

Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae)

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Abstract: Positive effects of fragmentation on plant reproduction are uncommon; in a literature review we found significant negative effects on fruit or seed set for 50 plant species, compared to 26 species showing no effect, and only nine affected positively. One of these is the declining New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae), and here we investigate the mechanism of this positive effect. *P. tetrapetala* requires visits from native bird or bee pollinators to produce fruit. Fruit set was consistently pollen limited at several South Island sites because of a shortage of pollinators, but within a site at Lake Ohau, plants on forest edges had higher fruit set than those in the forest interior. Previous work showed that this difference was not caused by a shortage of resources in interior plants, but was associated with higher bird visitation rates to flowers on edges. In this study, we tested whether native bees also show a preference for edge flowers. At two sites (Ohau and Craigieburn) edge mistletoes had higher visitation by native bees (*Hylaeus agilis* and *Leioproctus* sp.) and higher fruit set. Some, but not all, of the higher visitation to edge flowers was explained by a preference amongst bees for flowers in direct sunshine. Therefore, *P. tetrapetala* experiences higher fruit set on edges because both of its main groups of pollinators (endemic birds and bees) visit edge flowers more often. The other eight published cases of positive effects of fragmentation on fruit set also all reported increased visitation rates by pollinators.

Keywords: bee pollination; edge effects; fragmentation; *Hylaeus agilis*; *Leioproctus*; Loranthaceae; mistletoe; *Peraxilla tetrapetala*; plant reproduction; pollination mutualisms; pollinator visitation.

Introduction

Human activities have resulted in much forest clearance and fragmentation of natural habitats, both worldwide (Hobbs and Yates, 2003) and specifically in New Zealand (Ogden, Basher and McGlone, 1998). This has prompted extensive research on the consequences of fragmentation on habitat quality (Murcia, 1995; Ford *et al.*, 2001). Differences in microclimatic conditions on edges, increased densities of predators, herbivores and weeds, and an increased risk of windthrow and fire on edges may all have negative effects on native flora and fauna that inhabit forest remnants (Murcia, 1995). However, while anthropogenic fragmentation is often shown or presumed to negatively affect the native biota, the creation of edges can sometimes have positive effects.

One example of the variable effects of fragmentation is on plant reproduction, including plant/pollinator interactions — the subject of the present paper. Several recent studies show that fragmentation

often has negative effects on pollination systems. Aizen and Feinsinger (1994) showed that in an Argentinean dry forest, fruit set was significantly lower (at $P < 0.10$) in forest fragments than in continuous forest for five of 15 plant species, and the median decrease in pollination levels across all 15 species was 20%. Reviews by Hobbs and Yates (2003) and Harris and Johnson (2004) both showed that pollination is often negatively affected by fragmentation. Hobbs and Yates reviewed 60 species (including those in Aizen and Feinsinger's paper), some from multiple sites and/or years, and found significant declines in some measure of plant reproduction in 49 of 85 cases (58%).

In contrast, sometimes edges have no effects, or even beneficial effects, on pollination. Aizen and Feinsinger (1994) reported that two of 15 species had significantly better pollination in forest fragments. Hobbs and Yates (2003) found significant positive effects on reproduction in three (4%) of the 85 cases they examined. Recent studies on endemic mistletoes (*Peraxilla tetrapetala*, Loranthaceae) growing on

mountain beech (*Nothofagus solandri* var. *cliffortioides*, Fagaceae) trees in New Zealand found higher fruit set (and lower flower predation) by the native moth *Zelleria maculata* on forest edges than in the forest interior (Crowfoot, 1998; Kelly *et al.*, 2000).

To understand why edges can have such varied effects on plant reproduction, it is helpful to examine the mechanisms that alter plant-animal interactions near edges (Hobbs and Yates, 2003). In Chile, visitation rates to flowers of *Embothrium coccineum* (Proteaceae) were higher in small forest patches because of territorial behaviour by its primary pollinator, the flycatcher *Elaenia albiceps* (Smith-Ramirez and Armesto, 2003). In the case of *P. tetrapetala*, Montgomery *et al.* (2003) showed that the enhanced fruit set near edges was not due to higher light levels, which might enable plants to acquire more resources, but instead reflected higher visitation rates to edge flowers by bird pollinators. *P. tetrapetala* has a complex 'explosive' flower, which is dependent on animals for flower opening (Ladley and Kelly, 1995). Unopened flowers have extremely low fruit set, and fruit set overall is often strongly pollen limited because too few flowers are opened by pollinators (Robertson *et al.*, 1999; Kelly *et al.*, 2004; Robertson *et al.*, 2005). The primary animals which open flowers are two endemic species of birds: tui (*Prothemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*), both in the Meliphagidae (Ladley and Kelly, 1995; Ladley, Kelly and Robertson, 1997). In addition, two species of endemic short-tongued bees (*Hylaeus agilis* and *Leioproctus* sp.) also open *Peraxilla* flowers. Because of their small size (about one-fifth the size of a *P. tetrapetala* bud), the native bees seemed unlikely candidates for effective pollinators, but they have been shown both to deliver about as many pollen grains per visit as the birds do, and to significantly enhance fruit set (Kelly *et al.*, 1996; Robertson *et al.*, 2005).

Since these endemic bees are also now known to be important pollinators of *P. tetrapetala*, the response of bees to edges could alter the overall levels of *P. tetrapetala* fruit set on edges. If bees have no preference for edges, or the opposite preference to birds (i.e. higher visitation at interior sites), then the relative fruit set on edges versus interior sites would vary with the composition of the pollinating fauna. Moreover, invertebrate pollinators may be more affected than birds by inclement weather such as cold temperatures or rain (Szabo, 1980; Burrill and Dietz, 1981; Markwell, Kelly and Duncan, 1993; Robertson and Lloyd, 1993; Louadi and Doumandji, 1998; Horskins and Turner, 1999; Vicens and Bosch, 2000), so the relative numbers of vertebrates and invertebrate pollinators may change from day to day. Such a mechanism could produce variations over time or among sites in the strength of edge effects on pollination.

