

## Chapter 1. INTRODUCTION

### 1.1 OVERVIEW

In Australia, rainforest occurs as a thin strip along the eastern coast, and as small pockets in the Northern Territory and Western Australia (Webb & Tracey 1981b, Adam 1992). The rainforests are patchily distributed, as a result of both natural biogeographic history (Webb & Tracey 1981b, Walker 1990, Truswell 1990) and anthropogenic land clearance, drainage and logging practices (e.g. Adamson & Fox 1982, Winter *et al.* 1987) over the last 200 years (House & Moritz 1991). Along the eastern coast, the once extensive expanses of subtropical rainforest of the Atherton Tableland (north Queensland), southeastern Queensland, and the Big Scrub (northeastern New South Wales), have been extensively cleared for agriculture and settlement, reducing them to small isolated remnants, with larger tracts occurring mainly on the uplands and perimeters of the regions. This study was conducted within the Big Scrub area, which has important conservation significance for rare species, primitive plants (Webb & Tracey 1981b, Webb *et al.* 1984, Hunter 1991) and as part of MacPherson-Macleay overlap, a region of high diversity in Australia (Burbidge 1960).

A wide research literature demonstrates that forest fragmentation results in species extinctions, and changes in population size and distribution of animals (Chapter 2). These studies predict that fragmentation will also result in indirect effects on community processes. For example, interactions between animals and plants are likely to change. Interactions which affect plant reproductive success, such as seed predation, could lead to a change in abundance and distribution of plant species within habitat fragments. However, there have been few demonstrations of this in the literature. This study investigates seed predation and seedling survival of *Castanospermum australe*, in five remnants of subtropical rainforest in northeastern New South Wales.

Of the approaches to studying forest fragments, autecological studies are recommended for obtaining information that is useful for management and understanding ecosystem processes (Risdill-Smith 1987). Such studies are few both worldwide and in Australia (Chapter 2). Thus, this study is one of few to use such an approach to investigate the effects of forest fragmentation on a plant species. The results give insight into the ecological processes within rainforest, the importance of animal-plant interactions, and the effects of forest fragmentation on that ecology. Through this work, we have gained new understanding of

the functioning of rainforest systems, that can be used to predict the long term viability of populations and communities within forest fragments.

While much influential research on the effects of habitat fragmentation has been conducted in remnant sclerophyll vegetation of southern and western Australia (Saunders *et al.* 1987, Saunders & Hobbs 1991, Hobbs & Saunders 1993), far less attention has been paid to remnants of Australian rainforest. Further, little is known of the autecology of Australian rainforest plants. Few aspects of the ecology of *C. australe* have been previously studied, beyond some aspects of growth, photosynthetic rate, seed chemistry, and limited study of seed removal and survival of transplanted seedlings. There are no published studies on the seed ecology of *C. australe*. This thesis identifies two mammalian predators of *C. australe* seed, and provides detailed information on the level and pattern of seed predation, seed survival and seedling recruitment.

Throughout this thesis, investigation of the seed ecology of *C. australe* plays as important a role as the comparison between sites. This is because the paucity of information on *C. australe* made the collection of baseline data on the species and its interaction with fauna a prerequisite for interpretation of any differences between sites.

## 1.2 AIMS

This study had two main aims:

- (1) to investigate and compare the levels of seed predation and seedling recruitment of *Castanospermum australe* within remnants of subtropical rainforest of northeastern New South Wales, and
- (2) to investigate some of the mechanisms that influence levels of seed predation and seedling recruitment, that may be altered by forest fragmentation.

## 1.3 SCOPE OF THE STUDY

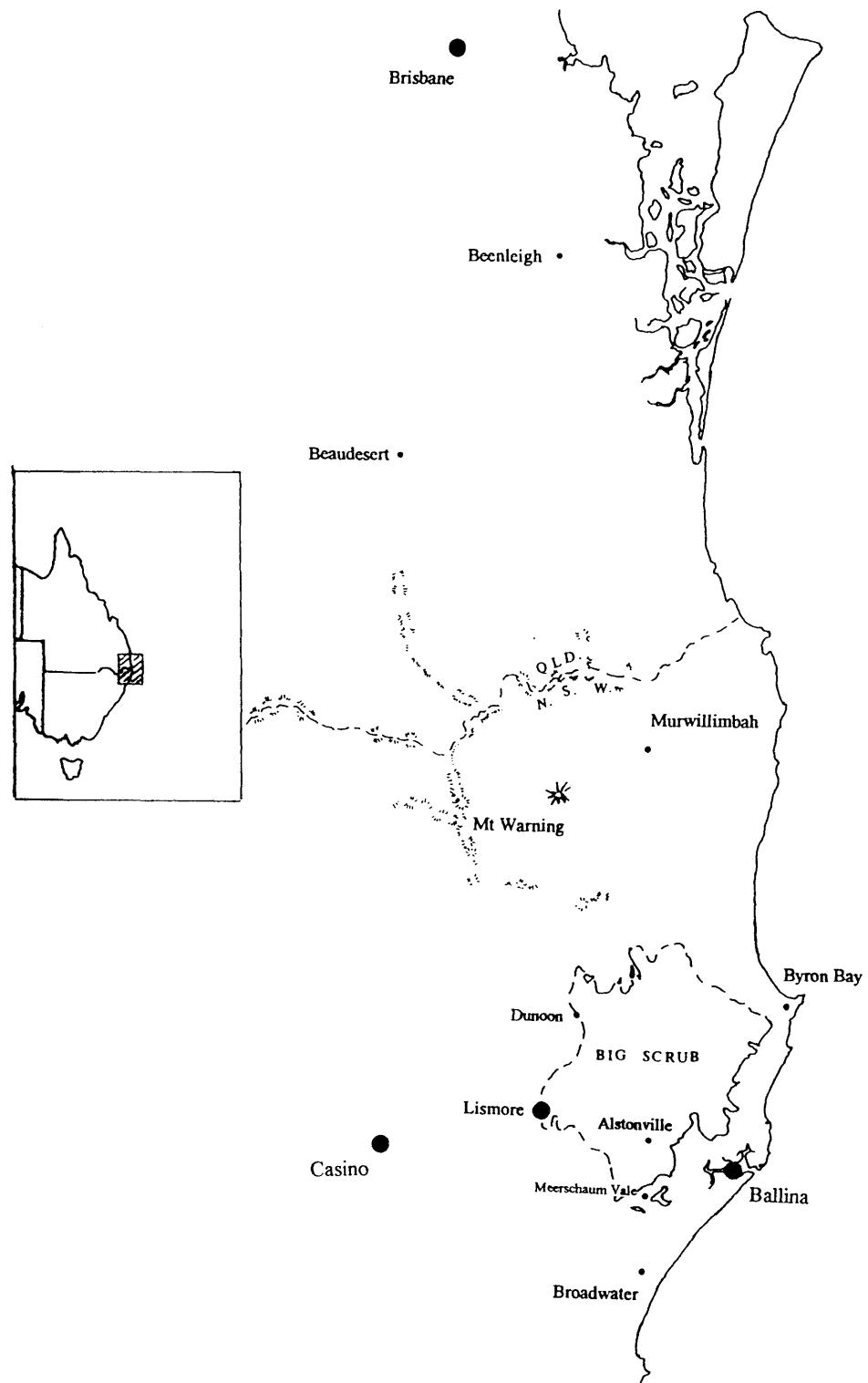
This study was carried out in subtropical rainforest remnants of the Big Scrub, near Lismore, northeastern New South Wales (Figure 1.1). This region is approximately 5 hours travel from the University of New England, Armidale, a distance which allowed regular commuting to study seed fate over time. The five sites selected for study span of a range of forest fragment sizes and were of the same vegetation association.

*Castanospermum australe* is a widespread and relatively common tree in subtropical and tropical rainforest. Its distribution ranges from the Orara and Bellinger Rivers, northeastern New South Wales, to Iron Range, Cape York Peninsula in northern Queensland, as well as New Caledonia and New Hebrides (Floyd 1989). It yields a valuable cabinet timber used for furniture, inlays and plywood finishes, and has been selectively logged throughout its range (Lewington 1990). More recently, it has become of interest to groups such as Queensland Forestry Service (Department of Primary Industries) and Community Rainforest Rehabilitation Program (North Queensland), for planting for its habitat and timber values (e.g. Nickles *et al.* 1994). The species also yields useful potential pharmaceuticals. The phenolic alkaloid castanospermine is one of a range of 'sugar mimic' alkaloids which have deterrent or toxic effects on insects and the digestive system of insects and some mammals (Lewington 1990). Castanospermine also has a dramatic effects on the AIDS virus H.I.V (Lewington 1990). Natural or synthesized castanospermine is also being tested in cancer and immunological research (Lewington 1990) and in a range of projects investigating the operation of glucose (e.g. Robinson *et al.* 1990, Howes *et al.* 1990, Winchester *et al.* 1990, Paul *et al.* 1992).

*C. australe* was chosen for study because it is a relatively common canopy tree species, and therefore is important in rainforest structure and function. Its previous and potential importance in forestry was also a reason for choice for study. It fruits in sufficient numbers to allow reliable study, and has a large seed potentially of importance to fauna. A large seed size is likely to influence seed attractiveness to predators and dispersers, the size and competitiveness of seedlings, and seedling response to shade and sunlight gaps. The very large seed also indicates that it may have specific dispersal requirements, or limited dispersal. These aspects could potentially be affected by altered animal-plant interactions in forest fragments. *C. australe* also fruits during winter, which allowed field trips to coincide with the restricted funding available at the commencement of the study.

The project was largely based on *in situ* field observation, with some additional manipulative field experiments. A laboratory feeding trial was also conducted. The main plant life history aspects investigated in the field were seed crop size and variability between trees, seedfall duration and variability over time, seed predation under parent trees, germination and seedling recruitment. The main types of seed predators were identified and their presence/absence in the five remnants correlated with levels of seed predation. The abundance of seedlings, immature plants and adults was compared between sites and compared with observed levels of seed predation and patterns of seedling recruitment. An emphasis on seed predation allowed investigation of a poorly known aspect of seed ecology in Australian rainforest.

**Figure 1.1** Map of northeastern New South Wales and southeastern Queensland, showing location of the Big Scrub.



#### 1.4 OUTLINE OF THE THESIS

Two review chapters (Chapters 2 and 3) introduce the subject material investigated in the thesis. Chapters 4-8 are written as independent papers, incorporating aims, methods, results and the relevant literature. Inevitably some repetition occurs as each paper was written to 'stand alone' as a publication. Chapter 9 contains a synthesis of the results of the study. Some chapters refer to a report by Lott and Duggin (1993), which is a report prepared for the Australian Heritage Commission (National Estate Program), available from the Department of Ecosystem Management, University of New England, or state and national libraries (ISBN 1 86389 149 8).

Figure 1.2 shows the main issues addressed in each chapter. The following outline summarizes the content of each chapter.

**Chapter 2** discusses the importance of animal-plant interactions, and reviews the literature on the effects of forest fragmentation, and the approaches to studying these effects. This provides a background to the study. Where possible, studies conducted in rainforest are used as examples. A brief review of rainforest research in Australia is given, in particular noting fragmentation and autecological studies. The criteria for selection of the study species are outlined.

**Chapter 3** gives a general description of the study region, and selection criteria for the study sites chosen. The description of *C. australis* incorporates a brief review of existing literature.

**Chapter 4** describes the annual variation in seed production by individual trees during the years 1989-1991, the timing of seed release within 1989, and some aspects of pod and seed size variation. Seed crop size was recorded for 15 trees between 1989 and 1991 and shows annual variation between and within trees, sites and years. A qualitative assessment of seed crop size for the nearest neighbours to these trees was made in 1990 and 1991, to estimate the proportion of the population in fruit each year.

