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The anatomy of fragmentation

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Abstract

The external and internal anatomy of fragments as well as the type of fragmentation process can influence the persistence of taxa within the remnants. This paper outlines some conceptual issues about fragment topology, habitat matrix and scale, and presents some caveats and directions for future research. For example, it is shown that owing to the specific pattern of fragmentation, even a vagile species can go extinct although a large proportion of its habitat is intact. Furthermore, the functionality of a landscape configuration is dependent on the perceptual abilities of the taxa experiencing the fragmentation. Fragmentation effects on immobile self-incompatible plants are mediated through the effects of landscape change on pollen vectors such as wind or animal taxa. Fragmentation research must therefore also focus on influence of landscape change on species interactions rather than on single species alone.

Keywords: Conservation biology, edge effects, fragmentation, metapopulations, scale effects.

1. Introduction

Fragmentation of natural habitats is the most serious threat to the long-term survival of the biological diversity of the earth.[1] Over the last few decades, ever since it became apparent that habitat conversion was accelerating at unprecedented rates, efforts have been made to understand the impact of fragmentation on various types of plant and animal taxa. Most of the studies involved post-fragmentation documentation of progressive declines in species richness or species diversity. Only a few documented pre- and post-fragmentation scenarios thus providing measures of the actual loss of original taxa as a result of fragmentation, i.e. the Biological Dynamics of Forest Fragments Project in central Amazonia.[2] In this paper, I point out some conceptual issues regarding the anatomy of fragmentation. I outline both external and internal features of fragments as well as their spatial arrangement and discuss how fragment topology may influence long-term species persistence.

2. Fragment anatomy

Fragments of habitats are situated within landscapes and form diverse types of mosaics. At a landscape level, the following features of the external anatomy of fragments are important to measure or are at least measurable[3] (Fig. 1): a) fragment size distribution, i.e. the frequency distribution of fragment sizes in a given landscape; b) perimeter : area ratio as a measure of fragment shape, c) fragment orientation, e.g. with regard to an altitudinal gradient or water flow gradient, d) context, i.e. the type of matrix in which the fragments are embedded, e) contrast, i.e. the difference between the inside and the outside of the fragment in terms of habitat