This study was designed to determine, firstly, what percentage of all studies of plant reproduction on edges show positive edge effects on fruit or seed set? We then set out specifically to determine how native bees visiting *P. tetrapetala* flowers are affected by forest edges. In particular, we asked: (1) Do native bees visit edge flowers of *P. tetrapetala* at a higher rate than interior flowers? (2) Do variations in *P. tetrapetala* fruit set on edges match changes in the abundance of insect pollinators? (3) Is the abundance of invertebrate flower visitors reduced by inclement weather such as wind and rain?

Methods

Literature review

To determine the relative frequency of positive versus negative effects of edges on plant reproduction, we compiled studies where some measure of fruit or seed set had been tested. We used recent reviews (Aizen *et al.*, 2002; Hobbs and Yates, 2003; Harris and Johnson, 2004) and the primary literature. Species were classified as showing a significant negative effect, no effect, or a significant positive effect of edges. If a species was measured at multiple sites, it was counted as showing an effect if this was found for at least one site; none of the species had sites with contradictory effects (positive at one and negative at another).

Study areas

We used two sites, Lake Ohau and Craigieburn, which are both in the Southern Alps of the central South Island and have both been used for previous mistletoe pollination studies (Ladley *et al.*, 1997; Robertson *et al.*, 1999; Montgomery *et al.*, 2003; Kelly *et al.*, 2004). *P. tetrapetala* is abundant on mountain beech (*Nothofagus solandri* var. *cliffortioides*) at both sites. Both Ohau and Craigieburn were once continuous forest but have since been fragmented to varying degrees, with the forest abutting open grassland and shrubland.

At Ohau (169° 49.1' E, 44° 12.4' S, 530 m altitude), a total of 38 study plants were chosen in three "edge" categories (interior, edge, isolated). In Round Bush, a 5.3 ha forest remnant surrounded by mixed pasture/shrubland on three sides and by Lake Ohau to the east (Kelly *et al.*, 2000), we sampled ten mistletoe plants in the forest interior (i.e. >50 m from the nearest edge of the remnant), and ten mistletoes on each of the upper (road) and lower (lake) edges. We also sampled eight mistletoes in total that grew in three isolated groups of three to seven beech trees surrounded by pasture/shrubland 3 km south of Round Bush (see map in Kelly *et al.*, 2000). In each habitat type, up to ten plants were

chosen haphazardly from the mistletoes which were within 2 m of the ground and had at least 100 flowers; only eight such plants could be found in the isolated groups. As plants on upper and lower edges at Round Bush did not differ significantly, they were combined for the analysis.

At Craigieburn (171° 42.5' E, 43° 9.1' S, 950 m altitude), we worked around roads, tracks, and other small clearings in continuous mountain beech forest (see Ladley and Kelly, 1996). This site is much less fragmented than Ohau, so the 31 study plants were selected in three habitat categories according to the availability of light. "Dark interior" plants were exposed to no direct sunlight throughout the day ($n = 14$), "light interior" plants were in forest but received some direct sunlight ($n = 11$) and "edge" plants were adjoining clearings and received full sunlight ($n = 6$). Again plants were selected from those near to the ground with sufficient flowers, using permanently tagged plants used in previous studies (Robertson *et al.*, 1999; Kelly *et al.*, 2004) where possible (18 of the 31 plants). The distribution of accessible mistletoes flowering in 2001/02 meant it was not possible to get equal numbers of plants in each habitat type.

Data collection

To measure insect visitation rates to *P. tetrapetala* flowers, a defined area on each plant was observed repeatedly and all insects on flowers at the moment of approach were counted. This instantaneous sampling was used to avoid the possibility of pollinators being deterred by the prolonged presence of the observer waiting near a plant. These counts were performed several times each day on six different days, giving a total of 18 counts on each plant at Lake Ohau between 3 and 14 December 2001, and 20 counts per plant at Craigieburn between 4 and 16 January 2002. All of the flowers on small plants were included, whereas only a subsection of larger plants was used so that approximately the same number of flowers was observed on all plants. Insect taxa recorded included the native bees *Hylaeus agilis* and an undescribed *Leioproctus* sp. (tag name 'species 10': B. Donovan, Landcare Research Ltd, Lincoln, pers. comm.), the introduced honeybee *Apis mellifera*, introduced bumblebees (*Bombus* spp.), introduced wasps (*Vespa* spp.), and "other spp." (largely Diptera).

Several environmental variables were estimated for each plant at the time of each count. Wind was scored on a scale of 0 (calm) to 5 (strong wind). Rain also was estimated from 0 (not raining) to 5 (heavy rain). The sunshine falling on the sampled flowers was estimated visually from 0 (no direct sun at the time of sampling) to 10 (all flowers in direct sun). At both Ohau and Craigieburn, the weather during sampling was generally wet and cloudy with occasional sunny

spells. The total volume (m^3) of the plant and the proportion used for counting insects were estimated. To see if bees were attracted to larger floral displays, the total number of available flowers on each plant was counted, or for large plants, estimated by taking the mean of independent estimates by two observers.

To measure fruit set on each plant, a branch with approximately 100 flowers was tagged and the flowers counted, along with the state of each flower (i.e. unripe bud, ripe bud, open flower). From this we could calculate the percentage of unripe buds, ripe buds (ready to be opened and pollinated) and open flowers on each plant. The percentage of flowers that were at the ripe bud stage was used as a predictor variable to determine if bees preferred plants with a higher proportion of buds ready to be opened. Fruit set on the tagged branch was calculated by counting developing fruits two months after flowering, and dividing by the initial number of flowers (for more details see Robertson *et al.*, 1999, 2005).

Statistical analysis

The insect count data were analysed using generalised linear models (GLMs) with a poisson error distribution and a log link function (Mathsoft, 1997). We first used a simple model for each insect taxon at each site with habitat as the main effect. Then we tested more complex models fitting the environmental variables first (sun, wind, rain, flower number, percent ripe), followed by habitat to determine if any detected habitat effects could be explained by the environmental variables. These analyses were not run for *Bombus* spp. at Craigieburn because of their infrequency at this site (Table 1). Fruit set data (each flower either made a single-seeded fruit or failed) were also analysed using GLMs, in this case with a binomial error distribution and logit link function.

Results

Literature review

We found published tests of edge effects on plant fruit set or seed set for 85 different plant species (Appendix 1). Negative effects on plant reproduction were prevalent, with 59% of species showing negative effects, 31% showing no effect, and only 11% (nine spp., including *P. tetrapetala*) showing positive effects. Publication bias could result in under-representation of the "no effect" category, although a quarter of the species are described in papers giving information for multiple species, which would reduce this bias. In any case, publication bias seems unable to explain the excess of negative effects over positive ones.