**Chapter 5** identifies the predators of *C. australis* seed, as background to the study of *C. australis*, and to allow later interpretation of any differences between sites in that seed ecology. A review of literature on the fauna of the Big Scrub and their diet, identified the potential vertebrate predators of *C. australis* seed in northeastern New South Wales. This is then tested by examination of seeds found eaten in the field, and by conducting a feeding trial with captive wild animals. The types of seed damage observed, are compared with the

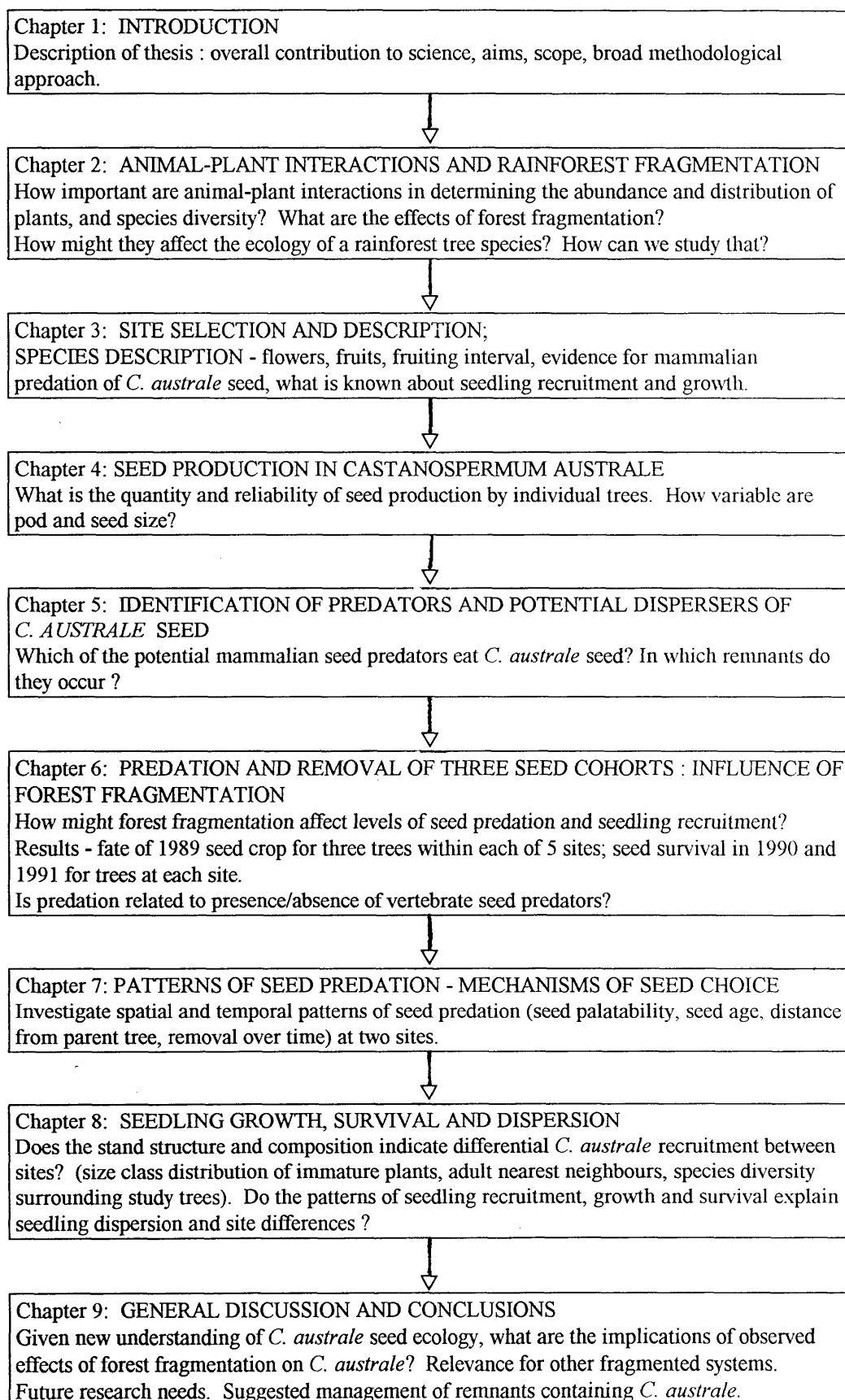
results of surveys of small mammal fauna at the 5 sites, to identify the presence/absence of seed predators from the study sites.

**Chapter 6** presents the main focus of this study, which was to compare levels of seed predation and removal in each of five remnants of forest. In 1989, three trees were studied in detail within each site. Individual seeds and pods were tagged and marked and their fate followed beneath the parent trees throughout the period of seedfall (April-September) and beyond. Measurements were made of seed survival, types of seed damage, timing and magnitude of predator response to seedfall, and differences in these variables among sites. Level of insect predation, seed crop size and overall seed survival were also assessed for a sample of trees in 1990 and 1991. The relative importance of the different predators and their role in limiting seed survival is discussed. The factors causing differential seed survival among sites are considered.

**Chapter 7** investigates the effect of seed palatability, seed age, and distance-dependent predation on patterns of seed removal at two sites. The proportional damage to individual seeds, and the germinability of damaged seeds are tested, to determine whether the seed predators could also act as seed dispersers.

**Chapter 8** continues the investigation of differences in seed ecology between remnants of forest. Data on seedling survival, seedling response to gaps and forest interior, floristic composition of the sites, and *C. australis* seedling and adult density and dispersion are used to further compare the sites and to consider whether the differences in seed predation represent an alteration to the ecology of the remnants.

**Chapter 9** outlines the main findings of the study regarding *C. australis* seed ecology, and the effects of forest fragmentation on that ecology. The implications for other fragmented rainforests, and some management options for remnants which contain *C. australis* are discussed.

**Figure 1.2** Outline of chapters and main issues addressed in thesis.

## Chapter 2. ANIMAL-PLANT INTERACTIONS AND RAINFOREST FRAGMENTATION

### 2.1 INTRODUCTION

Rainforest is characterised by high species diversity and structural complexity (Hutchinson 1959, Condit 1995, Leigh 1982, Webb & Tracey 1981a, Floyd 1990a). These characteristics mean that there are a large number of species interacting. Animal-plant interactions, in particular, are of great importance in maintaining biological diversity in the tropics (Howe 1984, Terborgh 1992). For instance, frugivore-plant relationships are of particular importance in rainforest. Compared with other vegetation types, rainforest has a large proportion of tree species with fleshy fruit adapted for animal dispersal (Howe & Smallwood 1982, Willson *et al.* 1989). These fruits are important as food to a diversity of frugivorous fauna, and they, in turn, are important for seed dispersal (Howe 1984). These relationships may affect one or more life stages of the plant, and thus affect a tree's ability to reproduce, the success of the reproductive effort (Lovejoy *et al.* 1983), and the long term genetic viability of the population (House & Moritz 1991).

Fragmentation of this complexity into small remnants of forest poses particular problems for conservation and management. The effects of fragmentation are both direct, negative effects on population survival and extinction, and indirect effects on interactions and community composition. Thus, habitat fragmentation negatively affects biological diversity, and should be considered important in conservation (e.g.. Janzen 1974, Picton 1979, Soule & Wilcox 1980, Lovejoy & Oren 1981, Whitcomb *et al.* 1981 in Wilcox and Murphy 1985).

The effects of forest fragmentation have been the subject of several reviews (e.g. Hobbs 1987, Usher 1987, Saunders *et al.* 1991) and a wide research literature. Early research into the effects of fragmentation contrasted natural fragments, such as continental islands, with those formed by humans modifying the landscape. These studies primarily documented species richness on islands or fragments. Later research investigated the effects of 'unnatural' fragmentation on minimum viable population size, habitat characteristics and more recently, on animal-plant interactions.

This chapter reviews the importance of animal-plant interactions to plant reproductive ecology, and the potential for the disruption of these interactions in fragmented rainforest. The main effects of habitat fragmentation, particularly on plants, the differing approaches to

the study of habitat fragmentation, and the criteria for choice of study species are also discussed. The chapter concludes with the rationale for the present project.

**Table 2.1** Life stages of a plant and interactions with fauna.

Life stage	Interactions (biotic)
Pollination	Pollinators
Seed set	Pre-dispersal seed predators
Seed survival	Seed predators (are they present in the fragments?)
Seed germination	Dispersal vectors Seed predators
Seedling survival	Dispersal vectors Herbivores
Sapling survival	Herbivores (Gaps/shade)
Adult	Parasites
All	Abiotic factors and competition may affect all of these

## 2.2 THE IMPORTANCE OF ANIMAL-PLANT INTERACTIONS

Interactions of animals with plant species include pollinators, seed predators, dispersers of fruit and seeds, herbivores, and parasites (Table 2.1). There is much evidence that animals have an important influence on the abundance and distribution of plants.

This may be by

1. direct influence, or
2. via a more complex set of interactions.

### 2.2.1 Direct influence

#### *Pollination*

Flowers offer nectar and pollen as food sources for animals, and in return, some animal species pollinate the flowers. Flowers exhibit general adaptations in terms of colour, shape, size and reward that correlate with broad types of pollinating agents (Howe & Westley 1986). Similarly, pollinators show general characteristics which allow them to access flowers. In some cases, plants demonstrate specialist adaptation to their pollinators. For example, in some orchids, the flower's appearance mimics the female insect pollinator, so that males attempt to copulate with the flower, thus pollinating it (Dodson 1975). The abundance of nectar (Law 1994) or flowers may influence the number of flower visitors present. Thus, the synchronous flowering of some tropical trees (Frankie *et al.* 1974) appears to be an adaptation to attracting pollinators; and pollination rate may be affected by the density of neighbouring conspecific trees (e.g. House 1992). However, the efficiency of pollinators varies. Fruit and seed set is influenced by the type of flower visitor (Auspurger 1980, 1981; Paton & Ford 1983) and visitation rate per flower (Vaughton 1990b).

#### *Seed predation*

Seed predation can remove up to 100% of the seed crop of a plant species (Crawley 1992), and seed predation is often very high beneath parent plants. Such observations indicate that seedling establishment occurs for one of two reasons: (1) some seeds escape predation by being dispersed beyond the parent (Janzen 1970, Connell 1971, Howe & Westley 1986), or (2) plant species which experience heavy seed predation, use synchronous flowering and fruiting (Auspurger 1980, 1981), and/or sporadic heavy crops (mast crops; Janzen 1971, Silvertown 1980), or a long fruiting season (e.g. Wright 1990) as a means of satiating or limiting predators, thus ensuring that at least in some years, some seeds escape predation and survive to germinate. Seeds obviously form an important food source to animals, however, the expectation is that seed predation tends to have little impact on plant recruitment. This is because seeds that escape predation may die anyway: seedlings that establish at high densities close to parents tend to show increased density-dependent mortality rates, due to microsite limitations (Harper 1977, Crawley 1992).

In investigating the first hypothesis, Hubbell (1980) noted that most adult tropical trees are clumped or randomly dispersed. This shows that despite high levels of density- or distance-dependent seed and seedling mortality near to adult trees, immature plants often establish near the parent. Hubbell (1980) concluded that seed predation does not produce the

expected low density and uniform spacing of trees, because variation in seed crop size between trees and years leads to differing levels of seed predation, and a range of temporal and spatial patterns of seedling establishment. Further, he concluded that factors other than seed predation limit the abundance of tropical tree species and prevent single-species dominance. For example, unequal suitability of microsite conditions for growth and survival, and local non-equilibrium conditions are most likely to prevent local single-species dominance (Hubbell 1980 and references within).

