

Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae)

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ABSTRACT

Fragmentation may disrupt mutualisms such as pollination or dispersal, adding indirect negative effects on native plant species to the direct effects of habitat loss. However the effect of fragmentation on mutualisms has been studied only rarely. Here we show that a limited degree of fragmentation improves reproduction in the endemic mistletoe *Peraxilla tetrapetala* (Loranthaceae) in New Zealand.

P. tetrapetala has declined since European settlement 150 years ago; the decline has been attributed partly to weakened pollination and dispersal mutualisms. The decline of native honeyeaters (Aves: Meliphagidae) has caused strong pollen-limitation for *P. tetrapetala* at some sites. A native lepidopteran, *Zelleria maculata*, also limits reproduction by destroying more than half the flower buds in some populations.

Here we report that flower predation by *Z. maculata* decreased and bird pollination increased with fragmentation over four sites at Lake Ohau, South Island. Flower predation decreased from 48% in continuous forest to 8% on isolated trees. Pollination was lowest in forest (14% seed set) and highest on isolated trees (45%). Fruit set therefore increased 4.4-fold with fragmentation. Plant density was also 2-3 times higher on fragment edges. Dispersal was good at all sites.

Therefore, *P. tetrapetala* seems to benefit from the forest edges created by fragmentation, provided that enough forest habitat survives to maintain bird densities. High levels of fragmentation beyond those measured here could possibly result in abrupt failures in the mutualisms. The benefits of moderate levels of fragmentation may partially offset declines in mistletoe numbers from habitat loss and introduced herbivores, which means that small fragments may still be of high value for mistletoe conservation.

INTRODUCTION

Habitat fragmentation has a number of direct and indirect effects on native plants and animals. Direct effects include the removal of vegetation (which alters the size of habitat patches), and physical changes associated with edges such as altered light, humidity and wind (which alter the nature of the patches). Indirect effects include alterations in the interactions between organisms, such as altered risks of predation, or disruptions of mutualisms. In this paper we study the effects of fragmentation on pollination and dispersal mutualisms.

There has been little work on the effect of fragmentation on mutualisms and how this affects the persistence of plant populations. The widely cited work of Aizen & Feinsinger (1994a, b) showed that in an Argentinian dry forest, increasing habitat fragmentation led to decreasing pollination rates (median decrease = 20%) in a range of plant species, due to a number of factors affecting both pollen quantity and quality. Fragmentation appeared to favour the introduced honeybee (*Apis mellifera*) and decrease visits by native pollinators.

Native mistletoes of the genus *Peraxilla* (Loranthaceae) in New Zealand provide a unique opportunity to test the effects of fragmentation on pollination and dispersal. Since European settlement of New Zealand around 1840, all six species of endemic loranthaceous mistletoes have declined in numbers (de Lange & Norton, 1997). The declines have been attributed to herbivory by introduced Australian brushtail possums (*Trichosurus vulpecula*) and destruction of forest habitat for farming. Native forest cover has been reduced from 78% in pre-human times to 23% today (Atkinson & Cameron, 1993). Habitat clearance has led to an overall decline in the distribution of the mistletoes, and extant populations have been reduced in size (de Lange & Norton, 1997). Perhaps the most graphic example of the effect of habitat loss is the extinction of *Trilepidea adamsii* (Loranthaceae), which may have disappeared primarily because of forest clearance (Norton, 1991), although pollination may also have been involved (Ladley & Kelly, 1995). The introduced brushtail possum has also negatively affected the extant species of mistletoe, by browsing adult plants (Wilson, 1984; Ogle & Wilson, 1985), although at some sites little damage to mistletoes is evident (Owen & Norton, 1995).

However, there has been no work on how habitat fragmentation affects the reproductive processes and population sizes of New Zealand mistletoes. The Loranthaceae is a large family (c. 75 genera and 900 species) with a predominantly southern hemisphere distribution (Barlow *et al.*, 1989).

Many mistletoes prefer high-light environments such as edges for germination and growth, both worldwide (Kuijt, 1964) and in Australia (Norton *et al.*, 1995), and anecdotal and distributional information suggests the same may be true in New Zealand (Norton & Reid, 1997). Kuijt (1964) also suggests that forest fragmentation may increase edges and thereby benefit birds, which could benefit mistletoes. However, loranthaceous mistletoes are less common along corridors in Western Australia, which Norton *et al.* (1995) attributed to reduced numbers of mutualist birds in these corridors. Therefore the net effect of fragmentation on mistletoe abundance is very dependent upon changes in reproductive mutualisms.

