

# Edge effects in a lowland temperate New Zealand rainforest

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# Edge effects in a lowland temperate New Zealand rainforest

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## ABSTRACT

This research assessed the effects of forest edges on microclimates, plants (vascular and non-vascular) and animals (forest floor and canopy invertebrates) in a south Westland lowland rainforest. Microclimate effects were apparent at north- and south-facing edges, but did not extend beyond c. 20 m into the forest. In contrast, vegetation responses to edges were apparent up to 70 m into the forest for some variables (e.g. tree ferns and bryophytes). The responses of canopy invertebrates appear similar to those of the vegetation, although the effect on predator abundance extended into the forest for at least 100 m. The extent of edge effects documented here is broadly comparable to that observed in other studies, both in New Zealand and elsewhere. Edge effects extending 50–100 m into the forest are likely to be a significant issue for small forest remnants.

**Keywords:** Fragmentation, edge effects, remnants, microclimates, vascular plants, bryophytes, invertebrates, forest, South Westland

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# 1. Introduction

The overall objective of this study was to better understand the effect of edges on the structure and composition of plant and animal communities within forest ecosystems and to determine how changes in these might affect the long-term viability of forest remnants. In particular, information on several aspects of the edge phenomenon, including microclimates, plants (vascular and non-vascular) and animals (forest floor and canopy invertebrates), is used to assess the effects of forest edges on the conservation management of small remnants.

Physical processes arising from the adjacent production (e.g. agriculture and forestry) matrix have major effects on the flora and fauna of remnant forest patches (Saunders et al. 1991; Bierregaard et al. 1992). As well as effects associated with reduced area and increased isolation, remnant forest patches, especially smaller ones, are characterised by a large amount of edge relative to area (Laurance 1991; Murcia 1995). Forest edges are transition zones between the wide climatic fluctuations of the external (usually unforested) environment and the relatively stable environment of the forest interior. It has been suggested that edges can affect forest remnants in three ways, through:

1. abiotic effects—those changes in environmental conditions associated with the edge;
2. direct biological effects—the changes in species abundances as a direct consequence of changes in the physical environment;
3. indirect biological effects—changes in species interactions (Murcia 1995).

Abiotic edge effects have been extensively documented. Elevated radiation levels, air and soil temperatures, wind speeds and vapour pressure deficits have been measured in forest adjacent to edges (Kapos 1989; Matlack 1993; Chen et al. 1995; Williams-Linera et al. 1998; Didham & Lawton 1999; Gehlhausen et al. 2000). In response to these abiotic effects, changes in the abundance and distribution of plant species is frequently observed close to edges, including changing species composition and higher stem densities and tree basal areas (Chen et al. 1992; Fraver 1994; Matlack 1994; Esseen & Renhorn 1998; Williams-Linera et al. 1998; Didham & Lawton 1999). Effects of forest edges on animals have been less well documented, although a variety of responses have been described. For example, forest understorey birds have been shown to vary in abundance in response to distance from the edge, edge age, season and guild (Restrepo & Gomez 1998), while the richness and diversity of small mammals increased away from edges (Stevens & Husband 1998). The responses of invertebrates to edges are less well understood. A variety of responses have been observed, including increases and decreases of numbers of individuals at forest edges (Margules et al. 1994; Didham et al. 1998); although, for beetles in tropical rainforest remnants, the vast majority of species were adversely affected by edges (Didham et al. 1998). Indirect effects of edges include increased numbers of invasive species (Scougall et al. 1983; Andrén & Angelstam 1988; Fraver 1994; Cadenasso & Pickett 2001), with flow-on effects on resident species (e.g. through nest predation or competition). The effects of edges on ecosystem processes are also poorly understood. Klein (1989) documented reduced dung decomposition in small forest remnants as a result of

changes in dung and carrion beetle communities. Laurance et al. (2000) highlighted the potential impact of elevated mortality of large trees at edge sites on food resources (nectar and fruit) and shelter for animal populations.

The extent to which edge effects penetrate into forest remnants varies depending on forest type, edge orientation, edge age and the variable being considered. Several studies have documented microclimate changes extending 50–60 m into forest remnants (reviewed in Murcia 1995) while Didham et al. (1999) and Chen et al. (1995) recorded microclimate effects extending 180 and 240 m in from edges. Edge-induced biotic changes have usually been recorded at distances of 20–50 m into remnants (reviewed in Murcia 1995), but effects at distances greater than 100 m have also been described. Chen et al. (1992) and Wilcove et al. (1986) suggested that elevated predation rates can occur 300–600 m in from the edge. Based on this type of data, several authors have highlighted the vulnerability of small forest remnants to edge effects. For example, Young & Mitchell (1994) suggested that regular-shaped remnants of less than 9 ha will be dominated by edge patterns and processes; while Laurance (1991) suggested that remnants may need to be larger than 2000–4000 ha, depending on shape, to ensure that > 50% of the area is unaffected by the edge.

It is clear that while changes in abiotic and biotic parameters across forest edges have been widely documented, there is little consensus on the extent of edge effects. Murcia (1995) suggested that this is due to poor experimental design, lack of consistency in methodology and an oversimplification of the edge phenomenon. These problems are further confounded by the wide range of forest types in which edge effects have been studied (ranging from boreal to tropic, and mesic to arid), differences in edge age and human impacts on remnants, and a paucity of studies that have simultaneously looked at the effect of edges on different taxonomic groups and on the abiotic environment. An exception to this is the study of Scougall et al. (1983) which considered plant, animal and abiotic responses across woodland edges in southwestern Australia. While edges have been extensively studied in northern boreal and temperate forests and in tropical forests, there have been fewer studies in southern temperate forests, with only three studies published from temperate New Zealand rainforests (Young & Mitchell 1994; Davies-Colley et al. 2000; Denyer 2000).

Murcia (1995) suggested that the failure of edge studies to generate any generalisations about the edge phenomenon may lead to an underestimation of the potential deleterious effects that edges have on forest remnants. Given the proliferation of small remnants as a result of ongoing habitat fragmentation and the isolation of these remnants in an often herbaceous-dominated matrix, a better understanding of the edge phenomenon would seem essential for conservation biology (Saunders et al. 1991; Bierregaard et al. 1992). This is particularly important given that even small forest remnants have important conservation values (Shafer 1995), and that remnants are increasingly being managed as part of the broader landscape (Norton & Miller 2000).

In contrast to other New Zealand edge studies, this study focused on relatively young edges (12–14 years old). This report presents an overview of the research project, highlighting the key edge patterns observed and discussing the implications for the conservation management of forest remnants in New Zealand. A formal scientific paper that will provide a more detailed analysis of the results is being prepared.

## 2. Study area

The study site is in Saltwater Forest (43°07'S, 170°24'E) on the west coast of New Zealand's South Island (Harihari Ecological District, Whataroa Ecological Region) at about 60 m a.s.l. This area was chosen for study because the ecology is well known (Norton et al. 1988; Ogden & Stewart 1995), edges of known age in similar forest types were present, and access was good.

The study area comprises outwash gravels and tills dating from the end of the last glaciation (14 000–16 000 years ago, Almond 1996). These gently undulating surfaces decrease in elevation and slope westwards towards the coast and have been dissected in places by fluvial action with current streams isolated in narrow stable channels. High rainfall and a water table close to the ground surface result in gleyed and leached soils with generally very low fertility (Almond 1996). The climate is moist and equable. Mean annual rainfall at Harihari, the nearest rainfall station (13 km to the east), is 3724 mm, and rainfall is evenly distributed through the year. Mean annual temperature at the study site is 11.7°C, with summer and winter means of 15.8°C and 7.2°C respectively (based on equations in Norton 1984).

The forest is dominated by the coniferous tree *Dacrydium cupressinum* which forms a dense canopy at 30–35 m. The conifers *Prumnopitys ferruginea* and *Manoao colensoi*, and the angiosperms *Quintinia acutifolia* and *Weinmannia racemosa* form a discontinuous subcanopy. The conifers *Phyllocladus* sp. aff. *alpinus* and *Podocarpus hallii* are also occasionally present. The understorey includes a number of angiosperm small trees and shrubs including *Griselinia littoralis*, *Pseudopanax crassifolius*, *Pseudopanax colensoi* var. *ternatus*, *Ascarina lucida*, *Myrsine australis*, *Coprosma* spp., *Neomyrtus pedunculata*, as well as the tree ferns *Cyathea smithii* and *Dicksonia squarrosa*. Bryophytes, pteridophytes, and herbaceous angiosperms carpet the forest floor, and lianes and epiphytes are common.

Saltwater forest has, until recently, been managed as a sustained yield production forest, based on the extraction of single trees or small groups of trees using helicopters (James & Norton 2001). However, 20 years of forestry operations prior to this have left the forest divided into a mosaic of patches with different logging histories (including clearfelling), as well as areas of unlogged forest. Saltwater forest has been used for a number of experimental logging operations, including selection logging and coupe logging. The creation of cleared coupes provided the edges used in this study.

## 3. Methods

### 3.1 STUDY SITE SELECTION

Three criteria were used in selecting study edges:

1. The forest type was uniform (mature canopy of at least 20 m tall *Dacrydium cupressinum*) and free of recent disturbance including logging for at least 200 m in from the edge.
2. There were no major landform discontinuities (including streams) either associated with the edge or extending at least 100 m in from the edge.
3. Edges had been created at approximately the same time (c. 1978–80).

Using these criteria, two north-facing and two south-facing edges were selected. Greater replication would have been desirable, but suitable sites were not available. At each site a 40-m baseline was established parallel to and immediately beyond the outermost canopy tree at the edge. Because edges had been created during experimental logging, they were straight and easily defined. A 100-m transect was then run back into the forest from the baseline and divided into 10 m × 10 m plots.

### 3.2 ENVIRONMENTAL VARIABLES

Substrate wetness and the amount of dead wood were subjectively estimated using a 4-point scale in each 10 m × 10 m plot. All measurements were made on the same day and under constant weather conditions. Substrate wetness was estimated as:

- 1 = substrate dry, no standing water,
- 2 = substrate wet, no standing water,
- 3 = substrate wet, some standing water,
- 4 = substrate wet, abundant standing water.

The amount of dead wood was estimated as:

- 1 = < 25%,
- 2 = 25–50%,
- 3 = 50–75%,
- 4 = > 75%.

Hemispherical canopy photographs were taken in the middle of each 10 m × 10 m plot and were used to determine percent canopy cover.