Table 1. The mean number of insects in each taxon or category observed on *Peraxilla tetrapetala* per visit according to edge category. The total number of each insect seen in each category is given in parentheses. Statistical values given are for edge effects on each taxon from poisson GLMs (percent deviance explained, *F* test of edge effect, and *P* value; for full details of analyses on Total native bees see Appendix 2).

(a) Ohau

Edge category	<i>Leioproctus</i> sp	<i>Hylaeus agilis</i>	Total native bees	<i>Apis mellifera</i>	<i>Bombus</i> spp.	Other spp.
Interior	0.033 (6)	0.067 (12)	0.100 (18)	0.000 (0)	0.006 (1)	0.050 (9)
Edge	0.150 (54)	0.156 (56)	0.306 (110)	0.045 (17)	0.111 (40)	0.139 (50)
Isolated	0.007 (1)	0.444 (64)	0.451 (65)	0.021 (3)	0.250 (36)	0.083 (12)
% dev. expl.	8.7	8.1	4.2	9.7	14.0	2.9
<i>F</i> value	5.62	10.56	5.09	8.54	24.43	3.54
<i>P</i> value	0.004	<0.001	0.006	<0.001	<0.001	0.030

(b) Craigieburn

Edge category	<i>Leioproctus</i> sp	<i>Hylaeus agilis</i>	Total native bees	<i>Apis mellifera</i>	<i>Bombus</i> spp.	Other spp.
Dense interior	0.000 (0)	0.021 (6)	0.021 (6)	0.011 (3)	0.000 (0)	0.139 (39)
Light interior	0.005 (1)	0.132 (29)	0.136 (30)	0.068 (15)	0.009 (2)	0.118 (26)
Edge	0.108 (13)	0.100 (12)	0.208 (25)	0.058 (7)	0.092 (1)	0.108 (13)
% dev. expl.	30.3	7.6	10.4	7.3	insufficient	0.2
<i>F</i> value	25.45	6.47	10.25	4.77	data	0.87
<i>P</i> value	<0.001	0.002	<0.001	0.009		0.145

Edge effects on insect visitation

At Ohau, the 38 plants varied in flower number from 94 to 12 500 flowers, with an average of 1982. Most flowers (96%) were ripe but very few of these (6% of all flowers) had been opened, reflecting the low bird visitation rates at this site (Robertson *et al.*, 1999, 2005). At Craigieburn, the 31 plants had fewer flowers (range 60 – 3400, average 856), of which 92% were ripe and 26% had been opened.

All of the insect groups studied at Ohau were significantly more common on edge or isolated mistletoes than on plants in the forest interior (Table 1a), with the percent deviance explained by habitat ranging from 7–13% and increases ranging from five- to twenty-fold (except for the “other insect spp.” category). Some taxa (*Leioproctus*, *Apis*) were most common along the forest edge, while others (*Hylaeus*, *Bombus*) were most common in the isolated sites. Native bees (*Hylaeus* plus *Leioproctus*) were least abundant in the forest interior and most abundant on the most exposed, isolated plants (Fig. 1a). Similarly at Craigieburn, all insect taxa except “other spp.” varied significantly among habitat categories, with highest numbers in the more exposed habitats (Table 1b). Native bees at this site again became more abundant with increasing habitat exposure, by a factor of 4.5 (Fig. 1b).

Effects of environmental variables and flower number

The environmental variables and the number of ripe flower buds usually explained a large fraction of the total deviance in visitation rates (Table 2). The native bees always showed significant positive associations with direct sunlight, whereas sunlight had no significant effect on the other taxa except for the “other” group at Craigieburn. High wind and rain had predominantly negative associations with all of the insect taxa, especially at Ohau where winds were stronger than at Craigieburn. The association between insect abundance and the number of ripe flower buds (total plant flower estimate, and percent of flowers that were ripe) varied among insect taxa and between the two sites.

After all of the above environmental and flowering-display variables had been controlled for, the models still usually found a significant effect of habitat on insect abundance. This suggests that variables like amount of direct sunlight contribute to the overall habitat effects shown in Table 1 and Fig. 1, but cannot account for all of the effect. This could be either because we did not include all the important variables, and/or because we included the important variables but did not estimate them with sufficient accuracy.

Fruit set

Mean fruit set by *P. tetrapetala* was highest on the most exposed plants at both sites (Fig. 1). The difference among the three habitat categories was marginally

Table 2. Effect of environmental factors, plant flowering display and edge category on insect visitation rates to *Peraxilla tetrapetala* flowers at two sites. The results presented are the percent deviance explained with significance test for each predictor, and the sign of significant effects (ie positive (+) or negative (-) effect) other than edge category, from separate GLMs for each taxon. See text for details of the predictor variables and Appendix 2 for more details of the analyses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns not significant.

(a) Ohau

Predictor	<i>Leioproctus</i> sp	<i>Hylaeus agilis</i>	Total native bees	<i>Apis mellifera</i>	<i>Bombus</i> spp.	Other spp.
Sun	10.8 *** +	12.8 *** +	14.3 *** +	0.4 ns	0.2 ns	0.1 ns
Wind	8.8 *** -	4.5 *** -	6.8 *** -	4.3 ** -	1.4 * -	2.7 ** -
Rain	2.9 *** -	1.7 ** -	2.3 *** -	2.0 * -	<0.1 ns	0.7 ns
Flower est.	1.1 ** +	23.8 *** +	15.8 *** +	0.5 ns	2.5 ** +	5.5 *** +
% ripe	3.6 *** +	0.9 ** +	1.9 *** +	1.2 ns	0.6 ns	2.1 ** +
Edge category	12.0 ***	0.6 ns	1.8 **	10.6 ***	9.0 ***	2.7 **
Total deviance						
% explained	43.7	45.2	45.2	19.6	14.2	14.9