Also, *Peraxilla* species have very exacting requirements for reproduction. They rely on native honeyeater birds to open and pollinate their flowers (Ladley & Kelly, 1995; Kelly *et al.*, 1996; Ladley *et al.*, 1997). Without birds, flower buds do not open and very little seed is produced. Several species of small native solitary bees (*Hylaeus agilis* and *Leioproctus* sp.) can open the flower buds and thus act as pollen vectors, but these are less important than birds (Kelly *et al.*, 1996). At several sites on the mainland of New Zealand, bird visits are too infrequent for sufficient pollen transfer, and seed production is much lower (5%–30%) than is achieved through hand pollination (50%–80% seed set: Robertson *et al.*, 1999). *Peraxilla* species also rely on the same native birds for seed dispersal, and without bird dispersal the seeds cannot germinate (Ladley & Kelly, 1996). Thus, changes in bird density or behaviour because of fragmentation could have a large effect on reproduction in *Peraxilla*.

Peraxilla fruit production is also affected by the predation of flower buds. Native caterpillars of *Zelleria maculata* (Yponomeutidae) eat out the interior of *Peraxilla* spp. flower buds (Patrick & Dugdale, 1997), and buds attacked by *Z. maculata* almost never produce seeds. At seven sites throughout the South Island in the 1997/8 season, *P. tetrapetala* lost from 8% to 44% of buds to *Z. maculata* (Crowfoot, 1998). Therefore the two main determinants of seed production at a site are the level of pollination and the extent of bud predation.

The aim of this study was to measure the effect of forest fragmentation on the reproductive biology of the mistletoe *Peraxilla tetrapetala* at Lake Ohau. This site was chosen for four reasons: (1) *P. tetrapetala* is consistently pollen-limited at the site (Robertson *et al.*, 1999); (2) it grows on a single host species (*Nothofagus solandri* var. *cliffortioides*) which is the sole canopy tree there; (3) the previously continuous forest cover has been fragmented into various sized remnants; and (4) *P. tetrapetala* occurs in many of these forest remnants. Robertson *et al.* (1999) considered that because of de-

clines in native pollinating birds, these mistletoe populations could well be seed-limited. We set out to measure how the density of mistletoe plants per unit area, the rates of pollination and bud predation, the overall fruit-set rate per flower, and the rate of dispersal of ripe fruits varied among four remnants differing in degree of fragmentation.

METHODS

Four mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest patches at Lake Ohau, central South Island, were chosen for comparison (Fig. 14.1). The most intact of the four forest sites, Temple Stream North Branch (NBT), was located within a 690-ha block of continuous forest, about 600 m from the forest edge. The Round Bush (RND) site was a 5.3-ha intact forest fragment, while Parsons Creek (PAR) was on the edge of a 100-m wide 6.5-ha riparian strip of forest containing many gaps and fallen trees. The final study site (ISO) consisted of three isolated groups of three to seven free-standing trees in pasture along the edge of Lake Ohau. The four patches were ranked by degree of fragmentation according to patch size, and how exposed the study mistletoes were to edge effects. At Temple Stream, all of the mistletoes were on host trees well within the interior of the forest. At Round Bush, two-thirds of the mistletoes were in the interior of the forest, and the other one-third were within 5 m of the edge of the patch. At Parsons Creek, all the mistletoes were on hosts on the edge of the patch of forest; the isolated mistletoes were on single host trees surrounded on all sides by pasture.

The main pollinating birds in this area are bellbirds (*Anthornis melanura*, Meliphagidae), which along with silvereyes (*Zosterops lateralis*, Zosteropidae) are also the principal dispersers of *Peraxilla tetrapetala* (Ladley & Kelly, 1996; Ladley *et al.*, 1997).