Four microclimate stations were established 5, 15, 30 and 90 m in from the edge at one north-facing and one south-facing edge, with an additional station in an adjacent clearing 100 m from the nearest edge. We measured windspeed, air temperature and relative humidity, ground surface temperature, and soil temperature. At the open station we also measured photosynthetically active radiation (PAR). Wind speed was measured using a Vector Instruments A101M anemometer placed c. 1.5 m above ground level. Relative humidity (RH) and air temperature were measured using Skye SKH2011 and Campbell 207 RH/temperature sensors at 0.5 m placed in Stevenson screens. Ground surface

temperature was measured using a Campbell 107 temperature probe placed under the forest floor bryophytes and soil temperature was measured using a Campbell 107B temperature probe at 10 cm depth. For the open climate station, incident PAR was measured using a LiCor LI190SB quantum sensor at c. 1.5 m and clear of all surrounding vegetation. All measurements were made at 10 sec. intervals and stored as 30 min. averages, using Campbell 21X and CR10 data loggers. Microclimates were measured simultaneously at all nine stations for a 19-day period in January (mid summer) 1992.

### 3.3 BIOTIC VARIABLES

Foliage cover abundance was visually estimated for each species in each 10 m × 10 m plot in five strata:  
ground (< 0.5 m including all ground ferns except tree ferns),  
shrub (0.5–1.9 m, including tree ferns),  
lower subcanopy (2–9.9 m),  
upper subcanopy (10–19.9 m) and  
canopy (> 20 m).

Cover abundance was recorded using seven abundance classes:

1 (< 1%), 2 (1–5%), 3 (6–10%), 4 (11–25%), 5 (26–50%), 6 (51–75%) and 7 (76–100%). The diameter of all trees > 5 cm diameter at 1.3 m height (dbh) were measured, and the number of seedlings (< 0.5 m tall) and saplings (> 0.5 m tall and < 5 cm dbh) of Podocarpaceae trees, and the number of tree ferns in three height/growth form classes (no trunk, trunk < 2 m tall, trunk > 2 m tall) were counted. The abundance of forest floor bryophytes (mosses and liverworts) was assessed by systematically locating ten 50 cm × 50 cm quadrats in each 10 m × 10 m plot. Bryophyte presence was recorded in five 10 cm × 10 cm squares within each of these quadrats, giving a total of 50 measures per plot.

Pitfall traps were located in the ten 10 m × 10 m plots along the right-hand side of each transect to sample forest-floor invertebrates. Within each plot, ten pitfall traps were located in an approximately circular fashion at least 1 m from the edge of the plot and c. 2 m apart. Traps were covered to prevent birds from accessing the traps and to minimise litter and rainfall into them. Pitfall traps were run for one week in every four for one year from February 1991 to February 1992, giving 13 sampling periods. The same position was used for each trap at each sampling period. All traps were laid out in one day, with 10 ml of 2% solution of formaldehyde placed in the bottom. Traps were collected seven days later and all invertebrate material placed in 70% alcohol in separate containers for each 10 m × 10 m plot. Samples were then taken back to the lab and sorted into identifiable species or species groups.

Canopy invertebrates were sampled by suspending 0.2 m<sup>2</sup> diameter collecting-funnels in the middle of each 10 m × 10 m plot. The canopy was then sprayed using a helicopter with standard formulation Permethrin spray, a synthetic pyrethroid insecticide. All four transects were sprayed on the same morning (28 January 1992), over an approximately 2-hour period. The collection funnels were left in place for 6 hours after spraying and then removed. Invertebrates were stored in 70% alcohol in separate containers for each funnel, and subsequently sorted into identifiable species or species groups.

### 3.4 STATISTICAL ANALYSIS

For vascular vegetation, cover classes were converted back to mid-points of their percentage cover ranges and summed for all species in each stratum to give a total stratum cover value. The bryophyte data were expressed as frequencies (percentage of 50 squares each species was recorded in). The pitfall data for each invertebrate taxon were combined across traps and seasons to provide one value for each plot. Both pitfall and canopy invertebrate taxa were sorted into functional groups based on either their known behavior or inferred behavior based on morphology. The groups were detritivores, herbivores, predators (including parasites) and sap suckers. Larvae were not included in the analyses.

Analysis of variance was used to test whether significant trends in species abundance and environmental variables occurred from the edge back into the forest, and between the north- and south-facing edges. Clearly, both the adjacent and the successive 10 m × 10 m plots at each edge are potentially correlated, thus likely violating the most critical assumption for standard analysis of variance application (Ostle & Malone 1988). To counter this, data from adjacent plots (the four plots at the same distance in from the edge) were pooled, thus giving more stability to the data. The effect of distance from the forest edge was then analysed using a mixed model (McCullagh & Nelder 1989) utilising an auto-regressive error structure (Littell et al. 1996). Significant correlations between successive plots were detected for many but not all variables but, for consistency, the error structure was maintained for all of them. Logically, adoption of the mixed model gave more conservative estimates of differences between edge orientation and distance from edge compared with standard analyses.

Indirect ordination of the species abundance data for each of the taxonomic groups (vascular plants, bryophytes, forest floor invertebrates and canopy invertebrates) was undertaken to investigate whether there were patterns in community composition that could be related to edge effects. Cover data for vascular vegetation over the five strata were combined to produce a single importance value for each species in each 10 m × 10 m plot. Importance value for each species was then calculated by summing the percent cover abundance for each stratum multiplied by  $\log_{10}$  stratum height (Norton & Leathwick 1990). Data from adjacent 10 m × 10 m plots at the same distance from the edge were combined to give ten sets of species abundances (vascular vegetation, bryophytes and canopy invertebrates) for each edge transect. Forest floor invertebrates had only been recorded from one 10 m × 10 m plot at each distance. The ordinations were undertaken for each data set independently using detrended correspondence analysis (DCA) within the program CANOCO (ter Braak & Smilauer 1998). Default options were used in the analyses, except that rare species were down-weighted to reduce their influence. Biplots of site and environmental variables were produced, but only those environmental variables with correlations of  $r > 0.4$  on at least one axis were plotted.

# 4. Results and discussion

## 4.1 MICROCLIMATES

The 19-day microclimate study period in January 1992 was characterised by a predominance of fine sunny days, with only five days with maximum PAR levels of  $< 1200 \mu\text{mol}/\text{m}^2/\text{s}$  (Fig. 1). Because no true replication was available (measurements were obtained from one north- and one south-facing edge only), no statistical comparisons were undertaken. However, it is clear that there are major differences in microclimates at the edge compared with the interior, and between south- and north-facing edges (Figs 2-4). The north-facing edge experienced elevated day-time temperatures and wind speeds, and lower relative humidities compared with the forest interior (95 m), with conditions more similar to those at the open site. This effect was apparent at the 5-m and 15-m climate stations, but was not evident at 30 m. In contrast, the south-facing edge (5 m only) had higher day-time relative humidities and lower wind speeds and temperatures compared with the forest interior.

Night-time temperatures were cooler at both north- and south-facing edges (5 m) than 95 m into the forest, while night-time relative humidity was higher at the south-facing edge (5 m) than at any other site. Night-time wind speeds were substantially higher at the 5 m north-facing edge site than at any other site including the open site. Reflecting these differences, the daily ranges for temperature, relative humidity and wind speed were also greater at the north-facing edge than in the forest interior (5 m and 15 m except wind speed, 5 m only), while the relative humidity and wind speed range were depressed at the south-facing edge (5 m and 15 m).

Marked differences in edge microclimates have been observed in other studies (reviewed in Saunders et al. 1991; Murcia 1995; Didham & Lawton 1999) and the patterns observed here are consistent with these, although edge penetration distances show considerable variation between studies. For example, Chen et al. (1995) measured edge penetration distances of  $> 100 \text{ m}$  for several

Figure 1. Daily photosynthetically active radiation (PAR) levels over the 19-day microclimate study period.

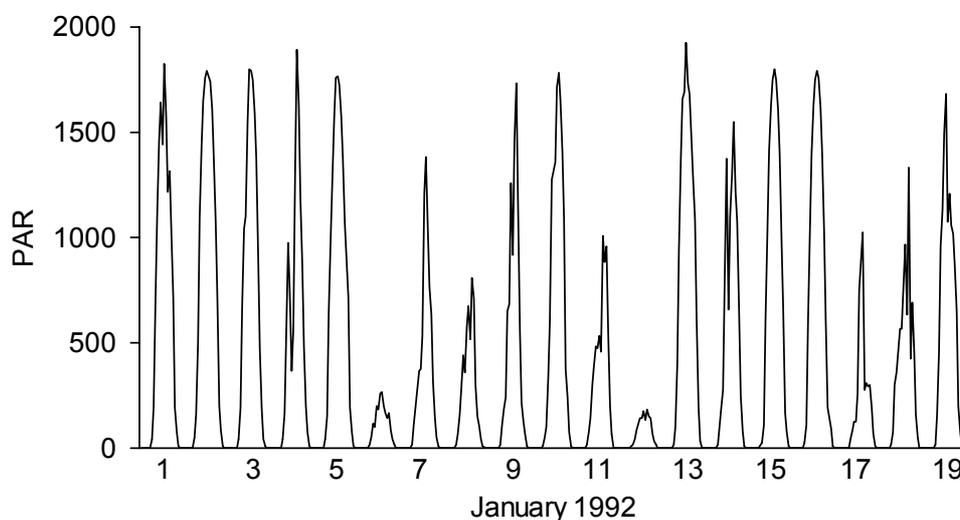
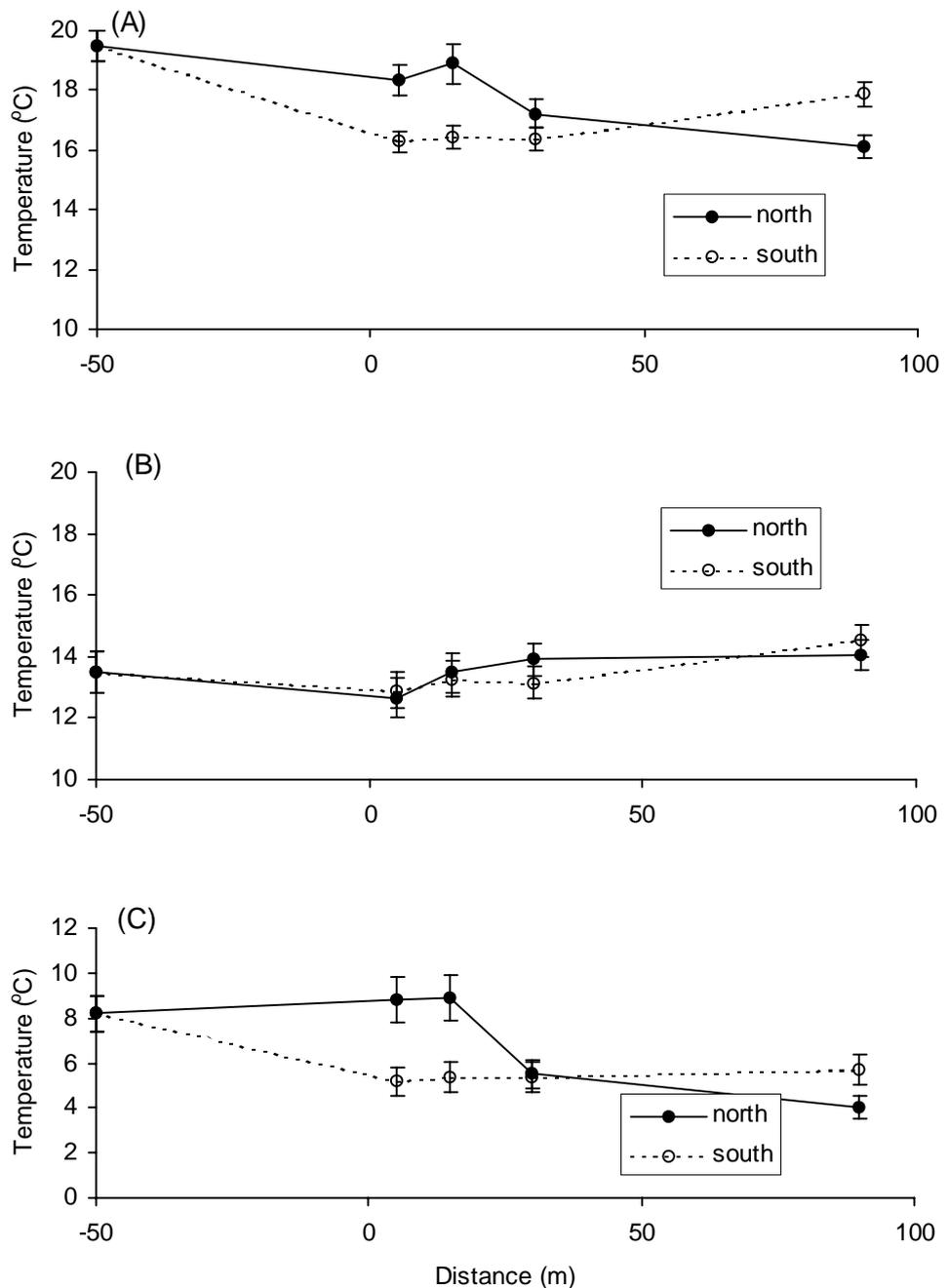