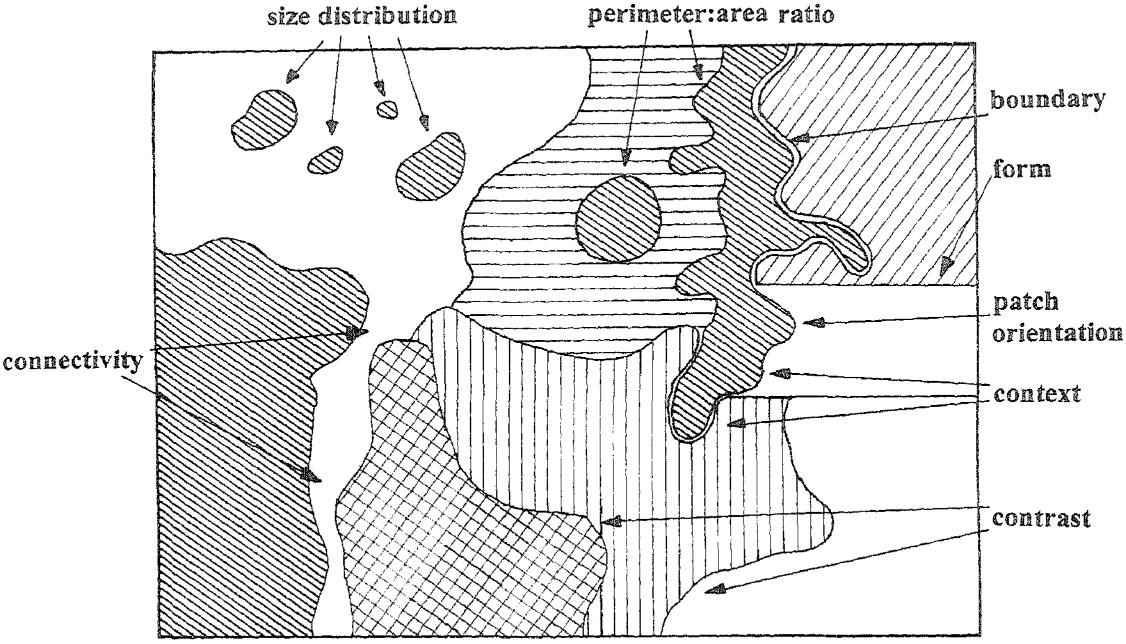

FIG. 1. A landscape-mosaic showing measurable features of fragments (adapted from Wiens *et al.*[3]).

characteristics, f) boundary form, e.g. boundary continuity and boundary length, g) connectivity, i.e. extent to which the patches are connected (however, this is a subjective measure because although it is possible to physically measure connectivity, the functional connectivity of fragments will vary from taxon to taxon), and h) dispersion, i.e. spatial arrangement of the fragments within the matrix.

With regard to the internal anatomy of fragments, the following parameters should be important in influencing the species persistence process: a) fragment edge, b) perforations along the horizontal and vertical axes, i.e. in edges of forest looking inwards or outwards as well as through the top of the fragment from the canopy to the understorey and the forest floor.

3. The fragmentation process

Essentially four types of sequences could be involved in the process of habitat conversion leading ultimately to fragmentation.[4] a) *Shrinkage*: In this case, the original habitat is impacted upon over one or more sides so that it persists only in one reduced region. A typical example of this type of conversion may involve gradual landfill or reclamation of a lake at one end. b) *Bisection*: In this process, the habitat is disturbed or converted in its middle region as might occur when a highway cuts through continuous forest resulting in two fragments which might get progressively smaller as the impact of fragmentation continues. c) *Fragmentation*: In this case, a whole habitat is simultaneously broken into smaller portions as might occur when a network of roads or canals breaks up a desert landscape. d) *Perforation*: In this process, foci of disturbance or habitat conversion begin at various points within the continuous lansdscape and then gradually grow outwards resulting in a perforated habitat as might occur when settlements are established in a grassland habitat. In all these cases, it can be expected that the nature of the impact will vary considerably based on the scale, timing of the impact and the taxa affected by the impact. In the first set of rigorous experiments to evaluate these different fragmentation processes, Collinge and Forman[4] conducted a microlandscape experiment with grassland insects. Beginning with 10 × 10 m grassland plots, they sequentially reduced the original habitat (Fig. 2), and documented changes in the grassland insect community. They found that although the shrinkage and perforation sequences resulted in substantially different fragment dispersions, yet, because of their higher connectivity, overall they showed similar results in species richness levels. The fragmentation and bisection sequences, which resulted in landscapes in which the fragments had lower connectivity, had considerable similarity in species compositions over the habitat conversion sequences. As expected, different taxa responded differently to the conversion process with the less vagile species being more affected than the more vagile species.

