Effects of landscape heterogeneity and clearfell harvest size on beetle (Coleoptera) biodiversity in plantation forests

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Abstract

Compared to natural forests, fast-growing plantations of exotic species such as *Pinus radiata* are often perceived as marginal habitat or unsuitable habitat for most native species. By studying Coleoptera (beetles) in a variety of landscape elements (pasture, native forest and different aged *Pinus radiata* stands) in a highly modified and fragmented landscape in New Zealand I aimed to determine the value of exotic plantation forests for native biodiversity, and how these species are affected by different sized clearfell harvest areas.

Pitfall trap sampling of beetles showed that plantation forest stands can provide suitable complimentary habitat to native forest for many species. Rarefied species richness of Carabidae, Scarabaeidae and Scolytinae was not significantly different between habitats, however, habitat types differed significantly in their beetle community composition. Comparing different production habitats, *Pinus radiata* stands had a beetle community composition most similar to native forest. However, a small minority of species, e.g., *Dichrochile maura*, were restricted to native forest habitat highlighting the importance of retaining indigenous ecosystems within plantations. Unlike human modified habitats, native forests did not provide suitable habitat for exotic species.

Clearfell harvesting is controversial and its impact on biodiversity is a key constraint for many forest certification programs, such as that administered by the Forest Stewardship Council (FSC). Despite this, no replicated manipulative experimental studies of the impact of different sized clearfell harvest areas on biodiversity have been undertaken at scales relevant to the New Zealand forest industry. One potential model of the impact of different clearfell harvest sizes is the concept of a threshold size. A threshold scenario may occur where clearfell harvest impacts increase at a rate disproportionate to the change in clearfell size over a small range of harvest areas, but impacts remain relatively unchanged either side of the threshold zone. I sampled Coleoptera in experimentally created 0.01, 0.05, 0.5, 5.0, 50 and 500 ha clearfells within *Pinus radiata* plantations in the central North Island of New Zealand. The wide range of clearfell harvest sizes, including some very small areas, such as 0.01 ha was instigated in an attempt to document potential clearfell harvest size thresholds.

Rarefied native beetle species richness was higher in harvest areas compared to adjacent mature plantation stands. The beetle species richness in 5 ha and 500 ha harvest areas was significantly greater species than that in small 0.01 – 0.5 ha harvest areas. Although, the high beetle diversity recorded in 500 ha clearfells should be treated with caution due to confounding spatial autocorrelation. The degree of change in beetle community composition increased with increasing clearfell harvest area. Beetle assemblages in large harvest areas were less similar to their paired adjacent mature forest than smaller harvest areas. Although, constrained multivariate ordination techniques did show a short-term change in beetle species composition between recently clearfelled harvest areas of as little as 0.05 ha and adjacent mature *P. radiata* stands. The colonisation by open-habitat disturbance-adapted species was a key driver of this change, some species dispersed into clearfelled stands in significant densities within days post-harvest. Overall, there were no distinct short-term trends to the change in species richness as a function of increasing harvest area that would suggest an ecological impact threshold response.

If short-term outcomes of clearfell harvesting are ameliorated by successful recolonisation, the long-term spatial arrangement of different aged stands becomes more important for the maintenance of biodiversity at the landscape level than short-term consequences of harvesting. By sampling selected beetle taxa in 1, 2, 4, 8, 16 and 26 year-old stands, I found that the abundance of seven out of eight of the species selected for analysis recovered to levels similar to those in adjacent mature forest within the timeframe of a single harvest rotation. Individual species utilised different aged stands, indicating different life-history strategies. For example, open-habitat, disturbance-adapted species such as *Cicindela tuberculata* and *Sitona discoideus* were prominent in young stands, and forest species such as *Pycnomerus sophorae* and *Paracatops phyllobius* were highly abundant in older stands. These alternative life-history strategies highlight the benefits of maintaining a mixture of different aged stands to increase biodiversity at the landscape level.

This thesis fills an important gap in our knowledge of biodiversity in production landscapes. I show that plantation forests have value as complimentary habitat to native forest and they make an important contribution to the maintenance of biodiversity at the landscape level. Although clearfell harvesting is a severe disturbance to the forest ecosystem, the long-term recovery of beetle populations suggests that harvesting is not the key limiting factor to the enhancement of biodiversity in the plantation forests studied. This unusual situation is possibly the result of prior land-use history, as many plantations were established on degraded pastoral land, and harvest-sensitive species are unlikely to have survived this initial land-use

change. As such, the severity of the long-term impacts of clearfell harvesting on biodiversity are likely to be context specific and will vary accordingly.

The importance of spatial heterogeneity of habitat elements, including different aged plantation stands and native forest remnants, needs to be investigated in more detail to determine what limits biodiversity in this plantation landscape. Key points to consider are the proximity to, and proportion of, native forest cover in the landscape and the degree of connectivity among native remnants. It is these landscape-level attributes that may determine biodiversity at a regional scale, and more emphasis should be placed on landscape scale factors and there interaction with stand specific forest management practices. For example, the spatial mosaic of harvesting areas may need to be of a finer-scale when there are fewer native remnants within the landscape.

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My family have encouraged me through these past few years with gentle prods and verbal reminders of ‘when are you finishing’ to keep me going. Though the distance of the Cooks Strait has meant family visits only occur a few times a year, your long distance love and support have kept the fires burning and the finish line in sight. As well as the love of my family a couple of people have shared a huge part of my life throughout the course of my PhD and their influence will be a lasting memory in my life.

Thanks and happy reading

Table of Contents

Abstract ..... **iii**

Acknowledgements ..... **vii**

Table of Contents ..... **ix**

List of Figures ..... **xiii**

List of Tables ..... **xvii**

List of Tables ..... **xvii**

List of Appendices ..... **xxi**

Declaration ..... **xxiii**

Chapter 1 - Introduction **25**

1.1 Background 25

1.11 Recent trends in fragmentation research 25

1.12 Plantations: habitat or matrix? 25

1.13 Forestry in New Zealand 27

1.14 Forest Stewardship Council (FSC) certification in New Zealand 27

1.15 Clearfell harvesting and harvest area 28

1.16 Rationale of thesis 29

1.2 Thesis Objectives 29

1.3 Thesis Structure 30

Chapter 2 - General methodology **33**

2.1 Introduction 33

2.2 Field Sites 33

2.21 Regional context 33

2.22 Selection of individual sites 35

2.23 Vegetation 36

2.3 Collection of beetle samples 36

2.41 Vegetation 41

2.42 Ground surface characteristics 42

2.42 Canopy cover 43

2.43 LENZ variables (covariables for ordination analyses) 43

2.5 Conclusion 44

Chapter 3 - Clearfell harvest impacts on biodiversity: Past research and the search for harvest size thresholds **47**

3.1 Introduction 47
3.2 Impacts of clearfelling.. 49
3.21 Abiotic 49
3.22 Clearfell harvest impacts on the biotic environment... 53
3.3 The impact of clearfell harvest size... 55
3.4 Reference points for testing clearfell harvest impacts 58
3.5 The search for thresholds 59
3.6 Discussion and Conclusions.. 63
Chapter 4. Non-native plantation forests as reservoirs for native biodiversity in a fragmented New Zealand landscape... 65
4.1 Introduction 66
4.2 Methods.. 68
4.2.1 Collection of beetles.. 68
4.2.3 Assessment of species richness and community composition 70
4.2.4 Assessment of community and individual responses between different habitat types 71
4.3 Results 72
4.3.1 Rarefied species richness 72
4.3.2 Relative beetle abundance in different habitat types.. 72
4.3.3 Variation in beetle community composition between habitat types 73
4.3.4 Individual species responses 73
4.3.5 Changes in the proportion of exotic beetles across habitat boundaries.............. 77
4.4 Discussion 81
4.4.1 High native beetle biodiversity in plantation forests.. 81
4.4.2 Low exotic dominance in plantation forests 82
4.4.3 Plantation forestry as a surrogate for native forest.. 83
Chapter 5 - Impact of clearfell harvest area on beetle biodiversity in an exotic *Pinus radiata* ecosystem 87
5.1 Introduction 87
5.2 Methods.. 89
5.21 Sampling design 89
5.22 Comparing species richness between treatments 90
5.23 Comparing species composition between treatments.. 91
5.24 Individual species responses 93

5.3 Results 94
5.31 Beetle species diversity and harvest size.. 94
5.32 Composition of beetle assemblages 95
5.33 Environmental variables as an explanation for community composition 98
5.34 Identifying species responsible for multivariate patterns................................. 100
5.4 Discussion 102
5.41 Effect of clearfell size on beetle species richness 102
5.42 Effect of clearfell harvest size on beetle species composition 107
5.43 Species richness of plantation habitat 109
5.44 Edge gradients.. 109
5.45 Limitations of the study design 110
5.5 Conclusions 111
Chapter 6 - A space-for-time substitution experiment to test long-term changes in the abundance of beetle species throughout an entire 26 year forest rotation. 125
6.1 Introduction 125
6.2 Methods.. 127
6.21 Study sites and experimental design 127
6.22 Selection of beetle taxa and analysis of data.. 128
6.3 Results 131
6.31 Understorey plant diversity 131
6.32 Beetle abundance.. 133
6.33 Changes in abundance as a function of stand age and distance from forest edge 133
6.34 Interaction terms... 134
6.4 Discussion 138
6.41 Dispersal into regenerating stands.. 138
6.44 Edge species 141
6.45 Exceptions to general abundance trends and their implications for forest management 141
6.5 Conclusions 142
Chapter 7 - Synthesis 145
7.1 Introduction 145
7.2 Non-native forests as reservoirs for native biodiversity in a fragmented New Zealand landscape 145

7.3 Impact of forest harvesting 146
    7.31 Short-term impacts 147
    7.32 Long-term implications 148
7.4 New Zealand forestry: modern biodiversity challenges, their implications and potential solutions. 149
7.5 Future research directions 151
References 155
Appendix A – Other publications produced during my PhD 179

List of Figures

Chapter 2

Figure 2.1. Map showing the location of study forests in the context of surrounding land cover in the central North Island of New Zealand. Land cover was defined by the New Zealand land cover database version 2 (LCDB2) (Terralink 2004). Note yellow circles document the rough centre of the major plantation forests and some of the native remnants used as study sites. (1) Broadlands Forest, (2) Kaingaroa Forest both central and northern, (3) Crater Forest, (4) Ngamotu Forest, (5) Matahina Forest, (6) Tarawera Forest, (7) Putuaki Forest, (8) non-protected native remnant owned by forestry company and (9) Paeroa Range – owned by Department of Conservation. 38

Figure 2.2 Pitfall trap design. I am holding the polypropylene plastic container that is buried to ground level beneath the junction of the two white plastic guide panels when the trap is operational. An ice cream container lid (lower corner of photo) is used as a rain cover and is held in place over the guide panels above the plastic container by wire pegs. Photo by Kennedy Warne. 39

Chapter 3

Figure 3.1. Spatial scale of studies that focus on the ecological changes resulting from different clearfell harvest sizes. Note that the scale is logarithmic. 56

Figure 3.2 (A) Null hypothesis of no-change (curve I), or a linear change (curve II) in ecological impacts with increasing harvest area. (B) Hypothetical scenarios for threshold ecological change across different clearfell sizes (curves III – VI). Ecological change might occur sharply at a defined point, or be spread over wider clearfell sizes. The magnitude and rate of change (slope of line) are likely to vary depending on the response variable studied. As such, there may not be a single identifiable threshold point, but rather a threshold zone might be likely to occur (denoted with shading). 61

Chapter 4

Figure 4.1. Species accumulation curves of, A) all beetle species and B) only native species were calculated for different habitat types by sample-based rarefaction. The x-axis is rescaled to the number of individuals and error bars denote 95% confidence intervals.

The Michaelis-Menten richness estimator was used to estimate the expected species richness asymptote. All rarefaction analyses were conducted using Estimate-S (Colwell 2004).. 74

Figure 4.2. The abundance of native species did not differ significantly across all habitat types, whereas the abundance of exotic species varied between habitat types and was very low in native forest. LSD (p = 0.05 with 26.06 d.f.).. 76

Figure 4.4. Average proportional abundance of exotic beetle species across gradients between habitats, A) Native forest versus clearfell, *P. radiata* and pasture, B) Pasture versus clearfell. Curves represent continuous response functions fitted using the methods of Ewers and Didham (2006b).. 80

Chapter 5

Figure 5.1. Sample based rarefied species richness, rescaled and expressed as individuals (x-axis), error bars are 95% confidence intervals. A) As a function of different sized clearfell harvest areas, and B) of mature *P. radiata* stands situated adjacent to the different size clearfell harvest areas.. 96

Figure 5.2. Sample based rarefied species richness, rescaled and expressed as individuals (x-axis) as a function of distance across a clearfell, mature forest gradient. Negative distances represent traps in mature *P. radiata* stand, positive distances those in clearfells. Error bars represent 95% confidence intervals calculated in Estimate-S Version 7.5..... 97

Figure 5.3. Correspondence analysis ordination diagram of axis 1 and 2 scores showing samples from different clearfell harvest sizes. Samples from 500 ha clearfell areas had very different community assemblages to other smaller harvest areas. Note: traps from the entire transects, including mature forest adjacent to the clearfell harvest areas are shown. 100

Figure 5.4. A) Partial CCA of all sites (forest and clearfell) with longitude and latitude removed as covariables. Significant environmental variables from a forward selection regression (Table 5.3) are given as lines from the origin, abbreviated environmental names are given in full in Table 5.2. B) Same pCCA showing only clearfell harvest sites. Comparisons show greater similarity between small clearfells and mature forest than with larger clearfell harvest areas.. 101

Figure 5.5. Difference in abundance of *Hylastes ater* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *H. ater* in

clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale and when abundance in deep forest sites was zero differences could not be calculated and thus no value is given. 103

Figure 5.6. Difference in abundance of *Pycnomerus sophorae* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *P. sophorae* in clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale and when abundance in deep forest sites was zero differences could not be calculated and thus no value is given. 106

Figure 5.7. Difference in abundance of *Cicindela tuberculata* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *C. tuberculata* in clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale, no *C. tuberculata* were caught in deep forest and thus the calculated values for the difference between clearfell and forest habitats when individuals were sampled from clearfells was infinity. 107

Chapter 6

Figure 6.1 Concept graph illustrating the experimental design of transects between mature forest control sites and adjacent regenerating stands of *P. radiata*. Transects were 580 m in length and were sampled from 290 m into mature *P. radiata* to 290 m into different-aged regenerating stands. In all graphs where the full transect is shown (Appendix 6.1) the mature forest control is given on the left and the regenerating stand on the right. Distances are measured in metres and presented on a $\log_5$ scale. 129

Figure 6.2. Average species richness of understorey vegetation decreased significantly with distance from mature forest in 1 and 4 year-old regenerating stands. a) year 1 ($Y= -0.58x + 3.85$ $R^2 = 0.49$, $P = 0.0001$), b) year 4 ($Y= -0.31x + 3.38$ $R^2 = 0.17$, $P < 0.0049$), c) year 8 ($R^2 = 0.10$, $P < 0.11$), d) year 16 ($R^2 = 0.001$, $P < 0.82$), and e) year 26 ($R^2 = 0.03$, $P < 0.29$) stands. Negative distances indicate sites in mature forest and positive into regenerating stands. Error bars are 95% confidence intervals of the sample based rarefied species richness; E) Similarity of understorey vegetation diversity increases with stand age, i.e., tends to zero. Significant of regression slopes is indicated by the use of alphabetical superscripts * = $P<0.05$, ** = $P<0.01$ and *** $P< 0.001$............................. 132

Figure 6.3. Scatter-plot with linear regressions of the difference in abundance of *Odontria ?piciceps* between regenerating stands and their adjacent mature forest control at a) year

1, b) year 2, c) year 4, d) year 8, e) year 16 and f) year 26. Slopes of the linear regression were significantly different from zero in year 1 and 2, where trap catch was greatest at the forest edge. Harvesting did not have a positive impact on all species. 135

Figure 6.4. Slope of relationship between abundance and distance was approximately zero in stands older than 8 years, indicating no difference in abundance along the habitat gradient. However, **a)** *Cicindela tuberculata* and **c)** *Hylastes ater* showed disparate responses in younger stands. *C. tuberculata* increased in abundance with distance into clearfell harvest areas, whereas *H. ater* decreased. Regression lines of the difference in abundance between mature and regenerating stands show that **b)** *C. tuberculata* and **d)** *H. ater* had greater abundance in young stands compared to adjacent mature controls. 136

Figure 6.5. Average difference in abundance between regenerating stands and adjacent mature forest controls of **a)** Latridiidae sp. 117 and **b)** *Pycnomerus sophorae* decreased immediately post-harvest and recovered as stands regenerated. **c)** *Paracatops phyllobius* showed a similar response with a time lag of 4 years, but did not appear to fully recover after 26 years. In contrast **d)** *Sitona discoideus* had higher abundance in young stands compared to the adjacent mature forest that decreased with stand age. Dashed lines indicate zero difference between mature *P. radiata* and adjacent regenerating stands. 137

List of Tables

Chapter 2

Table 2.1. Summary of the experimental design of individual chapters, including replicates and number of pitfall traps: note * denotes traps from the 50 ha clearfell harvest size treatments that are also used in Chapter 5, † denotes comparison also used in the Chapter 4 analysis of comparisons between landscape elements. 34
Table 2.2 Description of environmental variables collected and their units of measurement. 39
Table 2.3. Abundance and cover classes used to quantify the percentage vegetation cover at different tier heights. 42
Table 2.4. Vegetation height tiers used to obtain single importance values. 42
Table 2.5. Scoring system to provide a qualitative measurement of the amount of deadwood, drainage and litter surrounding each pitfall trap. 43

Chapter 3

Table 3.1 Summary of the known ecological changes in species abundance, richness and composition of different taxonomic groups and abiotic changes induced by clearfell harvesting. Change is recorded as positive (+), negative (-) or variable (-/+). 51

Chapter 4.

Table 4.1. Description and units of measurement of environmental variables included in constrained CCA ordination (Figure 4.4)... 69
Table 4.2. Results of repeated measures ANOVA of beetle species abundances with respect to habitat comparison type, habitat type, species origin and distance from habitat edge. A correction factor of 0.9658 was applied to the d.f. of the distance term and its interactions to adjust for potential correlation between pitfall traps sampled from the same trap gradient. Origin refers to whether the beetle was native or exotic.................................. 75
Table 4.3. Significant environmental variables and associated intraset correlations from partial canonical correspondence analysis. Eigenvalues, F-values and P-values are from forward selecting regression procedure, Canoco V. 4.02 (ter Braak and Smilauer 1999). Intraset correlations in bold are significant at P < 0.05... 77

Figure 4.4. A) Site-based partial constrained correspondence analysis (pCCA) of combined Carabidae, Scarabaeidae and Scolytinae in different habitat types. B) Biplot of significant environmental variables (Table 4.3) with the most abundant taxa and those with significant indicator values for at least one habitat type overlaid (abbreviations as in Table 4.4). Continuous environmental variables are shown as arrows, while categorical variables are expressed as a single black circle indicating its centroid........................... 78

Table 4.4. Indicator values for beetle taxa in different habitats, values were calculated using the methodologies of Dufrêne and Legendre (1997) on the basis of a priori selected habitat groupings using PC-ORD V. 4.01 (McCune and Mefford 1999). 79

Chapter 5

Table 5.1. The location of harvest treatments throughout 100-200 ha forest compartments in the central North Island plantations of New Zealand. Abbreviations: Kang = Kaingaroa Forest, Broad = Broadlands Forest, Tawa = Tarawera Forest, Crater = Crater Block, Roto = Rotoehu Forest, Puta = Putauaki Forest. Numbers reflect individual forest compartments, and * denotes the compartment that was not harvested in time. Note: that 500 ha sites were a combination of different forest compartments, only the compartment where the traps were actually sites is listed.. 90

Table 5.2. Site and landscape variables used as explanatory variables in multivariate ordination analyses. A description is given for each variable and where necessary identifies collinear composite terms. Units of measurement are specified..................... 92

Table 5.3. Significant environmental variables from a forward selecting regression (Canoco) both before (a) and after (b) assignment of significant spatial variables as covariables. Intraset correlations are given that define the strength of the relationship between environmental variables and the constrained ordination axes of the pCCA after the removal of spatial autocorrelation due to covariables. λ -A is the additional variance explained by each variable at the time it was included in the forward selection analysis, P is the significance of the F-value from a Monte-Carlo test with 500 replicates. 98

Table 5.4. Abundance of individual species in mature *Pinus radiata* 125 m from the forest edge, average abundance at 0, 5, 25 and 125 m into clearfells and the change in abundance of taxa highly correlated with ordination axes 1-3 of a constrained analysis of principal coordinates (Anderson and Willis 2003) at different clearfell harvest sizes. . 104

Chapter 6

Table 6.1. Observed patterns in the abundance of selected beetle taxa as a function of clearfell size (data presented in detail in Chapter 5). Exotic species are denoted by an-asterisk. 130

Table 6.2. Average species richness of native (N) and adventive (A) plants (excluding grasses, herbs and mosses) per 2 x 2m quadrat surrounding pitfall traps at different distances along an edge gradient sampled between mature 26 year *P. radiata* and regenerating stands of different ages. 131

Table 6.3. F-values and associated significance (<0.05 *, <0.01 ** and <0.001 ***) of a mixed model, random effects ANOVA to test for changes in species abundance by stand age, distance along transect (both linear and curvilinear) and the age*distance age*dist^2 (curvilinear) interaction. Random effects in the model were the age and age (compartment). 133

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List of Appendices

Chapter 4

Appendix 4.1. Average catch per 100 trap days of individual beetle taxa sampled at different distances from the habitat edge into clearfelled plantation forest, mature *P. radiata* forest, native forest, and pasture... 85

Chapter 5

Appendix 5.1 Raw species data of all 355 species and actual individual species catch in each habitat. 113

Chapter 6

Appendix 6.1. Average catch per 100 trap days of selected beetle taxa across pitfall trap gradients between mature forest and regenerating stands (positive distances) is presented. A) *Odontria ?piciceps* was attracted to edge habitat in young stands, where as B) *Pycnomerus sophorae*, C) *Paracatops phyllobius* and G) Latridiidae sp. 117 preferred mature forest stands. In contrast D) *Sitona discoideus*, E) *Cicindela tuberculata* and F) *Hylastes ater* were most abundant in the open habitat of young clearfells. Lines in all graphs are splines created using the curve fitting function of Sigma Plot (Version 7.0, SPSS Inc).. 142

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Declaration

I declare that the material in this thesis is my own work, except for the following assistance: (i) The trials undertaken in Chapter 4-6 were of my own design with input from Ecki Brockerhoff, Raphael Didham and David Norton, (ii) Cleland Wallace and Amy Leighton assisted in the collection of vegetation data and Chris Ecroyd identified our unknown plant specimens, (iii) Mike Watson, Sylvia McLaren, Jo Schaab, Marijn Zwart, Travis Cross and Nicolas Faust assisted in the monthly checking of pitfall traps, (iv) Carl Wardhaugh assisted with the sorting of beetle taxa for Chapter 4 & 6, all sampling for Chapter 5 was done by myself, (v) Species names were assigned by Stephen Thorpe to the morphospecies I had sorted in Chapter 5, (vi) Mike Watt provided statistical advice about mixed-model analyses in Chapter 4 and 6, (vii) The entire thesis including the submitted manuscript (Chapter 3) were written by myself with critical review from my supervisory committee, (viii) Esther Meenken conducted the repeated measures ANOVA in chapter 4 and provided general statistical advice, (ix) Barbara Hock (Ensis) provided the LCDB data of the proportion of native and exotic forest around my sample sites, (x) Publications given as appendices in Chapter 9 were largely written by myself with input from co-authors, except for the *Indigena* article in which I only contributed to sections relevant to my thesis and the New Zealand Geographic article that had significant contributions by Eckehard Brockerhoff.