(b) Craigieburn

Predictor	<i>Leioproctus</i> sp	<i>Hylaeus agilis</i>	Total native bees	<i>Apis mellifera</i>	<i>Bombus</i> spp.	Other spp.
Sun	48.4 *** +	2.5 * +	11.9 *** +	0.1 ns		16.1 *** +
Wind	0.0 ns	0.5 ns	0.5 ns	0.0 ns		7.4 *** +
Rain	0.3 ns	2.5 * -	14.6 * -	2.5 * -		1.4 * -
Flower est.	5.0 ** -	0.3 ns	1.6 * -	24.6 *** +		7.7 *** +
% ripe	1.7 ns	1.0 ns	1.4 * +	2.2 ns		0.0 ns
Edge category	4.3 *	8.6 ***	6.6 ***	2.3 ns		4.0 **
Total deviance						
% explained	67.4	21.8	32.2	31.8	insufficient data	36.9

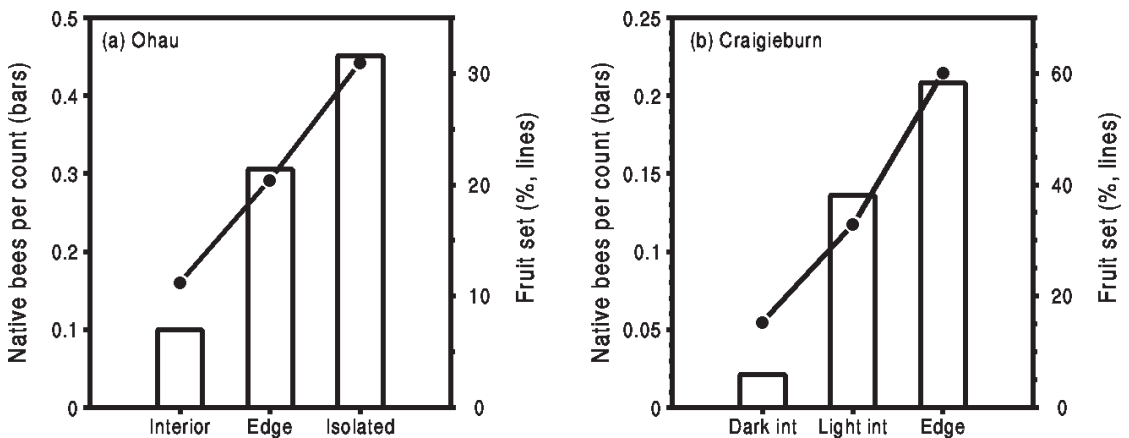


Figure 1. Visitation rate (bees per count, bars) by native bees (*Hylaeus agilis* and *Leioproctus* sp.) to flowers of *Peraxilla tetrapetala*, and % fruit set of *P. tetrapetala* plants (lines), in various forest habitats at two sites a) Ohau and b) Craigieburn in the central South Island of New Zealand in the 2001/02 season. For significance tests of each variable against habitat type, see Table 1 and Appendix 2.

non-significant at Ohau ($P = 0.061$, Appendix 2) but highly significant at Craigieburn ($P < 0.001$). Visitation rates by native bees were positively associated with fruit set (Fig. 1), although the absolute levels of visitation and fruit set varied between the two study sites.

Discussion

The rarity of positive effects of edges

Our review covering 85 species came to qualitatively similar conclusions as earlier reviews on smaller sample sizes (Aizen *et al.*, 2002; Hobbs and Yates, 2003). However, while positive effects are rare, we found a higher percentage of positive effects (11% of species) than Hobbs and Yates (2003) who reported 4% (of cases, rather than species). It is not known to what extent this difference comes from variation in the choice of papers to include (we used only papers giving data on fruit set or seed set, while the previous reviews included other metrics such as flower visitation rates and seedling abundances) or variation in methodology (cases versus species). There may also be a recent increase in reports of positive effects: seven of the nine cases listed in Appendix 1 were first published in 2001 or later.

Since positive effects are uncommon, *P. tetrapetala* represents an interesting case study into the mechanisms that can generate a positive effect. This is particularly true because the plant and pollinators are all endemic, so the effect is not a consequence of novel or maladapted species interactions.

The importance of edge effects for *Peraxilla tetrapetala* reproduction

The previously published finding that *P. tetrapetala* flowers had higher fruit set on edges at Ohau in 1997/98 (Kelly *et al.*, 2000) and 1999/2000 (Montgomery *et al.*, 2003) has been confirmed in a third season at Ohau, and at a second site (Craigieburn). Our results also show that the native bees *Leioproctus* sp. and *Hylaeus agilis* prefer flowers in edge habitat over those in the forest interior; at both our sites, native bees were more abundant at mistletoe flowers along edges and in isolated forest patches than in the forest interior. Moreover, approximately three times as many native bees were observed at Ohau which is much more heavily fragmented than Craigieburn. Montgomery *et al.* (2003) found that birds also preferentially visit *P. tetrapetala* plants exposed to high light. Higher visitation by both major groups of pollinators (birds and native bees) along forest edges probably explain the higher fruit set for *P. tetrapetala* on edges than in the interior. Fruit set in these plants has been repeatedly

shown to be pollen-limited (Robertson *et al.*, 1999; Kelly *et al.*, 2004; Robertson *et al.*, 2005), and a hand-pollination study showed that the higher fruit set on edges is not attributable to variation in plant resources caused, for example, by shading (Montgomery *et al.*, 2003). Both birds and bees are likely to contribute to the overall level of fruit set, as bees can effectively pollinate mistletoe flowers in cages which exclude birds, and bees were an order of magnitude more abundant as flower visitors at these sites (Robertson *et al.*, 2005).

Our key finding — better pollination on edges — is an exception to the generalisation that pollination will be impaired by the effects of fragmentation (Hobbs and Yates, 2003; Harris and Johnson, 2004). To improve our ability to predict which species will show reduced pollination on edges and which will show enhanced pollination, the key question is: what is it about the *P. tetrapetala* pollination system which makes it run counter to the general trend?

The answer is emphatically not that *P. tetrapetala* is “unfussy” in the sense of having an unspecialised pollination system (Robertson *et al.*, 2005; Newstrom and Robertson, 2005). The plants have specialised explosive flowers, which very few animals are known to open. Unopened flowers have very low levels of autogamous fruit set. Although a wide range of native and introduced birds and insects visit open flowers, almost the only important flower-opening animals are two endemic birds (tui and bellbird, of which only the bellbird is present at Ohau and Craigieburn) and two endemic bees (*Leioproctus* sp. and *Hylaeus agilis*).