Although seed predation does not explain the coexistence of large numbers of trees in tropical forests, it may have some role in determining the patterns of seedling establishment and community spatial patterns. It may also have some role in determining the relative commonness and rarity of individual species, because the importance of seed predation differs between plant species, due to differences in life history traits and in levels of seed attack.

Differing levels of seed predation (e.g. Terborgh *et al.* 1993) and differing competitive ability between species, indicate that removal of predation should cause a shift in plant species interactions. In the Chihuahuan desert, exclosure experiments have demonstrated that the abundance of small and large-seeded plants is determined by granivory by ants and rodents, in turn whose population abundance is interlinked with seed availability (Brown & Davidson 1977, Brown *et al.* 1979, Davidson *et al.* 1985, Samson *et al.* 1992). This is evidence for the importance of seed predation in controlling community composition and the abundance of plant species (within the limits outlined above). The other process which influences spatial pattern is seed dispersal (see below). Seed predators may also exert selection on the genetic character of the plant species (Smith 1975).

### *Seed dispersal*

Seed dispersal can limit local plant distribution (Primack & Miao 1992) and abundance. The coincident decline or failure to reproduce by a plant species, and the extinction of its seed disperser (e.g. *Calvaria major* and dodo *Raphus cucullatus*, Temple 1977) is evidence for the importance of animals for seed dispersal (but see Witmer & Cheke 1991). In Australia, the extinction of the burrowing bettong *Bettongia leseur* has been suggested as a factor contributing to the alteration of the vegetation composition in semi-arid areas. Noble and Cork (1993) suggested that mesomarsupials including *Bettongia leseur* and the central Australian *Trichosurus vulpecula* were important in regulating key mesoscale processes, such as dispersal of seeds (eg. punty bush), entrapment of seeds in burrows and regulation of seedling recruitment. Replacement of the native seed disperser could also have

implications for the fate of the plant. For example, in South Africa, rare species of Proteaceae may be in danger of extinction due to the replacement of native ants by non-native Argentine ants. Native ants transport and bury the seeds of several plant species, protecting them from fire damage, whereas the Argentine ants do not bury the seeds (Bond & Slingsby 1984).

### *Herbivory*

As animals feed and live on plants, they may change the quality, quantity and distribution of plants. In turn, plant diversity, abundance, structure and chemistry influence plant-herbivore interactions and the structure of herbivore communities (Hunter 1992). Experimental exclusions of herbivores are known to result in a marked regeneration of existing plant species and a shift in species composition (e.g. Smart *et al.* 1985). In the tropical rainforest at Los Tuxtlas, Mexico, it has been shown that there are low levels of seedling herbivory and dense mats of seedlings of large-seeded species compared with Montes Azules, a site at Lacandon forest in Chiapas (Dirzo & Miranda 1990, 1991). This appears to be correlated with an absence/low abundance of some components of the mammal fauna at Los Tuxtlas. However, these connections have not been investigated. Whether the lack of seedling herbivory will result in an increase in abundance of certain classes of tree as the forest ages has not been demonstrated. Due to the long life-span of tropical trees, the long term effect of herbivores in tropical forests is more difficult to determine.

#### **2.2.2 More complex interactions within a community**

While many interactions involve a discrete pair of species (or functional groups), others are more complex, potentially involving the same animal species at more than one life stage (such as a species which both eats and disperses seed), a range of species competing for the same plant part, or an animal-plant-fungi interaction.

For example, higher plants are dependent on mycorrhizal fungi which in temperate forest may be largely dependent upon small mammals for dispersal (Maser *et al.* 1978). In Western Australia the burrowing bettong *Bettongia penicillata* may be part of a complex three-way interaction between *Gastrolobium bilobum* plants, dispersal of its seeds and the mycorrhizal spores necessary for the plant's establishment (Lamont 1992). Interestingly, the seeds of *G. bilobum*, an aril containing legume, are also favoured by invertebrates, probably ants (Bell 1994).

## 2.3 THE EFFECTS OF HABITAT FRAGMENTATION

### 2.3.1 Introduction

Habitat fragmentation occurs when habitat is directly removed, and the remaining portions are left as small remnants or fragments isolated from other similar habitat, and often surrounded by a vastly different vegetation type and land use. Thus, habitat fragmentation has two components, habitat loss and insularization, both of which contribute to a decline in biological diversity (Wilcox 1980).

Much of the early theory and study of fragmentation was based on surveys of fauna assemblages on islands. Principles were extended to fragments in human-modified terrestrial environments, again with a faunal emphasis. Nevertheless, the theoretical effects of fragmentation apply both to plants and animals. Subsequent studies investigated habitat requirements and/or minimum viable population size of species or guilds. Some recent studies investigate the effects of fragmentation on animal-plant interactions and on plants.

### 2.3.2 Natural fragmentation

In some cases, natural fragmentation of habitat into islands has occurred either by a rise in sea level, or as a result of climatic changes or fragmentation of once large continental regions (Soule *et al.* 1979). These islands, once connected to the mainland, are called Land Bridge Islands. Recently isolated islands lose species, that is, the biota collapse or 'relax' (Diamond 1972, Wilcox 1980) to a new equilibrium level (Soule *et al.* 1979). This has been demonstrated for fauna on oceanic land bridge islands (reptile faunas, Wilcox 1978; bird faunas, Diamond 1972, 1973, Terborgh 1973, 1974, Terborgh & Faaborg 1973), communities on mountaintops (boreal mammal faunas, Brown 1971, Picton 1979; plant communities, Riebesell 1982, White *et al.* 1984), and plants on islands in Lake George, New York (Slack *et al.* 1975) and in Lake Mockeln, Sweden (Nilsson 1978). That is, species were surveyed on 'habitat islands' formed by virtue of their topography. These studies found that island size was the most important variable affecting rate of collapse (e.g. Diamond 1972, Terborgh 1974, Wilcox 1980). Distance from the mainland was also important.

### 2.3.3 Fragmentation in human-modified environments

A large number of studies have used the land-bridge approach to analyse the change in species richness in habitat remnants within a modified terrestrial landscape. For example,

Newmark (1987) used the land-bridge island approach to analyse the loss of mammalian species from western North American parks. Such studies also demonstrated a broad correlation between area of the fragment, and the number of species present some time after isolation, although this relationship is clearer if the species are separated into those that originate in the forest interior, edge, or are ubiquitous (e.g. Whitcomb *et al.* 1981).

Generally, small remnants appear to have lost a disproportionate number of original (core) species. Some forest interior species only occur in large areas. Species composition changes with fragment area. This has been demonstrated for mammals (Matthiae & Stearns 1981, Bennett 1987, Kitchener *et al.* 1980a), birds (Forman *et al.* 1976, Howe R. W. 1984, Blake & Karr 1987, Saunders 1989, Kitchener *et al.* 1982) and invertebrates (Wells *et al.* 1983, Klein 1989, Webb & Hopkins 1984). For reptiles (Kitchener *et al.* 1980b, Sarre 1995) and some invertebrates (see below) habitat variability may be more important.

Initially, the hypothesized effects of habitat fragmentation were considered analogous to island biogeography theory, where the size of the island and distance from the mainland are important in determining the number of species which can inhabit and recolonize an island (*sensu* MacArthur & Wilson 1967). In effect, fragmentation studies were applying island biogeography theory in reverse, that is, more extinctions than immigrations are expected, as the fragments lose species after isolation (Wilcox 1980). Species are expected to decline to an equilibrium that depends on island size and isolation. The likelihood of recolonization and population size within the remnants are key considerations.

However, in human-modified landscapes the relationship between size of remnant and species response is not restricted to size and isolation effects alone (e.g. Sarre 1995). Other factors such as topographic position and heterogeneity (Ehrlich & Murphy 1987), time since isolation, the taxon involved (Wilcox & Murphy 1985), disrupted community interactions and resultant indirect effects (e.g. see Ehrlich & Murphy 1987 and larval breeding in remnants) also determine species presence in a fragment and the rate and magnitude with which species loss occurs. These reasons and others mean that species-area curves have a limited use for the design of nature reserves (see review by Zimmerman & Bierregaard 1986).

Fragments within a human-modified landscape differ from oceanic islands in four main ways: (1) the intervening spaces between the fragments contain land uses and species which may interact with the fragments, (2) in the past, or potentially in the future, land clearing patterns may have removed the large 'continent' of habitat which acts as a source of immigrants (Harris 1984), (3) the fragments may vary topographically and climatically, more than is expected from recently denuded islands within an ocean, and (3) the process of

species extinction is, apparently, not directly the reverse of species colonization. In addition, ideas of species-area relationship and island biogeography apply to islands which have stabilized, that is, after the process of collapse of biotas precipitated by habitat fragmentation has occurred (Wilcox and Murphy 1985). The key factors affecting population survival, and the interactions between species were ignored (Wilcox & Murphy 1985). The following section discusses factors that affect population survival within fragments, and the interactions between species.

### **2.3.4 Mechanisms of species change**

The changes in species composition and abundance which follow fragmentation may be the result of :-

1. direct effects - population responses and stochastic factors; or
2. indirect effects resulting from the disruption of community processes and animal-plant interactions, and edge effects.

#### **Direct effects**

The direct effects of habitat fragmentation relate to population level responses (Wilcox & Murphy 1985):

- 1) demographic units may be destroyed outright, reduced in size, or subdivided (thus increasing their rate of extinction);
- 2) potential sources of immigrants may be lost (as a consequence of risk 1); and
- 3) immigration may be impeded by conversion of natural habitat between habitat patches.

In other words, the consequences of fragmentation for communities and for populations will depend on the sizes of populations within fragments, the amount of dispersal between fragments, and the degree to which small population size can be tolerated (House & Moritz 1991). Population viability may be reduced disproportionately with a decline in population size. Smaller remnants may lack numbers of individuals needed to maintain a breeding population, or lack suitable mates for breeding, for both plant and animal species.

Populations may also become extinct from random causes due to low population sizes within smaller islands (Willis 1974, Terborgh & Winter 1980). Species which have variable or unstable population sizes in response to environmental changes may be prone to local extinction (Leigh 1975, 1981; Karr 1982a). The magnitude of these effects is influenced by remnant size and distance (isolation) from a source of immigrants.

Hypotheses to explain 'relaxation' (reviewed by Karr 1982a) note that habitat diversity may also affect population response to fragmentation. For example, smaller islands have a lower

diversity of habitats, and species dependent on lost habitats may disappear (Able & Connor 1979, Wilcox 1980). Alternatively, species dependent on seasonal use of a range of habitats (Karr 1982b), or on resources likely to be variable and/or patchy in distribution are prone to extinction (Terborgh & Winter 1980, Karr 1982a).

Even within fragments of the same size, species composition may differ. The initial inclusion or exclusion of a species in a fragment may be entirely due to chance, in that a species may be absent from the fragment of suitable habitat at the time of isolation and cannot move in afterwards. For example, peccary wallows and periodically flooded pools are used as breeding hollows by Amazonian frogs and are important in determining the presence of the frogs. The periodically flooded pools and associated streams are clumped in space and time and may or may not be present in remnants of a range of sizes (Zimmerman & Bierregaard 1986). In five Amazonian rainforest fragments of equal size (9-10 ha), the occurrence of monkeys differed between sites (Lovejoy *et al.* 1986). Schwarzkopf and Rylands (1989) found that the presence of primates was correlated with habitat variables such as stream presence, a high number of small trees, low percentage of large trees and a high number of lianas. For invertebrates such as termites, community composition within fragments may be a result of the intrinsic patchiness of the original forest, random extinctions and altered microclimate caused by fragmentation (de Souza & Brown 1994).