Chapter 1 - Introduction

1.1 Background

1.11 Recent trends in fragmentation research

Deforestation and forest fragmentation are well-known threats to biodiversity, and are key drivers of global species extinctions (Tilman et al. 1994, Hanski et al. 1995, Sala et al. 2000, Ewers et al. In Press). Research into forest fragmentation has until recently focussed on three key areas: reduction of total forest area within the landscape, increased isolation of the remaining forest remnants and the creation of habitat edges (Kupfer et al. 2006), and their implications for organisms living in remnant habitat. For example, the size and shape of remnant forest patches and how these modify microclimate (Chen et al. 1995), dispersal and edge effects (Murcia 1995, Fagan et al. 1999), population viability and metapopulation dynamics (Hanski and Ovaskainen 2000, 2002, Ross et al. 2002, Steffan-Dewenter 2003) and the functional attributes of ecosystems (Didham et al. 1996). This focus has stemmed from the island biogeographic principles underpinning most of fragmentation research (MacArthur and Wilson 1967), in which remaining habitat was viewed for the most part as islands in an inhospitable matrix of unsuitable habitat (Haila 2002). However, it is now well recognised that remnant habitat fragments are only one component of a heterogeneous landscape made up of different elements that vary in habitat quality (Haila 2002, Kupfer et al. 2006). Evidence is now mounting that attributes of the matrix, including its extent, degree of contrast from remnant habitat, and permanence will affect the isolation of forest fragments (Sisk et al. 1997, Lindenmayer et al. 2001, Marzluff and Ewing 2001, Brotons et al. 2003).

1.12 Plantations: habitat or matrix?

Despite the international focus of research on natural ecosystems (Fazey et al. 2005), plantations are increasingly recognised as significant reservoirs of biodiversity, particularly in heavily modified landscapes (Humphrey et al. 2001, Carnus et al. 2006). This realisation comes at a time when researchers are beginning to recognise that there are few pristine native habitat remnants in some landscapes, and in such situations these will be insufficient to effectively preserve biodiversity. In such situations the modified production habitat (matrix habitat) will be important for the protection of biodiversity at the regional scale (Novacek and

Cleland 2001). These ideas are now incorporated in national government policies such as the New Zealand Biodiversity Strategy (NZBS, www.biodiversity.govt.nz), in an effort, perhaps, to change historical public and industry attitudes that conservation of biodiversity and economic production are mutually exclusive. This historical dichotomy in New Zealand has its roots in the Reserves Act 1977 and was an underlying feature of the New Zealand Forest Accord (August 1991) (Norton 1998).

Irrespective of government policy, extensive forest industry-led changes regarding biodiversity have occurred in the last decade; e.g., the New Zealand Institute of Forestry's biodiversity position statement. This recognises the value of plantation forests as a repository of biodiversity and the importance of maintaining and enhancing the value of plantations for biodiversity, as well as contributing to research and education (Shaw 1997). One of the main drivers for this change has undoubtedly been forest certification (for detailed explanation of certification in New Zealand see section 1.14) (Hock and Hay 2003), which in turn has evolved from a demand for sustainable forest products. However, the public have been slow to recognise the biodiversity value of plantation forests, largely because of historically perpetuated values and partially due to publications from environmental non-government organisations (e.g., Greenpeace), which have presented unbalanced views of plantation forestry (Rosoman 1994). Despite this, forestry is a significant production land use in New Zealand and has the potential to make a significant contribution to our international biodiversity obligations. Research has shown that plantation forests can act as a habitat reservoir for many species of birds, plants and insects (Clout 1984, Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003, Pawson and Brockerhoff 2005, Berndt et al. Submitted), including endangered species such as the kiwi, New Zealand falcon and the carabid beetle *Holcaspis brevicula* (Kleinpaste 1990, Brockerhoff et al. 2005). As such, plantation forests could play a major role in biodiversity preservation. As a low contrast matrix habitat compared to native forest they have the potential to act as conduit habitat, increasing the extent of forest habitat and providing connectivity between native forest remnants (Norton, 1998).

1.13 Forestry in New Zealand

Large-scale plantations dominate the New Zealand forest industry and cover c.1.87 million hectares (22.5% of total forest area in New Zealand) (Anon 2005). The exotic Monterey or radiata pine (*Pinus radiata*) is the principle species and comprises 89% of the current plantation area. The combination of the light-demanding regeneration requirements, fast rotation time and low timber value make clearfelling the most common harvesting technique for radiata pine. Clearfelling is defined as the removal of all trees from an area of sufficient size to break the continuity of the forest microclimate (Kimmins 1992). The result is a heterogeneous landscape of successional forest stages on a much larger and regular scale (the 'chequer board' landscape) than that created by natural disturbance processes. This has been condemned by environmental organisations (Rosoman 1994), whereas the main public concern about clearfelling appears to be its immediate visual impacts (McGee 1970, Hansis 1995), although no published research on this has been undertaken in New Zealand.

1.14 Forest Stewardship Council (FSC) certification in New Zealand

The Forest Stewardship Council (FSC, www.fsc.org) is an international non-governmental agency established in 1993 that certifies (through independent certification providers) forest management on the basis of 10 principles and 54 criteria. The aim is to ensure that forest management is sustainable and this can include an analysis of the 'Chain of Custody' of wood products from the forest through the supply chain to the end consumers. The concept of forest certification hinges on the willingness of consumers to pay a premium price for products derived from sustainably managed resources, this 'market edge' then pays for the compliance costs of certification. Hock and Hay (2003) reviewed FSC certification in New Zealand and found that by 2003 eleven forestry companies had certified 610,257 ha of forest, representing about 34% of our plantation estate. As part of the certification process, companies can be issued with major and minor corrective action request (CARs). Major corrective actions (also known as pre-conditions) indicate a major deficiency in a specific area that must be resolved before certification can proceed. Minor corrective actions are issues that must be resolved but are not considered a limiting factor for certification, and companies are generally given a period of time to rectify problems (Hock and Hay 2003).

Clearfell harvesting impacts and biodiversity are key areas of concern to the FSC process in New Zealand (Hock and Hay 2003). Forestry companies have responded to this by undertaking internal studies, contracting research, or supporting external research to address problems identified by FSC auditors.

1.15 Clearfell harvesting and harvest area

Clearfell harvest areas and young regenerating stands in a plantation landscape are the equivalent of matrix habitat in a fragmentation sense. As open habitat they present a discontinuity between the remaining unharvested forest stands. Like all other harvesting techniques, clearfelling has significant ecological consequences that have been the focus of much scientific study on both abiotic (Camargo and Kapos 1995, Chen et al. 1995, Chen et al. 1999) and biotic factors (Murcia 1995, Dijak and Thompson 2000, McGeoch and Gaston 2000, Campi and Mac Nally 2001, Barbosa and Marquet 2002, Honnay et al. 2002, Magura 2002). Despite the wealth of research into harvest impacts and their subsequent edge effects, very little is understood about the relative impacts of different sized clearfell harvest areas. A limited number of studies in North America have analysed whether the impact on biodiversity differs between small and large clearfell harvest areas, but most of these have only examined harvest areas of less than 10 ha, which is too small to be relevant to current forest harvesting practices in New Zealand (Pawson et al. 2002). It is surprising that so few published studies exist on the biological impacts of different sized clearfell areas given the world wide public concern regarding clearfell harvesting as a forestry practice. The public generally associate clearfell harvesting with a reduction in biodiversity, which is not necessarily correct (Niemela et al. 1993), and have demanded changes in forest harvesting policies to preserve biodiversity attributes (Ribe and Matteson 2002). In response, many research programs have been established to evaluate alternative harvesting systems (Hansen et al. 1995, Prescott 1997, Beese and Arnott 1999, Beese and Bryant 1999, Koivula 2002a). However, no-one has experimentally manipulated clearfell harvest size and measured the effect of harvest area on ecosystem attributes, including biodiversity. Perhaps small clearfell harvest areas have a lower impact on forest ecosystems and may be a suitable compromise between continuous cover forestry and large-scale even-aged silvicultural management.

1.16 Rationale of thesis

This thesis aims to fill a distinct gap in our understanding of forest ecology and the impact of forest harvesting on biodiversity. I achieve this by undertaking a replicated study that analyses the impact of different sized harvest areas, at a scale relevant to the New Zealand plantation forestry industry. The research described in my thesis will provide valuable information on the interaction between clearfell size and edge effects in a largely forested landscape and resolve important applied ecological issues relevant to environmental certification of forestry companies in New Zealand.

Pinus radiata plantations were chosen as an ideal study site to analyse the effects of clearfell harvest size for several key reasons: (i) as a managed forest ecosystem it was possible to experimentally clearfell specific areas of known size; (ii) past forest management history was well documented in a GIS framework; (iii) forest canopy had a simple structure of a single commercial species, which reduced variation between sites; and (iv) the sites were easy to access by a good road network.

1.2 Thesis Objectives

The objective of my PhD was to:

Compare the beetle fauna of Pinus radiata *plantation forests with other habitat elements within a fragmented landscape, and analyse by experimental manipulation the effects of clearfell harvest area on invertebrate biodiversity in an intensively managed* Pinus radiata *ecosystem.*

The thesis has a number of specific aims that are addressed in a series of chapters. These aims are:

- To synthesise currently available literature on the impacts of clearfell harvest size on biodiversity, and analyse this in an ecological threshold context.
- To determine the value of plantation forests as low-contrast matrix habitat for species that were historically associated with native forests.
- Quantify the change in beetle biodiversity as a function of different sized clearfell

harvest areas.

- Analyse the change in abundance of selected beetle species as a function of stand regeneration post-harvest.

1.3 Thesis Structure

The thesis is organised as a progression of chapters beginning with the known impacts of clearfell harvesting and potential implications of a change in harvest area. Plantations are evaluated for their potential as reservoirs of biodiversity before concluding with an analysis of the short-term and long-term impacts of clearfelling on Coleoptera (beetles). Thesis chapters are structured as follows:

Chapter 2 provides a description of general methods that are applicable to multiple thesis chapters. A detailed outline of the study area, collection of beetle samples, understorey vegetation, canopy-cover estimates, and site characteristics (deadwood, drainage and litter) is given to avoid repetition of these in subsequent chapters. Concise methods sections are given in individual chapters providing detailed explanation of methodologies and analyses relevant to each chapter.

Chapter 3 reviews the abiotic and biotic impacts of clearfell harvesting and provides a synthesis of available literature on the impacts of clearfell harvesting with respect to clearfell harvest area. The chapter finishes with a discussion of potential ecological threshold responses, which are currently being applied to fragmentation problems but have not been considered in a harvesting context. The material present in this chapter has been accepted as a manuscript for publication in the *Canadian Journal of Forest Research* as Pawson, S. M., Brockerhoff, E. G., Norton, D. A., and Didham, R. K., “Clearfell harvest impacts on biodiversity: Past research and the search for harvest size thresholds”.

The public often view plantations as ‘biological deserts’. To test this, Chapter 4 compares the Coleopteran and understorey vegetation diversity in *Pinus radiata* plantations versus other habitat elements (native forest and pasture) within a landscape of intensely managed land uses. The aim is to determine if managed forests can provide habitat for native biodiversity in a landscape that has a reduced and highly fragmented native forest area. This is important, as forestry is often compared unfavourably with other production land uses, such as intensive pastoral farming, even though preliminary evidence suggests that managed production forests can have considerable biodiversity benefits.

Chapter 5 evaluates the short-term impacts of clearfell harvesting on beetle biodiversity as a function of harvest area. Internationally there is intense public pressure to change from clearfelling to alternative silvicultural systems, due to the perceived ecological impacts of clearfell harvesting and aesthetic considerations. This chapter presents the results of the first large-scale, replicated experiment that compares the total beetle biodiversity in different sized clearfell harvest areas at a scale relevant to plantation forestry in New Zealand.

Chapter 6 presents results from a space-for-time substitution (chronosequence) experiment that evaluates the change in abundance of selected beetle species throughout an entire 26-year harvest rotation. Most overseas studies of clearfell harvest impacts have concentrated on short-term impacts, as long-term studies are difficult both logistically and financially. I circumvent the problems associated with a long-term project by comparing the abundance of selected invertebrate taxa in different-aged regenerating stands and adjacent mature stands. The aim is to determine habitat utilisation of these species as stands regenerate. This information can then be incorporated into harvest plans to ensure continuity of required habitat within plantations.

Chapter 7 provides a general synthesis of the results presented in previous chapters, and I discuss their ecological implications and relevance to forest managers. Finally my research is placed within the context of other international research on harvest impacts, fragmentation and the role of the matrix, and I consider future research directions.

Chapter 2 - General methodology

2.1 Introduction

Individual chapters of this thesis are designed to address specific thesis aims and are written as separate units for publication in peer-reviewed journals. As separate units they each have markedly different experimental approaches. Chapter 4 makes comparisons among different habitat types by sampling beetles across gradients running between different landscape elements (Table 2.1). Chapter 5 uses direct experimental manipulation of clearfell harvest size as a powerful method to assess ecological change to environmental perturbation and quantify the impact of clearfell harvest area on biodiversity (Table 2.1). To analyse long-term changes in species abundance with stand age (Chapter 6) I used a space-for-time (chronosequence) approach, sampling beetles in different aged stands and comparing them to adjacent mature forest sites (Table 2.1).

By approaching the thesis as a series of independent chapters there will inevitably be a certain degree of overlap in methods sections. To prevent unnecessary overlap between chapters common sections (field sites, collection of invertebrate samples, and the collection of environmental variables), are described in this chapter.

2.2 Field Sites

2.21 Regional context

The study area is within the Kaingaroa plateau that is part of a region of intensive volcanism known as the Taupo Volcanic Zone (Healy 1963). The geology is defined by a stratigraphic sequence of silicic and basaltic tephra's, and ignimbrite formations (Froggatt and Lowe 1990). The most northern study sites are dominated by the recent basaltic Tarawera tephra (from an eruption in 1886 AD), whilst southern and central sites have a thick mantle of the silicic Taupo tephra (from an eruption about 1850 ± 10 yr BP) (Froggatt and Lowe 1990). The Kaingaroa plateau is predominantly flat with dissecting gullies that were formed as a result of fluvial processes. Plateau dissection is most prominent in the northern Tarawera and Ngamotu forests and has resulted in a complex network of narrow valleys. In many cases these valleys have not been converted to plantation forests and a substantial network of native forest remnants exists. Alluvial areas are present to the west and east of the plateau including the Reporoa lowlands (the location of Broadlands Forest) and the Rangitaiki Plains. This is the result of depositional activity of the Waikato and Rangitaiki rivers, respectively (Healy 1963). The Tarawera eruption has created young soils in the Tarawera, Ngamotu, Matahina and Putuaki forests. These areas are prone to drought due to the poor moisture holding capacity of the coarse unweathered basaltic scoria that dominates the soil profile (Molloy 1988). Kaingaroa forest soils in general are characterised by the influence of pumice tephras from the Taupo eruption, which have a thick compacted C-horizon (Molloy 1988).

The altitude of sites ranged from 100 to 800 metres above mean sea-level, with rainfall throughout the region averaging 1200-1600mm dependent on topography and proximity to the coastline (Quayle 1983). Kaingaroa averages a single winter snowfall (Quayle 1983), however the region never experiences periods of snow accumulation.

Table 2.1. Summary of the experimental design of individual chapters, including replicates and number of pitfall traps: note * denotes traps from the 50 ha clearfell harvest size treatments that are also used in Chapter 5, † denotes comparison also used in the Chapter 4 analysis of comparisons between landscape elements.

Comparison	**Replicates**	**Number of pitfall traps**
Comparison between landscape elements Chapter 4		
P. radiata vs. Clearfell	3	21
P. radiata vs. Pasture	3	21
P. radiata vs. Native	3	21
Native vs. Clearfell	3	21
Native vs. Pasture	3	21
Pasture vs. Clearfell	3	21
Clearfell harvest size Chapter 5		
0.01 ha vs. adjacent *P. radiata*	6	30

0.05 ha vs. adjacent *P. radiata*	6	30
0.5 ha vs. adjacent *P. radiata*	6	36
5 ha vs. adjacent *P. radiata*	6	42
50 ha vs. adjacent *P. radiata*	6	42
500 ha vs. adjacent *P. radiata*	6	48
Comparison between different aged *P. radiata* Chapter 6		
1 yr vs. *P. radiata* †	3	27*
2 yr vs. *P. radiata*†	3	27*
4 yr vs. *P. radiata*†	4	36
8 yr vs. *P. radiata*†	4	36
16 yr vs. *P. radiata*†	4	36
26 yr vs. *P. radiata*†	4	36
Total		582

2.22 Selection of individual sites

Clearfell harvest study sites were located in the managed plantation forests of the central North Island, New Zealand (Figure 2.1). Comparisons were made with other landscape elements including pastoral areas (dairy and beef) adjacent to plantations, several unprotected native forest remnants within the plantations, and a single Department of Conservation managed reserve on the Paeroa Range. Plantation forests sampled included the central and northern regions of Kaingaroa forest, Broadlands forest, Ngamotu forest, Tarawera forest, Matahina forest, Crater forest and Putuaki forest (Figure 2.1). These plantations are dominated by *P. radiata*, which comprises over 90% of the total area. A number of alternative species such as Douglas-fir (*Pseudotsuga menziesii*) are grown in small amounts. All clearfell harvest study sites were within *P. radiata* stands that were surrounded on all sides by other *P. radiata* stands. The location of the central boundary trap was determined by selecting a random number (from a random number table) to represent the number of metres from the edge of the stand boundary. This was constrained by the condition that it was greater than 125 m from the forest stand boundary. Central traps were then located in the field using a hipchain distance measuring device. The New Zealand map-grid coordinates are given for the central trap in each of the 52 pitfall trap lines that were used in the three main experiments (Appendix 2.1).

2.23 Vegetation

The pre-human vegetation of the area was influenced by the intense volcanic activity in the region (Leathwick and Mitchell 1992, Wilmshurst and McGlone 1996). The central and southern Kaingaroa regions were originally dominated by tall lowland-montane conifer broadleaf forests, which were periodically destroyed by rhyolitic eruptions (McGlone 1989). After the colonisation by Polynesians, the vegetation was characterised by a shift to seral species (including *Pteridium esculentum*, *Leptospermum scoparium* and *Dracophylum subulatum* (McQueen 1961)) that were adapted to human initiated episodic burning (McGlone 1989). Northern areas of the Kaingaroa plateau had a slightly different forest composition, described by Nicholls (1991), including the emergent and canopy trees species *Dacrydium cupressinum*, *Metrosideros robusta*, *Beilschmiedia tawa* and *Litsea calicaris*, and a sub-canopy of *Weinmannia racemosa*, *Olearia rani* and *Melicytus ramiflorus*.

Plantation forests of exotic species were first established in New Zealand in the late 1890’s. However, the truly large state funded plantations such as Kaingaroa Forest were initiated during the great planting boom of 1925-1935 and a second planting boom between 1960-1987 (Roche 1990). The majority of Tarawera forest was planted in this second period (60,000 acres) and occurred after land consolidation was permitted by the Tarawera Forests Act 1967 (Roche 1990). Plantation forest establishment has continued throughout the 1990s, but in recent times a recession in the forestry industry (caused by rising costs and an unfavourable New Zealand currency exchange rate) has seen new plantings come to an almost complete standstill since 2005.

2.3 Collection of beetle samples

Resources were insufficient to make an attempt at sampling all invertebrates, or even all insects. As such, it was decided to focus on a particular group. The beetles were chosen because of their high species diversity, breadth of trophic levels, ubiquitous distribution

(Evans et al. 1996), sensitivity to different habitats (Dufrêne and Legendre 1997), and my personal familiarity with their taxonomy, which is well-known compared to most other New Zealand invertebrate groups. All of these are criteria are suggested as characteristics to consider when selecting indicator groups (McGeoch 1998).

Pitfall trapping, like other passive sampling methods, such as Malaise and flight intercept trapping, does not yield a direct measure of abundance, but a measure of insect activity which is sometimes referred to as activity-density (Greenslade 1964, Luff 1975, Halsall and Wratten 1988, Topping and Sunderland 1992, Lang 2000). Passive techniques are subject to inherent bias induced by factors such as the structural complexity of forest floor habitat that can alter the relative capture efficiency at different sites. These disadvantages of pitfall trapping are well known, but it continues to be a standard technique in ecological studies, and has a number of important benefits. Unlike direct measures of sampling insect density, such as litter or turf sampling, the passive nature of pitfall trapping allows the collection of samples over a long period of time, capturing rare species and those that may only be present at specific points in time. Therefore, pitfall trapping still remains the most efficient method for collecting highly mobile ground dwelling species that may spend the day in soil burrows or in refugia, such as beneath logs. Pitfall traps are also relatively easy to establish and maintain, which was a priority given the level of replication involved in this study.

All sampling used a standard pitfall trap design consisting of a circular, 680 ml polypropylene plastic container of 100mm diameter buried to ground level. White plastic guide panels 1.2 m long and 0.10 m high were placed at ground level in a cross-design over the central trap (Figure 2.2). Guide panels were used in an attempt to increase trap catch by channelling ground dwelling arthropods towards the central collecting cup. A 70% monoethylene glycol (antifreeze) solution was used as a preservative and changed at approximately monthly intervals. Samples were subsequently transferred into 70% alcohol for storage prior to analysis. Insects were sorted using a 6-50 × Zeiss stereomicroscope. All pinned material will be lodged with the Ensis entomology collection in Rotorua, however a reference collection is to be held at its Ilam office. The remainder of the unsorted material is stored in alcohol at the Ilam office.