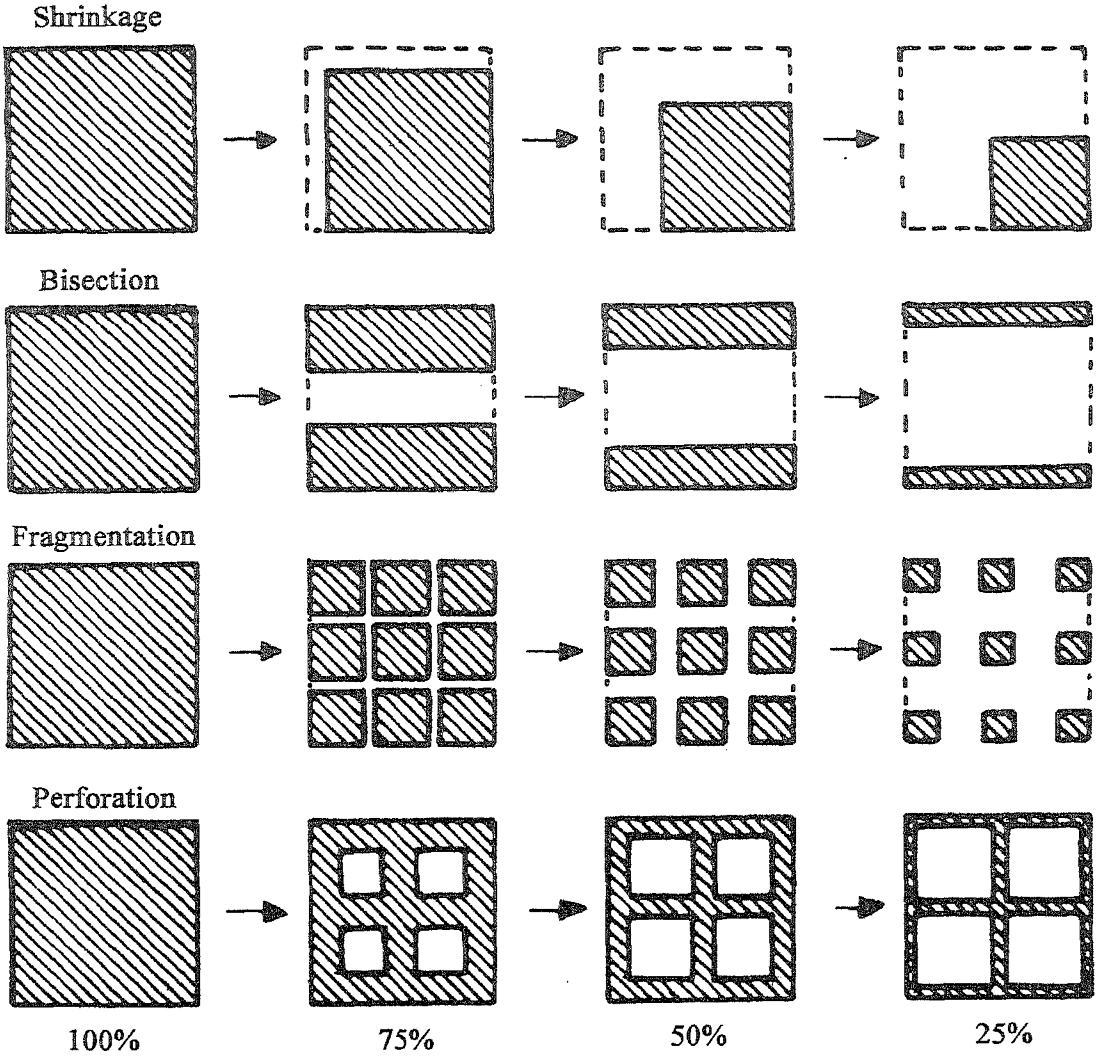

FIG 2. Four habitat conversion processes that could result in a fragmented landscape (adapted from Collinge and Forman[4]).

In the following sections, I use three examples to illustrate some important issues regarding the anatomy of fragmentation: a) species can go extinct even in large reserves before their habitat is fully fragmented, b) the perceptual capabilities of taxa must be considered while evaluating the response of species to patterns of fragmentation, and c) taxa that are involved in mutualistic relationships, such as plants and their pollinators, are especially vulnerable to the anatomy of fragmentation.