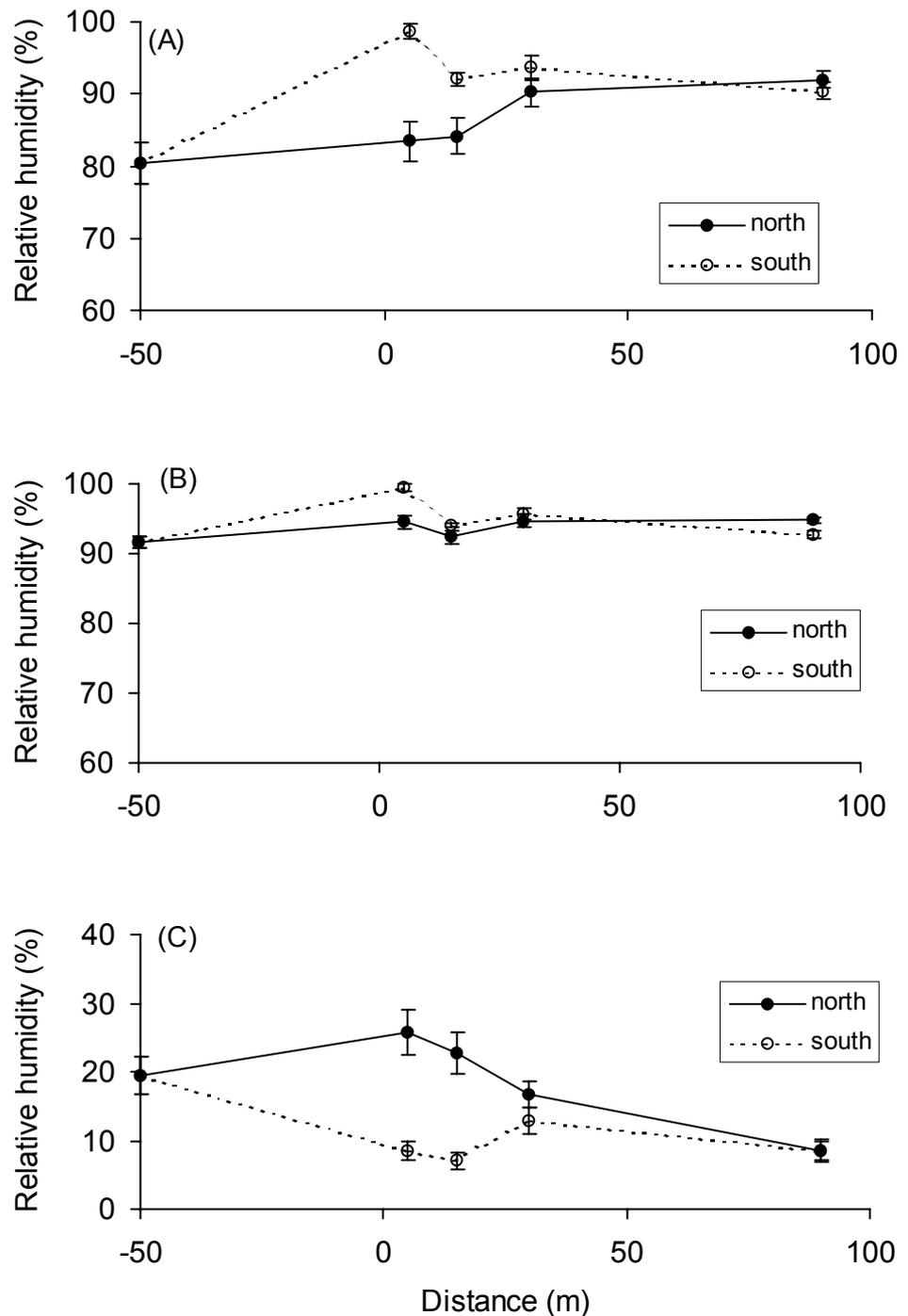
Figure 2. Temperature gradients over north- and south-facing edges. Error bars are standard errors of 19 daily means. (A) Day-time; (B) Night-time; (C) Daily range. Note different vertical scale in (C).



microclimatic parameters, while most other studies reported edge penetration distances of < 50 m (Murcia 1995). Previous studies of New Zealand forest edge microclimates (Young & Mitchell 1994; Davies-Colley et al. 2000; Denyer 2000) have focused on established edges (> 50 years old) in contrast to the relatively young edges studied here (12-14 years old). In general, these studies found a marked microclimate edge effect, with the most pronounced changes occurring within the first 10 m, but with elevated temperatures and vapor pressure deficits still evident 40-60 m into remnants.

Differences in microclimates at edges with respect to aspect (Young & Mitchell 1994) and adjacent land use (pasture versus plantation forest, Denyer 2000) have also been identified. While the difference in the extent and nature of microclimate change at north- and south-facing edges can be explained in terms

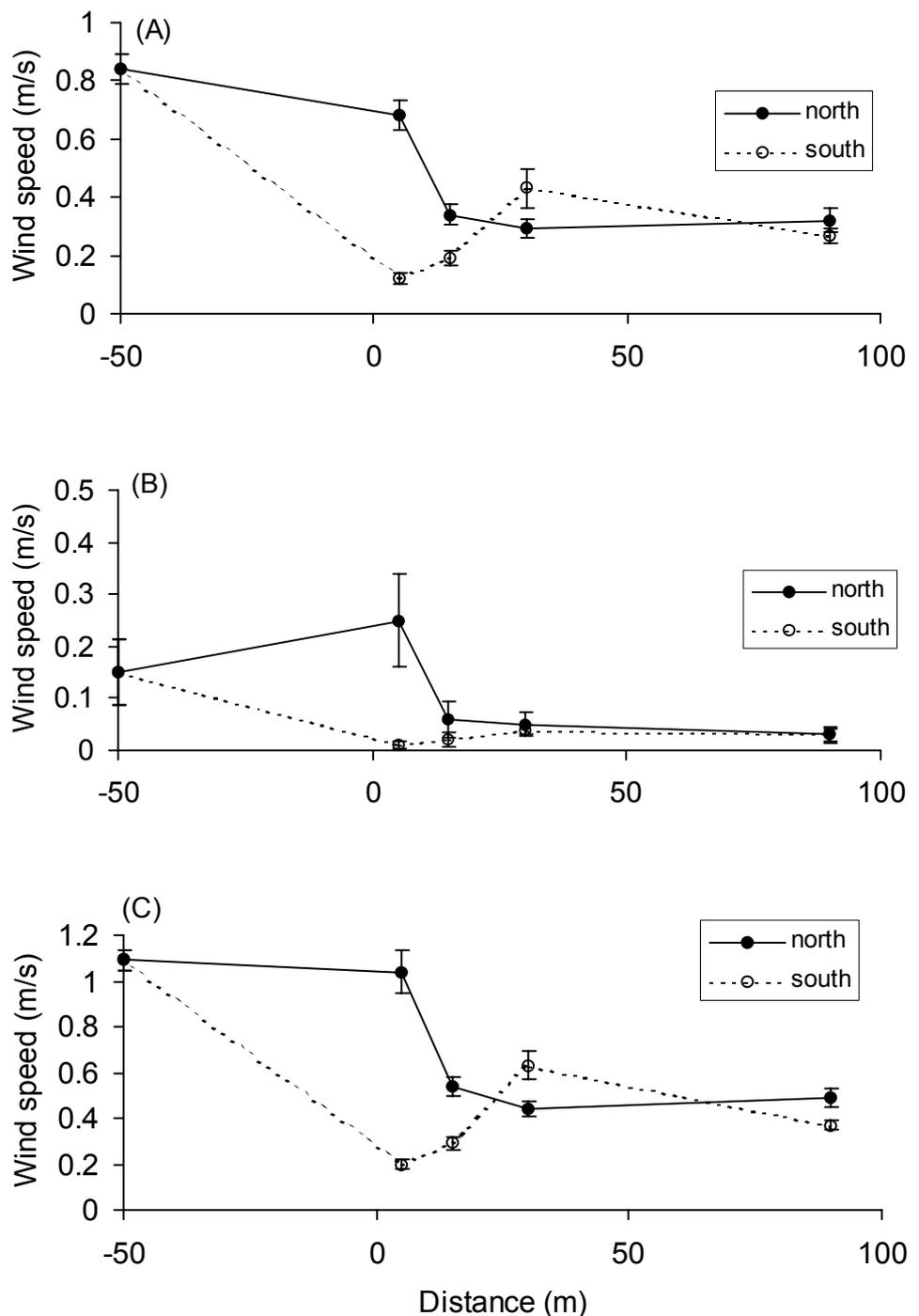
Figure 3. Relative humidity gradients over north- and south-facing edges. Error bars are standard errors of 19 daily means. (A) Day-time. (B) Night-time. (C) Daily range. Note different vertical scale on (C).



of edge orientation relative to solar angle, the dense vegetation associated with the south-facing edge has created a very closed edge which is likely to have further modified microclimate conditions (cf. Didham & Lawton 1999).