### **Interruption of processes**

The loss of even a few species may result in secondary extinctions through community level effects (Wilcox & Murphy 1985, Terborgh 1976). Thus, the potential effects of habitat fragmentation go beyond considerations of population level phenomena (Wilcox & Murphy 1985). As well as altered populations within the remnant, isolation effects may prevent reinvasion of pollinators, seed dispersers or herbivores, due to the distance between fragments and/or the inhospitability of the intervening landscape. For example, some insects and mammals, and many understorey bird species of Amazonian rainforest will not cross open area distances as small as 80m (Bierregaard *et al.* 1992). Plants with fleshy fruits that depend on such animals to carry their seeds will be affected. Other potential effects are altered pollination, reproduction or seed survival rates, or genetic inbreeding of the animals and plant species within the remnant.

Detailed information about the processes of ecosystem change in forest fragments of different sizes remains scarce (Bierregaard *et al.* 1992). There are few studies which directly measure the effects of fragmentation on plants or animal-plant interactions (Table 2.2). However, our knowledge of animal-plant interactions (Section 2.2), and of general

**Table 2.2** Studies of plants or animal-plant interactions in fragments or corridors.

Source	Life stage	Main findings
Ballal <i>et al.</i> 1994, Fore <i>et al.</i> 1992	embryo, seedling and adult tissue <i>Acer saccharum</i>	apparent gene flow evident in embryo subpopulation compared with canopy; genetic differentiation between woodlots greater for canopy than for juveniles in some patches, indicating long-distance gene flow by altered wind flux across fragmented landscape; but unlikely to indicate change in genetic diversity in future populations?
Prober & Brown 1994	genetics of seeds from fragmented <i>Eucalyptus albens</i>	significant relationship between population size and genetic diversity. Low diversity in populations <500 individuals. But low differentiation among populations (some interbreed with larger stands).
Aizen & Feinsinger 1994b	pollination, fruit set, seed set	decline in number of pollen tubes/style, fruit set, and seed set in fragments for 3-9 spp out of 14-16 species studied.
Lamont <i>et al.</i> 1994	crown size, seed mass and number	roadside plants larger and higher fecundity than non-edge plants, due to increased nutrient supply at roadside
Yates <i>et al.</i> 1994b	seed production, seed viability, pattern of seed fall	<i>E. salmonophloia</i> seeds in remnant woodlands had high viability, some other factor preventing regeneration in remnants
Santos & Telleria 1994; Telleria <i>et al.</i> 1991	seed predation	small woodlots had high densities of mice, high rates of predation, and less dispersal; large forests had higher densities of the disperser (thrush), more dispersal, higher densities of seedlings
Menges 1991	seed germination	germination increased with fragment size
Dirzo & Miranda 1991	seedling herbivory	lower species diversity, and higher densities of seedlings of some species in remnant
Estrada <i>et al.</i> 1993	frugivore species richness, seed dispersal	inter-island (agricultural crop, remnant forest) movement of forest birds and mammals; forest seeds found agricultural habitats
Putz <i>et al.</i> 1990, Leigh <i>et al.</i> 1993	flora survey of islands of Panama canal and adjacent mainland	non-random increase in abundance of large-seeded species on islands, absence of medium-sized mammal seed predators, and life-history of plants proposed as reasons.
Telleria & Santos 1995	habitat selection by birds in fragments	species that depend on relatively scarce resources occur only in large forests. Species that use ubiquitous resources occur through all the fragments.

habitat requirements for plants and animals, indicate that a range of types of processes may be altered or interrupted by forest fragmentation. Several studies show the potential for plants to respond to changed conditions, including habitat fragmentation (Table 2.2). Many fragmentation effects on plants are mediated by an effect on their animal partners in an interaction.

The following discussion reviews the potential effects of forest fragmentation on animal-plant interactions, with examples particularly relevant to rainforest where possible.

### *Pollination and seed set*

Seed set is affected by nutrient availability, and pollen limitation (Haig & Westoby 1988, Stephenson 1981). Increased water and nutrients within or at the edge of remnants may alter seed set (e.g. Lamont *et al.* 1994). The altered abundance (disappearance, decline or increase) of certain pollinators due to habitat fragmentation (Powell & Powell 1987, Sowig 1989, Aizen & Feinsinger 1994a) also has the potential to affect pollinator visitation and seed output (Menges 1991, Jennersten 1988). Menges (1991) found that *Silene regia* from large populations (>150 individuals) had a uniformly high germination rate. However germination of seed from small populations was relatively low and variable within and between populations. Likely explanations are that inbreeding depression has occurred in recently reduced populations, or that reduced hummingbird pollination has caused an increase in inferior geitogamously produced seed (Menges 1991). A decrease in the number of hummingbird species on land bridge islands has also been shown to affect flower visitation and nectar secretion. Plants were visited less regularly and with less fidelity (Feinsinger *et al.* 1982). No consequences for fruit or seed set were documented. However, several authors have suggested that more specialized pollination guilds may exhibit greater effects on populations within the guild (Feinsinger *et al.* 1982, Futuyma 1973, Janzen 1974 in Wilcox & Murphy 1985) as a result of environmental perturbation, than do generalised systems.

### *Seed predation*

There is circumstantial evidence for the effect on plant populations, when seed predators are absent: In the Panama canal, a survey of trees was conducted on small islands and the adjacent mainland. Comparison with the mainland indicated a non-random increase in abundance of large-seeded tree species on the islands. Small mammals which eat these seeds are absent from islands <2ha. The authors concluded that a combination of wind damage, germination requirements, absence of vertebrate seed predators and resistance to

insect seed predators appear to explain the increased abundance of these large-seeded trees (Putz *et al.* 1990, Leigh *et al.* 1993).

### *Frugivory and seed dispersal*

The population size of frugivores may be determined by fruiting seasonality and the abundance of fruits (Smythe *et al.* 1982). Due to habitat fragmentation, fruit-bearing trees may be a limiting resource in some reserves (H. F. Howe 1984). This could affect the food supply available for coexisting frugivores, resulting in reduced abundance of certain species. As a result, the regeneration of a range of plant species which rely on those frugivores for seed dispersal may be affected. In tropical forests, the disappearance of frugivores may prevent regeneration of plants dependent on animal dispersal (Terborgh & Winter 1980).

Where fruiting trees are visited in small remnants, there may be a high probability that a volant frugivore will deposit seed beyond the remnant edge, rather than within the forest, due to its flight patterns and the scattered distribution of food trees. Alternatively, rare or sparsely distributed fruiting resources may be unattractive to potential dispersers, further reducing the dispersal of the tree species. Many species with large fleshy fruits (e.g. Myrtaceae, Lauraceae) fall into this category (House & Moritz 1991).

As well as affecting the abundance of seedlings, seed dispersal is also important for the spatial distribution of seedlings. A change in the composition of the suite of dispersers due to fragmentation could therefore alter the spatial pattern of seedlings. Howe (1989) predicted that plant species which depend on scattered dispersal for recruitment would be especially vulnerable to loss of dispersal agents. This was because seedlings of scatter-dispersed species probably rarely survive near parents or in dense aggregations under frugivore roosts. Conversely, Howe (1989) predicted that seeds which are adapted for dispersal and germination in clumps should be less vulnerable to temporary loss of dispersal agents. Such species have offspring which consistently recruit near parents, and would tolerate germination without dispersal. Whether this applies to long term loss of dispersal agents has not been tested.

Species which establish under closed forest canopies in tropical and moist temperate environments tend to have larger seeds than those that establish in light gaps and less shaded locations (Foster & Janson 1985, Foster 1986). A large seed size is likely to influence seed attractiveness to predators, the size and competitiveness of seedlings, and seedling response to shade and sunlight gaps (Foster 1986). Such seeds may require larger animals for seed dispersal, and often seed predators large enough to handle the seed. These

animals may also have specific habitat requirements and seed caching behaviour, that are altered by fragmentation. Many of the larger mammal species may show a decline or extinction in small remnants. For example, in the Amazonian rainforest several species of primates are absent from small fragments (Lovejoy *et al.* 1983, Rylands & Keuroghlian 1988 in Bierregaard *et al.* 1992). In remnant islands in the Panama Canal, agoutis, squirrels and peccaries are absent from small fragments (Putz *et al.* 1990) and the abundance of spiny rats differed between islands (Adler & Seamon 1991). These animals are known to eat and/or disperse seeds. In Australia, several species of possum and tree kangaroos were found to be absent from small fragments (Pahl *et al.* 1988, Laurance 1990). These animals eat some fruit (Strahan 1983) and may also disperse seeds of some small-seeded or fleshy fruited species.

Large-seeded species appear unsuited for dispersal by the generalist frugivores and small granivores which often remain abundant in fragmented landscapes. Thus, they may be good indicators of altered plant-animal interactions in fragmented rainforests. However, there are some complications to this. In the neotropics, some medium-sized remnants retain higher abundances of seed predators, possibly due to the absence of large carnivores which have larger area requirements (e.g. Terborgh 1988, 1992; da Fonseca & Robinson 1990; Dirzo & Miranda 1991) (see next section). Thus seed predation rates may be higher, not lower, in fragments. In southern Australian rainforests, there is a range of large-seeded rainforest species (Webb & Tracey 1981b, Webb *et al.* 1986, Stocker & Irvine 1983) which have no known seed dispersers (Webb & Tracey 1981b). (These may once have been dispersed by cassowaries and diprotodonts (Pratt 1982)). It is possible that their ecology in fragmented systems does not differ from that observable in continuous forest. In contrast, in the neotropics, some gomphothere species are now dispersed by domestic livestock (Janzen & Martin 1982).

### *Seedling establishment, survival and dispersion*

Within a small remnant, there may be less chance of seeds landing in an environment suitable for establishment, due to the lack of heterogeneous habitat within the remnant, or due to altered germination conditions caused by edge effects (see next section). Seedling abundance and dispersion may also be altered depending on levels of seed predation, seed dispersal or seedling herbivory. There is evidence for altered seedling survival due to absence to herbivores in a large rainforest fragment (Dirzo & Miranda 1991), but no studies which demonstrate that this affects seedling dispersion, or subsequent abundance of larger size classes within the plant population.

### *Genetic effects*

Plant genetic dispersal may be directly affected by fragmentation if the dynamics of pollen and seed flow are altered or if conditions are made unsuitable for seedling establishment (House & Moritz 1991). Plant species which rely on animals for seed or pollen dispersal will be more affected than those which are wind dispersed and/or self fertile. Rare, or sparsely distributed species may be particularly affected, as discussed above. Thus, the genetic consequences of population fragmentation would be expected to be greater for some species than others, depending on their spatial distribution, breeding system, pollinator specificity and seed dispersal patterns (House & Moritz 1991). Mating systems and seed dispersal mechanisms are particularly important in defining genetic variation within and between populations, and breeding systems may be an important key for determining viable population sizes (House & Moritz 1991).

House and Moritz (1991) point out that several rainforest studies show that all known breeding systems (obligate outcrossers, facultative outcrossers and inbreeders) occur in tropical rainforest trees (e.g. Bawa 1974); that species may have flexible breeding systems (Ashton 1988), and that there may be important relationships between breeding systems, tree density, rarity and pollinator specialisation (House 1985, Kageyama 1990). These processes are equally relevant to Australian rainforest trees (Hopper 1980, Crome & Irvine 1986, Irvine & Armstrong 1988, House 1989, Sands & House 1990). The impact of fragmentation can be expected to be greater on species with density-dependent mating success (plants and animals) and may depend on the mechanism of dispersal (House & Moritz 1991). The effect may also depend on breeding system, such that in small populations the average amount of inbreeding increases. For species which typically outbreed, this usually results in decreased fertility and survivorship (e.g. Ralls *et al.* 1988).