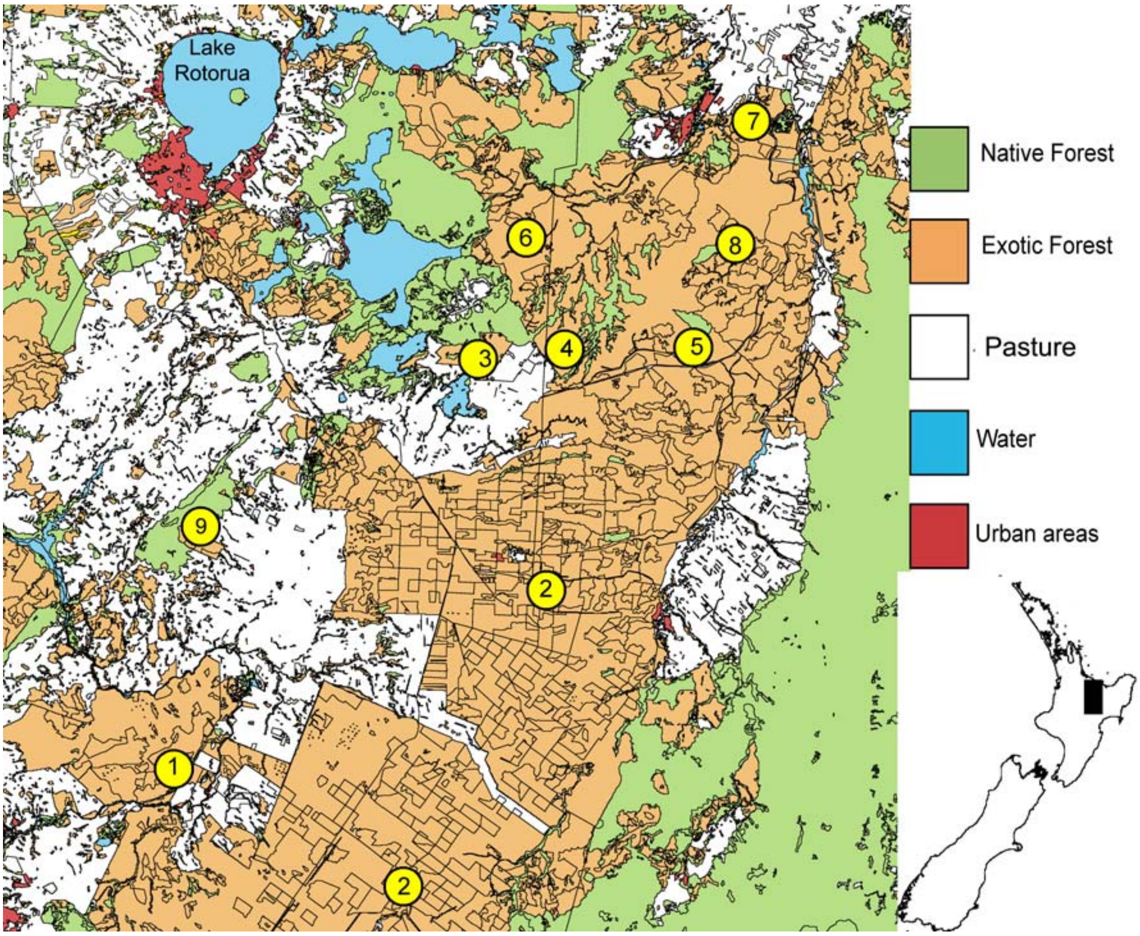

Figure 2.1. Map showing the location of study forests in the context of surrounding land cover in the central North Island of New Zealand. Land cover was defined by the New Zealand land cover database version 2 (LCDB2) (Terralink 2004). Note yellow circles document the rough centre of the major plantation forests and some of the native remnants used as study sites. (1) Broadlands Forest, (2) Kaingaroa Forest both central and northern, (3) Crater Forest, (4) Ngamotu Forest, (5) Matahina Forest, (6) Tarawera Forest, (7) Putuaki Forest, (8) non-protected native remnant owned by forestry company and (9) Paeroa Range – owned by Department of Conservation.

2.4 Collection of environmental variables

Environmental variables were recorded for each pitfall trap to aid interpretation of patterns in beetle abundance. Variables collected included – vegetation, ground cover, canopy cover, LENZ (Land Environments of New Zealand) and spatial attributes (Table 2.2)

Figure 2.2 Pitfall trap design. I am holding the polypropylene plastic container that is buried to ground level beneath the junction of the two white plastic guide panels when the trap is operational. An ice cream container lid (lower corner of photo) is used as a rain cover and is held in place over the guide panels above the plastic container by wire pegs. Photo by Kennedy Warne.

Table 2.2 Description of environmental variables collected and their units of measurement.

Abbreviation	**Description**	**Units**
Vegetation		
Vege 1	Axis 1 from PCO of vegetation composition	PCO Scores
Vege 2	Axis 2 from PCO of vegetation composition	PCO Scores
Vege 3	Axis 3 from PCO of vegetation composition	PCO Scores
500m-nat	Proportion of native vegetation within 500 m radius	Proportion
500m-exo	Proportion of exotic vegetation within 500 m radius	Proportion
1000m-nat	Proportion of native vegetation within 1000 m radius	Proportion
1000m-exo	Proportion of exotic vegetation within 1000 m	Proportion

	radius	
5000m-nat	Proportion of native vegetation within 5000 m radius	Proportion
5000m-exo	Proportion of exotic vegetation within 5000 m radius	Proportion
Ground Cover		
Litter	Qualitative assessment of litter within 2 m of trap	Categorical
Dead wood	Qualitative assessment of dead wood within 2 m of trap	Categorical
Drainage	Qualitative assessment of drainage within 2 m of trap	Categorical
Canopy Cover		
Canopy Cover	Percentage of canopy cover	Percentage
LENZ variables		
Acidp	Acid soluble phosphorous	Categorical
Age	Age of soil	Binary
VPD	Vapour pressure deficit	KPa
Tmin	Mean minimum temperature of coldest month	ºC
Slope	Slope defined from 25 m digital elevation model	Degrees
Chemlims	Chemical limitations to plant growth	Categorical
Calcium	Exchangeable calcium	Categorical
Drainage	Description of soil internal drainage	Categorical
R2pet	Water balance ratio	Ratio of rainfall to evaporation
Psize	Soil particle size	Mm
Mat	Mean annual temperature	°C
Mas	Annual solar radiation	MJ/M^2/day
Junes	Winter solar radiation	MJ/M^2/day
Induration	Soil parent material hardness	Discrete classes
Deficit	Annual water deficit	mm
Lenz_layer 4	Lenz_layer4 dummy variable	Binary

Lenz_layer 3	Lenz_layer3 dummy variable	Binary
Lenz_layer 2	Lenz_layer2 dummy variable	Binary
Lenz_layer 1	Lenz_layer1 dummy variable	Binary
Spatial Attributes		
Long	Longitude	NZ map grid
Lat	Latitude	NZ map grid
Lat^2	$Latitude^2$	NZ map grid
$Long^2$	Longitude	NZ map grid
Lat^2*Long	$Latitude^2 * Longitude$	NZ map grid
$Long^2*Lat$	$Longitude^2 * Latitude$	NZ map grid
$Long^2* Lat^2$	$Longitude^2 * Latitude^2$	NZ map grid
$Long^3$	$Longitude^3$	NZ map grid
Lat^3	$Latitude^2$	NZ map grid

2.41 Vegetation

Vegetation surveys were conducted between 4 - 12 April 2003 for the 2003 harvest replicates and from 21 - 25 April 2004 for 2004 replicates. Surveys were conducted within a 2.5 × 2.5 m quadrat centred on the pitfall trap. Individual plant species were quantified in four layers to incorporate information on spatial structuring (ground: 0.0 – 0.3 m, shrub: 0.3 m – 2 m, sub canopy: 2.0 - 10 m and canopy: >10 m). Shrubs and trees were identified to species and samples of plants that could not be identified in the field were taken for subsequent expert identification at the Ensis herbarium. Identified species were assigned to one of seven abundance classes that correspond to a percentage vegetation cover (Table 2.3). Vegetation data for each species were then converted to a single value for analysis using the following formula (D. Norton pers. comm.):

$$\text{Vegetation cover} = \sum_{N-tiers}^{i=1} \text{midpoint of \% cover} * \log_{10}(\text{tier depth} + 1)$$

Tier depths varied depending on forest type and *P. radiata* stand age (Table 2.4). Single importance values were ln(x+1) transformed and a principal coordinate analysis was conducted on the basis of Bray-Curtis dissimilarities using the Fortran program, PCO

(Anderson 2003b). The resulting principal coordinate axes scores were then used as environmental correlates (variables Vege1, Vege2 and Vege3) in ordination analyses of beetle abundance data.

Table 2.3. Abundance and cover classes used to quantify the percentage vegetation cover at different tier heights.

Abundance	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Cover Class	<1%	1-5%	6-10%	11-25%	26-50%	51-75%	76-100%

Table 2.4. Vegetation height tiers used to obtain single importance values.

Height (metres)	**Mature Pine**	**Native**	**4yr Pine**	**8yr Pine**	**16yr Pine**
Canopy	15	10	0	2	8
Sub-canopy	8	4	8	8	8
Shrub	2	2	2	2	2
Ground	0.3	0.3	0.3	0.3	0.3

The proportion of native and exotic plantation forests within a 500, 1000 and 5000 m radius of each study site was calculated using data from the Land Cover Database V2 (LCDB2) (Terralink 2004). These variables (500m-nat, 500m-exo, 1000m-nat, 1000m-exo, 5000m-nat and 5000m-exo) were then included as explanatory variables in multivariate ordination analyses.

2.42 Ground surface characteristics

Estimates of the percentage leaf litter cover, drainage and the quantity of deadwood were calculated on the basis of a 5-tier scale at the same time as understorey vegetation measurements were recorded (Table 2.5). Given the qualitative nature of these assessments all scoring was done by a single observer to reduce potential bias. These measurements were then incorporated as categorical binary variables into subsequent ordination analyses, i.e., a binary variable was created for each of n-1 levels of each ground surface factor (Table 2.5).

Table 2.5. Scoring system to provide a qualitative measurement of the amount of deadwood, drainage and litter surrounding each pitfall trap.

Score	**Dead-wood**	**Drainage**	**Litter**
1	None or very little deadwood (at most a few twigs)	Poor drainage (surface water present within the plot even during prolonged dry spells)	Little or no litter cover (< 5 % cover)
2	Intermediate, low - med	Intermediate, low - med	Intermediate, low – med
3	Medium amount of deadwood (at least one log > 10 cm diameter)	Medium drainage (at least one place within the plot that "squelches" when walked on)	Medium amount of litter (30-50 % cover of litter)
4	Intermediate med - high	Intermediate med - high	Intermediate med - high
5	Much deadwood (plot is difficult to move in due to the amount of deadwood)	Well-drained (no surface water even during prolonged rain)	Abundant litter (70% or more of the plot is covered in thick litter)

2.42 Canopy cover

Canopy cover was estimated as a percentage from hemispherical photographs analysed using Hemiview version 2.1. The hemispherical lens captures a 180-degree field of view and an adjustment was necessary to ensure that canopy cover was only calculated on the basis of a 90-degree arc directly above the pitfall trap, i.e., between 45-135^o of horizontal. Photographs were taken at ground level and the proportion of the circular photo selected for analysis was calculated as:

Radius of the portion of the hemispherical image to be analysed = radius of the photograph/sqrt2. Note: contrast was altered manually to account for differential light conditions between photographs.

2.43 LENZ variables (covariables for ordination analyses)

LENZ is a New Zealand wide classification of landscapes based on a comprehensive set of climate (7), landform (1) and soil variables (7) (Leathwick et al. 2003). LENZ variables for each site were obtained by creating a spatial join in ArcView between pitfall trap locations and each of the fifteen underlying LENZ data layers (Table 2.2). The resolution of LENZ data (c.1 ha) was insufficient to distinguish between individual pitfall traps so the entire transect is represented by a single value for the location of the central boundary trap. Individual landscape-level LENZ attributes were incorporated into composite variables by the use of principal components analysis (PCA) conducted in Canoco Version 4.02 (see Gates and Donald (2000)). LENZ attributes were not transformed, scaling was focussed on inter-sample distances and there was no centering or standardisation of samples. The first three axis scores were then incorporated as environmental variables (PCA1, PCA2 and PCA3) in ordination analyses of beetle data.

2.5 Conclusion

A total of 582 pitfall traps were used across all three main studies. Experimental designs made use of both the experimental manipulation of treatments and a mensurative (space-for-time) approach to data collection. A total of 35 environmental variables were collected to describe conditions surrounding trap locations and provide possible explanations of the observed beetle abundances. Individual methods sections that provide chapter-specific information should be used in consultation with the overall methods presented here to provide a comprehensive explanation of the techniques used to conduct experiments in this thesis.

Appendix 2.1. New Zealand map-grid location and plantation forest compartment (where particular treatment included a plantation forest component) for each study site. The geographic location given marks the central boundary (0m) trap from the pitfall trap gradient.

Comparison	**Forest Compartment (where applicable)**	**NZ-map-grid East**	**NZ-map-grid North**
Habitat Comparisons			
P. radiata vs Pasture	Goudies	2823620	6313960
P. radiata vs Pasture	Kaingaroa 1053	2813740	6299500
P. radiata vs Pasture	Kaingaroa 1054	2814490	6299440
P. radiata vs Clearfell	Kaingaroa 153	2816580	6285750
P. radiata vs Clearfell	Kaingaroa 240	2805440	6287760
P. radiata vs Clearfell	Kaingaroa 391	2819440	6280170
P. radiata vs Native Forest	Matahina 205	2834330	6323860
P. radiata vs Native Forest	Tarawera 94	2829410	6328990
P. radiata vs Native Forest	Tarawera 115	2838400	6330540
Clearfell vs Native Forest	Matahina 378	2835540	6324110
Clearfell vs Native Forest	Tarawera 155	2831450	6325540
Clearfell vs Native Forest	Tarawera 132	2821690	6323200
Clearfell vs Pasture	Kaingaroa 902	2814070	6296440
Clearfell vs Pasture	Kaingaroa 340	2811570	6311900
Clearfell vs Pasture	Kaingaroa 210	2808600	6315150
Native Forest vs Pasture		2796010	6306510
Native Forest vs Pasture		2821440	6321370
Native Forest vs Pasture		2822010	6321530
Clearfell harvest size			
0.01 ha	Kaingaroa 278	2808260	6278120
0.01 ha	Kaingaroa 1080	2815890	6300830
0.01 ha	Kaingaroa 1105	2819910	6308150
0.05 ha	Kaingaroa 278	2808450	6278220
0.05 ha	Kaingaroa 1080	2816440	6300840
0.05 ha	Kaingaroa 1105	2820240	6307570
0.5 ha	Kaingaroa 278	2808310	6278320
0.5 ha	Kaingaroa 1080	2817120	6300730

0.5 ha	Kaingaroa 1105	2820650	6308150
5 ha	Broadlands 3	2797390	6287570
5 ha	Kaingaroa 179	2812390	6284140
5 ha	Not sampled		
50 ha	Kaingaroa 153	2816580	6285750
50 ha	Kaingaroa 240	2805440	6287760
50 ha	Kaingaroa 391	2819440	6280170
200-500 ha	Kaingaroa 132	2822910	6324080
200-500 ha	Putuaki 191/192	2839320	6339330
200-500 ha	Matahina 205	2833350	6324250
Different aged stands			
P. radiata vs 4 yr	Kaingaroa 1028/1029	2812380	6300410
P. radiata vs 4 yr	Kaingaroa 1035	2812620	6306270
P. radiata vs 4 yr	Kaingaroa 1046/1061	2814720	6306150
P. radiata vs 4 yr	Kaingaroa 88	2817590	6295850
P. radiata vs 8 yr	Kaingaroa 185	2815630	6280440
P. radiata vs 8 yr	Kaingaroa 375	2819580	6283830
P. radiata vs 8 yr	Kaingaroa 46	2823180	6296440
P. radiata vs 8 yr	Kaingaroa 213	2808090	6292570
P. radiata vs 16 yr	Kaingaroa 224	2807490	6290720
P. radiata vs 16 yr	Kaingaroa 230	2807930	6289270
P. radiata vs 16 yr	Kaingaroa 233	2806370	6289150
P. radiata vs 16 yr	Kaingaroa 1068	2817260	6310740
P. radiata vs *P. radiata*	Kaingaroa 231	2808960	6288530
P. radiata vs *P. radiata*	Kaingaroa 377	2821490	6282440
P. radiata vs *P. radiata*	Kaingaroa 382	2820140	6281860
P. radiata vs *P. radiata*	Kaingaroa 1157	2825630	6301600

Chapter 3 - Clearfell harvest impacts on biodiversity: Past research and the search for harvest size thresholds

This chapter has been accepted in its present form (with the addition of an abstract) for publication in the *Canadian Journal of Forest Research*.

3.1 Introduction

As natural ecosystems are becoming increasingly degraded in many parts of the world, conservation of terrestrial biodiversity must increasingly look to production landscapes to achieve conservation goals (Knight 1999, Norton 2000, Novacek and Cleland 2001, Ewers et al. In Press). Managed natural or planted forests represent one type of production landscape that makes a significant contribution to biodiversity at both local and regional scales (Spellerberg and Sawyer 1995, Chey et al. 1997, Moore and Allen 1999, Brockerhoff et al. 2001, Hartley 2002). Plantations are known to provide alternative habitat for native species, improve connectivity between old-growth remnants, and buffer natural forests from edge effects, particularly in heavily-modified landscapes where there is little unmodified forest habitat left. These biodiversity benefits remained largely unpublicised, whilst forest management practices often face heavy public criticism.

Environmental issues associated with forestry are controversial, particularly the extensive even-aged monocultural plantations (especially of exotic tree species) and the large-scale clearfell harvesting that is typical of plantations and of many managed natural forests. It is indisputable that clearfelling results in substantial immediate on-site changes to the community structure and functional attributes of terrestrial ecosystems (Niemela et al. 1993, De Grandpre et al. 2000, Wardell-Johnson and Williams 2000, Roberts and Zhu 2002), their aquatic components (Rishel et al. 1982, Rowe and Taylor 1994, Stott and Marks 2000, Bubb and Croton 2002) and the aesthetic appeal of the landscape (McGee 1970, Hansis 1995). However, deep-seated underlying social values (which are difficult to influence and vary spatially) are used by people to interpret the visual changes associated with forest harvesting and are a strong determinant of the acceptability of such practices (McCool et al. 1986, Bliss 2000).

Condemnation of clearfell harvesting, especially by environmental non-government organisations (ENGOs), has been a significant driving force in forest policy (Schindler et al. 1993, Potton 1994, Rosoman 1994, Ribe and Robert 1999, Wilson and Wilson 2001). The acceptability of large-scale high impact clearfell harvesting is now reduced and in some countries restricted by voluntary mechanisms (industry led agreements, such as the New Zealand Forest Accord 1991 and forest certification schemes, such as the Forest Stewardship Council) or by legislation (e.g., the Forest Regeneration & Clearcutting Standards, Maine, USA 1999). These restrictions are partially responsible for the increased implementation of alternative silvicultural systems over the last 20 years, including shelterwood, green-tree retention methods and patch cuts. Numerous trials have assessed some of the impacts of these alternative harvesting techniques and these have often included comparisons with clearfelling (Schowalter 1995, North et al. 1996, Volin and Buongiorno 1996, Franklin et al. 1997, Prescott 1997, Beese and Arnott 1999, Beese and Bryant 1999, Bohonak 1999, Perry et al. 1999, Bartman et al. 2001, Duguay et al. 2001, Moorman and Guynn 2001, Huggard and Vyse 2002, Koivula 2002a, Knapp et al. 2003). However, as Koivula (2002b) and Spence (2001) point out, the full ecological consequences and long-term ecological sustainability of these alternative strategies are still not fully understood.

Given that clearfell harvesting has met with such strong opposition, it is surprising that few studies have investigated whether a reduction in the harvest area of individual clearfells might be a viable strategy to mitigate ecological impacts. After all, some forest policies around the world restrict clearfelling by prescribing maximum size cuts. One of the assumptions underlying these policies is that there is a threshold size above which ecological change occurs at a rate that is socially and environmentally unacceptable. The concept of ecological thresholds has been used in habitat fragmentation studies for some years (Andren 1994) and more recently in ecological restoration (Hobbs and Norton 1996). Thresholds have also found favour with land managers and territorial authorities as a mechanism for regulating land management policies (Huggett 2005). However, empirical evidence on which to base such policies is limited and individual studies are often contradictory (Lindenmayer and Luck 2005). As yet no one has experimentally tested forest harvest size thresholds. What limited work that has been conducted on clearfell size effects, at least at small spatial scales, was summarised by Bradshaw (1992), while a more extensive study in British Columbia is still in progress (Vyse 1999). In many ways it appears that the combined pressure of ENGOs and public opinion have circumvented research on the issue of clearfell harvest size impacts and most studies have focussed on evaluating alternative silvicultural systems instead.

In this paper I begin by providing a brief overview of the on-site ecological changes induced by clearfelling in the context of plantations (including those of exotic species) and managed indigenous forests. I then review the few available studies on clearfell harvest size influences and its impact on ecological change. This information is then combined to evaluate the possibility of a harvest size threshold at which ecological change occurs at a rate disproportionate to the change in harvest area. Different potential forms of this relationship are discussed in the context of recent ecological threshold studies in related disciplines of landscape ecology, with suggestions for designing empirical studies to test for threshold effects. The overall goal of this paper is to provide an increased understanding of the ecological consequences of harvest size in relation to large-scale clearfelling.

3.2 Impacts of clearfelling

3.21 Abiotic

The forest microclimate is strongly influenced by changes in overstorey canopy structure and is thus temporally and spatially variable (Chen et al. 1999). Harvesting practices such as clearfelling alter canopy structure and hence impact on the microclimate of forest stands (Chen et al. 1999, Burton 2002). Temperature, relative humidity, wind speed and solar radiation are significantly more variable (both spatially and temporally) in clearfelled areas compared to intact forest due to the removal of the buffering effect of the forest canopy (Chen et al. 1999, Zheng et al. 2000, Burton 2002, Spittlehouse et al. 2004) (Table 3.1). Furthermore, at forest boundaries steep edge-effect gradients can occur between stands due to their different microclimates (Chen et al. 1999).

Edge effects have received considerable attention recently by conservation biologists examining their effect on indigenous biodiversity (Murcia 1995, Didham et al. 1998, Laurance 2000, Ries et al. 2004). However, forest types differ in their vegetation structure and rates of secondary succession following disturbance (Brockerhoff et al. 2003). As a result the persistence and penetration of microclimatic edge effects, which are dependent on the rates of vegetative regrowth, will vary with biogeographic region, for example tropical forest edges rapidly produce an edge understorey that buffers the microclimate within the remaining forest (Didham and Lawton 1999).