4. The case of the army ant

Eciton burchelli is a Neotropical army ant that feeds voraciously on live insects, other invertebrates and small vertebrates. The colony has a single queen which lays about 10,000 eggs every 35 days. Once the eggs are laid, the colony bivouacs in a fixed spot for 20 days and the workers make regular feeding raids for live prey in all directions. At the end of this period, the eggs hatch and the colony becomes nomadic to meet the demands of the developing larvae until pupation which takes another 15 days. Once pupation occurs, a new bivouac is occupied and another batch of eggs is laid. The distance travelled from one bivouac to another is on average about 530 m.[5] Army ants tend to avoid areas of the forest which do not have adequate canopy cover;[5, 6] therefore, such areas serve as boundaries from which the ant columns recoil. With this knowledge of the natural history of the species, Boswell *et al.*[7] modelled the response of army ants to fragmentation using realistic values for the area parameters and applying realistic boundary conditions. They also took factors such as renewability of habitat into account vis-à-vis suitability for the ants in terms of prey availability within cells that had previously been visited by the ant columns. They started with an area of 9 × 9 km (the size of a forest patch that is conceivably present in an intact uninterrupted block in some parts of the Neotropics) and divided it into 2500 cells in a lattice (50 × 50 cells). By removing cells randomly from this lattice, i.e. the equivalent of deforestation or loss of canopy cover, they created boundary conditions for the ants into which the ants could not move (as, for example, owing to loss of canopy cover). They found that extinction of the colony was obtained when the proportion of randomly removed cells reached only 45%, i.e. with as much as 55% of the habitat still intact. Boswell *et al.*[7] interpreted this to be due to the pattern of fragmentation. The conceptual lesson from this simulation is that if 45% of the habitat is to be removed without detriment to the ant colony then it should be removed as a single block so that the remaining habitat is left as a large unit. These results are surprising and even counter-intuitive especially as the army ant is a symbol of a highly vagile taxon which by the conventional rules of thumb should be considered to be less vulnerable to extinction.

5. The case of the white-footed mouse

Forest-dwelling white-footed mice have often been featured in landscape-level studies[8, 9] and have been investigated in terms of navigation, homing and dispersal capabilities.[10, 11] Mice from forested woodlots were released in a variety of situations at different distances from their 'home' woodlots and their subsequent movements were tracked. Mice released into bare fields oriented towards forested woodlots only at distances up to 20 m from the point of release.[12] Mice released at 30 m from the woodlot appeared to be unaware of the woodlot (Fig. 3). Therefore, the perceptual range of mice for detecting the presence of woodlots when released into bare fields appeared to be about 20 m. Additional experiments seemed to indicate that the

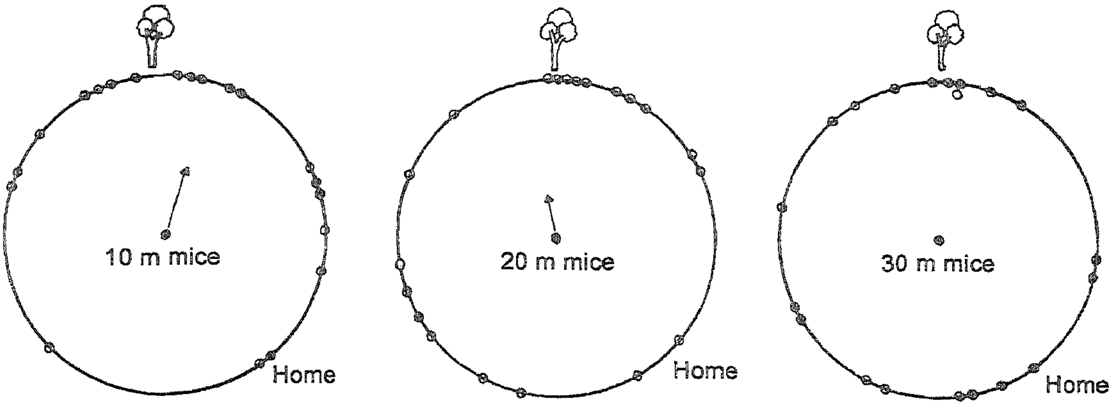

FIG. 3. Angular orientation of white-footed mice released into bare fields at varying distances (10, 20 and 30 m) from 'home' woodlots. The dots on each circle are the angular orientation of 20 individual mice; home indicates the woodlot from which the mice were captured; the tree symbol indicates that portion of the woodlot closest to the point of release; vectors indicate the average angle and degree of orientation for cases with statistically significant orientation (adapted from Zollner and Lima[12]).