Other processes which affect offspring survival, such as seed predation and seedling herbivory can also be expected to affect the heterozygosity of the surviving recruits. For example, seed dispersal and seedling recruitment patterns may be linked to the original seed density and location, the density of dispersers, and the occurrence of suitable establishment sites, all of which may be restricted with reductions in population and community size (House & Moritz 1991).

### **More complex effects on community processes**

Forest fragmentation can result in indirect community effects. These need to be considered when attempting to explain apparent effects of fragmentation on plant populations. For example, one animal at one life stage of a plant may compensate or show synergistic effects

from the absence of another animal interacting with the plant (e.g. Santos & Telleria 1994). The final outcome in terms of plant reproductive success may depend on the particular combination of presence/reduced abundance/absence of both the pollinators, seed predators, seed dispersers and seedling herbivores. This will depend on the species, community and the landscape matrix involved.

An example demonstrates the interconnectedness of different trophic levels: Many mammalian carnivores are in local or global decline due to habitat loss and large area requirements (Schonewald-Cox *et al.* 1991). In Brazil, da Fonseca & Robinson (1990) found that the absence of predators in small forest plots may alter community structure through competition between the remaining mammals. On Barro Colorado Island (BCI), there is an absence of large cats (jaguar and puma, Glanz 1982). Compared with a large mainland site at Cocha Cashu, Peru, BCI has a markedly higher number of small mammals (agoutis, paca, coati) (Terborgh 1988) which normally form the prey to large cats (Emmons 1987 in Terborgh 1992). As the cats potentially control the relative abundances of small mammals, which have differential fecundities, the absence of predators has potential indirect effects both on their prey and the plants upon which the prey feed (Terborgh 1988, 1992). However, there was no significant difference between Cocha Cashu and BCI in seed removal and seedling survival for *Dipteryx* spp., possibly because small rodents compensate for mortality (Terborgh & Wright 1994). Glanz (1990) cautions that although the lack of top predators appears to explain the high abundance of agoutis, paca and coati at BCI, it does not explain patterns for other fauna. Comparisons with large sites elsewhere must consider other human impacts, such as hunting and poaching, and their effect on abundance of mammals.

### *Edge effects and treefall gaps*

Another key consideration is that habitat remnants have a proportionally higher edge to area ratios compared with intact habitats. Edge effects include microhabitat change, invasion from outside, and a non-viable core area for some interior species. Remnant size and shape influence the magnitude of these effects (e.g. Lovejoy *et al.* 1983, 1984; Laurance & Yensen 1991).

Microhabitat change at the edge includes increased radiation, evaporation, and temperature, greater diurnal variation, changes in soil chemistry and structure, wind shear effects (Young & Mitchell 1994; and see review within Fraver 1994) as well as the incidence of fire (Lovejoy *et al.* 1986, Bierregaard *et al.* 1992). Edges may show an increased number of dead trees (Lovejoy *et al.* 1984; Young & Mitchell 1994) and treefall gaps (Wandelli 1991

in Bierregaard *et al.* 1992). These conditions favour shade-intolerant species which invade as shade-tolerant forest-interior species decline. As a result, forest edges often support an increase in shade intolerant, xeric species, a greater basal area and stem density of trees and saplings, and a higher species diversity (Ranney *et al.* 1981). Estimates of vegetation edge effect range from 10 to 500 m, depending on the vegetation type, aspect (e.g. Fraver 1994) and level of disturbance (Laurance 1991b). A recent review (Murcia 1995) compares various estimates of edge width, from studies measuring alteration in abiotic conditions, vegetation, fauna and processes.

The degree of edge effect will depend on the species. Roads form a barrier to mobility for some insects and mammals (Mader 1984), but others will cross small roads (Burnett 1992). While some birds and mammals of agricultural landscapes will cross fields (see above), others will not. California red-backed voles *Clethrionomys californicus* are virtually isolated in small (<4ha) remnants, and make little use of surrounding cleared land. The lack of hypogea sporocarps of mycorrhizal fungi in cleared areas and near the edges of remnants appears to explain the lack of use of these areas by the voles (Mills 1995).

Generalist or forest edge species may be favoured by the creation of a series of patches with high edge: area ratio. The increased heterogeneity in the landscape, and alteration in vegetation species and structure at edges offers different food, shelter, singing and nesting sites than in the forest interior (Yahner 1988). Edges also increase the invasion surface of the forest. Webb and Hopkins (1984) found an increase in diversity of invertebrate fauna in the smaller remnants, due to invasion from surrounding areas. An invasion, extending up to 300m, of second-growth 'edge' butterfly species was also found in recent Amazonian remnants (Brown in Lovejoy *et al.* 1986). In Victoria (Loyn 1987) and on the New England Tableland (Barrett *et al.* 1994), Australia, studies found that small patches supported more farmland birds such as noisy miners *Manorina melanocephala*. In North America, forest-edge bird species often achieve higher local densities in fragmented forests, but highly migratory species that specialise in forest interior habitat have shown the most severe declines in fragments (Lynch 1987). However, an increase in species at the edge does not always occur - Lovejoy *et al.* (1986) found a negative edge effect for birds, which extended at least 50m into the recently isolated (1980's) remnants in Brazil.

Other disturbances which function as edge effects (Hobbs 1987) include movement of livestock into remnants, invasion of agricultural and weed species into the native vegetation (e.g. Dunphy 1991, Jensen 1993), transfer of nutrients (e.g. Lamont *et al.* 1994), pesticides and organic matter from the field to the remnant, altered water regime (George *et al.* 1994), and possible secondary soil salinisation.

The structural complexity, and relatively stable, moist microclimate of rainforest indicates that edge effects would involve greater climatic contrasts than between other vegetation types and their adjacent agricultural land. For shade-tolerant rainforest species, edge effects could completely prevent suitable germination conditions. Insect, bird and mammal species differ in their response to edges, landscape mosaics and forest fragment size. This implies that the plants on which they feed will also be differentially affected. For example, understorey plants eaten by insects which form food to understorey birds could show higher levels of herbivory. Fruits dispersed by large canopy frugivores, such as primates, may show reduced dispersal distances in fragments.

Within small remnants, wind shear effects cause an increase in treefalls both at the edge and within the remnant (Lovejoy et al. 1986). This alters the amount of light entering the remnant, increasing the proportion of secondary species within the system, and altering the habitat available for plants and animals. Late succession, shade-tolerant species may decline within small remnants as a result. In addition, the composition of the seed rain into gaps is probably altered, as a result of altered abundances of edge plants, seed dispersers and foraging areas within the fragmented landscape (Janzen 1983).

Rainforest is a dynamic system - the vegetation is heterogenous, both spatially and temporally. In a natural system, treefall gaps create opportunities for light-tolerant species to regenerate, and for a variety of successional stages within the rainforest. An increased rate of treefall as a consequence of forest fragmentation could change the proportion of secondary and primary species throughout the remnants, rather than just at the edge. The location and abundance of treefalls, and of secondary species within regenerating vegetation within a remnant would depend on three things: (1) the combination of successional stages in the original forest at the time of clearing and fragmentation, overlaid by the spatial arrangement of patches, (2) the size and shape of the remnant, and the resultant ratio of edge to core forest, and (3) altered animal-plant interactions as a result of both the reduced forest area and the edge effects.

### *The landscape mosaic*

More subtle effects of fragmentation are caused by the break-up of previously continuous landscape mosaics (Hobbs 1987). Some effects of isolation distance have already been alluded to in the sections on pollination and seed dispersal. The dispersal of animals between remnants depends on their vagility and response to the intervening habitat. Some may be reluctant or incapable of moving across intervening regions. Other more mobile

species, such as fruit bats (Eby 1991b) and several species of frugivorous pigeon (Date *et al.* 1991), may move large distances within and between patches. For these, increased fragmentation may have little effect, except that the distribution of resources such as fruiting trees, is altered (House & Moritz 1991). Therefore, at the regional scale, fragmentation may affect plant species differentially. Species pollinated or dispersed by mobile animals are less likely to show the effects of fragmentation than species which depend on fauna which is confined to the remnant. However, it is unknown whether interactions at other life stages of the plant would counteract this. For example, a tree species pollinated by flying foxes may retain high pollination success and high genetic variability in its seed set, but show poor establishment if the fruit produced is large, requiring specific dispersers which are absent from the fragment, and if few seedlings are able to germinate under parent trees.

Distance effects could also prevent detection of flowering by pollinators, or prevent wind-borne cross-pollination from other plant populations. Fragmentation may also alter abiotic conditions, affecting processes such as wind pollination, germination and survival, thus affecting other species interactions.

Other effects may depend on the spatial arrangement of remnant vegetation within the landscape matrix. For example, Saunders and Ingram (1987) found that nesting hollows required by breeding populations of Carnaby's cockatoo *Calyptorhynchus funereus* occur in a different native vegetation type to that of their food. The cockatoos require corridors connecting remnant patches, and/or patches of remnant vegetation visible from neighbouring patches. Cockatoos can breed in extensively cleared areas, provided this spatial arrangement is met (Saunders & Ingram 1987). Other studies indicate that the spatial pattern of fragments and types of edges may influence the occupation and invasion of predators from outside: Although nest predation tends to be higher in smaller fragments, forest size appears to be poorly related to predation rate (Telleria & Santos 1992). In some cases, a 'packing effect' may cause densities of small predators to be higher in small fragments (Santos & Telleria 1992, Wilcove 1985). However, it appears that length and type of edge, the adjacent land use and proximity of adjacent forest are also contributing factors in determining the level of predation and frequency of invasion from outside (see Telleria & Santos 1992, Small & Hunter 1988).

Natural disturbance may occur in a spatial and temporal mosaic across the landscape. Hobbs (1987) pointed out that while disturbance causing local fluctuations within unaltered landscapes such as continuous forest may be in dynamic equilibrium (White 1979), fragmented landscapes are unlikely to be in such equilibrium (Sousa 1984). In attempting to manage the fragmented landscape at the regional scale, the problem is to distinguish the

natural disturbance regime, such as fire, from the altered one caused by clearing and fragmentation effects (Hobbs 1987). In the Scottish uplands, birch and pine do not regenerate well under their own canopies; rather, they probably regenerated after fires, with heathland a successional stage. Thus, the landscape was probably originally composed of a 'moving mosaic' of heath, birch woodland and pine forest (Hobbs & Gimingham 1986). Today, few areas of reserve are large enough to encompass the whole mosaic, and the remaining old growth woods are too precious to disturb to allow them to regenerate. As a result, problems arise with the lack of regeneration of old pinewoods (Hobbs & Gimingham 1986). Related problems occur where certain vegetation types were cleared preferentially and are, therefore, under-represented in the remaining landscape (Hobbs 1987). Often, only agriculturally poor, old growth, or long-unburnt areas are left as remnants. This means that only part of the mosaic is present and some ecosystem processes may have been interrupted. Thus, the temporal and spatial scale within which individual remnants and species are located is important.

In contrast, some landscape mosaics may retain much of the original fauna, depending on the time since fragmentation, the land use and spatial arrangement of remnants. Estrada *et al.* (1993) found that the landscape matrix that they studied in Mexico appears to support a higher diversity compared with that expected in intact rainforest. This was probably because the mosaic of pasture and agricultural tree crops can be utilized by native birds from the forest (see also Loman & von Schantz 1991). Barrett *et al.* (1994) point out the inevitability of a variegated landscape of woodland, scattered trees and pasture in most human-settled areas. In such landscapes, management that focussed on birds that are dependent on large areas of continuous forest may neglect the higher diversity of species in intermediate-sized woodlots (20-400ha). They proposed that we should be managing such agricultural landscapes to maintain core species that are tolerant of intermediate levels of habitat fragmentation. This approach may not be appropriate for rare plant species, which can have important strongholds in remnant vegetation (Hunter 1991).