In each forest patch, five variables were measured: mistletoe density, rate of predation of flower buds by *Z. maculata*, pollination rates, fruit-set rates, and fruit-dispersal rates. The density of *P. tetrapetala* plants at the different sites was measured by setting up a number of 20 × 20 m plots (Table 14.1). All mistletoes within these plots were mapped and their volume (m³) measured; the total number and trunk diameter of host trees was also recorded. At each site a smaller number of *P. tetrapetala* plants (Table 14.1) were tagged and used to measure the pollination rate, fruit set and rate of insect attack on flower buds. Flowering commenced in early December 1997. On each tagged plant a branch that had approximately 100 flowers on it was marked, and the exact number of flowers was recorded, along with

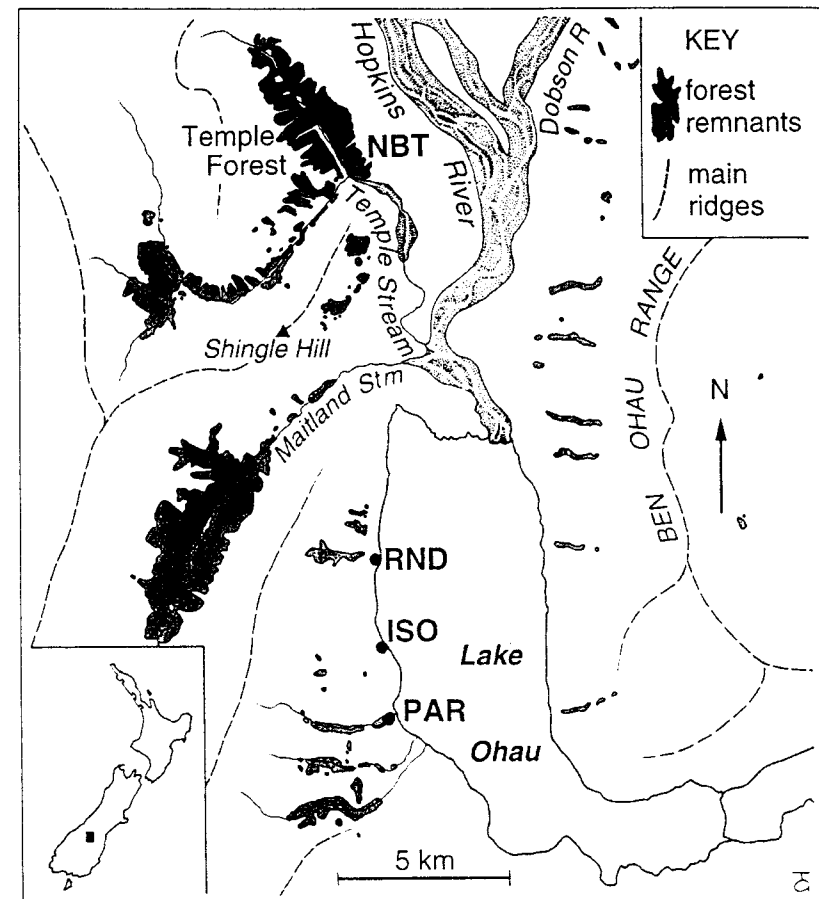


Fig. 14.1. Map of the study area at Lake Ohau, central South Island, New Zealand. Remaining forest areas are shaded, and the four fragments used in this study are labelled. NBT, Temple Stream North Branch (TCP was adjacent); RND, Round Bush; ISO, isolated plants; PAR, Parsons Creek. The inset shows the location of the main map within the South Island.

the number of flowers that had been attacked by *Z. maculata*. Approximately three months after flowering in March 1998 the number of ripening fruits was counted on the tagged branches. Like most of the Loranthaceae, *P. tetrapetala* has single-seeded fruits which are easily scored in the field for success or failure. From these numbers we calculated: the rate of *Z. maculata* attack (number of insect-attacked flowers, divided by the total

Table 14.1. Locations of the study sites, and number of *Peraxilla tetrapetala* mistletoe plants and plots used for the various analyses, at Lake Ohau, 1997/98 flowering season and 1998/99 fruiting season

Site	Longitude E	Latitude S	Altitude (m)	Number of plants, pollination ^d	Number of plants, predation ^d	Number of plants, dispersal ^d	Number of 20 × 20 m plots
Temple (NBT/TCP)	169° 48.9'	44° 06.4'	700	10	10	10	4
Round Bush (RND)	169° 49.0'	44° 12.6'	540	43	46	10	6
Parsons Creek (PAR)	169° 49.2'	44° 15.0'	540	10	8	9	4
Isolated plants (ISO)	169° 49.4'	44° 14.4'	540	7	8	7	3

^dNot all mistletoes in each plot were used for pollination, predation and dispersal measurements.

number of flowers); the pollination rate (the number of fruits set, divided by the number of flower buds not attacked by *Z. maculata*); and the overall fruit-set rate (number of ripening fruits divided by the total number of flowers).