Instead, this pollination system seems to work well on edges because the key pollinating animals not only persist in moderately modified landscapes, but crucially show an active preference for edge flowers. Bellbirds and tuis both remain widespread in New Zealand and are found in towns and other human-modified habitats (Bull *et al.*, 1985). At Craigieburn, we have found bellbirds nesting in both native *Nothofagus* trees and in exotic conifers (Kelly *et al.*, 2005). Both bird species visit the flowers of introduced plants (Bergquist, 1987; Higgins *et al.*, 2001), and the most important food type for bellbirds is invertebrates (Murphy and Kelly, 2001) which may be gleaned from native or exotic vegetation.

There is less information about the distribution and ecology of the native bee species, but native bees as a group are still widespread, including in areas with modified vegetation, and at least some species forage on the flowers of introduced plants. *Leioproctus* spp. nest in tunnels in bare soil, and most known nests are now in areas maintained free of vegetation by human activity (e.g. roadside banks), so these bees may be favoured or at least not disadvantaged by human habitat modification (Donovan, 1980).

Why the key pollinators prefer edge flowers is not known, but there are some pointers in our data and the literature. The two native bees were found to show a preference for flowers in bright sunshine at both our study sites. This may be because high light levels make flowers more easily spotted by foraging animals from a distance, but it is more likely that the light and associated warmth assist the bees to keep their body temperatures high enough for flight. Bees in general are known to be limited to foraging when ambient temperatures are above about 10°C (Szabo, 1980; Burrill and Dietz, 1981; Markwell *et al.*, 1993), and our sites are both at montane elevations (530 and 950 m) in the temperate latitudes where summer daytime temperatures are usually under 20°C. Thus, we hypothesise that bees prefer brightly lit flowers for energetic reasons.

It is less clear why our *bird* pollinators prefer edge flowers. The warmth from direct light is unlikely to be a factor, both because the birds are homeothermic, and also because they stay for much less time on the flowers, on average, than the insects (Kelly *et al.*, 1996 and unpublished observations). It may be that greater visibility from a distance is more important for birds, which have faster flight, larger potential foraging ranges, and more acute vision than bees. Easier access to edge plants from reductions in obstructing branches may also be a factor.

Whatever the reasons for the preferences, the key finding from this and Montgomery *et al.* (2003) is that the pollinators of *P. tetrapetala* do prefer flowers on the edges of forest, and for this reason plants have significantly higher fruit set there. Nonetheless, it remains unclear whether the long-term net effects of fragmentation for *P. tetrapetala* will be positive or not. *P. tetrapetala* plants do occur at higher densities on the edges of forest patches, which at least partially offsets the loss of habitat when continuous forest is cleared during fragmentation (Kelly *et al.*, 2000). In this study, a moderate level of forest fragmentation seemed to benefit *Peraxilla tetrapetala* by encouraging pollinators and thus enhancing reproduction. However, if fragmentation continued to decrease forest patches then the fragments might become too small or too far apart to sustain bird and bee populations. Moreover, an increase in generalist herbivores such as possums that thrive in fragmented landscapes could also decrease plant growth and reproduction (Sessions *et al.*, 2001; Sessions and Kelly 2001). On the other hand, a decrease in the abundance of a native caterpillar (*Zelleria maculata*) in highly fragmented areas increases fruit set rates for plants in such landscapes (Kelly *et al.*, 2000). The exact cumulative effect of these multiple relationships is not known and further research is needed to determine how management might mitigate the negative effects of fragmentation while taking advantage of its potential benefits.

Globally, *P. tetrapetala* is the most thoroughly studied case of a positive effect of edges on plant reproduction, but our causative mechanism (more pollinator visitation on edges) has also been reported in all of the other eight published cases where fruit set increased on edges (Appendix 1). Hence, information about the responses of pollinating animals to fragmentation helps to predict in specific cases whether fragmentation will have positive or negative effects on plant reproduction.

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References

- Aguilar, R.; Galetto, L. 2004. Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae). *Oecologia* 138: 513-520.
- Aizen, M.A.; Ashworth, L.; Galetto, L. 2002. Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science* 13: 885-892.
- Aizen, M. A.; Feinsinger, P. 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75: 330-351.
- Bergquist, C.A.L. 1987. Foraging tactics of tui (Meliphagidae). *New Zealand Journal of Zoology* 14: 299-303.
- Bruna, E.M.; Kress, W.J. 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). *Conservation Biology* Vol 16: 1256-1266.
- Bull, P.C.; Gaze, P.D.; Robertson, C.J.R. 1985. *The atlas of bird distribution in New Zealand*. Ornithological Society of New Zealand, Wellington. 296 pp.
- Burrill, R.M.; Dietz, A. 1981. The response of honey bees to variations in solar radiation and temperature. *Apidologie* 12: 319-328.
- Cascante, A.; Quesada, M.; Lobo, J.J.; Fuchs, E.A.M. 2002. Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. *Conservation Biology* Vol 16: 137-147.
- Crowfoot, L. 1998. (unpublished) *Factors limiting*