Land-use change and forest harvesting have considerable impacts on rates of snow accumulation and melt (Hudson 2000, Murray and Buttle 2003) and thus the local water balance. In high latitude forests snowmelt is a significant part of the annual water balance. Snow accumulation is often higher in harvest areas compared to intact forest, especially in small-to medium-sized harvest areas and to a lesser extent in large clearings, as snow is blown away from large clearfells into adjacent forest (Hudson 2000, Murray and Buttle 2003) (Table 3.1). However, the difference between clearfell and forest snow accumulation is greater in coniferous than hardwood forests due to the more open hardwood canopy allowing increased snow penetration (Murray and Buttle 2003). Snowmelt is greater in clearfell areas than forests under radiant melt conditions (Adams et al. 1998, Huggard and Vyse 2002). However, the difference in snow ablation between forest and clearfells, caused by rain falling on snow, is dependent on canopy snow loading (Beaudry, et al., 1997, cited in Hudson, 2000). Irrespective of clearfell harvesting or canopy cover, the spatial variation in snowmelt rates is most strongly influenced by geographical aspect, i.e., north vs south facing slopes (Murray and Buttle 2003).

In warmer climates the influence of tall vegetation (e.g., trees) on dry and wet leaf evaporation will be more important in determining catchment water yield (see recent review by Davies & Fahey, (2005)). Reduction in tall vegetation within catchments has been shown to increase stream flow (Bosch and Hewlett 1982) and create a temporary rise in stream temperature due to an increase in solar radiation on the water surface (Rishel et al. 1982, Rowe and Taylor 1994, Stott and Marks 2000, Kiffney et al. 2003), unless appropriate riparian management is undertaken (Young, 2000). However, preliminary data suggests that flow rates return to pre-harvest levels as regeneration proceeds (Bubb and Croton 2002) (Table 3.1). There are also significant regional differences in the change in water yield in response to afforestation and forest harvesting (Rowe 2003). In addition to altered evaporation, the decrease in litter and coarse woody debris (especially from site preparation, e.g., wind-rowing) can reduce rainfall infiltration rates, further increasing overland flow (France 1997, Costantini and Loch 2002).

Increased overland flow increases soil erosion, however clearfelling is not necessarily as damaging in this regard as other harvesting techniques. For example, group selection was shown by Hood (2002) to erode 25.1 t/ha more soil per 100-year rotation than clearfell harvesting. This is probably induced by the increase in temporary roads required for group selection harvesting. Sedimentation rates in stream channels can increase as a result of this enhanced erosion (France 1997) and affect surface communities as well as deeper streambed fauna (Trayler and Davis 1998). A buffer strip along a waterway is the management response designed to prevent increased sedimentation (Young 2000), however insufficient testing has been done at a catchment scale of commonly utilised buffer strip widths, some of which may prove to be inadequate (Kiffney et al. 2003).

Table 3.1 Summary of the known ecological changes in species abundance, richness and composition of different taxonomic groups and abiotic changes induced by clearfell harvesting. Change is recorded as positive (+), negative (-) or variable (-/+).

Response Variable	**Abiotic factor/taxon**	**Impact**	**Important points**	**Reference**
Abiotic Factors	Microclimate	-/+	Temperature, relative humidity, light and windspeed become more variable post-harvest.	(Chen et al. 1995, Zheng et al. 2000, Spittlehouse et al. 2004)
	Snowmelt, accumulation and ablation	-/+	Increased snow in harvested areas and increased rates of snow melt post-harvest compared to intact forest.	(Hudson 2000, Murray and Buttle 2003)
	Stream flows/hydrology	+	Stream flows increase post-harvest.	(Bosch and Hewlett 1982, Bubb and Croton 2002)
	Stream temperature	-/+	Stream temperature generally increases, however extent dependent on riparian buffer management strategies.	(Rishel et al. 1982, Rowe and Taylor 1994, Stott and Marks 2000, Young 2000)
	Soil loss due to erosion	+	Soil loss and stream sedimentation can increase post-harvest.	(France 1997)

Species abundance	Bats	-/+	Species specific, dependent on body size and foraging strategy.	(Patriquin and Barclay 2003)
	Spiders	-/+	Species specific, most impact on web-builders.	(Coyle 1981)
	Salamanders	-	Harvest impacts just as severe in leave tree, group selection or shelterwood.	(Knapp et al. 2003)
	Birds	-	Abundance still reduced for one third of all species after 14 years.	(Williams et al. 2001)
	Nematodes	-	Clearfell impact as severe as in shelterwood treatments	(Panesar et al. 2000)
	Stream macro-invertebrates	-	Returned to normal after spring rain, affected by increased sediment load associated with harvesting.	(Growns and Davis 1994)
	Plants	-	Decreased herbaceous layer cover.	(Gilliam 2002)
Species richness	Carabidae	+	Increased open habitat species in many cases led to increased overall species richness.	(Atlegrim et al. 1997, Beaudry et al. 1997, Heliola et al. 2001)
	Stream macro-invertebrates	-	Returned to normal after spring rain, affected by increased sediment load associated with harvesting. Dependent on depth in stream sediment	(Growns and Davis 1994, Trayler and Davis 1998)
	Lucanidae	+	Some species may not survive in long-term in clearfell areas and require old-growth conditions.	(Michaels and Bornemissza 1999)
Species composition	Birds	+	Some species did decline in abundance.	(Baker and Lacki 1997)
	Spiders	-/+	Different response from visual pursuit, micro-web and trap door spiders.	(McIver et al. 1992)
	Ectomycorrhizae	-/+	Driven by changes to soil biology and chemistry.	(Hagerman et al. 1999, Jones et al. 2003)
	Beetles	-/+	Changes between forest generalist and open habitat species.	(Niemela et al. 1993)

Plants	-/+	Changes in abundance of shade tolerant and open habitat species.	(De Grandpre et al. 2000)
Small mammals	-/+	Change in fauna in open habitat areas.	(Hansson 1994)

3.22 Clearfell harvest impacts on the biotic environment

The change in composition of biotic communities as a result of clearfell harvesting has been well studied. Despite this there is a paucity of information on some groups, particularly invertebrates, herbaceous vegetation and fungal communities, all of which provide important ecosystem services. Table 3.1 gives an overview of some research findings with respect to the impact of clearfelling on species richness, abundance and composition of different taxa.

Plants

Harvesting releases resources otherwise monopolised by the mature canopy species, allowing opportunities for surviving understorey plants and new colonisers originating from the soil seed bank and seed rain (Burton 2002). As a result of rapid colonisation by open-habitat specialists, plant species richness is usually greatest in the first few years following clearfelling (Freedman et al. 1994, De Grandpre et al. 2000, Burton 2002, Roberts and Zhu 2002) (Table 3.1). However, in many countries the presence of large numbers of exotic invasive species may significantly alter these regeneration patterns. For example, in New Zealand’s exotic plantation forests the dominant colonising grasses, herbs and shrubs following clearfelling are adventive, although some indigenous species present in the understorey prior to felling commonly re-sprout (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003).

Invertebrates

Most studies of the change in invertebrate community assemblage post-clearfelling have utilised single taxonomic groups, often ground beetles in the family Carabidae (Coleoptera). Unfortunately, these studies are often undertaken with little or no robust statistical justification as to the suitability of the chosen indicator species, citing abundance, sensitivity to environmental change, taxonomic and ecological knowledge, and ease of carabid sampling as justification for their use (Koivula 2002a, Magura 2002, Brouat et al. 2004).

Previous studies have shown that clearfelling results in the loss of some insect species, but just like plant communities there is often an increase in species richness associated with colonisation by open-habitat specialists, e.g., beetles (Lenski 1982, Niemela et al. 1993, Butterfield et al. 1995, Spence et al. 1996, Beaudry et al. 1997, Niemela 1997, Fahy and Gormally 1998, Ings and Hartley 1999, Heliola et al. 2001) and ground hunting spiders (Coyle 1981, McIver et al. 1992) (Table 3.1). The influx of open-habitat specialists is a transitory phenomenon, but in some Canadian and Finish managed indigenous forests species richness did not peak until approximately 10 years after harvest (Niemela 1997) and in some cases open-habitat species were still present after 27 years of stand regeneration (Spence et al. 1996). As such, the ecological impacts of these open-habitat species on forest specialist species may be of significance for very long time-periods, although this has not been tested in New Zealand.

Birds

Forest canopy structure determines the availability of nesting and foraging resources for birds (Williams et al. 2001), and therefore influences the species richness and composition of resident bird communities (Clout and Gaze 1984, Wardell-Johnson and Williams 2000). Clearfell harvesting typically creates large, even-aged, homogeneous stands with reduced resource diversity that has been shown to limit bird abundance and species richness (Beese and Bryant 1999, Moore and Allen 1999, King and DeGraaf 2000, Wardell-Johnson and Williams 2000, Williams et al. 2001). However, it is the concomitant change in species composition (Clout and Gaze 1984, Hansson 1994) that is probably of greater importance. Large-scale, even-aged forests tend to favour open-habitat and generalist bird species post-harvest. As such it is unsurprising that recent clearfells and young forests are dominated by early successional transient species and, in some countries, mainly exotic species (Clout and Gaze 1984, Hansson 1994, Wardell-Johnson and Williams 2000), while older regenerating and mature forests have higher proportions of forest generalist and old-growth bird species (Clout and Gaze 1984, Wardell-Johnson and Williams 2000).

Across all taxonomic groups there is concern that old-growth species in general may be lost from short rotation clearfell harvest systems due to a lack of suitable habitat, poor dispersal abilities and/or a lack of source populations (Clout 1984, Clout and Gaze 1984, Niemela et al. 1993, Spence et al. 1996, Wardell-Johnson and Williams 2000). However, conflicting evidence does exist, such as forest specialist carabid beetles that have colonised newly established plantation forests in the UK, despite a lack of obvious source populations in the immediate vicinity (Jukes et al. 2001). Similarly, a rare carabid beetle *Holcaspis brevicula* is only known from an isolated exotic pine plantation on the Canterbury Plains (New Zealand), an area retaining less than 1% of the original native forest and scrub communities (Brockerhoff et al. 2005). This indicates that some forest-specialist and rare species have sufficient dispersal capabilities and tolerance of disturbance to maintain populations in newly-established, and repeatedly clearfelled forests.. Whether these species represent exceptions from a general trend needs further investigation, as dispersal abilities are a key attribute to overcoming impacts of larger clearfells.

3.3 The impact of clearfell harvest size

Few published studies exist on the functional relationship between clearfell harvest size and the degree of ecological change at spatial scales relevant to current forestry practices. As such it is difficult to determine if there is a threshold clearfell size beyond which there is a disproportionate increase in ecological change with increasing harvest area. Indeed, few studies have even sampled different sized harvest areas, and most of these have focussed on gap-regeneration ecology at sizes of less than 1 ha (Figure 3.1). These studies concentrated largely on tree regeneration rates, but in some cases measured biodiversity attributes, including bird diversity (Moorman and Guynn 2001). However, there continues to be a lack of comparative sampling or experimentation over larger harvest areas, making it difficult to gauge the nature of the relationship between harvest area and ecological impact.

3.3.1 Plants

Phillips and Shure (1990) reported significantly greater vegetative re-growth in 2-10 ha clearfells (one year after clearfelling) compared with smaller 0.016 ha clearfells in the Southern Appalachians. By contrast, Moorman and Guynn (2001) failed to find similar vegetative trends in canopy gaps of the same size in bottomland hardwood forests of the Upper Coastal Plain of South Carolina. In Phillips and Shure's (1990) case, the increase in vegetative growth was a reflection of more prolific stump-sprouting in large clearfelled areas and was attributed mainly to increased solar radiation induced by larger-scale canopy removal. Coates (2000) in a study of commercial tree species showed that plant growth rates increased with harvest area up to 0.2 ha, yet growth rates increased little between 0.2 ha and 0.5 ha. This is probably attributable to edge effects limiting solar radiation in forest gaps up to one tree height in radius (Spittlehouse et al. 2004). In contrast York *et al.* (2003) extended the spatial scale of the study up to 1 ha gaps, and found that growth rates were still increasing at this maximum gap size. The lack of consensus between studies illustrates that further research is required, particularly at larger spatial scales.

Indirect evidence of clearfell size impacts suggests that even relatively large clearfells (100-120 ha) in plantation forests in New Zealand are recolonised by some indigenous forest plant species during a single rotation (ca. 27 years) (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003). However, the ability to colonise such large clearfells will be influenced by the relative dispersal abilities of different species, characteristics of the available seed bank and the proximity and size of source populations. The combination of dispersal ability and rotation length has significant implications for the recolonisation of clearfells of different sizes and requires further investigation.

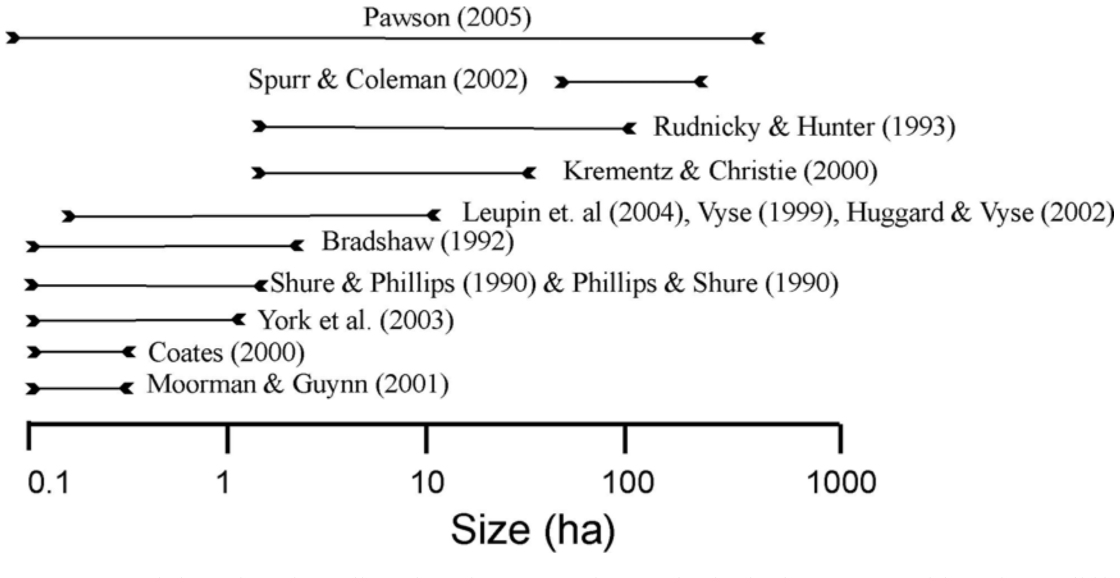

Figure 3.1. Spatial scale of studies that focus on the ecological changes resulting from different clearfell harvest sizes. Note that the scale is logarithmic.

3.3.2 Birds

Early successional bird species are currently in decline throughout parts of the United States (Krementz and Christie 2000). This may in part be a function of their populations being unnaturally high after centuries of habitat loss that created early successional habitat that is now being allowed to regenerate. Nonetheless clearfells provide important recently disturbed habitat for these species and manipulation of harvest practices has been suggested as a way of managing them in modified landscapes. Krementz and Christie (2000) found no decrease in reproductive effort, relative abundance or species richness of early successional bird species with increasing harvest area (2 – 57 ha) in a *Pinus palustris* forest in South Carolina. However, this is not surprising as early successional species might be expected to benefit from such harvesting practices. Other studies of entire bird communities have yet to show consistent changes in species richness per plot over different clearfell sizes. For example Leupin et al. (2004) observed no consistent changes in species abundances following clearfelling in smaller harvest areas (<0.01 - 10ha). Moorman & Guynn (2001) showed an increase in species richness with increasing harvest area from 0.06 – 0.5 ha, and Rudnicky and Hunter (1993) found similar results at slightly larger spatial scales up to 20 ha. At even larger spatial scales (48 - 132 ha and 218 - 240 ha), Spurr & Coleman (2002) found no difference in the species richness of birds as a result of clearfell harvest size.

Overall, it appears from the available evidence that clearfell harvest size has few (detectable) negative effects on the species richness of bird communities over the range of clearfell sizes and ages tested. Even Rudnicky and Hunter (1993) who found the most compelling evidence for an effect of harvest area recognised that clearfell size was not the most important factor for most bird species utilising managed forests. Clearfell size may have profound impacts on subsequent recolonisation by forest species as larger clearfells may impose greater constraints on individuals displaced by harvesting, however this is yet to be tested.

3.3.3 Insects

Both species richness and relative abundances of arthropods were similar across all clearfell sizes (0.016 - 10 ha) at the beginning of the season in Shure and Phillips' (1991) study in the Southern Appalachian Mountains. Later, during the growing season, abundance and species richness in the small and large clearfelled areas approximately doubled, but remained unchanged in mid-sized (0.08-0.4 ha) clearings. High arthropod diversity in the small and large openings was attributed to a confounding variable (greater vegetation cover), which supplied food and protection from the adverse microclimatic changes associated with clearfelling (Shure and Phillips 1991). Most importantly, different groups of arthropods responded differently to variation in clearfell size in two independent studies (Shure and Phillips 1991, Huggard and Vyse 2002). Millipedes, spiders, beetles and ice crawlers (Grylloblattoidea) decreased in abundance with clearfell size, whilst slugs and Homoptera tended to increase in abundance with increasing clearfell size (Shure and Phillips 1991, Huggard and Vyse 2002). Meanwhile, some spiders and ants exhibited non-linear responses and had decreased abundance in mid-sized clearfell areas (Shure and Phillips 1991).

3.4 Reference points for testing clearfell harvest impacts

The majority of studies of ecological change with respect to clearfell harvest size described above have utilised comparisons among clearfells, rather than against a fixed reference point, such as unharvested interior forest. However, a few studies have made direct comparisons, including Leupin et al. (2004) who compared bird abundance in different harvest sizes with a control forest and individual tree selection (30 % tree removal) and found that Golden-Crown Ringlet (*Regulus satrapa*) abundance decreased significantly in all harvest areas compared to control stands, whereas both individual tree selection systems and 10 ha clearfell harvest treatments had lower abundance than smaller 1 ha clearfells. Pawson et al. (2005) in a comparison between different clearfell sizes and uncut adjacent stands of *Pinus radiata* showed that *Pycnomerus sophorae* (Coleoptera: Zopheridae) had greater abundance in small 0.05 ha clearfells compared to uncut adjacent forest, but lower abundance than the reference stand in larger clearfell areas. The use of reference points as a baseline for comparison is critical to the interpretation of harvest impacts.

Perhaps because of the perception that clearfell harvest sizes might have to be very small to remain essentially unchanged from the ecological conditions in uncut forests, there has been a growing interest in legacy management techniques, e.g., variable retention harvest as a method for reducing the severity of ecological change of even-aged forest management (Mitchell and Beese 2002). However, it is only recently that studies such as Mazurek and Zielinski (2004) and Bebber et al. (2005) have provided direct evidence for the value of legacy management as a method of improving biodiversity conservation in even-aged harvesting systems. In this context, a comparison of clearfell harvest areas to uncut forest, with and without legacy management, would be particularly instructive. For example, does legacy management protect conservation values across the entire spectrum of clearfell sizes, or does the importance of legacy management change with increasing harvest area. Most importantly in all such comparative studies between clearfelling and uncut-forest, or alternative harvesting systems, there is a need to sample across a wide range of taxa and ecological processes to ensure that ecosystem-level responses are measured, rather than individual taxon responses that may not be representative of the majority of species.

Given the intense interest in the hypothesis that clearfell harvest areas may mimic natural disturbance processes, other potentially important reference points to consider include open-habitat created by natural disturbance processes, such as wind throws or catastrophic wildfires. The ecological similarity of clearfells and natural disturbances comparison, including the effects of post-harvest treatments, has been the subject of many studies (Gluck and Rempel 1996, Quine et al. 1999, Carignan et al. 2000, Lindenmayer and McCarthy 2002, Baker et al. 2004, Simon and Schwab 2005) and the issue remains contentious. As part of this debate consideration should be given to the fact that any similarity between clearfell harvesting and the results of natural disturbance processes may change with harvest area, a point yet to be studied in detail.

3.5 The search for thresholds

The key focus of future research, and the concept of greatest interest to land managers, is the potential existence of a threshold clearfell size, beyond which induced ecological change increases disproportionately to the linear increase in harvest area. The notion of ecological thresholds or discontinuities in response is not new (Muradian 2001, Huggett 2005), but it is only relatively recently that there has been a major focus on the theoretical and empirical importance of ecological thresholds. For example, in the extensive habitat fragmentation literature there is accumulating evidence of ecological thresholds in remaining habitat cover, below which there is a non-linear decrease in population persistence in habitat fragments (Andren 1994, Fahrig 2001). However, recent empirical studies highlight inconsistencies in the location (or existence) of ecological thresholds across species and sites (Drinnan 2005, Lindenmayer et al. 2005, Radford et al. 2005), and Muradian (2001) and Huggett (2005) raise caution about the limited predictive abilities of such empirical threshold estimates. Despite this, the concept of ecological thresholds has found great utility with territorial authorities to manage land for conservation purposes, particularly in Australia (Huggett 2005).

So what is the range of likely responses of ecological communities to clearfell harvesting (Figure 3.2)?

- Harvest impacts may follow the null hypothesis of no change in biodiversity and ecosystem function after harvesting (curve I in Figure 3.2a), although this is unlikely for the majority of response variables given the known changes in abiotic and biotic factors discussed earlier.
- Responses may be linear in that ecological change is proportional to harvest size (curve II in Figure 3.2a), i.e., there is no critical breakpoint or threshold in the system.
- A third possibility is that there is a threshold effect, in which ecological change increases disproportionate to the increase in harvest area, although there are several alternative scenarios for the location and shape of the threshold effect across harvest areas (Figure 3.2b). Ecological change may occur rapidly at very small harvest sizes and then plateau with little change beyond this small critical size (curve III in Figure 2.2b).
- Alternatively, threshold points may occur at larger clearfell sizes and the transition between low and high ecological impacts may be more gradual (curves IV-VI in Figure 3.2b).