It is difficult to compare in detail the results obtained here with those from other studies as each study has involved a different set of circumstances (e.g. variations in geographical location, time of the year, parameters measured, and location of measurement points relative to edge) and adequate replication is lacking in most studies. Nonetheless, the general trends are similar, suggesting that the overall nature of the edge effect on forest microclimates is similar for edges with similar adjacent vegetation and aspect. In southern New Zealand

Figure 4. Wind speed gradients over north- and south-facing edges. Error bars are standard errors of 19 daily means. (A) Day-time. (B) Night-time. (C) Daily range. Note different scales on vertical axes.



cool-temperate rainforests, edge creation results in elevated temperatures and wind speeds and reduced relative humidities for at least 15 m into north-facing forest edges. In contrast, south-facing edges experience similar temperatures to the forest interior, but have higher relative humidities and lower wind speeds (at least at 5 m), probably reflecting the dense growth of tree ferns (see below) that occurs after edge creation.

## 4.2 VEGETATION

A number of pronounced changes in vegetation occurred across the study edges. We measured a highly significant distance effect on total canopy cover (Table 1, Fig. 5A) with both north-facing edges showing cover reductions 40 m into the forest. In contrast, the south-facing edges showed no edge effect, with a significant interaction between aspect and distance (see Table 1). While total cover changed with distance from north-facing edges, there was no significant interaction between aspect and distance for tree basal area (Table 1, Fig. 5B). Tree fern densities and bryophyte frequencies both showed significant edge effects (Table 1), with a decrease in tree fern densities towards north-facing edges and an increase towards south-facing edges (Fig. 5C). In contrast, bryophyte frequencies declined significantly towards both north- and south-facing edges (Fig. 5D)

Canopy foliage cover showed a significant distance effect at both north- and south-facing edges, with a reduction in cover most apparent in the first 10 m in from the edge (Table 1, Fig. 6A). In contrast, the upper subcanopy and, especially, the lower subcanopy showed much more pronounced edge effects in terms of reduced foliage cover. At the north-facing edge, reduced upper subcanopy cover was evident at least 30 m in from the edge, while little change was apparent at the south-facing edge (Fig. 6B). The lower subcanopy cover declined over the whole length of the transects at the two north-facing edges, while there was an increase in cover for the first 30 m in from the south-facing edge (Fig. 6C), with a significant interaction between aspect and distance. Shrub cover showed a significant increase towards the edges at both north- and south-facing edges (Fig. 6D), although this appeared strongest at the south-facing edge. There was no significant edge effect on ground cover, although at one of the south-facing edge transects cover increased markedly in the 20 m closest to the edge (Fig. 6E).

Indirect ordination of the vascular vegetation data resulted in 44.7% of the total variation being explained by the first three axes (Table 2), although species turnover along all three axes was limited (1.36–1.46 standard deviation units), suggesting that all plots were floristically similar. There was little obvious sorting of plots with respect to either distance or edge orientation, and distance

TABLE 1. VEGETATION STRUCTURAL VARIABLES AND DISTANCE OF EDGE INFLUENCE FOR NORTH- AND SOUTH-FACING EDGES IN A SOUTHERN NEW ZEALAND COOL TEMPERATE RAINFOREST.

VARIABLE	<i>P</i>		
	ASPECT	DISTANCE	ASPECT×DISTANCE
Total cover	0.394	<b>0.003</b>	<b>0.006</b>
Basal area	0.333	0.631	0.785
Canopy	0.412	<b>0.015</b>	0.070
Upper subcanopy	0.528	<b>&lt;0.001</b>	0.155
Lower subcanopy	0.890	0.489	<b>0.006</b>
Shrub	0.817	<b>0.028</b>	0.211
Ground	0.763	0.069	0.313
Tree ferns	0.961	0.208	<b>&lt;0.001</b>
Bryophytes	0.772	<b>0.038</b>	<b>0.006</b>

Figure 5. Trends in biotic variables across the two north- and two south-facing edges. Values are means for the four contiguous 10 m × 10 m plots located at the same distance from the edge. Values are plotted at the mid point for each plot (e.g. 5 m value is for the 0-10 m plot). (A) Total canopy cover. (B) Basal area. (C) Tree fern density. (D) Bryophyte frequency.

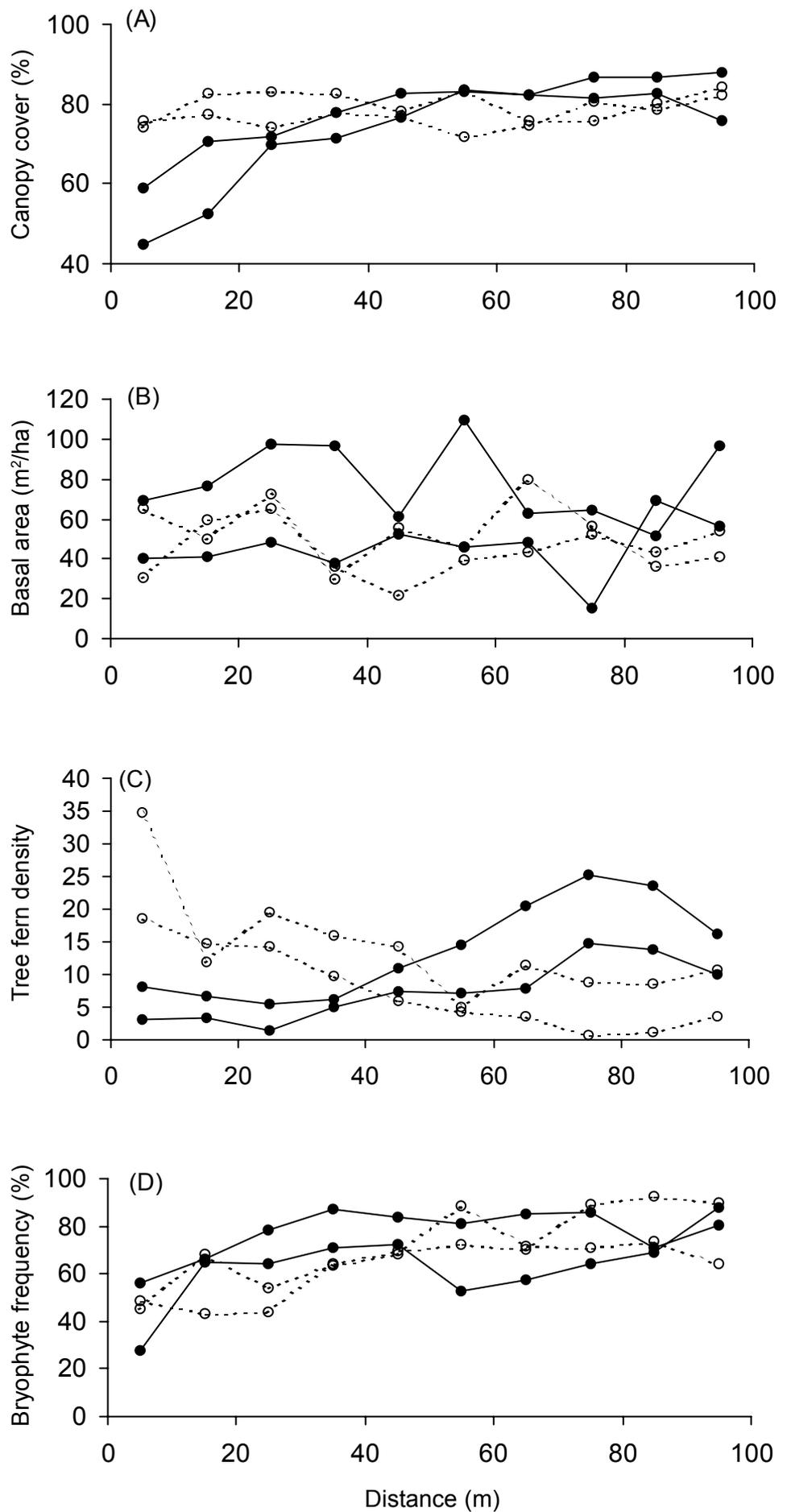


Figure 6. Trends in biotic variables across the two north- and two south-facing edges. Values are means for the four contiguous 10 m × 10 m plots located at the same distance from the edge. Values are plotted at the mid point for each plot (e.g. 5 m value is for the 0–10 m plot). (A) Canopy foliage cover. (B) Upper subcanopy foliage cover. (C) Lower subcanopy foliage cover. (D) Shrub foliage cover. (E) Ground foliage cover.

