies, we also need improved standardisation both for quantifying species traits and ecological parameters, especially the spatial and temporal degree of fragmentation. We particularly encourage an Internet based co-operation for setting up comparative studies along these lines in different ecosystems and biomes. Likewise, adequate models must view fragmentation with the eyes of the species, since a landscape with the same physical changes is perceived as fragmented by some but not by other, even closely related species (Diffendorfer et al. 1995). To predict the sensitivity of a particular species, we need to better understand how traits interact with environmental changes following the fragmentation process. Most importantly, however, we need to integrate biological studies with socio-economic studies that try to identify instruments and policies that can contribute to halting the fragmentation process and to re-integrate fragmented landscapes.

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