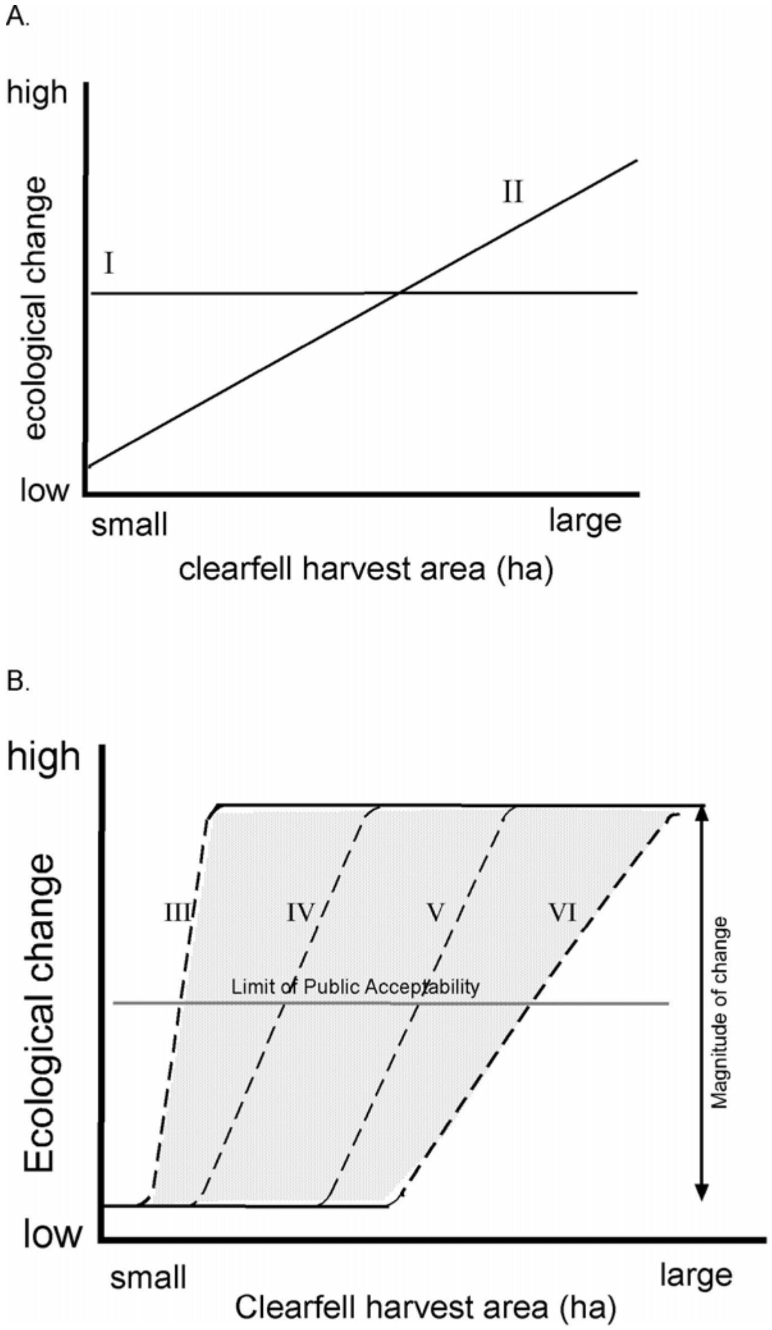

Figure 3.2 (A) Null hypothesis of no-change (curve I), or a linear change (curve II) in ecological impacts with increasing harvest area. (B) Hypothetical scenarios for threshold ecological change across different clearfell sizes (curves III – VI). Ecological change might occur sharply at a defined point, or be spread over wider clearfell sizes. The magnitude and rate of change (slope of line) are likely to vary depending on the response variable studied. As such, there may not be a single identifiable threshold point, but rather a threshold zone might be likely to occur (denoted with shading).

The species responses discussed in previous sections, e.g., lack of change in bird species richness in clearfells over 20 ha (Rudnicky and Hunter 1993), suggest that non-linear responses to clearfell harvesting do exist in at least some circumstances. Given these non-linear responses, at what harvest size might threshold points occur and where should research effort be concentrated to quantify potential threshold sizes? The magnitude of the change post-harvest will vary depending on the response variable measured, as well as broad-scale biogeographic factors such as forest type and fine-scale factors such as aspect and slope (Figure 3.2). Consequently, there is most likely to be a threshold zone of ecological transition (indicated by the shaded area in Figure 3.2b) and exact thresholds will vary spatially and temporally depending on response variables (e.g., species abundance, community composition and so on) and stand specific factors.

In many cases the definition of clearfelling focuses on the changes in microclimate with increasing disturbance to the mature forest stands. Given that microclimate is a key variable that determines species distributions, community composition and influences biological processes (Krebs 2001), the harvest area where the forest microclimate changes to an open-habitat microclimate seems a logical starting point to assess ecological thresholds in the response of biodiversity to forest harvesting. Most definitions of clearfells have assumed an area with a radius greater than 1 - 2 tree heights (Bradshaw 1992). Recent research into microclimatic changes induced by clearfelling at Sicamous Creek supports this showing that the greatest rate of change occurred within one tree height of the forest edge (Spittlehouse et al. 2004). Therefore, clearfell areas above or below 1 to 2 tree heights in radius become a logical starting point to test for clearfell thresholds and changes in forest biodiversity. This size will vary depending on forest type, topography and local climate.

In addition to potential ecological thresholds resulting from clearfelling there is a strong social element of public acceptability to take into consideration. It is likely that there are limits to public acceptability of clearfell harvest impacts that may differ greatly from the amount of ecological change observed (Figure 3.2b). As yet there is no empirical evidence to define where (or if) these ecological thresholds in clearfell size exist, and as such one cannot reconcile any potential differences between forest policy and public perceptions. However, a mismatch between the ecological threshold and public acceptability creates potential conflict, especially if the ecological threshold is higher than the limits of public acceptance.

3.6 Discussion and Conclusions

Disturbances of the magnitude produced by clearfell harvesting will cause significant changes in abiotic factors such as microclimate and hydrology, which in turn affect local biotic communities. In the past, clearfelling has been promoted as a mimic of natural processes, such as wild fire and wind-throw, although in recent years such comparisons have been questioned. Clearfelling may be an adequate mimic of disturbance in some forest systems (Seymour and Hunter 1999), but the extent of similarities can in some cases be quite superficial, with forestry providing a poor substitute (Spence 2001, Pedlar et al. 2002).

Clearfell harvest size has been reduced or replaced by alternative silvicultural systems in recent years, due largely to public pressure, but in some cases also for specific ecological reasons (e.g., concern over population decline in the Spotted Owl (*Strix occidentalis*) Noon, 1996) It appears, generally speaking, as if there has been an *a priori* assumption that large clearfells are ‘bad’, yet from the available research there is conflicting empirical support for this generalisation (Phillips and Shure 1990, Shure and Phillips 1991, Rudnicky and Hunter 1993, Huggard and Vyse 2002, Spurr and Coleman 2002, Leupin et al. 2004).

Public acceptability is partially driven by science and to a large degree by social values. Unfortunately the data for critically assessing ecological change as a function of clearfell size is lacking. As such, forest managers lack crucial information to facilitate consultation with the public over their management practices. Further complications will occur when comparing managed native forests with plantations formed by the reforestation of previously agricultural land. Public perception of plantations is different to that of managed native or old-growth forests and these differing attitudes will affect the acceptability of clearfelling depending on the forest context. In addition, the actual impact of clearfelling may also be context dependent, because the process of afforestation to create plantations may select for species with good dispersal abilities and generalist habitat requirements that are better suited to cope with clearfell harvesting methods. As a result, many species in recently reforested agricultural landscapes may be less affected by large sized cuts than those present in managed indigenous forests.

Currently, large-scale clearfelling may be the most cost-effective form of harvesting currently available, especially for low-value timber species. However, considerable research is still required to determine the ecological change induced by different sized clearfell harvest areas across the spectrum of currently managed forests, including different forest types (managed indigenous, exotic and native plantations), as well as a range of biogeographic zones. This research is important to identify possible thresholds where the severity of ecological damage changes dramatically. Previous work on microclimatic changes induced by clearfelling would indicate that a large amount of change occurs in forest gaps greater than one tree length in radius. As such, research should be targeted at assessing impacts from <1ha to 10ha to identify potential threshold points. However, comparisons with uncut forests and with larger clearfell areas will also be necessary to confirm the shape and magnitude of the impact curve (Figure 3.2) and to determine responses of other abiotic and biotic variables.

Threshold sizes, if they exist, can guide forest management, enabling the development of improved harvesting policies. However, potential thresholds of 1-2 tree lengths in radius will be significantly smaller than current forest harvesting practices in many countries. This will be a contentious issue that will need addressing in due course.

Research and policy design needs to be followed by a process of public education. The point needs to be made that forestry is not all bad for biodiversity (Pawson and Brockerhoff 2005), especially with respect to plantation forestry in areas that have otherwise lost the majority of native tree cover. In some instances, establishing plantations on marginal agricultural land can be beneficial for regional forest biodiversity. In such cases silviculture can have positive conservation outcomes, but to ensure its sustainability and gain broad public acceptance it must be based on sound science.

Chapter 4. Non-native plantation forests as reservoirs for native biodiversity in a fragmented New Zealand landscape

This chapter has been submitted in a modified form to Biodiversity and Conservation for inclusion in a special issue on biodiversity in plantation forests as:

Non-native plantation forests as reservoirs for native biodiversity in a fragmented New Zealand landscape

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4.1 Introduction

Habitat loss and fragmentation are recognised as critical agents of species decline (Tilman et al. 1994, Sala et al. 2000, Brooks et al. 2002, Fahrig 2003, Reed 2004, Ewers and Didham 2006a). In New Zealand, the impacts of habitat loss on biodiversity have been most severe in the fertile lowland forest environments that were best suited for conversion to pastoral agriculture (Norton 2001), where over 90 % of the original forest cover has been destroyed in some regions (Ewers et al. 2006). Significant changes in land use still occur (Ewers et al. 2006, Walker et al. 2006), and in lowland regions recent reforestation for plantation timber production has established large areas of forest habitat that have been missing from these landscapes for many decades. In a landscape matrix otherwise dominated by pastoral farming, low contrast matrix habitats such as plantation forests are increasingly recognised for their potential contribution to biodiversity preservation (Humphrey et al. 1999, Anon 2000, Carnus et al. 2006).

Because plantation forests are intensively managed for the commercial production of timber and other forest products, they are typically composed of just one or a few tree species (predominantly *Pinus radiata* in New Zealand) grown in even-aged stands with a simplified canopy structure, that are repeatedly harvested by clearfelling. As a consequence, plantation forests are often assumed to support a low abundance and diversity of indigenous species, and they are frequently referred to as 'biological deserts' (Brockerhoff et al. 2001). Contrary to such perceptions, research has shown that managed plantation forests can support a diverse array of native understorey plants (Allen et al. 1995, Geldenhuys 1997, Ogden et al. 1997, Brockerhoff et al. 2003), birds (Ryder 1948, Weeks 1949, Clout 1984, Clout and Gaze 1984), and invertebrates (Humphrey et al. 1999, Hutcheson and Jones 1999, Bonham et al. 2002, Woodcock et al. 2003, Humphrey 2005, Mesibov 2005, Oxbrough et al. 2005, Carnus et al. 2006). Furthermore, plantation forests contribute to ecosystem integrity by buffering native forest remnants from the microclimatic influence of surrounding matrix habitat (Norton 1998, Brockerhoff et al. 2001, Hartley 2002, Denyer et al. 2006), and provide a low contrast forest environment suitable for many species dispersing between remnant native habitats in the landscape (Norton 1998, Hale et al. 2001).

Internationally, there is increasing pressure to reduce the real and perceived negative environmental effects of plantation forestry, and to enhance sustainable timber production

(Hock and Hay 2003). An array of stand-level initiatives to increase forest heterogeneity and enhance biodiversity has been evaluated in managed production forests. Most are encompassed by the concept of legacy management (manipulation of organisms or organically-derived biological structures that survive a disturbance event and provide propagules, habitat, food or other ecosystem services to recovering biological communities, as summarised in Franklin et al. 2000) which includes management of harvest debris and manipulation of stand composition, vertical structure and age (Kerr 1999, Franklin et al. 2000, Bonham et al. 2002, Mazurek and Zielinski 2004). However, external influences at larger spatial scales, such as landscape composition and connectivity, are now emerging as equally critical determinants of biodiversity within plantations, and the influence of stand level management should be considered within a landscape context (Humphrey et al. 2004, Lindenmayer and Hobbs 2004, Barbaro et al. 2005). Unfortunately, advances in this vein are hampered because most landscape ecological research continues to focus on natural ecosystems (Norton 2001, Fazey et al. 2005), and there is little understanding of the contribution managed habitats, such as plantation forests, can make to regional biodiversity conservation relative to native remnants.

The objective of this study was to determine the role of modified habitats, particularly non-native plantation forests as reservoirs of native biodiversity in heavily fragmented landscapes. This is particularly important in regions that have undergone extensive deforestation, where plantation forests may provide significant ‘surrogate’ forest habitat throughout the landscape. For example, afforestation in New Zealand from 1900 onwards has created 1.8 million hectares of exotic (primarily *Pinus radiata*) forest (ca. 25% of New Zealand’s total forest cover) in the form of intensively-managed plantation forest habitat (Anon 2005). In some regions of the central North Island and the eastern South Island, plantation forests dominate the matrix habitat that surrounds remnant native habitat. I compared invertebrate biodiversity in native forest habitat and three human-modified ecosystems (pasture, mature production forest stands, and recent clearfell-harvested stands) in the highly fragmented landscape of the central North Island. Sampling focused on beetle diversity within three dominant families, ground beetles (Carabidae), chafer beetles (Scarabaeidae) and bark beetles (Curculionidae: Scolytinae), which are known to occur in high abundance within New Zealand’s exotic plantations (Chapter 5) and include critically endangered species of conservation concern

(Brockerhoff et al. 2005). Sampling across gradients between habitats was an attempte to investigate the presence of edge-mediated changes in the abundance of beetles.

4.2 Methods

4.2.1 Collection of beetles

The study was conducted in the central North Island of New Zealand, a region historically subject to infrequent catastrophic disturbances, predominantly from the Taupo Volcanic Zone (Froggatt and Lowe 1990, Wilmshurst and McGlone 1996). Before European colonisation the vegetation of this volcanic plateau was a mosaic of seral shrub-heaths and frost flats at higher altitudes, and lush mixed podocarp-broadleaved forests on lowland terraces (Wardle 1991). Current patterns of indigenous vegetation are a reflection of drastic changes in land use over the last 200 years (McGlone 1989, Roche 1990). Exotic pasture species (predominantly ryegrass, *Lolium perenne*, and clover, *Trifolium repens*) and plantation forests of *P. radiata* are now dominant and surround highly fragmented, isolated patches of native habitat. Native vegetation is limited to a few large intact areas of forest (managed by the Department of Conservation), many small privately-owned forest remnants (including a substantial network throughout plantation forests along riparian margins and steep gullies), pockets of indigenous shrubland, areas of fire-induced shrubland, and the significant but often unrecognised native plant component within the understorey of plantation forests (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003).

Invertebrates were collected along three independent replicate edge gradients in each of the six possible comparisons between pairs of the following habitats: mature 26 year-old *P. radiata*, recently clearfelled *P. radiata* stands, native forest and pasture. Along each of the 18 edge gradients, individual pitfall traps were placed at seven distances from the habitat boundary, at -125, -25, -5, 0, +5, +25 and +125 m perpendicular to the edge (negative distances arbitrarily assigned to one of the habitats, giving 126 pitfall traps in total. The logarithmic scale applied to the sampling design reflects the *a priori* assumption that changes in species abundances would occur most rapidly near habitat edges (Didham et al. 1998, Ewers et al. In Press). Carabidae, Scarabaeidae and Scolytinae (Curculionidae) were identified to species level from the pitfall samples. These three taxonomic groups were chosen to provide a balance between identifying all Coleoptera (which was not technically feasible due to resource limitations) and the other extreme of relying on a single taxonomic ‘indicator’ group. The families were selected to provide a range of trophic groups: Scarabaeidae are herbivores, Scolytinae are phloem feeders in wood, and Carabidae are generally predators. Little is currently known about the diet of New Zealand carabids, but it is assumed that they have similar trophic roles to those found in other countries (Larochelle and Larivière 2001).

Trap monitoring was undertaken six times at monthly intervals between November 2002 – February 2003 and December 2003 – February 2004. Total abundance of each species within traps was used in rarefaction analysis, however, for other analyses the abundance of individual species was unit-standardised by converting to abundance per 100 trap-days to account for minor differences in sampling duration between traps that resulted from the schedule of sample collection. For detailed discussion of study sites, pitfall trapping procedures and the collection of environmental variables see Chapter 2.

Table 4.1. Description and units of measurement of environmental variables included in constrained CCA ordination (Figure 4.3).

Abbreviation	**Description**	**Units of measurement**
Dist	Distance along transect	Metres
Long	Longitude (also expresses collinear effects of $Long^2$, $Long^3$, $Long^2 * Lat$ and $Long * Lat^2$)	NZMG Longitude/1,000,000
Lat	Latitude (also expresses collinear effects of Lat^2 and Lat^3)	NZMG Latitude/1,000,000
500m-nat	Proportion of native vegetation within 500 m radius	Proportion
500m-exo	Proportion of exotic vegetation within 500 m radius	Proportion
1000m-nat	Proportion of native vegetation within 1000 m radius	Proportion
1000m-exo	Proportion of exotic vegetation within 1000 m radius	Proportion
5000m-nat	Proportion of native vegetation within 5000 m radius	Proportion
5000m-exo	Proportion of exotic vegetation within 5000 m radius	Proportion
Adj-N	Adjacent stand to site is native	Categorical
Adj-P	Adjacent stand to site is pasture	Categorical
Adj-M	Adjacent stand to site is *Pinus radiata* 26 yr	Categorical

Adj-C	Adjacent stand to site is clearfell	Categorical
DW-1-5	Dead wood, categorical scale 1-5, i.e., 4 levels	Categorical
D-1-5	Drainage, categorical scale 1-5, i.e., 4 levels	Categorical
L-1-5	Leaf litter, categorical scale 1-5, i.e., 4 levels	Categorical
PCA-Veg1	PCA axis 1 scores of understorey vegetation surveys	Ordination scores
PCA-Veg2	PCA axis 2 scores of understorey vegetation surveys	Ordination scores
PCA-Veg3	PCA axis 3 scores of understorey vegetation surveys	Ordination scores
PCA-LENZ 1	PCA axis 1 scores of LENZ environmental information	Ordination scores
PCA-LENZ 2	PCA axis 2 scores of LENZ environmental information	Ordination scores
PCA-LENZ 3	PCA axis 3 scores of LENZ environmental information	Ordination scores

4.2.3 Assessment of species richness and community composition

Expected species accumulation curves were calculated using the sample-based rarefaction index (Mau-Tau, in Estimate-S 7.5.0), rescaled and expressed in terms of number of individuals (Colwell 2004). Associated confidence intervals were calculated by a general binomial mixture model with 100 randomisations (Colwell et al. 2004). The expected asymptote of the rarefaction curve was calculated by extrapolation beyond the sampled data range using the Michaelis-Menten richness estimator (Colwell and Coddington 1994, Colwell 2004).

Variation in beetle species composition between habitats was analysed using multivariate ordination techniques. An unconstrained correspondence analysis (CA) was conducted on log-transformed species abundances. A total of 39 variables characterising spatial attributes, vegetation structure and local environmental factors were collected for each of the sampling sites (Table 4.1). After removing collinear variables, the remaining factors were included in a canonical correspondence analysis (CCA), and a forward selection procedure was used to identify potential confounding variables (such as spatial autocorrelation among trap locations) that explained significant variation in beetle community composition (Ter Braak 1995). Both longitude and latitude were significant and thus considered to represent spatial autocorrelation in the data, and were subsequently added to the model as covariables (Borcard et al. 1992). A final partial CCA was then conducted on 29 environmental variables and the two covariables, using inter-sample distances and biplot scaling. All ordination analyses were conducted in Canoco V. 4.01 (ter Braak and Smilauer 1999).

4.2.4 Assessment of community and individual responses between different habitat types

The abundance of native and exotic beetles in different habitat types was analysed with a split-plot repeated measures ANOVA (Genstat Version 9). Habitat comparisons (e.g., pasture versus clearfell) were assigned as the main plot and individual habitat types as sub-plots. A factor was created called 'compartment group' which provided an identifier for each unique pairing of habitat types. By nesting habitat type within 'compartment group' it is possible to assess the effect of adjacent habitat on beetle abundance (measured as average catch per 100 trap days). For this particular analysis, the 5, 25 and 125 m pitfall traps were assigned as repeated measures within the sub-plot. Treatments were beetle origin (native or exotic), habitat type (native, pine, clearfell and pasture) and distance from boundary between the habitats. Examination of residual plots indicated a log transformation was required, but 0 values in the data set forced the use of an adjusted log transformation, i.e., log(x + 0.01).

Species characteristic of particular habitats were identified by the Indval procedure of Dufrêne and Legendre (1997). Indval sample groupings were assigned *a priori* on the basis of habitat type (clearfell, pasture, native forest and mature *P. radiata*). Habitat types were constructed by grouping pitfall traps along transects, whereby traps at 125 m and 25 m in each habitat were considered representative of their particular habitats. This was a conservative approach to avoid the most severe edge-effects that are present at the habitat boundaries and at pitfall traps 5 m either side.

Differences in the relative abundance of native and exotic species were then further analysed across entire habitat gradients to determine whether the shape of the edge response function varied between habitat types. Variation in the proportional representation of exotic beetles across habitat edges was modelled by testing the fit of five continuous response functions of increasing complexity: null, linear, power, logistic and unimodal (Ewers and Didham 2006b). Response functions were calculated in R version.2.4.0 (Team 2006) using a single average proportional abundance of exotic species for each trap, which was the average value pooled across the six trapping periods (so as to avoid pseudoreplication). The best-fit model, out of the five response functions tested, was selected using Akaike weights (calculated from Akaike information criterion, AIC, values), which give the probability that a particular model is the best fit to the data from the set of models that are evaluated.

4.3 Results

4.3.1 Rarefied species richness

There was no significant variation in beetle species accumulation curves as a function of habitat type, either for all species combined (Figure 4.1a), or for native beetles species considered separately (Figure 4.1b). In both cases, clearfell habitats had the highest expected species richness, whereas native forest had a lower total expected species richness asymptote than production habitats. The principle cause of this was the low exotic beetle species richness in native forest (Appendix 4.1), this was further illustrated by an increase in the slope and expected asymptote of the native forest species accumulation curve relative to other habitat types when comparing native beetles only, as opposed to all beetles (Figure 4.1b).

The target species groups were very well characterised by the level of sampling effort employed, as illustrated by the curves approaching an asymptote (Figure 4.1a). Pooling across all habitats, the actual species richness was equivalent to 97.7% of the expected species richness asymptote as calculated by Michaelis-Menten running means.

4.3.2 Relative beetle abundance in different habitat types

A combined total abundance of 9,974 Carabidae (28 species), 1,433 Scarabaeidae (11 species) and 633 Scolytinae (3 species) were collected from all habitat types. The majority of species (75 %) were native, however eight carabid species, one scarabaeid species and two scolytine species were exotic species (Appendix 4.1). There was strong evidence of an interaction between the origin of beetle species (exotic versus native) and their abundance in different habitat types ($F_{3,78} = 25.55$, $P < 0.001$, Table 4.2). Recent clearfells had the greatest pooled mean abundance of the four habitats sampled (140.8/100 trap days), due largely to the dominance of one native species, *Cicindela tuberculata* (78 % of individuals). Exotic beetle abundance in native habitat was extremely low compared to all other habitat types (Figure 4.2). There was evidence of lower exotic species abundance in mature *P. radiata* habitat compared to recent clearfells (Figure 4.2). However, there was no significant difference in the abundance of native beetles between habitat types (Figure 4.2).