Dispersal measurements were carried out in February–July 1999. The same four patches were used, except that the Temple Stream site (TCP), while still within the large Temple Forest, was located closer to the edge of the forest due to logistic problems in monitoring the NBT site. At each site branches were tagged on seven to 10 plants and fruits on the branches were recorded on seven occasions at three-week intervals. At each date fruits were classified as unripe, ripe, or overripe (withered: see Ladley & Kelly, 1996). To measure dispersal efficiency, for each plant we summed the number of ripe and overripe fruits seen over all dates through the season, and calculated the overripe fruits as a percentage of all ripe and overripe fruits. With more efficient dispersal, ripe fruits would be removed before they turn overripe (which takes four to six weeks), and the overripe percentage would be lower.

RESULTS

The trend was for density of *P. tetrapetala* plants to be higher at more fragmented sites (Fig. 14.2a). The greatest densities of *P. tetrapetala* mistletoes were recorded in the edge habitats (Isolated and Parsons Creek) with 2- to 3-fold more mistletoes than were located in larger forest patches (Temple Stream and Round Bush). The same result was found for mistletoe volume divided by basal area of host trees per plot, so the result was due largely to changes in mistletoes per host, not hosts per plot. The confidence intervals were wider for the Isolated site, because there were fewest plots at this site (Table 14.1), and perhaps also because of stochastic factors in mistletoe colonisation of isolated trees.

Flower bud predation by *Z. maculata* was markedly lower at the more fragmented sites (Fig. 14.2b). The greatest rate of flower bud destruction by *Z. maculata* larvae was recorded at the continuous forest site (Temple Stream), and there were very low levels of predation at the two edge habitats (Parsons Creek and Isolated).

Pollination rates in unattacked flowers were higher in the more fragmented patches (Fig. 14.2c). The variance was higher for isolated plants, and this cannot wholly be attributed to a smaller sample size, so the exact location of the isolated plants in relation to movement patterns by pollinating birds may be important for adequate pollination.