mice were detecting the woodlots primarily by vision.[12] Experimental work of this nature indicates how the anatomy of fragmentation can influence which fragments dispersing animals can actually perceive and that the ecological utility of a given fragment mosaic with regard to species persistence and metapopulation dynamics is dependent on the perceptual ability of the taxon under consideration.[13]

6. The case of stationary plants and mobile pollinators

Heterophragma quadriloculare is a tree of the crest forests in a highly fragmented seasonal cloud forest environment in the Western Ghats of Maharashtra. It is usually found at the edge of forest fragments and is pollinated at night by carpenter bees.[14] Owing to the highly fragmented system, trees can be separated by distances of several kilometres. Yet, the bees are highly vagile and there was no effect of tree isolation on the reproductive success of individual trees.[15, 16] The case of *Lasiosiphon eriocephalus* is however different. This plant is a shrub in the same environment and is pollinated by sedentary beetles. Isolated plants had lower reproductive success than plants in clumps possibly because they were not found as easily by the beetles or owing to the isolation, they were not a sufficiently profitable resource.[15, 16] The dioecious *Diospyros montana* in the same fragmented environment was investigated over two years in a natural and a fragmented population (altered by human disturbance as plants were selectively removed). Flowering females and males were separated by greater distances in the fragmented population and in the natural population during a lean flowering year compared to the natural population in the normal flowering year (Table I). These larger female–male distances translated into much lower reproductive success in the fragmented population and in the natural population in the lean flowering year compared to the natural population in the normal flowering year in terms of per cent fruit set owing to the isolation effect of these plants which are visited by a host of generalist insects.[17] All these examples show clearly that the fate of plant taxa after isolation depends almost entirely on the mobility and possibly the perceptual abilities of the pollinator. Plant taxa cannot be considered as independent taxa in fragmentation studies and, therefore, the internal anatomy of fragmentation for plants critically interacts with

Table I
Female–male nearest neighbour distances and reproductive success in *Diopsyros montana*

	Natural population (1995)	(1996)	Fragmented population (1996)
Female–male distances (Mean ± S.E.)	84.15 ± 36.56 (3)	13.05 ± 1.35 (35)	81.19 ± 12.57 (12)
Per cent fruit set (Mean + S.E.)	5.11 ± 2.02 (3)	31.08 ± 2.07 (35)	4.31 ± 0.94 (12)

Values in parentheses are samples sizes (data from Somanathan and Borges[17]).

the consequences of the fragmentation for their pollinators or for pollinating agents such as wind to determine the response of such plants to fragmentation. Other studies have also shown similar effects. For example, euglossine bees that are important pollinators of many Neotropical plants were found to be unable to cross cleared areas of greater than 100 m width.[18] Strong winds were found to affect forest fragment edges up to distances of 100 m inside the fragment.[19] The consequences of these effects for wind-pollinated plants also need to be considered in the impact of fragmentation.

7. The matrix problem

Fragments are embedded within a matrix, e.g. partially submerged mountains in an oceanic or freshwater matrix as occurs during canal or dam construction or tree islands within a matrix of agriculture or of secondary vegetation. The matrix serves as a filter and the pore size of the matrix filter will determine the connectivity of the fragments (Fig. 4). Very few studies have looked at the properties of the matrix in determining or supporting species richness in remnants.[20] Using a 19-year database, Gascon *et al.*[21] found that species richness of small mammals and frogs increased in fragments after isolation while those of ants and birds declined. Furthermore, those taxa that avoided the matrix declined in the fragments while those that tolerated the matrix increased in the fragments. Therefore, the properties of the matrix, i.e. the external anatomy of the fragment, is very important in determining species survival.