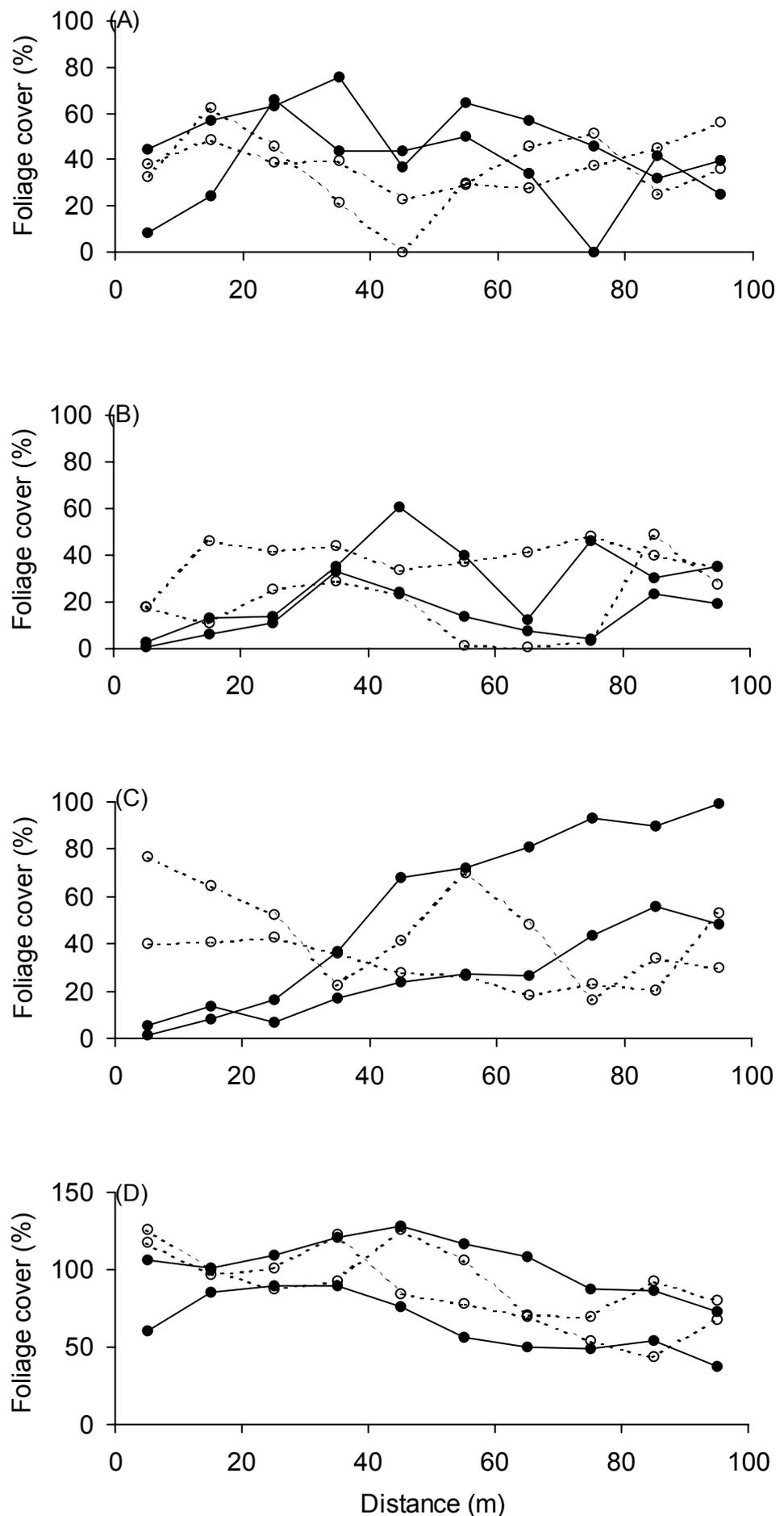


Fig. 6 contd.

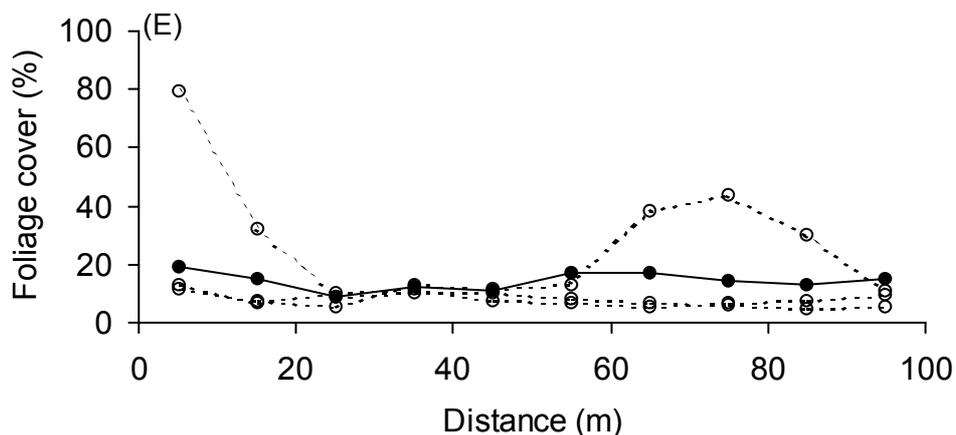


TABLE 2. VEGETATION ORDINATION SUMMARY STATISTICS. ALL ANALYSES WERE FOR 40 SAMPLES.

	AXIS 1	AXIS 2	AXIS 3
<b>Vascular vegetation (101 taxa)</b>			
Gradient length	1.46	1.40	1.36
Variance explained	25.8	12.2	6.7
<b>Bryophytes (65 taxa)</b>			
Gradient length	1.40	1.78	1.03
Variance explained	26.8	10.4	5.7

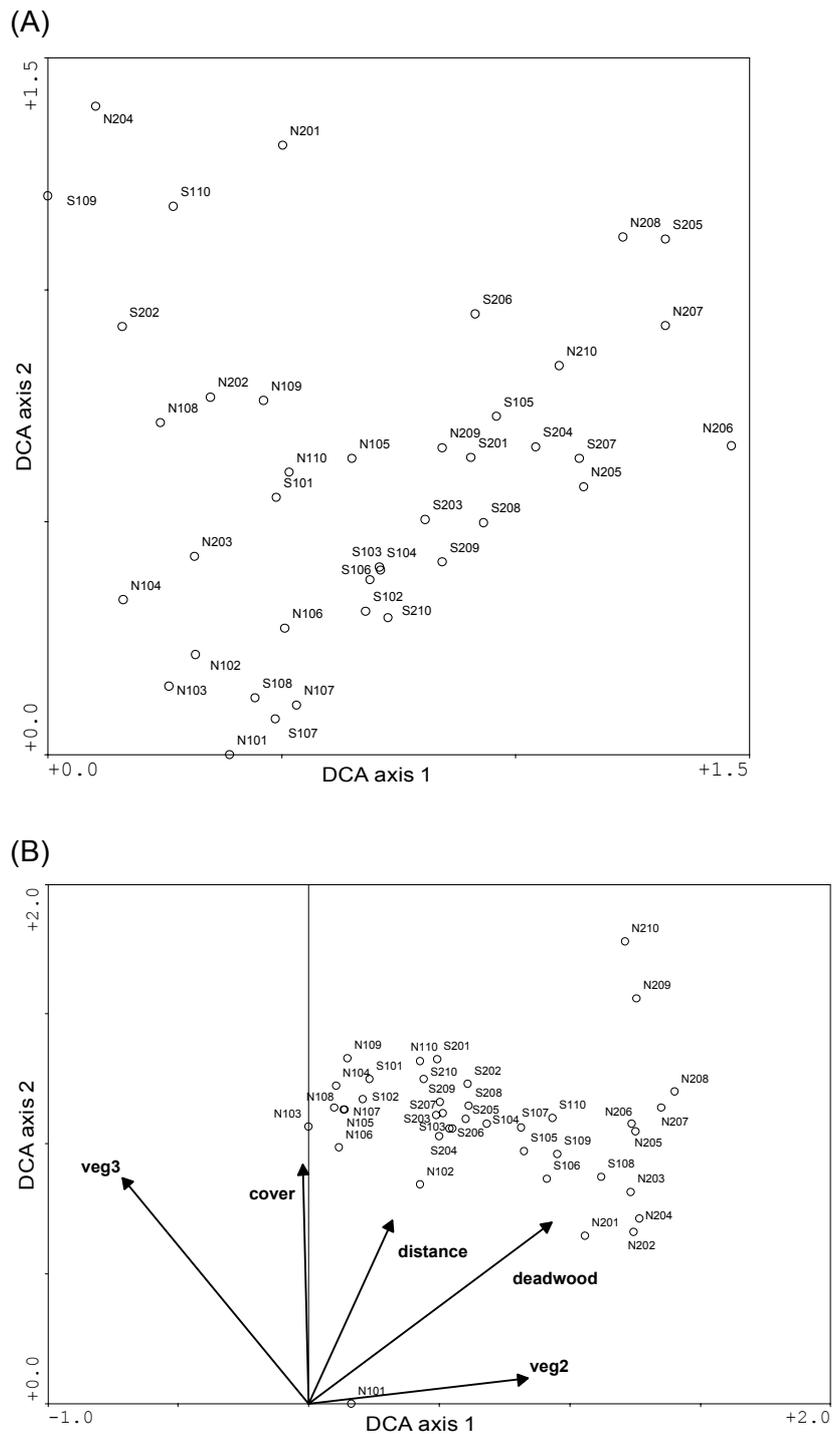
was not strongly correlated with either axis (Fig. 7A). The first three axes of the bryophyte ordination explained 42.9% of the total variation and species turnover was again limited (1.03–1.78 standard deviation units; Table 2). Plots along the two north-facing edge transects occurred at opposite ends of axis 1, with the south-facing edge transect plots intermediate. North-facing edge transect plots were well sorted along axis 2, with plots closest to the edge having the lowest values (Fig. 7B), but no such sorting occurred along the other axes. The first axis of the bryophyte ordination was correlated with vegetation axis 2 scores and the second axis was correlated with total canopy cover. Vegetation axis 3 scores, distance and deadwood were correlated with both axes (Fig. 7B).

In summary, the data on overall cover and abundance of particular structural or functional plant groups showed pronounced edge effects, with evidence for some groups (subcanopy vegetation, tree ferns and bryophytes) that edge effects might extend into the forest for 80–100 m. There was, however, little evidence for an edge effect on vascular plant community composition, suggesting that while the edge has caused changes in the abundance of plant species, it has not affected the relative abundance of different species. In contrast, there was a strong edge effect along the second axis of the bryophyte ordination, at least for north-facing edges, suggesting that edge effects have resulted in some changes in bryophyte community composition.

A diversity of vegetation responses to edge creation have been documented; although, in general, edge vegetation tends to be dominated by high densities and basal areas of shrub and tree species, and differences in species composition compared with interior vegetation (Murcia 1995). There appears,

Figure 7. Detrended correspondence analysis ordination of the vegetation data.

(A) Vascular vegetation.  
 (B) Forest floor bryophytes.