- fruit set in *Peraxilla tetrapetala* (Loranthaceae). B.Sc.Hons. thesis, University of Canterbury. 55 pp.
- Cunningham, S.A. 2000. Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London, B* 267: 1149-1152.
- Dick, C.W. 2001. Genetic rescue of remnant tropical trees by an alien pollinator. *Proceedings of the Royal Society of London, B* 268: 2391-2396.
- Donaldson, J.; Nanni, I.; Zachariades, C.; Kemper, J.; Thompson, J.D. 2002. Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology* 16: 1267-1276.
- Donovan, B.J. 1980. Interactions between native and introduced bees in New Zealand. *New Zealand Journal of Ecology* 3: 104-116.
- Ford, H.A.; Barrett, G.W.; Saunders, D.A.; Recher, H.F. 2001. Why have birds in the woodlands of south Australia declined? *Biological Conservation* 97: 71-88.
- Ghazoul, J.; McLeish, M. 2001. Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. *Plant Ecology* 153: 335-345.
- Gross, C.L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biological Conservation* 102: 89-95.
- Harris, L.F.; Johnson, S.D. 2004. The consequences of habitat fragmentation for plant-pollinator mutualisms. *International Journal of Tropical Insect Science* 24: 29-43.
- Higgins, P.J.; Peter, J.M.; Steel, W.K. (Editors) 2001. *Handbook of Australian, New Zealand, and Antarctic birds. Vol 5. Tyrant-flycatchers to Chats*. Oxford University Press, Melbourne. 1272 pp.
- Hobbs, R.J.; Yates, C.J. 2003. Impacts of ecosystem fragmentation on populations: generalising the idiosyncratic. *Australian Journal of Botany* 51: 471-488.
- Horskins, K.; Turner, V.B. 1999. Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. *Australian Journal of Ecology* 24: 221-227.
- Huang, S.Q.; Guo, Y.H. 2002. Variation of pollination and resource limitation in a low seed-set tree, *Liriodendron chinense* (Magnoliaceae). *Botanical Journal of the Linnean Society Vol 140*: 31-38.
- Jacquemyn, H.; Brys, R.; Hermy, M. 2002. Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. *Oecologia* 130: 617-625.
- Karrenberg, S.; Jensen, K. 2000. Effects of pollination and pollen source on the seed set of *Pedicularis palustris*. *Folia Geobotanica* 35: 191-202.
- Kelly, D.; Ladley, J.J.; Robertson, A.W. 2004. Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. *New Zealand Journal of Botany* 42: 89-103.
- Kelly, D.; Ladley, J.J.; Robertson, A.W.; Edwards, J.; Smith, D.C. 1996. The birds and the bees. *Nature* 384: 615.
- Kelly, D.; Ladley, J.J.; Robertson, A.W.; Norton, D.A. 2000. Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae). In: Young, A.G.; Clarke, G.M. (Editors), *Genetics, demography and viability of fragmented populations*, pp. 241-252. Cambridge University Press, Cambridge.
- Kelly, D.; Brindle, C.; Ladley, J.J.; Robertson, A.W.; Maddigan, F.W.; Butler, J.; Ward-Smith, T.; Murphy, D.J.; Sessions, L.A. 2005. Can stoat (*Mustela erminea*) trapping increase bellbird (*Anthornis melanura*) populations and benefit mistletoe (*Peraxilla tetrapetala*) pollination? *New Zealand Journal of Ecology* 29: 69-82.
- Ladley, J.J.; Kelly, D. 1995. Explosive New Zealand mistletoe. *Nature* 378: 766.
- Ladley, J.J.; Kelly, D. 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *New Zealand Journal of Ecology* 20: 69-79.
- Ladley, J.J.; Kelly, D.; Robertson, A.W. 1997. Explosive flowering, nectar production, breeding systems and pollinators of New Zealand mistletoes (Loranthaceae). *New Zealand Journal of Botany* 35: 345-360.
- Lee, S.L. 2000. Mating system parameters of *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae) in three different forest types and a seed orchard. *Heredity* 85: 338-345.
- Liu, H.; Koptur, S. 2003. Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: Impacts of the urban-wildland interface. *American Journal of Botany* 90: 1180-1187.
- Louadi, K.; Doumandji, S. 1998. Diversity and gathering activity of bees (Hymenoptera, Apoidea) in a therophyte lawn in Constantine (Algeria). *Canadian Entomologist* 130: 691-702.
- Markwell, T.J.; Kelly, D.; Duncan, K.W. 1993. Competition between honey bees (*Apis mellifera*) and wasps (*Vespula* spp.) in honeydew beech (*Nothofagus solandri* var *solandri*) forest. *New Zealand Journal of Ecology* 17: 85-93.
- Mathsoft, Inc. (1997). *S-Plus 4 Guide to Statistics*. Mathsoft, Inc, Seattle, Washington. 877 pp.
- Matsumura, C.; Washitani, I. 2000. Effects of population size and pollinator limitation on seed-

- set of *Primula sieboldii* populations in a fragmented landscape. *Ecological Research* 15: 307-322.
- Molano-Flores, B.; Hendrix, S.D.; Heard, S.B. 1999. The effect of population size on stigma pollen load, fruit set, and seed set in *Allium stellatum* Ker. (Liliaceae). *International Journal of Plant Sciences* 160: 753-757.
- Montgomery, B.R.; Kelly, D.; Robertson, A.W.; Ladley, J.J. 2003. Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Lorantheaceous mistletoe. *New Zealand Journal of Botany* 41: 277-286.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58-62.
- Murphy, D.J.; Kelly, D. 2001. Scarce or distracted? Bellbird (*Anthornis melanura*) foraging and diet in an area of inadequate mistletoe pollination. *New Zealand Journal of Ecology* 25: 69-81.
- Mustajarvi, K.; Siikamaki, P.; Rytkonen, S.; Lammi, A. 2001. Consequences of plant population size and density for plant-pollinator interactions and plant performance. *Journal of Ecology* 89: 80-87.
- Navarro, L.; Guitian, J. 2002. The role of floral biology and breeding system on the reproductive success of the narrow endemic *Petrocoptis viscosa* rothm. (Caryophyllaceae). *Biological Conservation* 103: 125-132.
- Newstrom, L.; Robertson, A.W. 2005. Progress in understanding pollination systems in New Zealand. *New Zealand Journal of Botany* 43: 1-59.
- Ogden, J.; Basher, L.; McGlone, M.S. 1998. Fire, forest regeneration and links with early human habitation: evidence from New Zealand. *Annals of Botany London* 81: 687-696.
- Quesada, M.; Stoner, K.E.; Lobo, J.A.; Herrerias-Diego, Y.; Palacios-Guevara, C.; Munguia-Rosas, M.A.; Salazar, K.A.O.; Rosas-Guerrero, V. 2004. Effects of forest fragmentation on pollinator activity and consequences for plant reproductive success and mating patterns in bat-pollinated bombacaceous trees. *Biotropica* 36: 131-138.
- Robertson, A.W.; Ladley, J.J.; Kelly, D. 2005. The effectiveness of short-tongued bees as pollinators of apparently "ornithophilous" New Zealand mistletoes. *Austral Ecology* 30: 298-309.
- Robertson, A.W.; Lloyd, D.G. 1993. Rates of pollen deposition and removal in *Myosotis colensoi*. *Functional Ecology* 7: 549-559.
- Robertson, A.W.; Kelly, D.; Ladley, J.J.; Sparrow, A.D. 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conservation Biology* 13: 499-508.
- Roll, J.; Mitchell, R.J.; Cabin, R.J.; Marshall, D.L. 1997. Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). *Conservation Biology* 11: 738-746.
- Rovira, A.M.; Bosch, M.; Molero, J.; Blanche, C. 2004. Pollination ecology and breeding system of the very narrow coastal endemic *Seseli farrenyi* (Apiaceae). Effects of population fragmentation. *Nordic Journal of Botany* 22: 727-740.
- Sessions, L.A.; Kelly, D. 2001. Heterogeneity in vertebrate and invertebrate herbivory and its consequences for New Zealand mistletoes. *Austral Ecology* 26: 571-581.
- Sessions, L.A.; Rance, C.; Grant, A.; Kelly, D. 2001. Possum (*Trichosurus vulpecula*) control benefits native beech mistletoes (Loranthaceae). *New Zealand Journal of Ecology* 25: 27-33.
- Severns, P. 2003. Inbreeding and small population size reduce seed set in a threatened and fragmented plant species, *Lupinus sulphureus* ssp. *kincaidii* (Fabaceae). *Biological Conservation* 110: 221-229.
- Smith-Ramirez, C.; Armesto, J. J. 2003. Foraging behaviour of bird pollinators on *Embothrium coccineum* (Proteaceae) trees in forest fragments and pastures in southern Chile. *Austral Ecology* 28: 53-60.
- Somanathan, H.; Borges, R.M. 2000. Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India. *Biological Conservation* 94: 243-256.
- Somanathan, H.; Borges, R.M.; Chakravarthy, V.S. 2004. Does neighborhood floral display matter? Fruit set in carpenter bee-pollinated *Heterophragma quadriloculare* and beetle-pollinated *Lasiosiphon eriocephalus*. *Biotropica* 36: 139-147.
- St Denis, M. Cappuccino, N. 2004. Reproductive biology of *Vincetoxicum rossicum* (Kleoe.) Barb. (Asclepiadaceae), an invasive alien in Ontario. *Journal of the Torrey Botanical Society* 131: 8-15.
- Steffan-Dewenter, I.; Munzenberg, U.; Tschamtker, T. 2001. Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London, B* 268: 1685-1690.
- Szabo, T.I. 1980. Effect of weather factors on honeybee flight activity and colony weight gain. *Journal of Apicultural Research* 19: 164-171.
- Tomimatsu, H.; Ohara, M. 2002. Effects of forest fragmentation on seed production of the understory herb *Trillium camschatcense*. *Conservation Biology* 16: 1277-1285.
- Vicens, N.; Bosch, J. 2000. Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera : Megachilidae and Apidae). *Environmental Entomology* 29: 413-420.