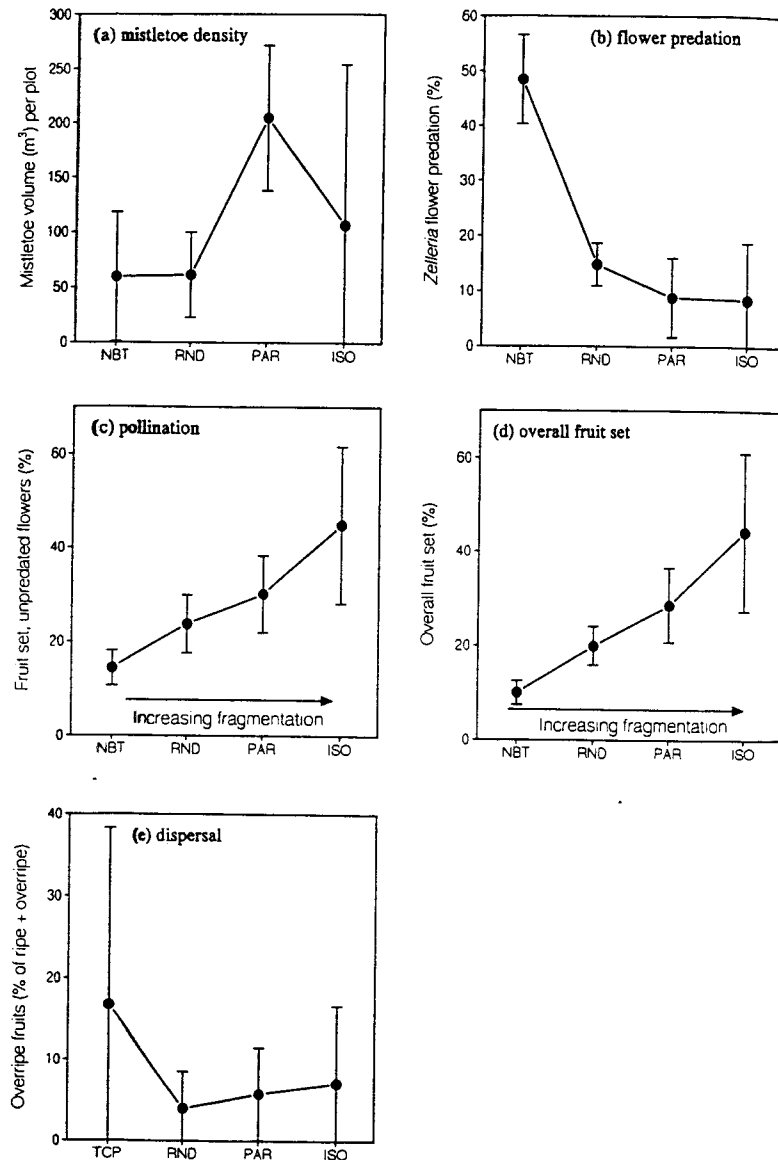


Fig. 14.2. Reproduction of *Peraxilla tetrapetala* mistletoes at Lake Ohau in four forest sites varying in their degree of fragmentation from undisturbed forest (NBT/TCP) to single isolated trees (ISO). (a) Density of adult mistletoes in 20 × 20 m plots (m³ per plot). (b) Percentage of flower buds eaten by the native moth *Zelleria maculata*. (c) Percentage of non-*Z. maculata*-attacked flowers which set seed (a measure of pollinator visitation rates). (d) Overall chance of a flower producing a seed. (e) Rates of dispersal (percentage of ripe and overripe fruits through the season which were overripe). Error bars are 95% confidence intervals; sample sizes are given in Table 14.1.

Because smaller fragments had both a lower rate of flower predation and a higher rate of pollination, the overall fruit-set rate (Fig. 14.2d) was very much higher at fragmented sites (Isolated, mean 44.9%, and Parsons Creek, 28.6%) than in continuous forest (Temple Stream, 10.0%). Combined with the higher density of adult mistletoes on edges (Fig. 14.2a), there will be very much greater numbers of seed produced per unit area of forest on the edges of forest and in small fragments than in undisturbed continuous forest, even though *P. tetrapetala* grows successfully throughout the upper canopy of the tall intact forest at Temple Stream North Branch.

Dispersal service was good at all sites (Fig. 14.2e). The overripe-to-total-ripe ratio was less than 17% at all sites and showed no clear trend with fragmentation. This suggests that fruit removal by birds normally occurs before fruits have withered.

DISCUSSION

Zelleria maculata, the native moth that consumes the flower buds of *Peraxilla tetrapetala*, was less common at more fragmented sites. A parallel study in the same area showed that this was also true at the individual plant level, with mistletoe plants located on edges having lower rates of *Z. maculata* attack than plants located in the interior of patches (Crowfoot, 1998). There may be various reasons why *Z. maculata* attacks more flowers inside forest patches, such as more favourable pupation sites (e.g. Montllor & Bernays, 1993), lower predation by parasitoid wasps (e.g. Rausher, 1979), or preferential oviposition by the female moths, in forest interiors. In any case, the effect is that mistletoe seed set is higher on edges, apparently because the native moth is itself affected by the creation of edges during fragmentation.

Pollination is also more effective on edges, which almost certainly means that bird visits per flower are more frequent there. Previous work suggests that fruit set is essentially determined by the number of pollen grains delivered by animal visitors (Robertson *et al.*, 1999). Therefore, it seems that bird visits per flower were highest on the isolated plants, and lowest in intact forest. The more frequent visits to edge mistletoes could be due to a range of aspects of bird behaviour including: greater accessibility to birds of flowers on forest edges; local increases in the relative attractiveness of mistletoes in predominantly pasture areas with few other nectar-producing plants; or, if mistletoes flower more profusely on edges, preferential foraging by birds in areas with higher densities of flowers. The mistletoes

produce showy bright red flowers which are visible from great distances (> 1 km) across open country. Aizen & Feinsinger (1994b) also found higher visitation rates in isolated fragments for two hummingbird-pollinated plants in Argentina. At Lake Ohau, the main limit to seed set is pollinator availability (Robertson *et al.*, 1999), and thus enhanced attention by birds to edge mistletoes increases the seed set there.