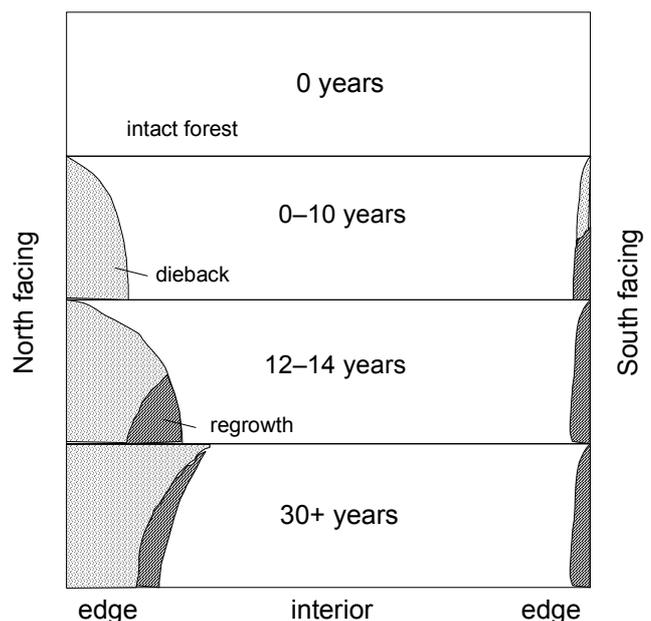


however, to be little consensus on the distances over which edge effects on vegetation occur, with vegetation responses from 15–150 m into unmodified forest recorded (Murcia 1995). Differences in stem density and species composition have also been observed in New Zealand. Young & Mitchell (1994) found that the overall density and basal area for mature individuals was higher at the forest edge than in the forest interior, while there were some differences in species composition between edge and interior plots. Denyer (2000) also observed that stem density was greater in edge plots than interior plots, but did not find any difference in basal area. However, she did observe a very pronounced floristic difference between edge and interior plots, especially for edges bounding pasture.

The results we obtained in our south Westland study are not as strong as those reported elsewhere, although there is good evidence for an edge effect. Our data showed no basal area effect, suggesting that there has been minimal tree mortality since the edge was created, although many canopy trees appeared very unthrifty (with marked foliage dieback) and other studies have documented canopy mortality at edges in this forest type (James 1987). We did, however, observe significant decreases in foliage cover at north-facing edges in the canopy, upper subcanopy and lower subcanopy, suggesting that vegetation dieback has occurred, but that it has not yet been sufficient to result in substantial tree mortality. In contrast, shrub cover appeared to have increased at north-facing edges, at least for 40 m into the forest, suggesting a rapid response in the shrub vegetation to edge creation, although it is unclear if this followed an initial period of shrub dieback. A similar response was also apparent at the south-facing edges, where both the lower subcanopy and shrub foliage cover have increased, especially in the first 30 m in from the edge. Much of this increase in foliage cover at south-facing edges can be attributed to the rapid growth of tree ferns, which showed elevated densities at least 50 m in from the south-facing edges, while tree fern densities appeared to be depressed 60–70 m in from north-facing edges.

It would seem clear that vegetation at the recently created edges we studied is still responding to the microclimate changes that have occurred. Our data do, however, indicate that the vegetation changes occur soon after edge creation. For north-facing edges, dieback occurs rapidly as previously sheltered plants are exposed to elevated light and temperature, and reduced humidity levels. The shrub stratum appears to respond first, with increased foliage cover apparent after 12–14 years. However, dieback is still occurring in the subcanopy and canopy strata and it is likely that, with time, trees will die and the edge zone will retreat from the original edge line to form a new edge, perhaps behind the zone of increased shrub growth (Fig. 8). In contrast, at south-facing edges tree mortality appears to be limited, and rapid regrowth in the shrub and subcanopy strata suggests that edge position is likely to be relatively stable (Fig. 8).

Figure 8. Possible temporal changes in south Westland forest edge vegetation.



### 4.3 INVERTEBRATES

We observed no significant distance or aspect effects for forest floor invertebrates (Table 3, Fig. 9), but we did find significant distance effects for three of the canopy invertebrate functional groups (Table 3, Fig. 10). Canopy detritivores and herbivores decreased towards both north- and south-facing edges, especially in the final 40 m from the edge (Fig. 10A & B), while canopy predators decreased over the full 100 m of all transects (Fig. 10C). In contrast, sap suckers showed a weak and non-significant distance effect (Fig. 10D).

Ordination of the forest floor invertebrate data explained only 25.6% of the variation along the first three axes (Table 4). Plots from closer to both north and south edges tended to have lower values than interior plots along axis 1, while plots from north edge transects tended to have lower values than plots from south edge transects along axis 2 (Fig. 11A). Bryophyte ordination axis 1 scores, dead wood and distance were all correlated with the first axis of the forest floor invertebrate ordination. The first three axes of the canopy invertebrate ordination explained 40.6% of the variance, but species turnover was again limited (0.73–1.37 standard deviation units; Table 4). With the exception of one north transect, plots close to the forest edge tended to have low values on axis 1 while forest interior plots had high values (Fig. 11B). Some separation of edge plots also occurred on axis 3. Axis 2 was correlated with vegetation axis 1 scores while distance was correlated with both axes (Fig. 11B).

The forest edges have affected both the abundance and composition of canopy invertebrates, but appear to have had little impact on forest floor invertebrates, although we did not look in detail at the response of individual invertebrate taxa. There is no other data for edge effects on invertebrates from New Zealand forests, although results from studies elsewhere have suggested that, in general, invertebrate species abundance and community composition is affected by edge creation, with fewer species and simpler communities close to edges (Didham et al. 1998). It had been anticipated that changes in forest floor invertebrate abundance and community composition would be observed, at least for those plots closest to the north-facing forest edges, but little evidence of this was found. In contrast, the dramatic response of canopy invertebrates to edge creation was unexpected, but there is no other data to compare this with. Edge creation appears to be having a major effect on these canopy invertebrates.

TABLE 3. INVERTEBRATE FUNCTIONAL GROUPS AND DISTANCE OF EDGE INFLUENCE FOR NORTH AND SOUTH FACING EDGES IN A SOUTHERN NEW ZEALAND COOL TEMPERATE RAINFOREST.

VARIABLE	P		
	ASPECT	DISTANCE	ASPECT×DISTANCE
Forest floor detritivores	0.388	0.655	0.143
Forest floor herbivores	0.337	0.174	0.224
Forest floor predators	0.156	0.792	0.272
Forest floor sapsuckers	0.090	0.111	0.133
Canopy detritivores	0.598	<0.001	0.539
Canopy herbivores	0.972	<0.001	0.900
Canopy predators	0.974	<0.001	0.948
Canopy sapsuckers	0.935	0.057	0.985

Figure 9. Trends in biotic variables across the two north-facing and two south-facing edges. Values are plotted at the mid-point for each plot (e.g. 5 m value is for the 0-10 m plot).  
 (A) Forest floor detritoveres. (B) Forest floor herbivores. (C) Forest floor predators. (D) Forest floor sapsuckers.

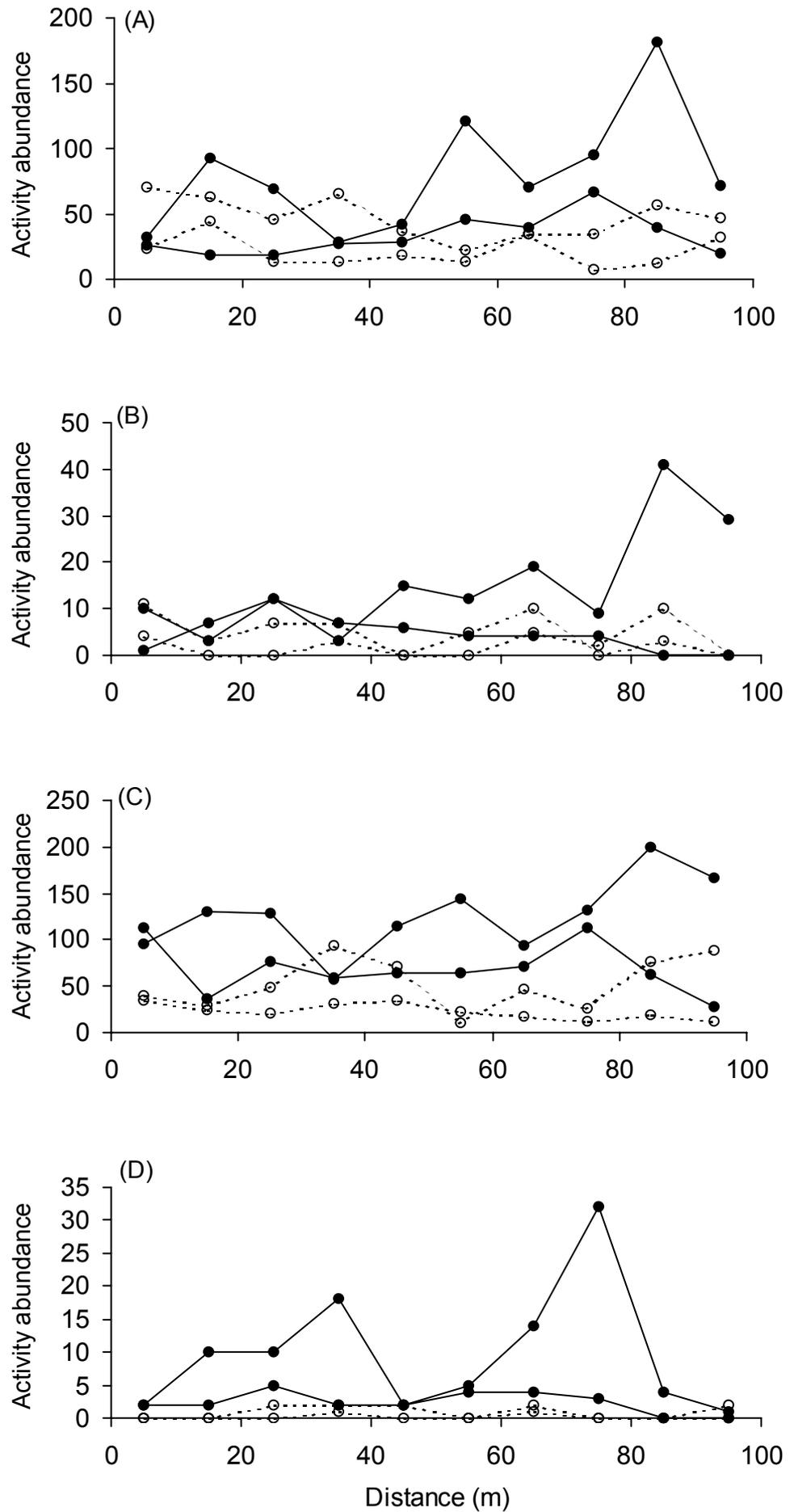


Figure 10. Trends in biotic variables across the two north- and two south-facing edges. Values are means for the four contiguous 10 m × 10 m plots located at the same distance from the edge. Values are plotted at the mid point for each plot (e.g. 5 m value is for the 0–10 m plot). (A) Canopy detritovores. (B) Canopy herbivores. (C) Canopy predators. (D) Canopy sapsuckers.