Average beetle abundance did not change with distance into habitat, or distance as an interaction with other factors in the repeated measures ANOVA (Table 4.2). However, a number of species, including *Hypharpax australasiae*, *Scopodes* spp., *Demetrida natsuda* and *Lecanomerus sharpi* were present in open habitats, such as clearfells and pasture, but not in mature forest (Appendix 4.1). Four species were specific to a single habitat type, three of which, *Scopodes edwardsi* (clearfell), *Ataenius brouni* (forest) and *Notagonum submetallicum* (pasture), may be transient species given their low abundance, whereas the fourth species, *Acrossidius tasmaniae*, is a common pasture pest (Appendix 4.1).

4.3.3 Variation in beetle community composition between habitat types

Twelve of the 29 environmental variables tested in the forward selection procedure of the canonical analysis were significant predictors of variation in beetle community composition between sites (Table 4.3). Given their potential as confounding factors, latitude and longitude were incorporated as covariables in a partial canonical correspondence analysis (pCCA). Axes 1 and 2 of the pCCA explained 6.3 and 5.6 % of the total variance in species abundances, respectively, and 17.7 and 15.8 % of the species environment relationship, respectively (Figure 4.3a). The four habitat types formed distinct groupings (Figure 4.3a). Although mature *P. radiata* sites shared multivariate space with other habitat elements they were the most similar to native forest (Figure 4.3a). Overall, variation in beetle species composition was best explained by the proportion of native forest within 500 m of the sample location, with sites most strongly correlated with this environmental variable along pCCA axis 1 (Table 4.3). The second strongest correlation with Axis 1 was the axis 1 scores of the PCA analysis of understorey vegetation, PCA-Veg1 (Table 4.3). Axis 2 was most strongly correlated with the PCA axis 1 of the LENZ data layers (Table 4.3).

4.3.4 Individual species responses

In general, indicator values for individual taxa were low, but values for two species exceeded 50 (*C. tuberculata* in clearfells and *C. zealandica* in pasture) indicating a strong habitat association. A further 14 species had maximum indicator values greater than 25 (Table 4.4). Clearfell and native forest had the most distinctive assemblages, with 8 and 5 species, respectively, exceeding an indicator value of 25. In contrast to native forest that was

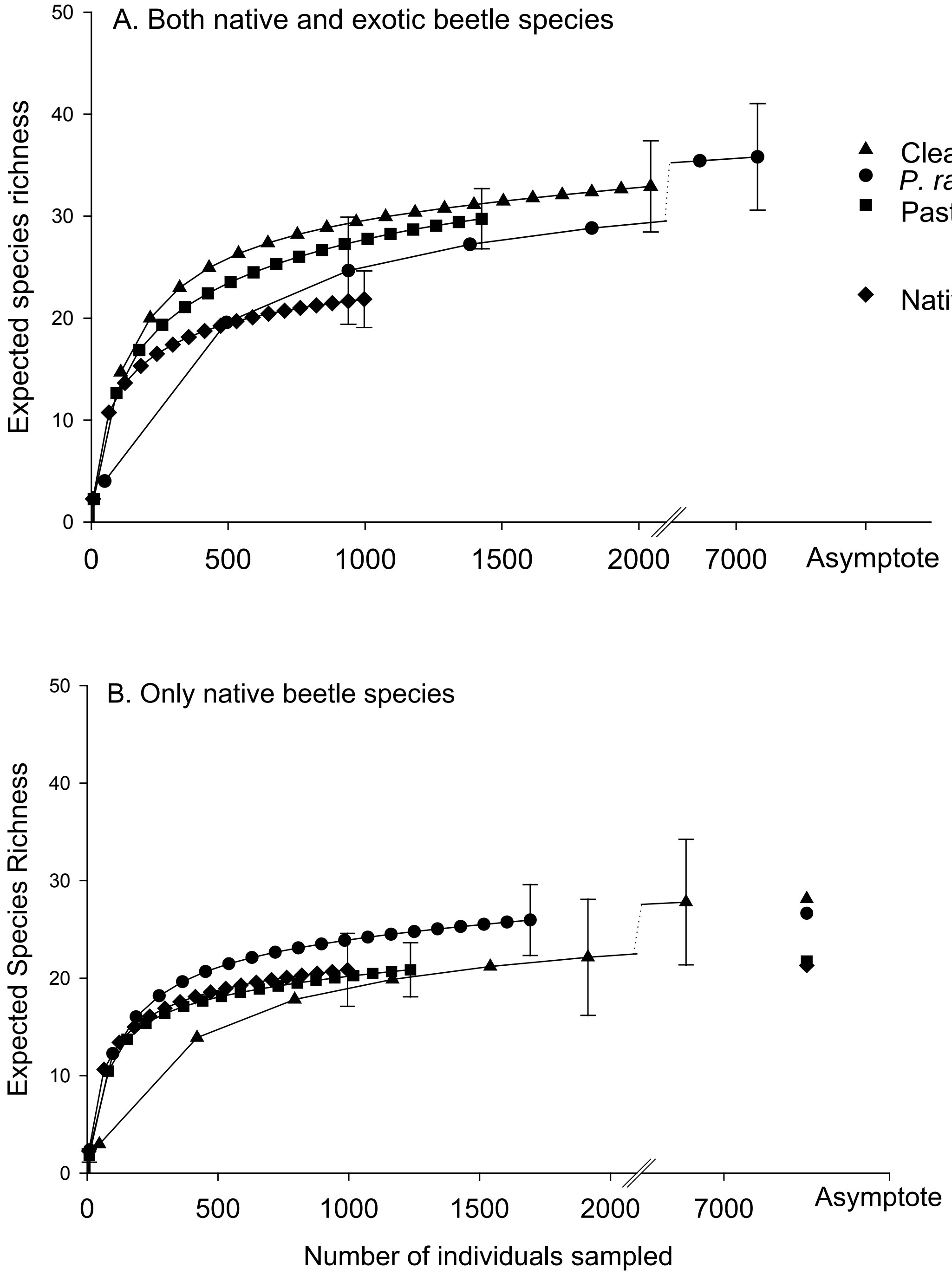

Figure 4.1. Species accumulation curves of, A) all beetle species and B) only native species were calculated for different habitat types by sample-based rarefaction. The x-axis is rescaled to the number of individuals and error bars denote 95% confidence intervals. The Michaelis-Menten richness estimator was used to estimate the expected species richness asymptote. All rarefaction analyses were conducted using Estimate-S (Colwell 2004).

Table 4.2. Results of repeated measures ANOVA of beetle species abundances with respect to habitat comparison type, habitat type, species origin and distance from habitat edge. A correction factor of 0.9658 was applied to the d.f. of the distance term and its interactions to adjust for potential correlation between pitfall traps sampled from the same trap gradient. Origin refers to whether the beetle was native or exotic.

Source of variation	**d.f.**	**Sums of Squares**	**Mean Square**	**F**	**P**
Compartment stratum					
Habitat Comparison	5	324.66	64.93	11.07	<0.001
Residual	12	70.41	5.87	2.79	
Compartment * Subplot stratum					
Habitat Type	3	114.47	38.16	18.16	<0.001
Habitat Comparison. Habitat Type	3	32.49	10.83	5.16	0.016
Residual	12	25.21	2.10	0.97	
Compartment . Subplot * Distance stratum					
Distance	2	6.30	3.15	1.45	0.244
Distance.Habitat Comparison	10	12.40	1.24	0.57	0.828
Distance.Habitat Group	6	7.03	1.17	0.54	0.774
Distance.Habitat Comparison.Habitat Group	6	22.15	3.69	1.70	0.140
Residual	48	103.95	2.17	1.70	
Compartment . Subplot * Distance * Replication stratum					
Origin	1	303.13	303.13	237.68	<0.001
Distance.Origin	2	0.41	0.20	0.16	0.853
Habitat Comparison.Origin	5	94.28	18.86	14.79	<0.001
Habitat Group.Origin	3	96.06	32.02	25.11	<0.001
Distance.Habitat Comparison.Origin	10	21.03	2.10	1.68	0.101
Distance.Habitat Group.Origin	6	10.58	1.76	1.41	0.233
Habitat Comparison.Habitat Group.Origin	3	11.28	3.76	3.00	0.038
Distance.Habitat Comparison.Habitat Group.Origin	6	5.91	0.99	0.77	0.594
Residual	78	97.38	1.25		
Total	215	1353.56			

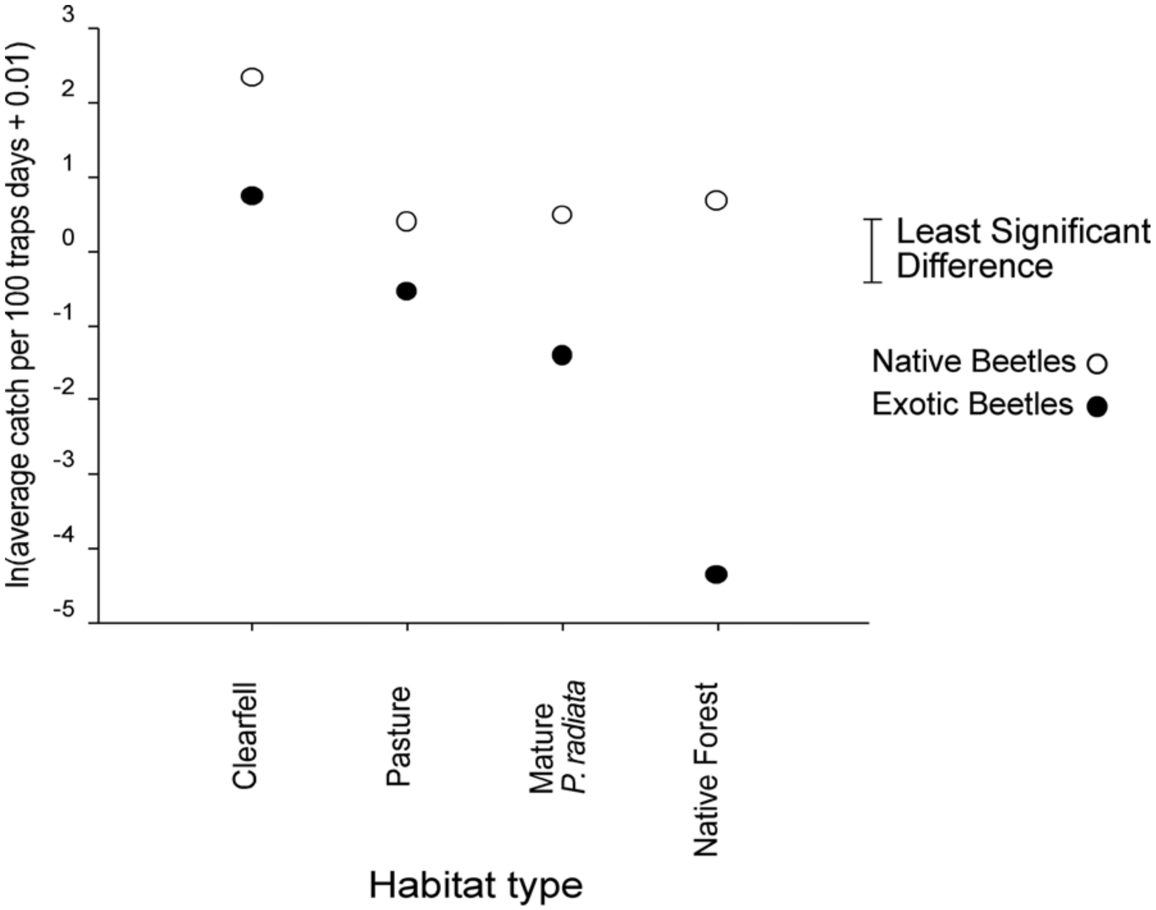

Figure 4.2. The abundance of native species did not differ significantly across all habitat types, whereas the abundance of exotic species varied between habitat types and was very low in native forest. LSD (p = 0.05 with 26.06 d.f.).

Table 4.3. Significant environmental variables and associated intraset correlations from partial canonical correspondence analysis. Eigenvalues, F-values and P-values are from forward selecting regression procedure, Canoco V. 4.02 (ter Braak and Smilauer 1999). Intraset correlations in bold are significant at $P < 0.05$.

Environmental Variables	**Eigenvalue, Σ of eigenvalues = 1.49**	***F***	**P**	**Intraset correlations**	
				Axis 1	**Axis 2**
500 m Native forest	0.16	4.88	0.002	**0.67**	-0.03
PCA LENZ 1	0.15	4.45	0.002	**-0.24**	**-0.51**
PCA Vege 1	0.11	3.52	0.002	**0.60**	0.04
500 m Exotic	0.10	2.96	0.002	-0.10	**-0.37**
Adjacent pasture	0.10	3.43	0.002	-0.15	-0.07
5,000 m Exotic	0.09	3.04	0.002	0.08	-0.10
PCA LENZ 3	0.09	2.81	0.002	**-0.18**	-0.09
5,000 m Native	0.08	2.89	0.002	**0.24**	0.12
Drainage 5	0.06	1.83	0.014	-0.05	**-0.24**
Litter 1	0.08	1.50	0.042	**-0.28**	-0.01

dominated by native indicator species, many of the clearfell species were exotic in origin. Pasture and mature *P. radiata* had a predominantly generalist fauna, with only 2 and 3 indicator species respectively. Partial canonical correspondence analysis axis scores of beetle species with significant indicator values greater than 25 were superimposed on the plot of

4.3.5 Changes in the proportion of exotic beetles across habitat boundaries

Exotic and native beetle abundance varied significantly between habitat types, but this was dependent on the adjacent habitat type ($F_{3,78} = 2.95$, $P < 0.038$, Table 4.2). There was negligible invasion by exotic beetles at all distances into native forest despite the presence of exotic species in adjacent production habitats (Figure 4.4a). Proportional representation of exotic beetles in *P. radiata* was low at all distances from the native forest edge, but increased with distance into pasture (Figure 4.4a). There was an unusual unimodal abundance pattern in recent clearfells; exotic beetle abundance peaked 5 m into the clearfell habitat before declining with increasing distance from the forest boundary (Figure 4.4a). Plantation stands of *P. radiata* and recently disturbed clearfell habitat had a much lower proportional abundance

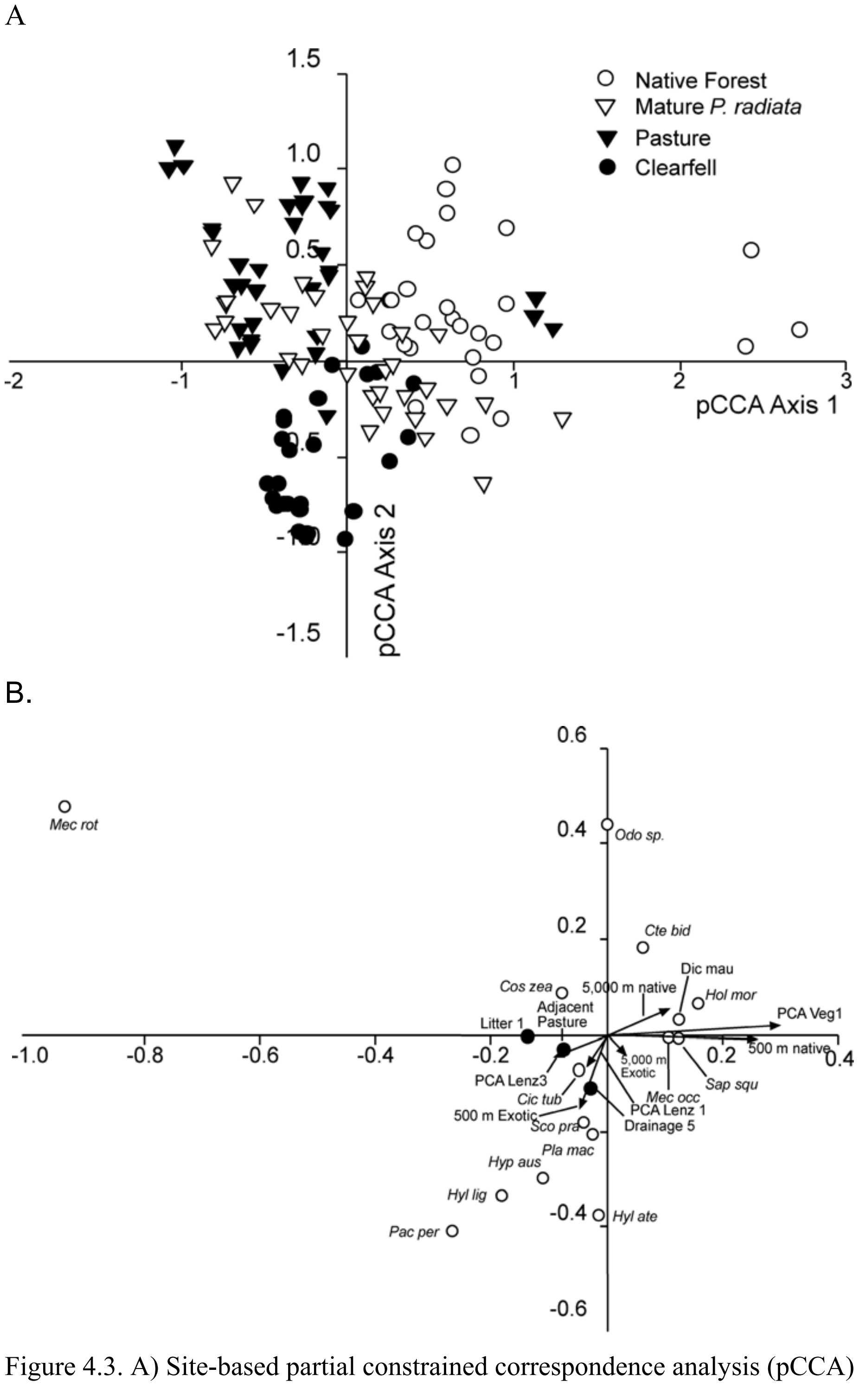

Figure 4.3. A) Site-based partial constrained correspondence analysis (pCCA) of combined Carabidae, Scarabaeidae and Scolytinae in different habitat types. B) Biplot of significant environmental variables (Table 4.3) with the most abundant taxa and those with significant indicator values for at least one habitat type overlaid (abbreviations as in Table 4.4). Continuous environmental variables are shown as arrows, while categorical variables are expressed as a single black circle indicating its centroid.

Table 4.4. Indicator values for beetle taxa in different habitats, values were calculated using the methodologies of Dufrêne and Legendre (1997) on the basis of a priori selected habitat groupings using PC-ORD V. 4.01 (McCune and Mefford 1999).

Family	Species	Abbreviation	Clearfell	Native	Pasture	Mature *P. radiata*	Significance
Carabidae	*Cicindela tuberculata*	*Cic tub*	85	0	1	0	0.001
Scarabaeidae	Costelytra zealandica	*Cos zea*	2	0	53	4	0.001
Carabidae	Platynus macropterus	*Pla mac*	39	0	0	0	0.001
Scarabaeidae	*Odontria* sp.	*Odo sp.*	15	5	5	36	0.005
Carabidae	*Ctenognathus bidens*	*Cte bid*	2	34	2	2	0.003
Carabidae	*Mecodema occiputale*	*Mec occ*	12	34	1	9	0.004
Carabidae	*Dichrochile maura*	*Dic mau*	0	33	2	1	0.001
Carabidae	*Hypharpax australis*	*Hyp aus*	31	0	0	5	0.001
Carabidae	*Rhytisternis miser*	*Rhy mis*	27	0	31	2	0.003
Scarabaeidae	*Saphobius squamulosus*	Sap squ	5	31	0	4	0.002
Scolytinae	*Hylastes ater*	*Hyl ate*	31	0	0	27	0.005
Carabidae	*Mecyclothorax rotundicollis*	Mec rot	30	0	15	0	0.002
Carabidae	*Holcaspis mordax*	*Hol mor*	10	29	7	16	0.038
Carabidae	*Scopodes prasinus*	*Sco pra*	29	1	0	0	0.001
Scolytinae	*Hylurgus ligniperda*	*Hyl lig*	26	0	0	15	0.001
Scolytinae	*Pachycotes peregrinus*	*Pac per*	19	0	0	25	0.004

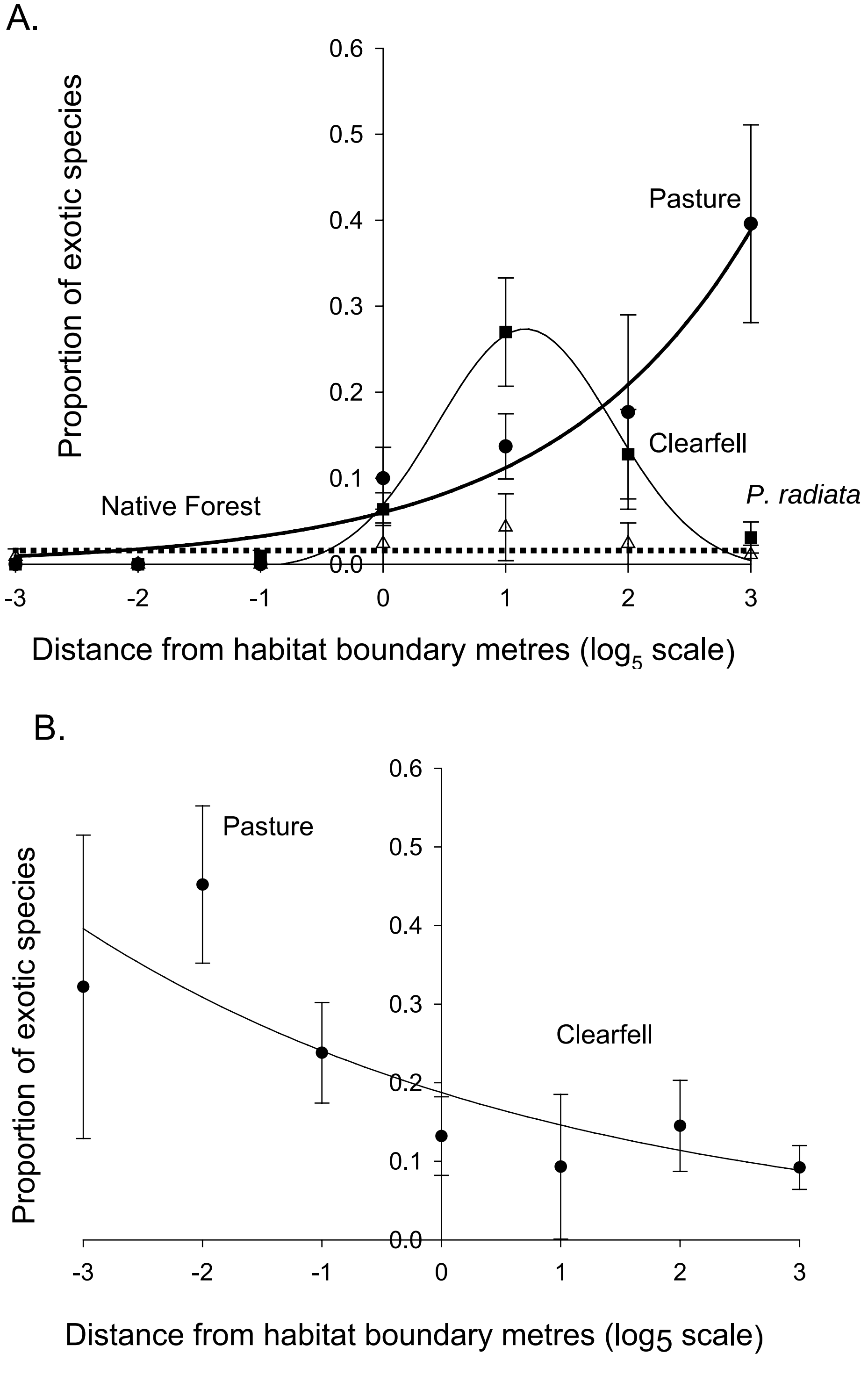

Figure 4.4. Average proportional abundance of exotic beetle species across gradients between habitats, A) Native forest versus clearfell, *P. radiata* and pasture, B) Pasture versus clearfell. Curves represent continuous response functions fitted using the methods of Ewers and Didham (2006b).

of exotic beetles than intensively managed pastoral grassland adjacent to native forest (Figure 4.4a). Despite the fact that both clearfells and pastoral grassland are structurally open habitats, the proportional abundance of exotic species was much higher in pasture, even when pasture was directly adjacent to clearfell habitat (Figure 4.4b).