### **2.3.5 Managing remnants within the landscape matrix**

Because the surrounding landscape is not as isolating as true islands within an ocean (e.g. Harris 1984), remnants are part of a dynamic interaction with other components of the landscape matrix (Burgess & Sharpe 1981). We can expect that over time, the size of remnants and degree of isolation may change as more land is cleared (Hobbs 1987), or as agricultural land is allowed to regenerate. Thus, recent concern for conservation and management of the fragmented landscape as a matrix (e.g. Fahrig & Merriam 1994, Hansson *et al.* 1994) must anticipate future changes. Studies of forest fragmentation have

yet to deal with the need for long term studies of abundance of several species (but see Lovejoy *et al.* 1986, Bierregaard *et al.* 1992), but these are needed to distinguish permanent changes from short term changes caused by management, climate, and disturbance (Risdill-Smith 1987; see Yates *et al.* 1994a). In the meantime, the use of vegetation corridors and revegetation in agricultural areas (e.g. Mwalyosi 1991, Hobbs 1993) have been proposed as measures to maintain and enhance the long term viability of fragmented landscapes. There has been some discussion as to the value of corridors (Simberloff *et al.* 1992, Hobbs 1992), nevertheless, these are the best available options, which potentially allow animal movement and maintenance of essential ecosystem processes. Current research is examining faunal use of corridors and 'ribbons' (Bennett, Henein & Merriam 1994; Crome *et al.* 1994), habitat resources in remnants (Bennett, Lumsden & Nicholls 1994) and ecological principles (Lindenmayer & Nix 1993) for corridor design.

### **2.3.6 Effects of fragmentation on rainforest trees**

#### *Temporal scales*

As plants are often longer-lived than fauna, we can expect that extinction effects will operate over longer time scales. Tree species, and understorey species which continue to reproduce at least partially, will continue to be present in a remnant for some time, i.e. the life span of the adult tree. However, the invasion of plant species from outside the fragment, and the alteration in plant-animal interactions (through the loss of fauna, and breakdown in dispersal and reproductive success of both plants and animals) may occur on a shorter time scale. Thus, the effects of fragmentation on plants may first be evident as changes in species abundance - some species may be lost, others may assume greater importance (Curtis 1956 in Hobbs 1987). For trees, the effects of fragmentation may be measured as differential phenology, reproductive effort, mortality and growth of existing individuals and/or as differential seedling recruitment and survival (Lovejoy *et al.* 1983, Bierregaard *et al.* 1992).

The long-lived nature of rainforest tree species means that the short term effects of habitat isolation will not be perceived through extinctions at the species level (e.g. loss of all individuals of a species in a patch), but rather through changes in, or disappearance of ecological relationships critical to maintaining a successfully reproducing population (Lovejoy *et al.* 1983). Thus, the tropical tree is the classic example of an organism which can become ecologically extinct long before the last remaining individual dies (Janzen 1973, Ng 1983). Tropical trees present additional reasons to consider long term studies of forest fragmentation which include an assessment of reproduction.

### *Genetic changes*

In addition, alteration in plant population dynamics and reproductive processes may be evident as genetic change, long before it is evident as species extinction. Small population size has a range of theoretical genetic consequences (reviewed by Miller 1979, Harris *et al.* 1984, Frankel & Soule 1981, Usher 1987). Complicating these, the genetic effects of forest fragmentation will depend on the size of the plant population's neighbourhood (the area within which a group of plants interbreeds) and the breeding system (House & Moritz 1991, Hamrick 1994). It may not always be the case that forest fragmentation results in greater isolation of local plant populations (Fore *et al.* 1992). Therefore, the genetic effects of fragmentation on a plant species can only be understood once its reproductive biology, and prior geographic distribution and genetic variability are known. In Australia, some species (e.g. *Eucalyptus caesia*, Moran & Hopper 1987) and vegetation types (e.g. rainforest) are naturally fragmented, and this is likely to have some bearing on genetic composition after fragmentation.

## **2.4 RAINFOREST ECOLOGY AND FRAGMENTATION RESEARCH IN AUSTRALIA**

Apart from classifications of forest types (Webb *et al.* 1984 and related papers; Floyd 1990a,b), and taxonomic reviews (e.g. Whiffin 1982), most studies on Australian rainforest plants have been community studies on phenology or succession, or studies of an animal species and the plants they eat (Table 2.3). Detailed studies of the ecology of rainforest plant species in Australia are few.

Overall, interactions between fauna and Australian rainforest plants are poorly known. Flower visitors and breeding system are known for only a handful of rainforest plant species: *Myristica insipida* (Armstrong & Irvine 1989a,b), *Eupomatia laurina* (Armstrong & Irvine 1990), *Flindersia brayleyana*, *Alphitonia petriei* (Irvine & Armstrong 1988), *Syzygium tierneyanum* (Hopper 1980), *S. cormiflorum* (Crome & Irvine 1986), *Neolitsea dealbata*, *Litsea leefeana*, *Diospyros pentamera* (House 1985, 1989) and *Melastoma affine* (Gross 1993). Some dietary studies document the species and plant parts eaten by rainforest fauna (e.g. Goudberg 1990, Crome 1975a,b, Innis 1989), but there have been few studies which determine the influence of herbivores or seed dispersers on the survival of rainforest plants. Several studies demonstrate that flying foxes are probably an integral part

**Table 2.3** Research on aspects of rainforest plant ecology in Australia.

Topic	References
Rainforest structure and classification	Webb <i>et al.</i> 1984 and other papers; Floyd 1990a,b
Boundaries / fire	Smith & Guyer 1983, House 1986, Ash 1988, Turton & Duff 1992, Hopkins <i>et al.</i> 1993.
Nutrients, environmental variables	Turner & Kelly 1981, Lambert & Turner 1986
Succession along gradient	Myers <i>et al.</i> 1987.
Gaps	Nicholson <i>et al.</i> 1988, Abdulhadi & Lamb 1988, West <i>et al.</i> 1988.
Regeneration after logging/cyclones	Westman 1990, Hopkins & Graham 1984a.
Revegetation	Stocker 1981, King & Chapman 1983,
Germination	Horne & Gwalter 1982, 1987; Unwin <i>et al.</i> 1988,
Seedfall / phenology	Olsen & Lamb 1988, Congdon & Herbohn 1993.
Seed banks	Stockard 1991, various articles in Phillips (1991), Buchanan 1989, Kooyman in prep.
Seedling survival	Tompsett (1982) and later; few others.
Litterfall	House 1986, Willson & Crome 1989,
Leaf size, photosynthesis	Hopkins & Graham 1989, Hegarty 1990,
Light interception	Nadolny 1991, Stewart 1995.
Herbivory	Hopkins & Graham 1984b, 1987; Hopkins <i>et al.</i> 1990,
*Pollination	Graham & Hopkins 1990, Abdulhadi & Lamb 1988,
Seed predation	Stewart 1995, Waugh 1993,
Frugivory & seed dispersal	Russell-Smith & Lucas 1994.
- Birds	Connell <i>et al.</i> 1984, McGee 1990, *Nadolny 1991,
- <i>Pteropus</i> spp.	Stewart 1995.
Rainforest fragmentation	Lowman 1988, Hegarty 1991,
	Herbohn & Congdon 1993.
	*Langenheim <i>et al.</i> 1984, Myers <i>et al.</i> 1987,
	Thompson <i>et al.</i> 1988, Herwitz 1993,
	Osunkoya <i>et al.</i> 1993.
	Lowman 1986, Osunkoya & Ash 1991, Turton 1992.
	Lowman & Box 1983, *Lowman 1982, 1985a,b;
	*Jackson 1995,
	Basset 1990, 1991, Basset & Arthington 1992.
	Hopper 1980, Crome & Irvine 1986;
	Irvine & Armstrong 1988, Armstrong & Irvine 1989a,b;
	House 1985, 1989, 1992, 1993; Gross 1993.
	Willson 1988, *Lott and McIntyre 1991,
	*Goldberg 1994, *Lott <i>et al.</i> 1995,
	*Harrington <i>et al.</i> in prep., A. Dennis in prep.
	Crome 1975a,b; Innis 1989, Date <i>et al.</i> 1991,
	Green 1993,
	Richards 1990; Parry-Jones & Augée 1991a,b;
	Eby 1990, 1991a; Eby & Palmer 1991
	Hopkins <i>et al.</i> 1990, Laurance 1991b,
	Laurance & Yensen 1991, Waugh 1993.

\* autecological studies

of the ecology of seed dispersal (McWilliam 1986, Richards 1990, Eby & Palmer 1991, Parry-Jones & Augee 1991a). Recently, the role of seed predators has been investigated in northern Queensland (Lott & McIntyre 1991, Lott *et al.* 1995, Goldberg 1994, Harrington *et al.* in prep., A. Dennis in prep.). Incidental observations on seed predation can also be found in other studies (e.g. Freeland 1972, Redenbach 1982, Osunkoya *et al.* 1992).

In Australia, much of the investigation of forest fragmentation, and the use of habitat corridors and remnants by fauna has been located in sclerophyll vegetation types (*vegetation*: Yates *et al.* 1994b, Prober & Brown 1994, Norton *et al.* 1995; *fauna*: Bennett 1987, 1988, 1990, 1993; Saunders 1989; Barrett *et al.* 1994). In some cases, these give useful information on species composition and habitat correlates of some fauna found both in sclerophyll and rainforest communities, for example *Rattus fuscipes*, and *Trichosurus caninus*.

There is some information on the effect of fragmentation on Australian rainforest seed dispersal processes. Eby and Palmer (1991) presented preliminary results from a study of flying foxes in rainforest remnants in northern New South Wales. Flying foxes defaecate soon after returning to the day roost, after foraging elsewhere. Seeds from a total of 15 species from 4 families were shown to pass through the gut, of which 11 species were viable (Eby & Palmer 1991). This indicates that flying foxes are important dispersers of seed into remnants. These animals have been accused of spreading weeds into remnants, due to their widespread foraging habits, and damage to the forest canopy. Eby and Palmer (1991) found that although exotic plants were found in 90% of the understorey vegetation quadrats at one site, there were none at the other site. This indicates that other factors, such as disturbance from paths, edges, and treefalls influence the invasion of exotics more than canopy degradation due to flying fox colonies (Eby & Palmer 1991). Size of remnant and surrounding vegetation are also likely to have affected weed invasion at these sites.

The effect of fragmentation on rainforest fauna species composition has been surveyed for birds and mammals. Avifauna species richness (Holmes 1987) and distributions (Howe *et al.* 1981) in subtropical rainforest remnants in northeastern New South Wales were found to be related to size of remnant, isolation and disturbance. Across this region, Date *et al.* (1991) found that several species of frugivorous rainforest pigeon travel between remnants, and between forest on the coast and uplands. This demonstrated the importance of retaining fragments as 'stepping stones' across the birds' seasonal migration. Mammal species in north Queensland rainforests are also affected by remnant area and proximity to corridors (Pahl *et al.* 1988; Laurance 1990, 1991a, 1994). For *Melomys cervinipes*, preliminary evidence from one island and 3 fragments indicated that the populations in

fragments were not less heterozygous than the control, and that animals may migrate between sites (Leung *et al.* 1993). However, other species do not use small fragments.