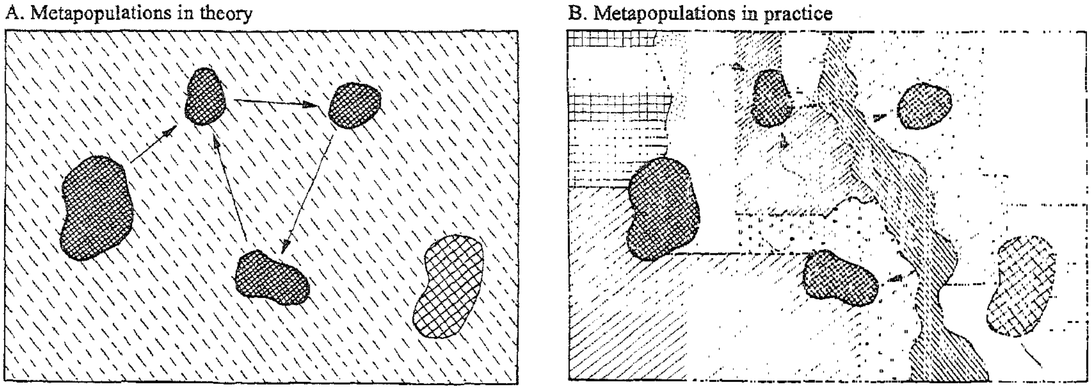

FIG. 4. Metapopulations in theory do not consider the anatomy of the intervening matrix. A) Individuals are theoretically free to move between fragments containing populations of the taxon through a matrix whose properties are not usually considered within theoretical analyses. B) In reality, the matrix properties may impede the movement of individuals between fragments. Consequently, metapopulations in reality may be smaller than those in theory. Figure adapted from Wiens.[24]

8. The scale problem–the issue of fragmented fragments

Anatomy and scale are inseparable as are their combined effects (which are not necessarily mutually exclusive). A single fragment at one scale could be perceived as many small fragments at scales appropriate to diverse taxa, e.g. a tree fall gap causing a break in the canopy and influencing one taxon such as shade-intolerant saplings of a species could have its smaller scale equivalent in a branch break off on the crown of a tree canopy causing a gap with consequences for epiphytes on the trunk immediately below the break. Canopies have varying degrees of porosity to light[22] and other elements and thereby fragmentation of the fragment varies accordingly. Similarly, fragment boundary length for a large carnivore is measured on a very different scale for dung beetles which might be more responsive to fractal dimensions of the same landscape.[23]

9. Conclusions

The army ant, white-footed mouse and pollination examples provided in the paper illustrate a few important features of the consequences of the anatomy of fragmentation. a) Even a vagile species can go extinct although a large proportion of its habitat is intact owing to the pattern of fragmentation. Even for vagile species a highly dispersed fragmented pattern is less desirable than a pattern where the fragments are closely opposed. b) The functional value of a given landscape configuration (pattern of fragmentation and associated matrix) is dependent on the perceptual ability of the animal taxon under consideration. c) In two-species interaction systems such as pollination systems, the effect of fragmentation anatomy on the fixed partner, i.e. the plant, is mediated via its effect on the mobile partner. Therefore, plants that need agents for pollination such as animal taxa or wind cannot be considered as independent taxa in fragmentation studies. It appears, then, that many earlier approaches to the study of fragmentation need to be re-examined and greater attention be given to the intervening matrix, the pattern of fragmentation, the perceptual abilities of the taxa under consideration, and to the role of the mobile partner in two-species interactions such as pollination.