4.4 Discussion

4.4.1 High native beetle biodiversity in plantation forests

In New Zealand's central North Island, intensively-managed exotic plantation forests supported significant native beetle biodiversity. This is consistent with other recent invertebrate studies in New Zealand (Brockerhoff et al. 2005, Pawson 2006, Berndt et al. Submitted) and Australia (Bonham et al. 2002, Mesibov 2005). The expected total species richness was higher in plantations (including recently clearfelled stands) than native forest (Figure 4.2a). However, low beetle diversity in native forest was partially a reflection of the resilience of native forest to invasion by exotic species. *Hylastes ater*, a common bark-beetle pest species of *P. radiata* was the only exotic species recorded in native forest sites. In contrast, clearfell-harvested sites had seven exotic species, and *P. radiata* and pasture sites had eight. Harris and Burns (2000) also observed apparent resilience to exotic species invasion in native kahikatea (*Dacrycarpus dacrydioides*) forest fragments of the Waikato district (~ 120 km from our study site), despite the dominance of exotic species in adjacent pasture. Harris and Burns (2000) attributed this to the difference in light levels between native forest and pasture, preventing the establishment of adventive plant species and their host-specific adventive beetles. Our results do not support this conclusion as the canopy closure of native forest and plantations was very similar (calculated using hemispherical photographs, see Chapter 2), yet *P. radiata* stands supported many more exotic beetle species. However, few of the species considered here were host-specific species, unlike many of the Malaise-trapped flying species of Harris and Burns (2000). Alternative explanations include the difference in disturbance history of the native forest compared to the managed production habitats and the origin of the tree species and their potential flow-on effects to the invertebrate community, and the choice of taxa sampled. Disturbance is much more frequent and intense in plantation forests or pasture, and disturbance processes are known to facilitate establishment of invasive species (Hobbs and Huenneke 1992, Lozon and MacIsaac 1997).

If exotic species are excluded from the analysis the expected species richness falls into two groups, mature plantation habitat and clearfells with higher richness, and native forest and pasture with lower richness (Figure 4.2b). The lower native beetle species richness in pasture may reflect both the lack of native host plant species in managed exotic grass swards (Harris and Burns 2000, Ecroyd and Brockerhoff 2005)and the historical rarity of natural grasslands and their associated beetle communities in the central North Island (see appendix Kennedy et al. 1978).

4.4.2 Low exotic dominance in plantation forests

Beetle abundance varied significantly between habitat types, but this was dependent on the adjacent habitat type and on beetle species origin (exotic versus native) (Table 4.2). Exotic beetles were almost absent from native forest, irrespective of the adjacent habitat type, implying that there may be some attributes of undisturbed native forest that promote resistance to the establishment of exotic species. Plantation forests are already recognised as a suitable microclimatic buffer for native remnants (Denyer et al. 2006), and the low proportion of exotic species in mature *P. radiata* stands (Figure 4.4a) suggests that they may also provide a ‘temporary’ biological buffer from exotic species dominance, compared to alternative pasture land uses. The word temporary is important to bear in mind, as pine plantations are harvested regularly and the proportion of exotic beetles was high immediately adjacent to the native forest boundary in recent clearfell habitats (Figure 4.4a). Furthermore, plantation forests may reduce the equilibrium density of exotic species in the landscape, by increasing the risk of mortality to individuals dispersing between isolated regions of pasture (Barlow and Kean 2004). Forest boundaries are known to act as a barrier to the dispersal of some insect species (Cant et al. 2005), and this may partially explain the unimodal relationship in exotic species dominance with distance away from the forest edge in clearfells.

The dominance of exotic beetles in pasture decreased exponentially with increasing proximity to native forest (Figure 4.4a), suggesting that there may be increased spill over of native species into the adjacent pasture habitat (Magura et al. 2001). This may partially explain the greater than anticipated total native beetle diversity in pasture sites as a whole. Whether the native beetles in the pasture samples represent resident populations is unclear, as the dispersal of invertebrates between managed and natural ecosystems is common (see review by Rand et al. (2006)). However, additional sampling of pasture sites that are more isolated from natural and plantation forests is required before a definitive statement can be made about the relative importance of dispersal versus resource utilisation in the matrix. In contrast, comparisons between mature *P. radiata* stands and clearfells in our study were conducted deep within the plantation estate, often many kilometres from the influence of alternative habitat types. As such, there is a very low probability that the rich native beetle community sampled in plantation-clearfell comparisons were the result of dispersal from adjacent non-plantation habitat.

4.4.3 Plantation forestry as a surrogate for native forest

Mature *P. radiata* stands provided the best surrogate habitat to augment remaining native forest remnants in this study area. Beetle species composition of mature plantation stands was more similar to native forest than of either pasture or recent clearfells (Figure 4.3a). The environmental drivers regulating the similarity in species composition between the two habitats is unknown. However, I would have expected plantation forests to provide an equivalent microclimate to native forest due to their similar canopy cover and known ability to ameliorate microclimate edge effects (Denyer et al. 2006). Furthermore, the depth of leaf-litter and soil chemical properties in *P. radiata* stands are more likely to be analogous to native forest than open pastoral habitat (Parfitt et al. 1997, Alfredsson et al. 1998). However, plantation forests are dynamic and individual stands are clearfelled about every 28 years in New Zealand. Although harvesting can be locally destructive, it is not necessarily detrimental to landscape-level species persistence if a spatial mosaic of different successional forest stages can be maintained within the landscape (Butterfield 1997, Magura et al. 2003).

The high species richness in clearfells (36 species), and their distinctive fauna (Table 4.4), is consistent with European studies (Niemela et al. 1993, Koivula et al. 2002) which have shown that both open-habitat species and surviving populations of forest generalist species co-exist (at least temporarily) in clearfells. In our study area a number of exotic species that are known to prefer open habitat colonised recent clearfells, e.g., *Anisodactylus binotatus*, *H. australis*, *H. australasiae*, *L. verticalis*, *L. vestigialis* and *R. miser* (Larochelle and Larivière 2001). However, this has been found to be a transient phenomenon, with the abundance of these species decreasing in nearby plantation stands greater than four years old (unpublished data).

Despite the richness of the beetle fauna in clearfells and mature plantation stands, native forest had a distinct fauna (reflected in the Indval indicator species analysis results, Table 4.4) characterised by a higher abundance of some species. This, combined with the fact that proximity to native forest was the strongest environmental predictor (Table 4.3) of beetle community composition in non-native habitats, highlights the importance of retaining native forest within the plantation matrix (Humphrey et al. 2004, Lindenmayer and Hobbs 2004)

4.5 Conclusions

In New Zealand, extensive habitat loss and fragmentation have left scattered, isolated native forest remnants spread throughout a landscape matrix dominated by plantation forest and improved pastoral grassland. These modified production ecosystems provide a considerable extension to the potential habitat of many native beetle species that were previously perceived to be restricted to native habitat. However, different matrix habitats are not equivalent in quality or habitat-suitability for native beetles. Mature *P. radiata* plantations support native beetle communities that are most similar to those in native forest. Disturbed and open habitat areas are more prone to invasion by exotic species than native forests or pine plantations, where exotic beetle species were uncommon.

Further work is required to understand spatio-temporal variation in the relationship between the mosaic of different-aged plantation stands and how they interact with native habitat at a landscape scale. In particular, some of the most important questions to address are how insects disperse between regenerating stands, whether this is affected by proximity to native habitat, and whether stand-level management techniques, such as legacy management, influence these dispersal processes. Despite the importance of proximity to native habitat, many existing exotic tree species plantations currently contain few native remnants. Further research is required to determine the value of restoring small native remnants within existing plantations, and their role as source populations for invertebrate recolonisation of regenerating plantation stands.

Appendix 4.1. Average catch per 100 trap days of individual beetle taxa sampled at different distances from the habitat edge into clearfelled plantation forest, mature *P. radiata* forest, native forest, and pasture

	Clearfell (1 yr)			***P. radiata* 26 yr**			**Native Forest**			**Pasture**		
Species	**5 m**	**25 m**	**125 m**	**5 m**	**25 m**	**125 m**	**5 m**	**25 m**	**125 m**	**5 m**	**25 m**	**125 m**
Exotic												
Carabidae												
Anisodactylus binotatus	0.07	0.06		0.03		0.02				0.07		
Anomotarsus illawarrae				0.02								
Hypharpax australasiae	0.12		0.25							0.05	0.05	0.19
Hypharpax australis	0.97	0.37	0.68	0.21	0.06	0.18				0.04		
Lecanomerus verticalis	0.05	0.28	0.37	0.02	0.05	0.05				0.34		0.24
Lecanomerus vestigialis	0.24	0.55	0.25	0.05	0.09	0.25					0.07	0.04
Rhytisternis miser	1.06	2.46	2.41	0.08	0.08	0.47				2.03	2.64	2.11
Scolytinae												
Hylastes ater	3.02	4.78	2.36	3.02	2.32	2.12	0.05		0.05	0.60		
Hylurgus ligniperda	0.64	1.30	0.69	0.60	0.19	0.19				0.06	0.06	
Scarabaeidae												
Acrossidius tasmaniae											2.74	
Native												
Carabidae												
Allocinopus sculpticollis		0.05			0.02					0.12		
Amarotypus edwardsii	0.05	0.24	0.40	0.19	0.08	0.09	0.37	0.07		0.33	0.12	
Aulacopodus calathoides	0.52	1.16	1.26	0.38	0.34	0.42	0.99	1.51	0.29	0.73	0.41	1.09
Cicindela parryi	6.94	7.34	2.23	1.28	16.28	0.37	2.27	0.14		1.97	0.10	
Cicindela tuberculata	88.98	105.60	136.40	0.09	2.28	0.92		0.08		22.77	0.48	0.42
Ctenognathus adams[i]	0.18	0.91	1.76	0.09	0.40	0.40	1.04	1.79	1.10	1.32	0.57	1.84
Ctenognathus bidens	0.13	0.45	0.18	0.18	0.19	0.13	6.18	1.46	1.39	0.50	0.64	0.26
Demetrida natsuda			0.05									
Dichrochile maura		0.06		0.06		0.06	0.23	0.71	0.24	0.16	0.16	0.10
Holcaspis mordax	1.53	1.47	1.03	2.93	1.68	1.57	1.94	3.27	2.69	2.30	1.72	2.94
Holcaspis mucronata	0.15	0.10	0.05	0.11	0.15	0.15						
Lecanomerus sharpi	0.11	0.10	0.05				0.26	0.37				
Mecodema occiputale	2.91	1.57	0.80	3.73	3.06	2.06	4.33	3.40	2.94	0.81	0.97	0.05

Mecyclothorax rotundicollis	0.40	1.19	2.26		0.05	0.23				0.51	1.42	1.39
Notagonum submetallicum												0.07
Pentagonica vittipennis		0.06		0.18	0.32	0.37						
Platynus macropterus	0.34	1.21	14.16		0.09	0.15					0.06	0.12
Scopodes edwardsi	0.06											
Scopodes multipunctatus	0.07	0.05										
Scopodes prasinus	0.32	1.14	0.10			0.05	0.06	0.12				
Syllectus anomalus		0.15		0.07	0.02				0.05			
<u>Scolytinae</u>												
Pachycotes peregrinus	1.12	0.66	0.38	0.54	0.73	0.49	0.04			0.04		
<u>Scarabaeidae</u>												
Ataenius brouni						0.03						
Costelytra sp a	0.89	0.30	0.16	0.05	1.36	0.19						
Costelytra zealandica	0.88	0.71	0.16	0.88	0.51	0.05	0.41	0.07		7.35	2.31	6.86
Odontria magnum				0.03	0.03	0.05	0.13	0.07				0.10
Odontria ?piciceps.	2.58	1.36	0.74	2.09	4.84	1.44	1.11	0.55	0.63	1.31	0.72	1.03
Odontria sylvatica	0.75	0.30	0.56	0.14	0.02	0.02	0.86	0.52	0.12	0.27	0.24	0.10
Pyronota "red form"				0.05	0.02					0.25	0.21	1.20
Pyronota festiva	0.13	0.44	0.06	0.46	0.15	0.08	1.17	0.62	0.17	1.35	0.58	0.31
Saphobius squamulosus	0.24	1.07	0.51	0.56	0.49	0.49	1.93	3.70	2.43			
Saphobius sp.							0.42		0.05	0.15		
Stethaspis longicornis	0.12	0.13	0.06	0.03	0.02		0.06	0.05	0.11			

Chapter 5 - Impact of clearfell harvest area on beetle biodiversity in an exotic *Pinus radiata* ecosystem

5.1 Introduction

Plantation forests of native or exotic tree species provide suitable habitat for a wide range of non-production species including plants, invertebrates, fungi, mammals and birds (Humphrey et al. 1999, Hartley 2002, Carnus et al. 2006). However, plantations are production environments and the management practices associated with the forestry industry can have significant impacts on native biodiversity. Quantification of these impacts has concentrated on changes in species composition and species richness associated with harvesting (Niemela et al. 1993, Baker and Lacki 1997, Heliola et al. 2001, Williams et al. 2001, Grove 2002a, Koivula et al. 2002, Clayton 2003). However, the causal mechanisms for such changes, e.g., changes in microclimate and how they influence species traits such as survival, competition and reproduction are less frequently studied and remain poorly understood.

The dominant management model in New Zealand's plantation forests is the planting of large-scale, even-aged stands that are subsequently clearfelled. Globally, plantation managers have adopted clearfell harvesting on the basis of ecological requirements for the growth of saplings, reduced risk of wind damage and marginal economic returns from low value crop species (Kimmins 1992). However, public acceptability of clearfelling has decreased, and the combination of growing environmental awareness and changes in consumer demand has promoted a shift toward environmental certification of forest management practices, such as forest stewardship council certification (Fletcher and Hansen 1999). To meet such environmental standards and to quell growing public concern over clearfell harvesting, many forestry companies have begun to implement alternative harvesting techniques. The impact of these alternative techniques on biodiversity and comparisons with existing clearfell harvesting regimes has been the focus of much recent research (Schowalter 1995, North et al. 1996, Volin and Buongiorno 1996, Prescott 1997, Beese and Arnott 1999, Beese and Bryant 1999, Perry et al. 1999, Bartman et al. 2001, Duguay et al. 2001, Moorman and Guynn 2001, Huggard and Vyse 2002, Knapp et al. 2003), however the true extent of their impacts relative to clearfelling remains unknown (Spence 2001, Koivula 2002b)

In a New Zealand review of environmental certification assessments under the Forest Steward Certification (FSC) scheme, Hock and Hay (2003) highlighted the recurring theme of large clearfells with no size limit as a common area of concern. Given the widespread and longstanding public dislike of clearfell harvesting (McGee 1970, Ribe and Robert 1999) and pressure to move to alternative harvesting techniques (or a pure preservationist ideal), it is surprising that very little research has been undertaken on the impact that clearfell size has on biodiversity (Chapter 2), especially since several alternative-harvesting strategies are merely a series of disconnected small clearfells.

To test the impact of different sized clearfell harvest areas on coleopteran biodiversity, a large-scale project was established in the *Pinus radiata* plantation forests of the central North Island volcanic plateau of New Zealand. Plantation forests present excellent opportunities for ecological research, with a single-species, even-aged canopy structure, and a known forest management history that allows selection of similar stands as replicates of different treatments. As a study taxon, Coleoptera were chosen in order to build on previous community level ecological studies in *P. radiata* plantations and native forest in New Zealand (Hutcheson and Jones 1999, Harris and Burns 2000), and similar European studies of beetle taxa, particularly the family Carabidae (Niemela et al. 1993, Koivula et al. 2002). However, long term monitoring of the ecological impacts of clearfell harvesting on groups such as Coleoptera is difficult. Large-scale complete inventories at a species level are prohibitive in terms of both time and cost. As a solution, the use of indicator taxa have frequently been promoted as an alternative to comprehensive surveys (McColl 1975, Butterfield et al. 1995, Dufrêne and Legendre 1997, McGeoch 1998, Ferris and Humphrey 1999, Panesar et al. 2000). To succeed, such an approach requires robust statistical confirmation of a relationship between the indicator species and the factors under scrutiny (McGeoch 1998). Comprehensive assessments of harvest impacts that utilise species rich groups such as Coleoptera thus have the potential to identify individual taxa that are most sensitive to harvesting treatments so that they may be utilised in the future for targeted monitoring.

This chapter examines the short-term changes in coleopteran biodiversity in response to the experimental creation of different sized clearfell harvest areas in an exotic *Pinus radiata* plantation ecosystem. The main aim was to test the post-harvest change in species richness and community composition of Coleoptera and determine if they are affected by the size of the harvest area.

5.2 Methods

5.21 Sampling design

Short-term changes in coleopteran biodiversity were monitored in six different clearfell harvest sizes, 0.01, 0.05, 0.5, 5, 50 and 500ha. Three replicates of each clearfell size were harvested in 2002, except 5 ha plots that were only represented by two replicates because one replicate was unfortunately not harvested in time (Table 5.1). Smaller clearfells (0.01-5.0 ha) were custom created as squares to the exact size required. Larger clearfells were selected from scheduled forest operations in consultation with the forest manager and varied within 20 % of the desired size. For harvesting reasons small clearfells (0.01-0.5 ha) were located within the same three forest compartments, but individual replicates were separated by a minimum of 150 metres. Larger clearfells were located in different forest compartments. Commercial harvesting crews using standard clearfelling practices were contracted to create all harvest areas.

Pitfall sampling was conducted between 7th December 2002 and 22nd January 2003. Sampling consisted of traps placed at eight distances on a $\log_5$ scale (-125, -25, -5, 0, +5, +25, +125, +625 m, note: positive distances indicate traps placed in clearfell areas and negative distances those in adjacent mature forest stands, transects were also sequentially truncated, where appropriate, to account for the different sized clearfell harvest areas) along edge gradients perpendicular to the boundary between mature *P. radiata* stands and clearfell areas. The 0 m trap was placed at the drip-line of the mature forest stand. Pitfall traps were placed in the mature forest as reference points for comparison with the adjacent samples from clearfelled sites. The pairing of these traps was designed to provide localised “control” traps that reduce the issue of spatial heterogeneity in beetle communities throughout the forest that can be problematic when control sites are located at considerable distances from treatment plots.

Table 5.1. The location of harvest treatments throughout 100-200 ha forest compartments in the central North Island plantations of New Zealand. Abbreviations: Kang = Kaingaroa Forest, Broad = Broadlands Forest, Tawa = Tarawera Forest, Crater = Crater Block, Roto = Rotoehu Forest, Puta = Putauaki Forest. Numbers reflect individual forest compartments, and * denotes the compartment that was not harvested in time. Note: that 500 ha sites were a combination of different forest compartments, only the compartment where the traps were actually sites is listed.

		Harvested 2002	
0.01 ha	Kang 1080	Kang 1105	Kang 278
0.05 ha	Kang 1080	Kang 1105	Kang 278
0.5 ha	Kang 1080	Kang 1105	Kang 278
5 ha	Kang 1017	Kang 1017*	Broad 3
50 ha	Kang 153	Kang 240	Kang 391
200-500 ha	Tawa 132/133	Puta 191/192	Roto 205

All Coleoptera were individually dry mounted on pins and sorted to morphospecies based on external morphological characters. Most species of Aleocharinae (Staphylinidae) and Scydmaenidae were excluded from the analysis due to the poor condition of specimens and the lack of resources to undertake genitalic dissections to ensure accurate species identification. Subsequent catch data were converted to number of individuals per 100 trap days for multivariate analyses (ordinations), in order to account for different sampling durations among traps. Refer to chapter 2 for a comprehensive outline of the study area, pitfall trap design, beetle sampling programme and collection of environmental data.

5.22 Comparing species richness between treatments

The inherent nature of pitfall trap sampling produces data with uneven sample sizes due to the variable number of insects captured in any given trap. To account for this our analysis of species richness used a recently derived moment-based interpolation method (Colwell et al. 2004) that allows direct statistical comparison of species richness between different harvest areas and distances from clearfell edge. Sample based species rarefaction analyses were conducted using untransformed actual catch data in Estimate-S Version 7.5, with random replications set to 100 (Colwell 2004). The pitfall trap gradient was split into clearfell traps (that included the boundary trap) and the adjacent mature forest traps and rarefaction curves were calculated separately. Data are presented as traditional species accumulation curves (with associated 95% confidence intervals), where the x-axis has been rescaled from samples to individuals. The expected asymptote was calculated using the Michaelis Menten running means method (Colwell and Coddington 1994), also in Estimate-S Version 7.5.

5.23 Comparing species composition between treatments

An unconstrained correspondence analysis (CA) was performed to assess absolute variation in species composition among pitfall samples in ordination space, using Canoco V4.02 on log transformed species abundance data (expressed as catch per 100 trap days), with inter-sample distances and biplot scaling (ter Braak and Smilauer 1999).