Plant species composition and abundance in the soil seed bank have also been investigated in a small number of rainforest remnants (Hopkins & Graham 1984b, Hopkins *et al.* 1990, Waugh 1993). Seed bank studies showed an increase in weed seed and seeds dispersed by vertebrates in the soil near the edge of small remnants. Some vertebrate dispersed weed seeds were also present in soil from the core of remnants and larger sites, but these were not evident in the standing vegetation (Waugh 1993). Laurance also found an increase in *Calamus* spp. and vines near the edge of rainforest remnants in North Queensland. This edge effect could extend up to 500m into the remnant (Laurance 1991b).

In Australia, the effects of fragmentation on dispersal, demography and genetics of individual species, and the effects of fragmentation on interspecific interactions, particularly predation and interactions essential for plant dispersal, are two of the main areas where our knowledge of rainforest is deficient (House & Moritz 1991). House and Moritz (1991) recommended that there be long term studies on the effects of fragmentation, which focus on dispersal, recruitment and survival of selected species of plant and animal. However, they noted that these are costly in time and resources, even for common species. Therefore, species which are relatively abundant should be selected, with the goal to span a range of life histories and breeding systems.

Can we expect any differences in the effects of fragmentation on Australian rainforest, based on our knowledge of Australian ecosystems? Structurally and floristically, Australian vegetation communities can be related to communities elsewhere (Adam 1992). However, some of our fauna is distinctive and differs from those in rainforests of Asia and the neotropics. Australia has a lack of top predators, and a paucity of large mammalian frugivores and large rodents, relative to other rainforest systems. The largest mammals in rainforest are marsupials, most of which are folivorous (see Strahan 1983), but their role in frugivory, seed dispersal and seed predation is as yet poorly understood. Australia has a range of frugivorous megachiroptera and avifauna, including the cassowary in North Queensland. Although seasonal migrations are not as conspicuous in Australia, plant species pollinated or dispersed by mobile fauna (bats, birds, cassowaries) may well correspond to those visited by migratory birds and terrestrial mammals in the neotropics. Generalist plant-pollinator relationships are likely to be more common, at least in the subtropical rainforests. This may mean that the ecosystem has some resilience to environmental perturbation (Williams & Adam 1994). However, species with specialist

pollinators, and species which are strongly density-dependent in breeding success may be at risk if populations are fragmented (Williams & Adam 1994).

Because Australian rainforest occurs as numerous discrete patches, it is likely that species were already functioning within isolated remnants or refugia, albeit large, prior to human interference. This natural fragmentation offers the chance for some fascinating insight into the long term genetic effects of isolation on species (e.g. Joseph & Moritz 1994, Joseph *et al.* 1995), but complicates interpretation of the effects of human-induced fragmentation on animal-plant interactions. Overlaid on the natural fragmentation, we need to consider the droughts and the unreliable rainfall experienced in Australia (and South America, e.g. Olmos 1993), which may mean that animals and plants within fragments have unreliable food, and may be more prone to extinction than those in less seasonal rainforests.

Because of the paucity of information on habitat requirements, and the effects of environmental variability on rainforest animal-plant interactions, it is too early to answer whether patterns of frugivory, dispersal and seed predation in Australian rainforests are different. We still need to describe the general ecology of the species present, and understand their role in Australian rainforest ecosystems. Such studies can incorporate an investigation of the effects of forest fragmentation.

## **2.5 APPROACHES TO STUDYING THE EFFECTS OF HABITAT FRAGMENTATION**

### **2.5.1 Difficulties in design and implementation**

The majority of the studies on habitat fragmentation have been community studies, based on one-off or monitoring surveys. Most studies of forest fragmentation have been comparisons based on a survey of species richness of fauna (Levenson 1981), or less frequently flora (Dzwonko & Loster 1989) within fragments, compared with a more continuous tract of similar forest. Such studies document current species assemblages and infer that observed differences in species diversity and abundance represent changes following habitat fragmentation. Some aspects of the vegetation may be measured, as habitat correlates for the fauna. As noted above, although such surveys of remnants indicate which species are present in the forest, and may provide guidelines for refuge design based on the number of species that can be maintained in a given area (island biogeography theory, Diamond 1975, Lovejoy & Oren 1981), they give little direct understanding of the functioning of the forest and remnants, or susceptibility of individual species.

Relevant studies have either (1) demonstrated the effect on plants of a reduced interaction with associated fauna but with fragmentation effects uncertain, (2) shown a difference in plant function in fragments without demonstrating the cause, or (3) demonstrated an alteration in animal-plant interactions in fragments, but not the resultant effect on plants.

### *1. Time scale involved*

The difficulty is that the transfer of effects from one trophic level to the next, and from offspring to adult size classes, takes an unidentified period of time after habitat fragmentation. In long-lived plants, the standing stock of individuals should indicate the relative survival of different size classes, both within and between sites. However, without information on the longevity and natural variability in survival rates between size classes, and the past disturbance at the sites, it is difficult to determine whether an alteration in abundance of seedlings represents a long term change in population parameters. Similarly, judging whether the change in abundance of one animal species in a trophic web is the result of altered abundance of another requires prior information on those species' interactions, and their population resilience over time.

### *2. Identification of suitable sites*

Comparison between large and small remnants of forest offers a chance to understand the ecology of species with and without some components of the system. The unnatural fragmentation of the forest forms the experiment, although it often suffers from lack of site replication due to the vagaries of human land clearance patterns. It may not be possible to select sites of similar size, slope and vegetation type within the same region. This means that between-site variation will complicate interpretation of the effects of fragmentation, as will differing disturbance regimes between sites. Also, the definition of small, medium, large and control sites differs between studies, presumably depending on the size of the remnants left after fragmentation (Table 2.4). This complicates comparisons between studies. Sadly, there are few large tracts of forest which can be regarded as truly intact (Janzen 1983).

### *3. Dearth of information about plant-animal interactions*

The inconclusive outcomes of much earlier research may be because studies either concentrated on community aspects, or did not investigate animal-plant interactions in autecological studies. Potentially, studies of animal-plant interactions within fragments of a range of sizes could give a greater insight than studies solely in natural systems.

**Table 2.4** Number of sites studied in fragmentation projects (including studies of edge).

Number of sites	Size range (ha)	Source
<b>SPECIES ASSEMBLAGE</b>		
*4 (6)	60,80,860,36000	da Fonseca & Robinson 1990
6 (primates)	10, 100	Lovejoy <i>et al.</i> 1986
*7 (birds)	1,10	Lovejoy <i>et al.</i> 1986
10	0.1-0.8,7,cont.	Putz <i>et al.</i> 1990, Leigh <i>et al.</i> 1993
17	2-74, cont.	Pahl <i>et al.</i> 1988
13	0.1-350	Telleria & Santos 1995
14	144-21000km <sup>2</sup>	Newmark 1987
15	2.5-500	Blake & Karr 1987
16	<10-200	McCoy & Mushinsky 1994
22	0.1-500	Webb 1989
22	0.7-40	Matthiae & Stearns 1981
23	34-5119	Kitchener <i>et al.</i> 1980a,b
25	1.1-905	Whitcomb <i>et al.</i> 1981
29, 35 (2 regions)	0.1-7, cont.	R. W. Howe 1984
30 + 15 agric islands	1- >200	Estrada <i>et al.</i> 1993
39	0.3-82	Bennett 1990
43	0.03-40	Levenson 1981
*50	0.3-17.1	Adler & Seamon 1991
185		Bennett, Lumsden & Nicholls 1994
294	<6- >400	Barrett <i>et al.</i> 1994
<b>AUTECOLOGY / EDGE</b>		
2 P	6.6 sq mile, cont.	Terborgh & Wright 1994
4 P	20-150	Yates <i>et al.</i> 1994a
4 GP	0.5-1.6	Ballal <i>et al.</i> 1994
4 E	1, 100	Kapos 1989
4 + 18 corridors	~2-10	Bennett, Henein & Merriam 1994
5 E	1.4-50	Young & Mitchell 1994
5	9-10	Schwarzkopf & Rylands 1989
7	1,10,100,cont.	Powell & Powell 1987
8 E	20-1040	Small & Hunter 1988
9 E	2.2-14.5	Ranney <i>et al.</i> 1981
10 P	0.2-16,150,270	Santos & Telleria 1994
14 + 14 corridors	2.4-60.5	Norton <i>et al.</i> 1995
15 P	0.2-20.5, cont.	Aizen & Feinsinger 1994b
15 E	1.4-590, cont.	Laurance 1991b
15 G	0.4-2.3	Fore <i>et al.</i> 1992
17	0.1-280	Telleria <i>et al.</i> 1991
23 G	10-1200 individuals	Menges 1991
25 G	0.3->1000	Prober & Brown 1994
30	0.1-350	Telleria & Santos 1992

\* species abundance or monitoring study.

E= study of edges within fragments, G= laboratory isozyme or germination study from field collections, P=study of plant process in fragments.

### 2.5.2 Importance of autecological studies

Studies of the biology of individual species have been concerned with predicting the minimum viable population size or density for particular species (e.g. Ashton 1976, Shaffer 1987). These have usually ignored genetic effects, interspecific interactions and the breeding system (House & Moritz 1991). Areas in which autecological studies have been identified as having particular importance are:

#### *1. Species area relationships*

Species-area relationships are unreliable in the absence of autecological bases to provide special insights (Zimmerman & Bierregaard 1986). Such autecological information can be used to determine whether a remnant contains sufficient heterogeneous habitat to satisfy a species' requirements. In Panama, Adler and Seamon (1991) found that, although presence/absence of rat species was positively related to island size and negatively to isolation, abundance was not related to either of these. Abundance was probably related to availability of fruit, floristic composition of the islands, and proximity to the mainland which allows short term invasion when food is available.

#### *2. Differential fragmentation effects on species*

Species do not respond to fragmentation in the same manner. Both as a result of population size and their habitat requirements, certain taxon are more likely to become extinct in fragments. In cloud forest of the western Andes, bird species at their geographical limit of distribution were more likely to become extinct, and as were certain guilds of birds (understorey insectivores and large canopy frugivores) (Kattan *et al.* 1994). Other studies have also found that birds of the understorey (Newmark 1991) and foothills (Karr 1982b) are more prone to extinction. Specialists tend to be more vulnerable to habitat destruction, and to successional changes in fragments, the collapse of coevolved mutualisms or food webs, or to edge effects (references within Estrada *et al.* 1993). An added complication is that ecological correlates of species success may differ between disturbance regimes or sites (Fimbel 1994).

Secondly, it should also be noted that not all species decline in abundance due to forest fragmentation. Margules *et al.* (1994) provide preliminary evidence that scorpions are not affected by remnant size. Main (1987) found that a diversity of spiders existed in relatively small areas (104, 400, 1750 ha), although the ecology of individual species ('capacity to persist') will affect the probability of their long term persistence. Trapdoor spiders appear

to be suited to continuing existence in small areas (ca 25 ha), providing a buffer area is available to supplement food supply and microhabitat sites for burrows. Large herbivores such as elephants may (temporarily) increase in abundance due to compression into the remaining area (Walker 1981). Plant populations may show increased fecundity due to increased nutrient or water resources provided by the surrounding agricultural land or roadside (e.g. Lamont *et al.* 1994).

### 2.5.3 Recommended approaches

Four main means of measuring the dynamics of remnants were identified in a workshop (Risdill-Smith 1987) held during the 'Nature Conservation: the Role of Remnants' conference (Saunders *et al.* 1987). Three of the methods involve long term study.