References

1. WHITMORE, T. C. — Tropical forest disturbance, disappearance, and species loss. In *Tropical forest remnants: Ecology, management, and conservation of fragmented communities* (W. F. Laurence and R. O. Bierregaard, Jr, eds), University of Chicago Press, 1997, pp. 3–12.
2. LOVEJOY, T. E. *et al.* — Edge and other effects of isolation on Amazon forest fragments. In *Conservation biology: The science of scarcity of diversity* (M. E. Soulé, ed.), Sinauer Assoc., Sunderland, Mass., 1986, pp. 185–257.
3. WIENS, J. A., STENSETH, N. C., VAN HORNE, B. AND IMS, R. A. — Ecological mechanisms and landscape ecology, *Oikos*, 1993, **66**, 369–380.
4. COLLINGE, S. K. AND FORMAN, R. T. T. — A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects, *Oikos*, 1998, **82**, 66–84.
5. WILLIS, E. O. AND ONIKI, Y. — Birds and army ants, *A. Rev. Ecol. Syst.*, 1978, **9**, 243–263.
6. STOUFFER, P. AND BIERREGAARD, R. O. JR — Use of Amazonian forest fragments by understory insectivorous birds: effect of fragment size, surrounding secondary vegetation, and time since isolation, *Ecology*, 1995, **76**, 2429–2443.

7. Boswell, G. P., Britton, N. F. and Franks, N. R. Habitat fragmentation, percolation theory and the conservation of a keystone species, *Proc. R. Soc. Lond. B*, 1998, **265**, 1921–1925.

8. Fahrig, L. and Merriam, G. Habitat patch connectivity and population survival, *Ecology*, 1985, **66**, 1762–1768.

9. Bowers, M. A. and Dooley, J. L. jr. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects, *Oecologia*, 1993, **94**, 247–254.

10. Drickamer, L. C. and Stuart, J. *Peromyscus*: snow tracking and possible cues for navigation, *Am. Midl. Nat.*, 1984, **111**, 202–204.

11. Anderson, P. K. Foraging range in mice and voles: the role of risk, *Can. J. Zool.*, 1986, **64**, 2645–2653.

12. Zollner, P. A. and Lima, S. L. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat, *Oikos*, 1997, **80**, 51–60.

13. Lima, S. L. and Zollner, P. A. Towards a behavioural ecology of ecological landscapes, *Trends Ecol. Evol.*, 1996, **11**, 131–135.

14. Somanathan, H. and Borges, R. M. Nocturnal pollination by the carpenter bee *Xylocopa tenuiscapa* (Apidae) and the effect of floral display on fruit set of *Heterophragma quadriloculare* (Bignoniaceae) in India, *Biotropica* (in press).

15. Borges, R. M., Mali, S. and Somanathan, H. *Status, ecology, and conservation of the Malabar Giant Squirrel Ratufa indica.* Final Report, United States Fish and Wildlife Service and Wildlife Institute of India Collaborative Project, Dehradun, 1999.

16. Somanathan, H. *Community phenology and reproductive success of some insect-pollinated plants in Bhimashankar Wildlife Sanctuary, Western Ghats*, Ph.D. dissertation, University of Bombay, India, 1998.

17. Somanathan, H. and Borges, R. M. Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India, *Biol. Conserv.*, 2000, **94**, 243–256.

18. Powell, A. H. and Powell, G. V. N. Population dynamics of male euglossine bees in Amazonian forest fragments, *Biotropica*, 1987, **19**, 176–179.

19. Ferreira, L.V. and Laurance, W. F. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia, *Conserv. Biol.*, 1996, **11**, 787–801.

20. Mesquita, C. G., Delamônica, P. and Laurance, W. F. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments, *Biol. Conserv.*, 1999, **91**, 129–134.

21. Gascon, C. *et al.* Matrix habitat and species richness in tropical forest remnants, *Biol. Conserv.*, 1999, **91**, 223–257.

22. Endler, J. A. The color of light in forests and its implications, *Ecol. Monogr.*, 1993, **63**, 1–27.

23. With, K. A. Using fractal analysis to assess how species perceive landscape structure, *Landscape Ecol.*, 1994, **9**, 25–36.

24. Wiens, J. A. Metapopulation dynamics and landscape ecology. In *Metapopulation biology: Ecology, genetics and evolution* (I. Hanski and M. E. Gilpin, eds), Academic Press, 1997, pp. 43–62.