- Ward, M.; Johnson, S.D. 2005. Pollen limitation and demographic structure in small fragmented populations of *Brunsvigia radulosa* (Amaryllidaceae). *Oikos* 108: 253-262.
- Weidema, I.R.; Magnussen, L.S.; Philipp, M. 2000. Gene flow and mode of pollination in a dry-grassland species, *Filipendula vulgaris* (Rosaceae). *Heredity* 84: 311-320.
- Wolf, A.; Brodmann, P.A.; Harrison, S. 1999. Distribution of the rare serpentine sunflower, *Helianthus exilis* (Asteraceae): the roles of habitat availability, dispersal limitation and species interactions. *Oikos* 84: 69-76.
- Wolf, A.T.; Harrison, S.P. 2001. Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. *Conservation Biology* 15: 111-121.
- Yates, C.J.; Ladd, P.G. 2004. Breeding system, pollination and demography in the rare granite endemic shrub *Verticordia staminosa* ssp. *staminosa* in south-west Western Australia. *Austral Ecology* 29: 189-200.
- Yates, C.J.; Ladd, P.G. 2005. Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape. *Conservation Biology* 19: 239-249.

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Appendix 1. Published studies of the effect of habitat fragmentation on pollination and fruit set.

Species	Reference
Negative effect (n = 50)	
<i>Acacia aroma</i>	Aizen and Feinsinger (1994)
<i>Acacia brachybotrya</i>	Cunningham (2000)
<i>Anacardium excelsum</i>	Ghazoul and McLeish (2001)
<i>Atamisquea emarginata</i>	Aizen and Feinsinger (1994)
<i>Brunsvigia radulosa</i>	Ward and Johnson (2005)
<i>Caesalpinia gilliesi</i>	Aizen and Feinsinger (1994)
<i>Calystegia collina</i>	Wolf and Harrison (2001)
<i>Cassia aphylla</i>	Aizen and Feinsinger (1994)
<i>Catasetum viridiflavum</i>	Harris and Johnson (2004)
<i>Ceiba grandiflora</i>	Quesada <i>et al.</i> (2004)
<i>Centrosema virginianum</i>	Aizen <i>et al.</i> (2002)
<i>Cercidium australe</i>	Aizen and Feinsinger (1994)
<i>Cestrum parqui</i>	Aguilar and Galetto (2004)
<i>Chamaecrista keyensis</i>	Liu and Koptur (2003)
<i>Clarkia coccinea</i>	Aizen <i>et al.</i> (2002)
<i>Dianthus deltoides</i>	Aizen <i>et al.</i> (2002)
<i>Diospyros montana</i>	Somanathan and Borges (2000)
<i>Dombeya acutangula</i>	Harris and Johnson (2004)
<i>Dryobalanops aromatica</i>	Lee (2000)
<i>Enterolobium cyclocarpum</i>	Aizen <i>et al.</i> (2002)
<i>Eremophila glabra</i>	Cunningham (2000)
<i>Gentiana lutea</i>	Harris and Johnson (2004)
<i>Gentianella campestris</i>	Harris and Johnson (2004)
<i>Ipomopsis aggregata</i>	Aizen <i>et al.</i> (2002)
<i>Justicia squarrosa</i>	Aizen and Feinsinger (1994)
<i>Lasiosiphon eriocephalus</i>	Somanathan <i>et al.</i> (2004)
<i>Lesquerella fendleri</i>	Roll <i>et al.</i> (1997)
<i>Liriodendron chinense</i>	Huang and Guo (2002)
<i>Lupinus sulphureus</i> ssp <i>kincaidii</i>	Severns (2003)
<i>Lychnis viscaria</i>	Aizen <i>et al.</i> (2002)
<i>Lythrum salicaria</i>	Aizen <i>et al.</i> (2002)
<i>Nepeta cataria</i>	Aizen <i>et al.</i> (2002)
<i>Oenothera macrocarpa</i>	Aizen <i>et al.</i> (2002)
<i>Opuntia stricta</i>	Aizen <i>et al.</i> (2002)
<i>Panax quinquefolius</i>	Harris and Johnson (2004)
<i>Passiflora mixta</i>	Harris and Johnson (2004)