With lower predation and higher pollination, the chance of a *P. tetrapetala* flower ripening a seed is much higher on edges. Also, adult mistletoes are much more abundant on edges. It is possible that more successful flowering on edges in the past has resulted in a locally elevated seed source for establishing more mistletoes on the edges. However, other factors apart from elevated flowering have probably independently increased the density of mistletoes on edges. Firstly, seeds are more likely to be deposited on an edge host tree if the dispersing birds (bellbirds and silvereyes at Ohau) favour edges (see above). Dispersal did not vary greatly between fragmented and less-fragmented sites, but this was because dispersal was efficient at all sites. We were unable to measure where dispersed seeds were deposited after passing through the bird, and this could still show a bias towards edges if birds roost or perch there. Second, higher light conditions may favour the establishment of seeds, or subsequent growth of *P. tetrapetala*. Overseas studies have often shown better germination or growth of mistletoes in higher-light (Kuijt, 1964; Lamont, 1983; Norton *et al.*, 1995). The New Zealand species appear to be relatively unfussy in their general germination requirements, apart from a requirement for removal of the exocarp (Ladley & Kelly, 1996), but have not been tested for light effects. Establishment success of the closely related mistletoe *Alepis flavida* is known to vary with branch size (Norton & Ladley, 1998), but an unpublished experiment shows little effect of light levels on establishment in *A. flavida* or *P. tetrapetala* (D. Norton & J. Ladley, personal communication). There are no published data on growth rates of these species in relation to light intensity but it is possible that edge mistletoes have higher growth rates and therefore will be larger after a given time interval.

Our results are limited to the scale of fragmentation that we studied. Even our most isolated host trees were no more than 2–3 km from other patches of forest containing mistletoes, and birds readily move over these distances. However, if fragmentation proceeded, then fragments might be too far apart to sustain bird populations (or the birds might be unable to move out to the mistletoes from more intact areas where populations are sustained). In those cases, then we would expect a collapse of the mutualism at very high levels of fragmentation, especially since exotic bird species

which are more likely to inhabit highly fragmented landscapes (Williams & Karl, 1996) rarely serve as effective pollinators for *Peraxilla* (Ladley *et al.*, 1997). While exotic birds may serve as useful dispersers of mistletoes (Keast, 1958), it is pollination which is limiting reproduction in the New Zealand species (Robertson *et al.*, 1999).

Also, our results are limited to a short time-scale. We have shown that mistletoes on the edges of forest patches produce more seeds per flower, but these mistletoes cannot persist long term without a supply of young regenerating mountain beech trees. Edges and clearings generally favour *Nothofagus solandri* regeneration (Wardle, 1984), but at most of our sites beech regeneration is limited by fires, and grazing by sheep and cattle, and mistletoes seem to be largely establishing on large, old, even moribund trees. In the longer term, without effective beech regeneration, the mistletoe edge population cannot persist even if there is abundant seed produced on edges.

CONCLUSION

A moderate level of forest fragmentation appears to benefit this declining native mistletoe, principally by creating more edge habitat. While fragmentation may sometimes serve to disrupt mutualisms, worsening the performance of the surviving native species (e.g. Aizen & Feinsinger, 1994b), clearly this will not always be the case. In our study, fragmentation improved mistletoe reproduction by reducing flower predation by a native moth, and concentrating visits by native pollinating birds, on edges and exposed trees. However, this may partly be an artefact of the extensive changes in the New Zealand biota, with greatly reduced densities of the pollinating birds due to introduced mammalian predators like rats, cats and stoats (Atkinson & Cameron, 1993). Had these predators not reduced densities of bellbirds in the Ohau area, there might have been enough birds to adequately pollinate the *P. tetrapetala* plants at all sites, including in the intact forest. Concentrating the mistletoes on to easily accessible edges may be beneficial now mainly because it gives the highest possible fruit set with the current low densities of surviving birds.

Also, around sites like Parsons Creek and Isolated, the past loss of *P. tetrapetala* forest habitat (> 95%; Fig. 14.1) exceeds the increase in density and reproduction on edges (7- to 9-fold). Consequently, there would still be more mistletoe seeds produced per square kilometre in intact forest than in this mosaic of small fragments and pasture. But given that the forest was cleared in the past, enhanced reproduction of mistletoes in small frag-

ments means that even small remnants can be valuable habitat for the conservation of these endemic plants. The higher seed production per flower on edges partially compensates for the loss of forest habitat and herbivore damage by possums, thus enhancing the survival prospects of the mistletoes. However, extensive regeneration of *Nothofagus solandri* will be required for the long-term persistence of these endemic mistletoe populations at Lake Ohau.

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