- 1) A short-term approach is to conduct a 'snapshot survey' of species richness and abundance at a range of sites. The resultant data is analysed for pattern and correlated with habitat or management differences between sites. Where a sufficiently large number of remnants are surveyed, species richness may be correlated with site statistics (for example size of remnant), and used to estimate the size of remnant needed to maintain most native species. The species-area relationship (insular biogeography) adapted from island biogeography theory and applied to forest fragments is such an example. Although a general answer is obtained in a short time, a problem with the method is that spatial heterogeneity obscures temporal patterns, and little understanding of mechanism is gained (Risdill-Smith 1987).
- 2) Monitoring of communities is the easiest and quickest of the long term studies. Species richness and the abundance of a number of species are estimated in repeated surveys. By analysing patterns, data from a large number of sites can be used to determine distribution and biogeography of species. Correlations with environmental variables at the sites, over time, allow interpretation of the health of the remnant, but give little understanding of the functioning of the system (Risdill-Smith 1987).
- 3) A study of community ecology incorporates many species in a remnant and their interactions. An example would be a frugivore-fruit dispersal community, such as have been studied in Africa (Gautier-Hion *et al.* 1985) and the mediterranean (Debussche & Isenmann 1989), with more selective studies in Asia (Lambert 1989) and Australia (Green 1993). These kinds of study are long term, and provide information on the interactions in the system, but are difficult to interpret due to the complexity and number of interactions (Risdill-Smith 1987). Rather, most studies have recorded the animal visitors to one species of tree (e.g. Howe 1977, 1980; Coates-Estrada & Estrada 1986), or the foods eaten by one species of frugivore (e.g. Estrada & Coates-Estrada 1984, Wrangham *et al.* 1994).

However, H.F. Howe (1984) recommended that prior to adopting management strategies for reserves, a census of phenology throughout the year, and a systematic census of animal use of different fruits should first be carried out (this would be more difficult for Australia's predominantly nocturnal mammals). This would allow, for example, the identification of plants which attract a disproportionate number of fruit-eating animals, that may be pivotal for maintaining the community. A related approach could be used at the regional level to identify functional groups of organisms, which are important for ecosystem processes and have least 'ecological redundancy' in the biological composition of ecosystems (Walker 1992).

4) Autecology involves the detailed study of one species, its interactions with other species, and the mechanisms influencing the abundance and distribution of that species.

Autecological studies attempt to understand the basis for the status and performance of individual species within the fragmented system. These studies are long term, and the species will usually be studied at one or a number of sites. Autecological studies potentially give better information concerning the function and health of the remnant, providing an appropriate species is chosen. This approach was favoured by participants of the workshop (Risdill-Smith 1987).

Concurrently, the case for autecological studies rather than species-area relationships was presented strongly by Zimmerman and Bierregaard (1986), who cited a long list of supporting papers as evidence of a widespread opinion among ecologists. Zimmerman and Bierregaard point out that 'predictions derived from the equilibrium theory of island biogeography and species-area relations concerning design of nature reserves have been neither helpful nor warranted and there now exists an urgent need for autecological studies on the species to be preserved'.

Bennett (1987) pointed out that insular biogeography and autecology are complementary approaches, which can both provide useful but different information relevant to conservation within fragmented environments. Insular biogeography documents observed changes in faunal assemblage following habitat fragmentation, while autecological studies attempt to understand the basis for the change. Bennett combined these approaches to survey the fauna of 39 remnants, and to study the ecology of *Potorous tridactylus* within the fragmented environment.

#### **2.5.4      Choice of species for autecological study**

Compelling reasons for pursuing an autecological approach to the study of the effects of fragmentation have emerged from this study of the literature and from the experience of

participants in the workshop above. However, the study of some species will predictably be more useful than the study of others.

Several authors have proposed the kind of species which should be chosen for autecological studies. Those most appropriate for study are ones that are:

- a) important economically or socially ( results can have a wider application to conservation, forestry and general biology),
- b) rare,
- c) keystone animal or plant species (which are important in maintaining the community), or
- d) 'indicator' tree species (sensitive to changes with isolation).

Species which are important socially or economically, or rare, may also act as an 'umbrella' species, giving the opportunity to study another ecologically more meaningful species (Risdill-Smith 1987). For example, they are more likely to receive public concern and funding, and to galvanise subsequent management action for forests. Keystone plant species are important in sustaining frugivores through periods of general food scarcity, and are characterized by reliable fruiting (Terborgh 1986). This includes species such as figs and palms, which sustain obligate frugivores, seed predators and other opportunistic species (Terborgh 1986). The 'host' keystone plant (*sensu* Mills *et al.* 1993) and members of its 'ecologically interdependent constellation' might be expected to change together with the effects of isolation (Lovejoy *et al.* 1983). By virtue of their interactions with other species, keystone species can be expected to be important in maintaining the community within fragments.

Indicator species (species sensitive to changes due to remnant isolation) can be either:

- a) species which rapidly colonize disturbed open sites or reserve margins;
- b) shade tolerant species with low dispersability requiring closed forest sites for germination and successful establishment; or
- c) species for which the relative abundance in the patch is high enough to permit statistical analysis and detection of very small changes in population parameters (Lovejoy *et al.* 1983).

Species which are 'representative' and thus a good indicator of the health of the remnant could also be chosen from one or more trophic levels (eg. tree, herbaceous plant) or life history attributes, such as a woody perennial, an obligate seed regenerator, a serotinous species, long-term seed viability, or limited seed fertility (Risdill-Smith 1987).

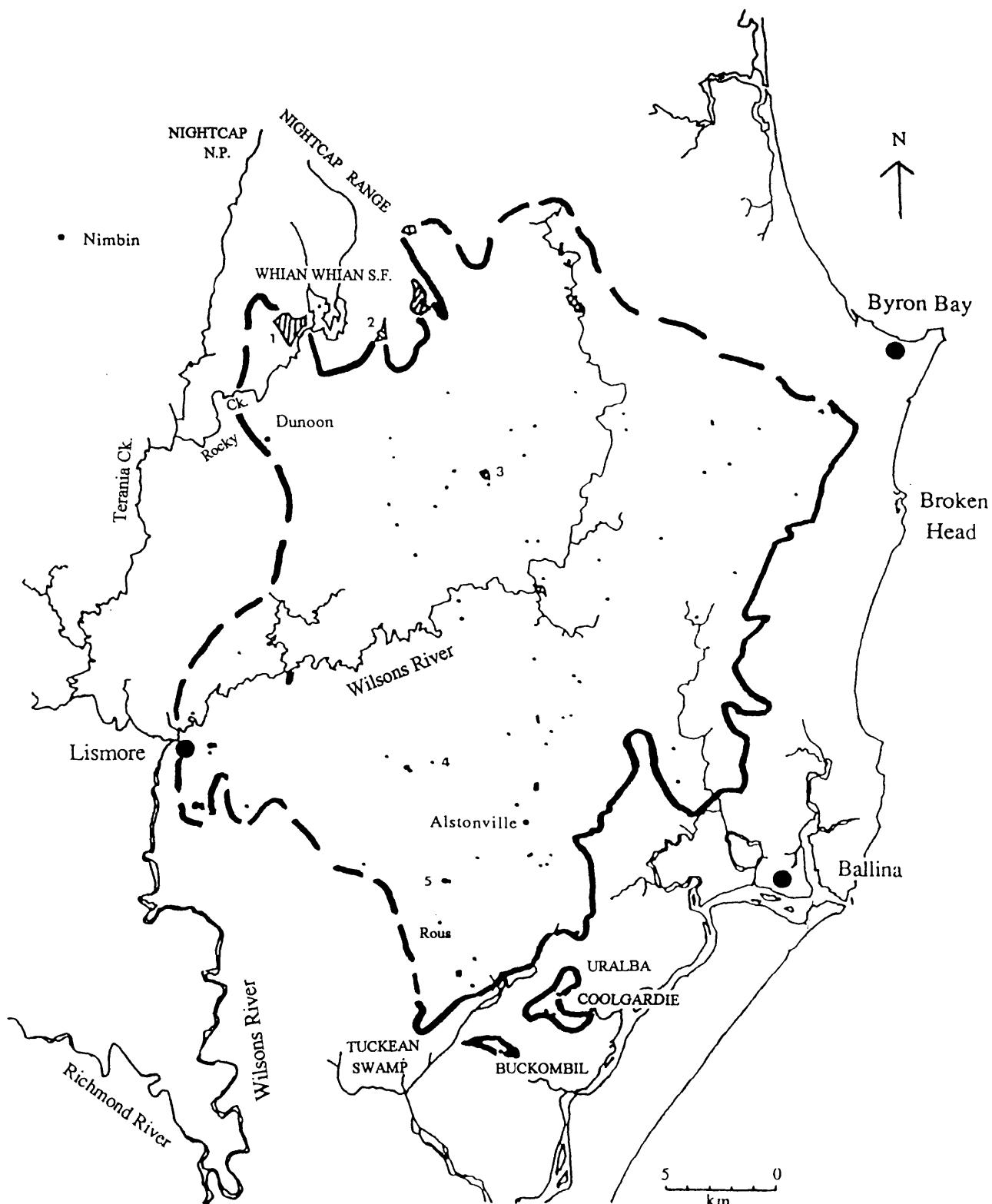
## 2.6 RATIONALE FOR THIS STUDY; CHOICE OF STUDY SPECIES

The literature review revealed that forest fragmentation leads to a decline in species richness, and a change in species composition within remnants. The loss of fauna, and the evidence for their importance in processes such as seed dispersal, led to the prediction that a breakdown of animal-plant interactions (process) would occur within forest fragments, leading to community-level changes, such as a shift in plant community composition.

Most studies used one-off surveys of a large number of fragments to investigate patterns in species richness. However, of the methods of studying forest fragments, autecological studies are preferred as they investigate processes within the habitat. Such studies are few both worldwide and in Australia. For an autecological study, the species chosen should fulfill at least one of the criteria outlined in the previous section, as well as being likely to show changes due to loss of fauna from fragments, i.e. an indicator species, or a keystone plant species. In Australia, there are few studies of rainforest fragmentation, and little is known of the autecology of rainforest plants. Insufficient information exists to identify keystone species in rainforest, with the probable exception of figs. However, an indicator species with low dispersability (e.g. a large seed potentially dispersed by mammals) and which requires closed forest sites for germination and successful establishment is more readily identifiable.

A combination of pragmatic reasons and the above recommendations were used to select *Castanospermum australe* for study in rainforest remnants of the Big Scrub. This species is a canopy tree species, which yields a valuable cabinet timber. It fruits in sufficient numbers to allow reliable study, and has a large seed potentially of importance to mammalian fauna. Studies within continuous forest indicated that seed predation was unlikely to influence (long term) plant recruitment, although it could affect patterns of plant distribution. As forest fragments represent an altered system, this gave the opportunity to investigate the importance of seed predation by comparison between fragments of a range of sizes, potentially with differing fauna. The large seed size would also make such processes readily observable. The large seed also indicated that *C. australe* may have specific dispersal requirements, or limited dispersal. These aspects could potentially be affected by altered animal-plant interactions in forest fragments. Thus it satisfies the selection criteria for autecological study. *C. australe* also fruits during winter, which allowed field trips to coincide with the availability of restricted funding. The emphasis on seed predation allowed investigation of a poorly known aspect of seed ecology in Australian rainforest.

**Figure 3.1** Map of the area of the Big Scrub and location of the study sites.



Boundary of Big Scrub is indicated by a heavy line. Southern and eastern boundaries represent the edge of the basalt plateau (solid line). Western and northern boundaries lie within the area of basalt parent material and are determined by vegetation type and rainfall (hatched line).

Map shows remnants of Big Scrub >1 ha in size. Larger sites are mapped to scale; mapped size of remnants <5 ha size is exaggerated. Study sites numbered: 1 Big Scrub F. R., 2 Boomerang Falls, 3 Johnston's Scrub, 4 Wollongbar, 5 Davis Scrub.