<i>Portulaca umbraticola</i>	Aizen and Feinsinger (1994)
<i>Primula elatior</i>	Jacquemyn <i>et al.</i> (2002)
<i>Primula sieboldii</i>	Matsumura and Washitani (2000)
<i>Primula veris</i>	Harris and Johnson (2004)
<i>Prosopis nigra</i>	Aizen and Feinsinger (1994)
<i>Pterygodium catholicum</i>	Donaldson <i>et al.</i> (2002)
<i>Raphanus sativus</i>	Aizen <i>et al.</i> (2002)
<i>Rhaphalis lumbricoides</i>	Aizen and Feinsinger (1994)
<i>Rutidosia leptorrhynchoides</i>	Aizen <i>et al.</i> (2002)
<i>Seseli farrenyi</i>	Rovira <i>et al.</i> (2004)
<i>Shorea siamensis</i>	Ghazoul and McLeish (2001)
<i>Sinapis arvensis</i>	Aizen <i>et al.</i> (2002)
<i>Spondias mombin</i>	Aizen <i>et al.</i> (2002)
<i>Trillium camschatcense</i>	Tomimatsu and Ohara (2005)

No significant effect ($n = 26$)

<i>Acacia atramentaria</i>	Aizen and Feinsinger (1994)
<i>Acacia furcatispina</i>	Aizen and Feinsinger (1994)
<i>Acacia praecox</i>	Aizen and Feinsinger (1994)
<i>Allium stellatum</i>	Molano-Flores <i>et al.</i> (1999)
<i>Aster curtus</i>	Harris and Johnson (2004)
<i>Berkheya armata</i>	Donaldson <i>et al.</i> (2002)
<i>Brassica kaber</i>	Aizen <i>et al.</i> (2002)
<i>Ceiba aesculifolia</i>	Quesada <i>et al.</i> (2004)
<i>Cyanella lutea</i>	Donaldson <i>et al.</i> (2002)
<i>Dillwynia juniperina</i>	Gross (2001)
<i>Filipendula vulgaris</i>	Weidema <i>et al.</i> (2000)
<i>Gladiolus liliaceus</i>	Donaldson <i>et al.</i> (2002)
<i>Helianthus exilis</i>	Wolf <i>et al.</i> (1999)
<i>Heliconia acumin</i>	Bruna and Kress (2002)
<i>Leucochrysum albicans</i>	Harris and Johnson (2004)
<i>Mimosa detinens</i>	Aizen and Feinsinger (1994)
<i>Opuntia quimilo</i>	Aizen and Feinsinger (1994)
<i>Ornithogalum thyrsoides</i>	Donaldson <i>et al.</i> (2002)
<i>Pedicularis palustris</i>	Karrenberg and Jensen (2000)
<i>Petrocoptis viscosa</i>	Navarro and Guitian (2002)
<i>Samanea saman</i>	Cascante <i>et al.</i> (2002)
<i>Tillandsia ixioidea</i>	Aizen and Feinsinger (1994)
<i>Trachyandra hirsuta</i>	Donaldson <i>et al.</i> (2002)
<i>Verticordia staminosa</i>	Yates and Ladd (2004)
<i>Verticordia fimbriolepis</i>	Yates and Ladd (2005)

Positive effect ($n = 9$)

<i>Babiana ambigua</i>	Donaldson <i>et al.</i> (2002)
<i>Centaurea jacea</i>	Steffan-Dewenter <i>et al.</i> (2001)
<i>Dinizia excelsa</i>	Dick (2001)
<i>Embothrium coccineum</i>	Smith-Ramirez and Armesto (2003)
<i>Ligaria cuneifolia</i>	Aizen <i>et al.</i> (2002)
<i>Lychnis viscaria</i>	Mustajarvi <i>et al.</i> (2001)
<i>Peraxilla tetrapetala</i>	Montgomery <i>et al.</i> (2003)
<i>Symphonia globulifera</i>	Aizen <i>et al.</i> (2002)
<i>Vincetoxicum rossicum</i>	St Denis and Cappuccino (2004)

Appendix 2. Full Analysis of Deviance tables for *P. tetrapetala* flowers at two sites. (a) Predicting native bee abundance (*Hylaeus* plus *Leioproctus*) using only habitat category, or (b) using all terms as predictors, in GLMs with poisson errors and log link functions. (c) Predicting fruit set using habitat category, in GLMs with binomial error and logit link functions.

Test and Site	Model	df	Deviance	Residual df	Residual deviance	F-value	P
(a) effect of Edge only							
Ohau	Null			683	973.82		
	Habitat	2	41.26	681	932.57	5.0877	0.006
Craigieburn	Null			619	373.37		
	Habitat	2	38.81	617	334.56	10.25	0.000
(b) Effect of all terms							
Ohau	Null			683	973.82		
	Sun	1	139.34	682	834.48	75.06	0.0000
	Wind	1	66.47	681	768.02	35.80	0.0000
	Rain	1	22.33	680	745.69	12.03	0.0006
	Flower est	1	153.81	679	591.88	82.85	0.0000
	% Ripe	1	18.70	678	573.19	10.07	0.0016
	Habitat	2	14.39	676	558.80	3.88	0.0212
	Craigieburn	Null			619	373.37	
Sun		1	44.28	618	329.08	25.18	0.0000
Wind		1	1.77	617	327.31	1.01	0.3155
Rain		1	7.97	616	319.35	4.53	0.0337
Flower est		1	5.81	615	313.54	3.30	0.0696
% Ripe		1	5.40	614	308.13	3.07	0.0801
Habitat		2	37.89	612	270.24	10.78	0.0000
(c) Fruit set							
Ohau	Null			36	817.568		
	Habitat	2	125.965	34	691.603	3.047	0.0606
Craigieburn	Null			30	886.273		
	Habitat	2	403.46	28	428.815	13.109	0.0001