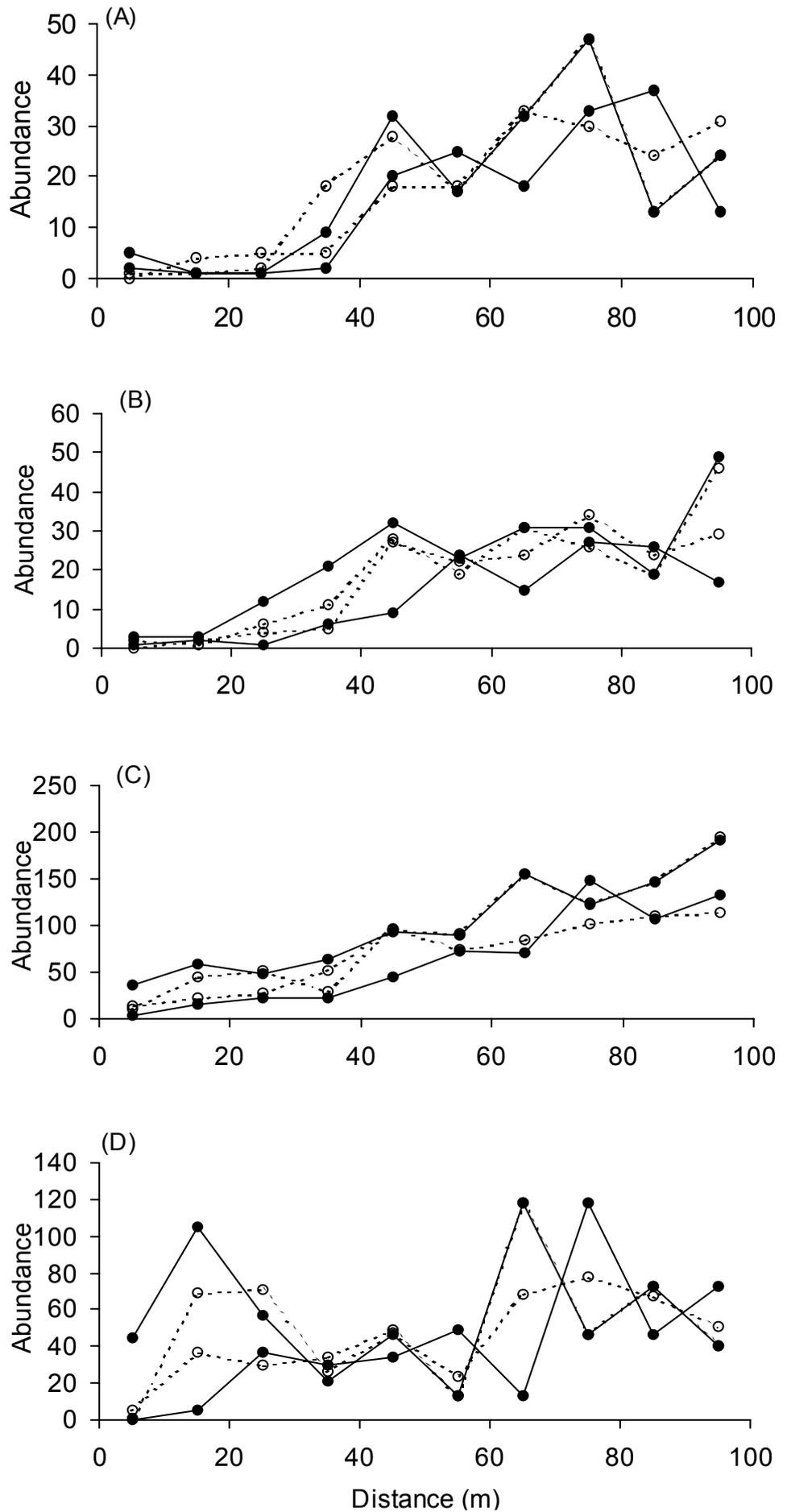
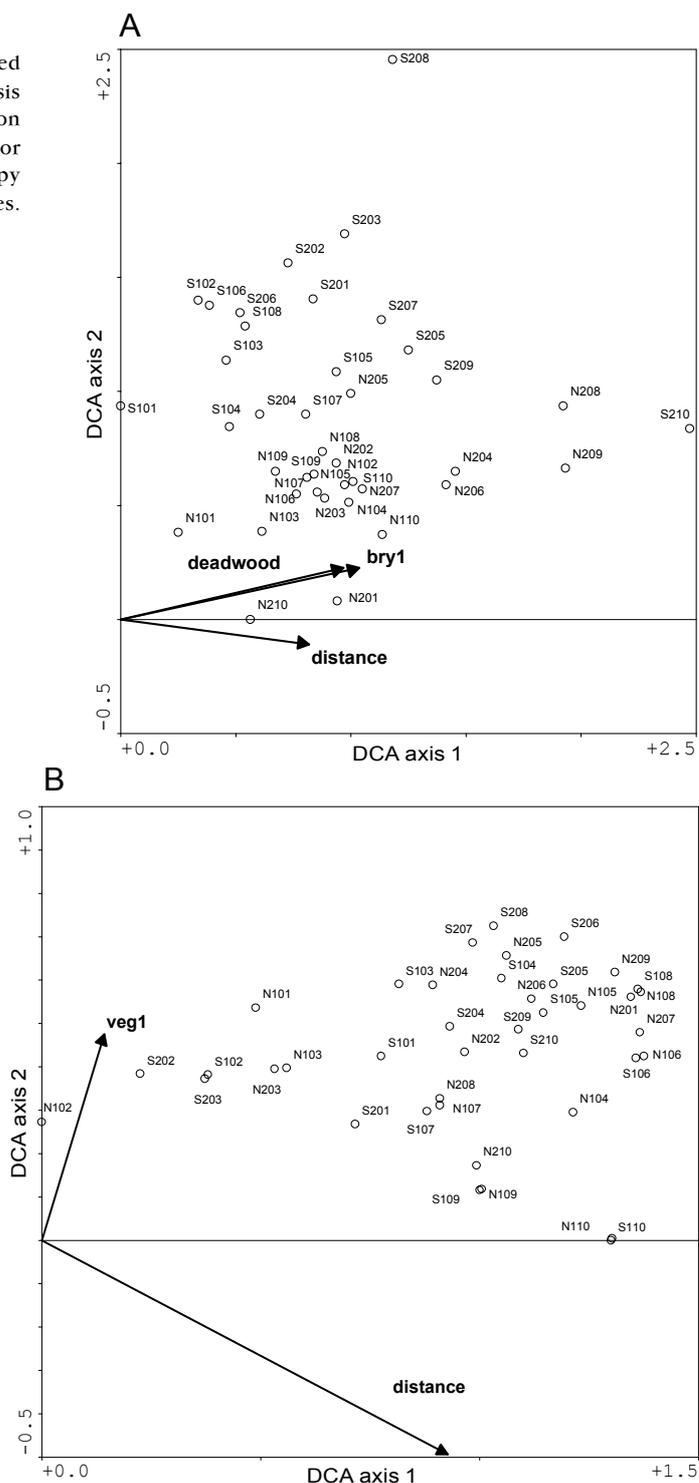


TABLE 4. INVERTEBRATE ORDINATION SUMMARY STATISTICS. ALL ANALYSES WERE FOR 40 SAMPLES.

	AXIS 1	AXIS 2	AXIS 3
<b>Forest floor invertebrates (58 taxa)</b>			
Gradient length	2.47	2.45	1.33
Variance explained	12.4	8.5	4.7
<b>Canopy invertebrates (43 taxa)</b>			
Gradient length	1.37	0.73	1.16
Variance explained	24.5	11.0	5.1

Figure 11. Detrended correspondence analysis ordination of the vegetation data. (A) Forest floor invertebrates. (B) Canopy invertebrates.



#### 4.4 EXTENT OF THE EDGE EFFECT

There is considerable variation in edge response between the different attributes examined, which highlights the complex nature of edge effects (cf. Murcia 1995). Microclimate effects were apparent at north- and south-facing edges, but did not extend beyond c. 20 m into the forest (Table 5). In contrast, vegetation responses were apparent up to 70 m into the forest for some variables (e.g. tree ferns and bryophytes). The responses of canopy invertebrates appear similar to those of vegetation, although the effect of edge on predator abundance appeared to extend into the forest for at least 100 m. The extent of the edge effect documented here is broadly comparable to that observed in other studies, both in New Zealand and elsewhere, and suggests that edge effects of 50–100 m are a significant issue for small forest remnants.

As discussed by other authors (e.g. Matlack 1994; Young & Mitchell 1994) the edge effect has important implications for reserve size. A theoretically circular remnant needs to be at least 9 ha to ensure that 50% of the forest is unaffected by edge effects for a 50 m edge effect, c. 35 ha for a 100 m edge effect and c. 900 ha for a 500 m edge effect (Fig. 12). Comparable values for a square remnant are 11 ha (50 m edge effect), c. 41 ha (100 m edge effect) and > 1000 ha (500 m edge effect). Given that most remnants are likely to have a much greater edge/interior ratio than either circular or square remnants, the areas necessary to ensure that 50% of the remnant is not affected by the edge

TABLE 5. EXTENT OF EDGE INFLUENCES AT NORTH- AND SOUTH-FACING EDGES. Numbers indicate how far effect extends into forest (in metres).

VARIABLE	NORTH-FACING EDGE	SOUTH-FACING EDGE
<b>Microclimates</b>		
Day time temperature	23	0
Night time temperature	10	10
Day time relative humidity	23	10
Night time relative humidity	0	10
Day time wind speed	10	23
Night time wind speed	10	0
<b>Plants</b>		
Total cover	40–50	0–10
Basal area	0	0
Canopy	20	0
Upper subcanopy	30	0
Lower subcanopy	70	30 <sup>+</sup>
Shrub	70 <sup>+</sup>	70 <sup>+</sup>
Ground	0	0
Tree ferns	70	50 <sup>+</sup>
Bryophytes	70	50
<b>Invertebrates</b>		
Forest floor detritivores	0	0
Forest floor herbivores	0	0
Forest floor predators	0	0
Forest floor sapsuckers	0	0
Canopy detritivores	40	40
Canopy herbivores	30	30
Canopy predators	100	100
Canopy sapsuckers	10	10

<sup>+</sup> edge effects have resulted in elevated values for the variable.

will be much greater. The remaining lowland New Zealand forest is now predominantly in small remnants. For example, in the north-western Waikato Region, 82% of all indigenous forest blocks are < 25 ha (Denyer 2000), while on the West Coast 88% of alluvial floodplain forest remnants are < 10 ha (Craig Miller pers. comm.). Clearly, many of the remnants of lowland forest throughout New Zealand will be subject to some degree of edge effects.

## 5. Conservation management implications

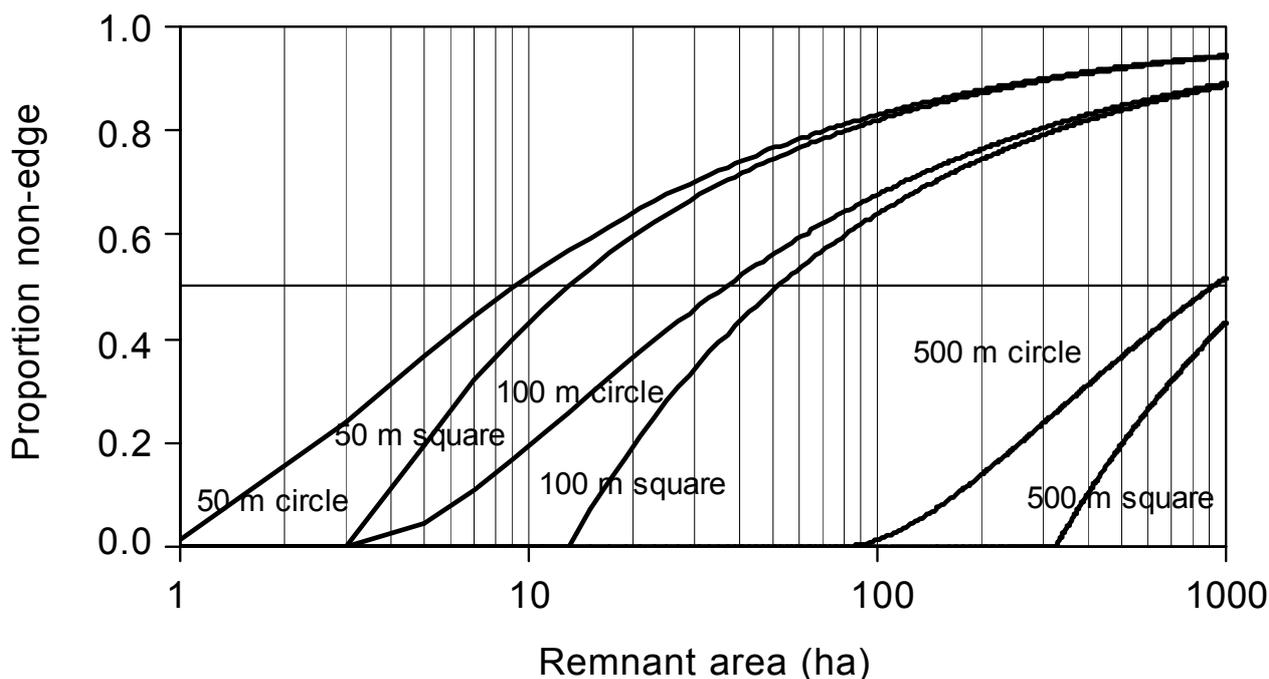
### 5.1 MODIFIERS OF EDGE EFFECTS

In considering the implications of the results of this and other edge studies for the conservation management of forest remnants it is important to emphasise that the effects of edges at any particular site are modified by a number of factors. Because of these modifiers it is often difficult to make generalisations about edge effects (Murcia 1995), although the relative direction and magnitude of their influence is known. Four main modifiers can be identified.

#### 5.1.1 Edge age

Figure 12. Relationship between remnant size and proportion of remnant that is non-edge for three different edge penetration distances and for two remnant shapes.

Most edge studies have focused on a single-aged edge, as was the case with the present study and other New Zealand edge studies. However, where different edge ages have been considered, marked differences in the extent of the edge effect have been described. For example, Matlack (1994) observed that edge-related patterns in vegetation were most frequently observed at recently created edges, but edge effects were still apparent at some 55-year-old edges,



although considerably reduced. A characteristic feature of recent edges is that they tend to be open, with little vegetation regrowth. However, regrowth appears to be rapid under favourable conditions, such as at the south-facing edges studied here, effectively ‘sealing’ the forest interior from external influences. The importance of vegetation regrowth at the forest edge is highlighted by Didham & Lawton (1999) who observed considerably reduced microclimate effects across closed compared with open edges.

### **5.1.2 Edge location**

As already discussed here and shown in numerous other studies, the orientation (aspect) of the edge can have a major influence on the extent and magnitude of edge effects within the forest. Edge effects can also be modified by the nature of the local topography. For example, a north-facing edge on a flat site will have different edge microenvironment than a north-facing edge located at the bottom of a gully.

### **5.1.3 Vegetation type**

The nature of the vegetation can have a marked influence on the way the forest ecosystem is influenced by edge creation. For example, edge effects in Mediterranean climate *Eucalyptus* woodlands in Western Australia appear to be far less marked than in closed-canopy rainforests (Scougall et al. 1983, cf. the results of the present study). This difference arises because of the very open nature of these woodlands with canopy covers in undisturbed woodland usually < 50% cf. > 70% observed here. As a result, the woodland ecosystems are already strongly influenced by open-site microclimate conditions similar to those that occur as a result of edge creation. However, it is important to acknowledge that while the microclimate effects of edges might be less important in these systems, other aspects of edges such as biological invasions can still have major impacts on remnant vegetation (Scougall et al. 1983). Vegetation type is responding to broad climatic gradients and it would seem likely that as conditions change from mesic to xeric, direct edge effects associated with microclimate changes are likely to reduce.

### **5.1.4 Adjacent land use**

The nature of the surrounding matrix can also have a major influence on edge effects, as has been elegantly illustrated by Denyer (2000). In her study Denyer (2000) observed that native forest edges that abutted plantation forests had very different edge environments to those that abutted pasture, with edge effects far more pronounced at the latter.

## **5.2 DO EDGES MATTER FOR NATURE CONSERVATION?**

The results of this research and those of the many other studies that have looked at the effects of edges all show that edges do have a significant influence of the abiotic and biotic environment and that these effects can extend for some distance into the forest. However, because of the influence of the edge

modifiers discussed above, it is difficult to provide specific guidelines on how conservation management should deal with edge effects. I offer the following observations as a guide for conservation management of forest edges in New Zealand.

### 5.2.1 Edges and small remnants

Edges are a significant feature of the multitude of small forest remnants that characterise lowland New Zealand (see earlier discussion on edge extent and remnant size). Edge effects will be directly modifying the biota in these remnants and are likely to result in long-term changes in their composition and structure. Unfortunately, there is virtually no long-term data on the changing composition of small forest remnants in New Zealand. One exception is Riccarton Bush, Christchurch, where the number of indigenous plant species declined from 106 to 67 over the period 1870–1993 (D.A. Norton unpubl. data). This decline is likely, at least in part, to result from edge effects (although remnant size *per se* and isolation are also likely to contribute). This decline in species number in remnants after fragmentation has been referred to as ‘relaxation’ (Diamond 1972) and refers to the period of time taken for the biota of a remnant to return to some sort of equilibrium with environmental conditions in the remnant. For organisms such as long-lived trees, this will be very long, and current biotas may not truly reflect the actual potential or equilibrium biota of the remnant. Edge effects are unlikely to be important in large remnants (> 1000 ha) except, perhaps, at particular sites.

The impact of edges in small remnants will be increased if external disturbances such as grazing and fire occur. There is good evidence that external disturbances can substantially enhance edge effects. For example, in Western Australia Scougall et al. (1983) observed that the abundance of invasive plant species was higher at grazed edges than at ungrazed edges, while grazed woodlands typically have fewer perennial native plants, elevated soil nutrient levels, increased soil compaction and higher soil temperatures than ungrazed woodlands (Yates et al. 2000).

It is important to acknowledge that conservation problems in small remnants are not just related to edges. Size in itself is likely to present a major problem for many organisms through limited gene pools, reduced habitat diversity, and reduced opportunities for patch dynamics to occur, while the isolation of many small remnants also impacts on the long-term viability of the species present within these remnants. Edge management needs to be undertaken in the context of broader landscape management, as edges are only one component of highly fragmented systems (see below).

Management approaches for dealing with edge effects in small forest remnants should include:

- development of some form of buffer zone, either by encouraging the regeneration of vegetation at the edge or through restoration plantings. A buffer zone will reduce microclimate changes within the forest and the biotic effects resulting from these.
- Reduction of external effects such as grazing, as it is these that are likely to sustain edge effects within the remnant.

### 5.2.2 Indirect edge effects

While most of the literature is concerned with the direct impacts of edges through microclimate and biotic changes, indirect biological edge effects (Murcia 1995) are likely to be as important or more important and will affect a much wider range of remnant sizes than direct effects. Edges are the key sites for biological invasions into remnants, especially for plants. Biological invasions are likely to have much more profound long-term impacts on remnants, including the larger remnants that are less vulnerable to direct edge effects. There are numerous examples of biological invasions through edges both in New Zealand and elsewhere (Ogle et al. 2000). Biological invasions can be enhanced by external disturbances (Hobbs & Huenneke 1992). There has also been considerable concern in North America about the impact of cowbirds as predators of forest interior bird nests (Wilcove et al. 1986). Cowbirds are normally birds of open sites but will invade forest remnants and have been documented preying on nests as much as 1500 m from edges. Magpies may play a similar role in New Zealand, although the evidence for this is still largely anecdotal.

Management approaches for biological invasions are limited, as the control of biological invaders is difficult (particularly for plants) from both a technical and financial perspective, but the best option is:

- local control and continual vigilance at forest edges, as is the currently practice of many land managers in New Zealand (e.g. for possums).

### 5.2.3 Landscape management

Edge effects do not occur in isolation, and the whole issue of edges and remnants needs to be considered within the context of the broader landscape (Forman 1995). The external environment has a strong influence on all aspects of edges and the problems they pose for the conservation of forest fragments. For example, the external environment is the source of biological invaders and of external influences such as grazing. Management of the environment at the landscape level is therefore likely to be the best approach to managing remnants with edges, especially in the highly fragmented lowland of New Zealand.

Management approaches towards edges at a landscape scale should include:

- buffer zone management, either within the remnant or in the surrounding landscape, to reduce the direct effects of edges and potentially reduce biological invasion and other external effects.
- integrated pest control, including intensive control around remnants (e.g. keeping weeds such as *Clematis vitalba* out of surrounding agricultural areas).
- Restoration, which is likely to be a key component in combating the effects of habitat fragmentation in general, and hence of edge effects. This essentially involves rebuilding the landscape (Hobbs & Saunders 1993). In many areas this will have direct benefits for productive activities such as farming as well as conservation through improving water management (e.g. in western Australian wheatbelt) and providing refuges for many predators of potentially harmful agricultural pests (Norton & Miller 2000).

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