Because variation in beetle community composition is not only a function of clearfell harvest treatment effects, but is also influenced by environmental variables and spatial autocorrelation among sampling locations a constrained canonical correspondence analysis (CCA) was conducted, incorporating 50 measured environmental variables in Canoco V 4.02 (ter Braak and Smilauer 1999). A forward selection regression procedure was used to test significance of individual environmental variables. Significant collinearity was detected among some environmental variables and was dealt with in two ways: collinear site-level attributes were subsumed into larger more inclusive categories, whereas landscape-level LENZ attributes were incorporated into composite variables by the use of principal components analysis (PCA) (see Gates and Donald (2000)). This resulted in a reduced set of 25 environmental variables (Table 5.2), which were used in subsequent analyses.

If any of the measures of spatial autocorrelation explained significant variation in beetle species composition among sites they were subsequently treated as covariables in a partial canonical correspondence analysis (pCCA). A pCCA conducts an ordination of the species data but removes (‘partials out’) variation attributable to significant environmental variables identified as representing ‘background’ variation (these are termed covariables) priori to testing other environmental factors. This analysis was conducted in Canoco (Version 4.02, GLW-CPRO 1999) using log transformed species abundance data (expressed as catch per 100 trap days), latitude and longitude as covariables and twenty-three environmental variables (Table 5.2).

Table 5.2. Site and landscape variables used as explanatory variables in multivariate ordination analyses. A description is given for each variable and where necessary identifies collinear composite terms. Units of measurement are specified.

Abbreviation	**Description**	**Units**
Site Variables		
Size	Size of harvest area (representing also the collinear interaction terms: Clearfell size * Habitat, Clearfell size * Distance and Clearfell size * Habitat * Distance)	Hectares
Clear	Clearfell or mature forest	Binary dummy variable
Dist	Distance along transect	Metres
Longitude	Longitude of site (representing also the collinear terms: $long^2$, lat * long, $long^3$, $long^2$ * lat, lat^2 * long and $long^2$ * lat^2)	NZMG 260/ 1,000,000
Latitude	Latitude of site (representing also the collinear terms: lat^2 and lat^3)	NZMG 260/ 1,000,000
Canopy Cover	Canopy cover as calculated from hemispherical photographs	Proportion
Dead wood	Dead wood at site	Four binary dummy variables for each factor, see chapter 3 for assessment scale.
Drainage	Drainage of site	
Litter	Leaf litter	
Vege 1	Axis 1 from PCA of vegetation composition	PCA Scores
Vege 2	Axis 2 from PCA of vegetation composition	PCA Scores
Vege 3	Axis 3 from PCA of vegetation composition	PCA Scores
Landscape Level Variables		
500m-nat	Native vegetation within 500m radius	Proportion
500m-exo	Exotic vegetation within 500m radius	Proportion
1000m-nat	Native vegetation within 1000m radius	Proportion
1000m-exo	Exotic vegetation within 1000m radius	Proportion

5000m-nat	Native vegetation within 5000m radius	Proportion
5000m-exo	Exotic vegetation within 5000m radius	Proportion
PCA-1	Axis scores from a PCA analysis of underlying attributes of the LENZ (Land Environments of New Zealand) classification Variables included; water balance ratio, soil particle size, mean annual temperature, annual solar radiation, winter solar radiation, soil parent material hardness and annual water deficit	PCA Scores
PCA-2		PCA Scores
PCA-3		PCA Scores

5.24 Individual species responses

A canonical analysis of principal coordinates (CAP) was conducted to provide a measure of the correlation between individual species and constrained ordination axes. The advantage of the CAP procedure is that the discrimination function can constrain axes such that they are most strongly correlated with pre-defined groups (Anderson and Willis 2003), in this case clearfell harvest size. The analysis was conducted on clearfell data only, i.e., 0, 5, 25 and 125 m traps in clearfell habitat, using the discriminant function of the Fortran program CAP (Anderson 2003a), log-transformed data, automatic selection of the number of principal coordinate (PCO) axes to be retained (in this case 23) and Bray-Curtis distances. Individuals with a correlation greater than $|r| = 0.40$ with CAP axes 1-3 were then selected for further evaluation. Candidate species with a mean trap catch less than 1 per 100 trap days were removed. These species are unlikely to be suitable as indicators of community assemblage change as insufficient specimens would be caught to ensure statistical rigour and repeatability. Changes in the abundance of more common taxa were then compared between different clearfell harvest areas. This was expressed as the percentage change in abundance (ΔN) relative to the adjacent mature forest traps and was calculated as follows.

$$\Delta N = ((C - F)/F)*100$$

Forest insect abundance (F) was calculated as the mean catch per 100 trap days of traps installed at 125m into mature forest. This was to reflect species abundance within ‘deep’ forest and avoid possible edge effects. Abundance within different clearfell sizes (C) was calculated as the mean catch per 100 trap days of the combined 0, 5, 25 and 125 metre traps as appropriate (i.e., smaller clearfells only had 0 and 5m traps due to their smaller size).

5.3 Results

5.31 Beetle species diversity and harvest size

A total of 18,270 beetles were extracted from the 107-pitfall trap samples collected from late December 2002 to late January 2003 (4,841 active trap days). A total of 355 species from 45 families were collected (the number of families recorded includes the Scydmaenidae that were excluded from other analyses, see methods). This represents 55% of the 82 families reported from the New Zealand sub-region (Klimaszewski and Watt 1997). Expert identification of morphospecies is important (Ward and Larivière 2004) and in this case resolved 24 cases of incorrect morphospecies, due to in most cases over-splitting of morphologically variable taxa. Staphylinidae and the Curculionidae dominated the fauna. The trap catch of individual species showed a typical, highly skewed distribution of a few common species and many rare species, with 106 species represented by a single specimen. The most common species were *Thalycrodes australis* (1793 individuals, Family: Nitidulidae), *Cicindela tuberculata* (1544 individuals, Family: Carabidae) and *Pycnomerus sophorae* (1476 individuals, Family: Zopheridae). Only 21 species (5.9%) were known adventives, including some significant forestry and agricultural pests, e.g., *Hylastes ater* and *Sitona discoidea* pests. A detailed breakdown of species and their actual catch in different harvest areas is given in Appendix 5.1.

Rarefied native beetle species richness in clearfells increased idiosyncratically with harvest area throughout the range of clearfell sizes. Accumulation curves (Figure 5.1a) show lower species richness in smaller harvest areas compared to large 500 ha clearfells. The steep slope of the 500 ha curve suggests that the total number of species from these sites is much greater than was actually sampled. In contrast the slope of the accumulation curve in smaller harvest areas is lower, indicating that a larger proportion of the total species pool was sampled (Figure 5.1a). Among the smaller harvest areas, 5 ha sites had significantly greater species richness than 0.01-0.5 ha harvests (based on 95% confidence intervals (Colwell 2004)), whereas the species richness of 50 ha harvest areas was marginally, but not significantly, greater than 0.01-0.5ha treatments (Figure 5.1a).

Native beetle species richness in mature *P. radiata* stands showed similar patterns to their adjacent clearfells. Mature stands adjacent to large 500 ha clearfells had significantly greater species richness than those of other harvest area treatments (Figure 5.1b). Also, the 50 ha and 5 ha treatments were slightly higher than the smaller 0.01- 0.5 ha harvest areas.

Rarefied native beetles species richness changed with distance from the forest-clearfell boundary (Figure 5.2). However, the slope of individual accumulation curves was more similar at all distances except 625 m. The steep slope of the accumulation curve at 625 m into clearfells reflects the higher diversity in 500 ha replicates (Figure 5.1a & b) as this distance was only present in the 500 ha stands. Note: The asymptote was not calculated for 625 m as its validity would be questionable given the extrapolation from only three samples. Species richness in deep forest (125 m into mature *P. radiata*) was significantly lower (based on 95% confidence intervals) than forest edge samples and all distances into adjacent clearfell harvest areas except at 25 m.

5.32 Composition of beetle assemblages

There were distinct differences in beetle community composition among clearfell harvest treatments (Figures 5.3 & 5.4). Axes 1 and 2 of an unconstrained correspondence analysis of beetle species composition clearfell pitfall traps explained 5.4 % and 3.9 %, of the variation respectively, and showed a clear separation between the beetle communities in 500 ha sites versus other clearfell areas (Figure 5.3). Changes in the community composition among the remaining harvest areas are difficult to determine due to the dominant effect of 500 ha sites in ordination space.

Eleven of the 25 environmental factors (Table 5.3) explained significant variation in beetle community composition in a forward selection regression procedure in a CCA analysis (Table 5.3). Both composite spatial variables (latitude and longitude, Table 5.2) proved significant predictors of species distributions. This combined with a significant correlation observed between harvest area and latitude, as well as between harvest area and longitude (Spearman Rank Correlation, Latitude; $R = 0.412$, $P<0.001$, Longitude; $R = 0.406$, $P<0.002$) led us to assign them as confounding spatial effects and the model was rerun as a partial-CCA with these coded as covariables.

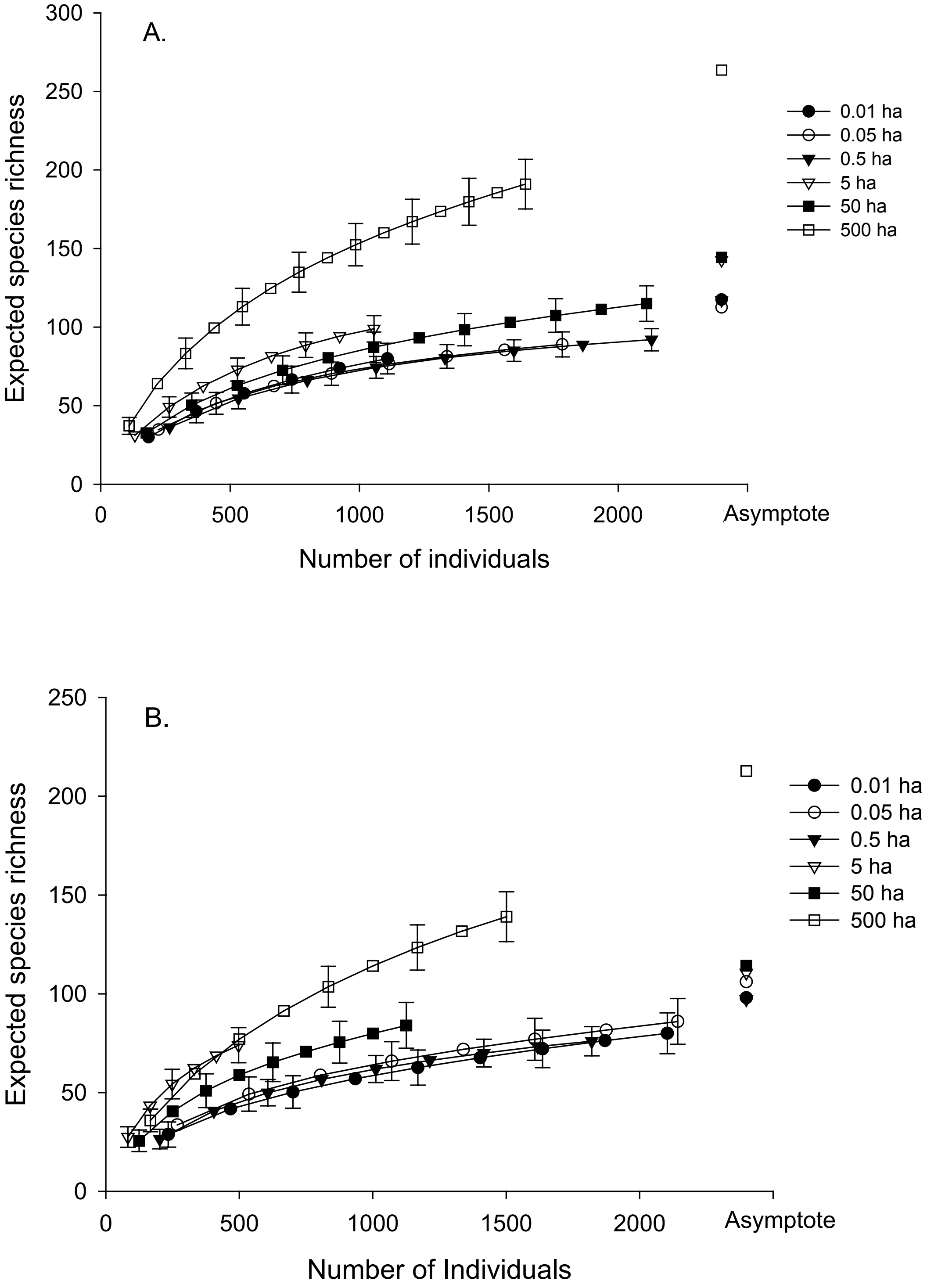

Figure 5.1. Sample based rarefied species richness, rescaled and expressed as individuals (x-axis), error bars are 95% confidence intervals. A) As a function of different sized clearfell harvest areas, and B) of mature *P. radiata* stands situated adjacent to the different size clearfell harvest areas.

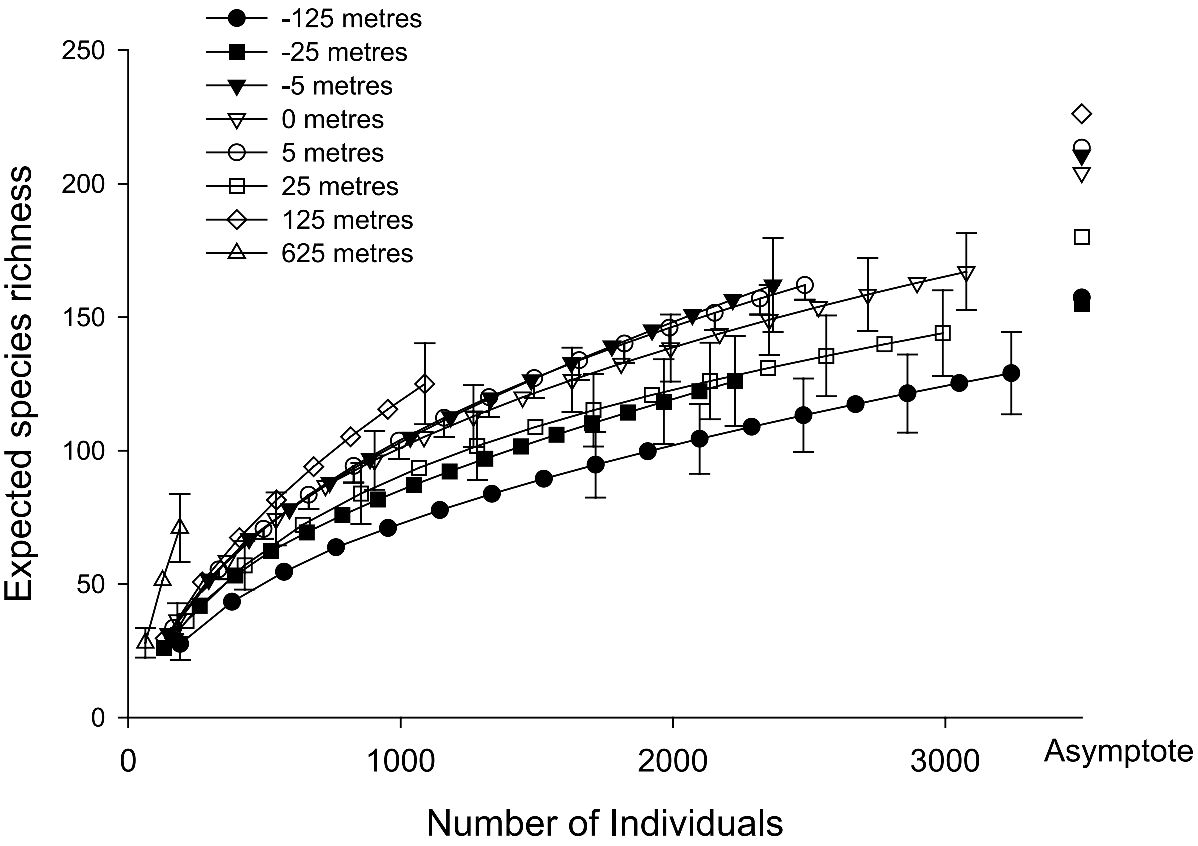

Figure 5.2. Sample based rarefied species richness, rescaled and expressed as individuals (x-axis) as a function of distance across a clearfell, mature forest gradient. Negative distances represent traps in mature *P. radiata* stand, positive distances those in clearfells. Error bars represent 95% confidence intervals calculated in Estimate-S Version 7.5.

Plotting all sites (clearfell and adjacent mature forest controls) on axes 1 and 2 of the pCCA showed a trend from small harvest areas at negative axis values to larger clearfells at higher axis values (Figure 5.4a). Eight sites formed two distinct, closely related clusters at highly positive values of axis 1. These sites correspond to a single 500 ha replicate situated on the north-eastern flank of Mt Tarawera. The two groups of four sites represent the clearfell samples and the adjacent forest control samples respectively. Comparing a pCCA plot of axes 1 & 2 of only clearfell sites (Figure 5.4b) with the full plot of clearfell and adjacent forest controls (Figure 5.4a) it shows that the species assemblages of small clearfell areas have greater similarity with their forest controls than the larger harvest areas.

5.33 Environmental variables as an explanation for community composition

Intra-set correlations of environmental variables (that were shown to add significant explanatory power to the ordination by a forward selection procedure) show that axis 1 is most highly correlated with the proportion of native vegetation within 500 m of the site (Figure 5.4). However, the 500 ha plot mentioned above from the north-eastern flank of Mt Tarawera was the only site with significant amounts of native vegetation within 500m. This is reflected in the position of the native-500m environment arrow, indicating a major influence of the proximity of native forest on beetle species composition at this site (Figure 5.4a). Clearfell harvest size and larger-scale landscape attributes, such as the proportion of exotic and native vegetation within a 1000m and 5000m radius were also highly correlated with changes in beetle species composition (Table 5.3).

Table 5.3. Significant environmental variables from a forward selecting regression (Canoco) both before (a) and after (b) assignment of significant spatial variables as covariables. Intraset correlations are given that define the strength of the relationship between environmental variables and the constrained ordination axes of the pCCA after the removal of spatial autocorrelation due to covariables. λ -A is the additional variance explained by each variable at the time it was included in the forward selection analysis, P is the significance of the F-value from a Monte-Carlo test with 500 replicates.

a)

Environmental Variable	**Without covariables**		
	λ-A	**F**	**P**
Clearfell size	0.35	5.22	0.002
Proportion of native vegetation within 500m	0.25	3.81	0.002
Clearfell vs. Forest	0.18	2.70	0.002
longitude	0.13	2.02	0.002
Distance along transect	0.13	2.00	0.002
PCA LENZ Axis 3	0.11	1.78	0.002
Proportion of exotic vegetation within 1000m	0.11	1.74	0.002
Latitude	0.10	1.70	0.002
PCA LENZ Axis 2	0.10	1.50	0.002
PCA LENZ Axis 1	0.10	1.73	0.002
Proportion of exotic vegetation within 5000m	0.10	1.60	0.002

Table 5.3b)

Environmental Variable	**With covariables**			**Intraset correlations with pCCA**	
	λ -A	**F**	**P**	**Axis-1**	**Axis-2**
Proportion of native vegetation within 500m	0.25	3.76	0.001	0.854	-0.42
PCA LENZ Axis 2	0.18	2.86	0.001	-0.655	-0.461
Clearfell vs. Forest	0.17	2.64	0.001	0.323	0.521
Distance along transect	0.13	2.02	0.001	0.123	0.090
PCA LENZ Axis 3	0.11	1.77	0.001	0.073	0.340
Proportion of exotic vegetation within 1000m	0.11	1.76	0.001	-0.706	0.344
Clearfell size	0.09	1.5	0.001	0.737	0.371
PCA LENZ Axis 1	0.11	1.73	0.001	0.351	-0.106
Proportion of exotic vegetation within 5000m	0.1	1.6	0.001	-0.706	0.344
Latitude Longitude	Added as covariables to model				

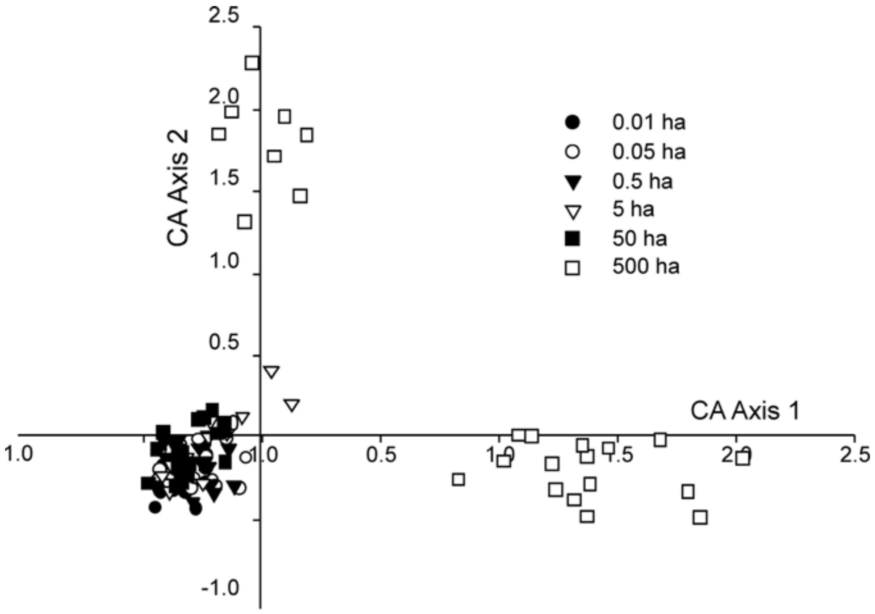

Figure 5.3. Correspondence analysis ordination diagram of axis 1 and 2 scores showing samples from different clearfell harvest sizes. Samples from 500 ha clearfell areas had very different community assemblages to other smaller harvest areas. Note: traps from the entire transects, including mature forest adjacent to the clearfell harvest areas are shown.

5.34 Identifying species responsible for multivariate patterns

Eighteen species had a correlation with CAP axes greater than |r| = 0.40 and an abundance greater than 1 per 100 trap days. All of the nine species correlated with axis 1 of the CAP ordination showed negative correlations, indicating a preference for forested areas or small clearfells of 0.01 and 0.05 ha (Table 5.4). This was reflected in the change in abundance of these species between clearfells and their adjacent forest areas, e.g., *Hylastes ater* (Figure 5.5) and *Pycnomerus sophorae* (Figure 5.6) that were much more numerous in traps from small harvest areas compared to larger clearfells. In contrast *Cicindela tuberculata* that is negatively correlated with CAP axis 2, had higher abundances in medium sized clearfell areas, peaking at 0.5 ha (Figure 5.7). *Sitona discoideus* was the only species to be highly correlated with axis 3 of the CAP analysis and had greater abundance in clearfell areas compared to mature forest, in all harvest sizes except 5 ha (Table 5.4).

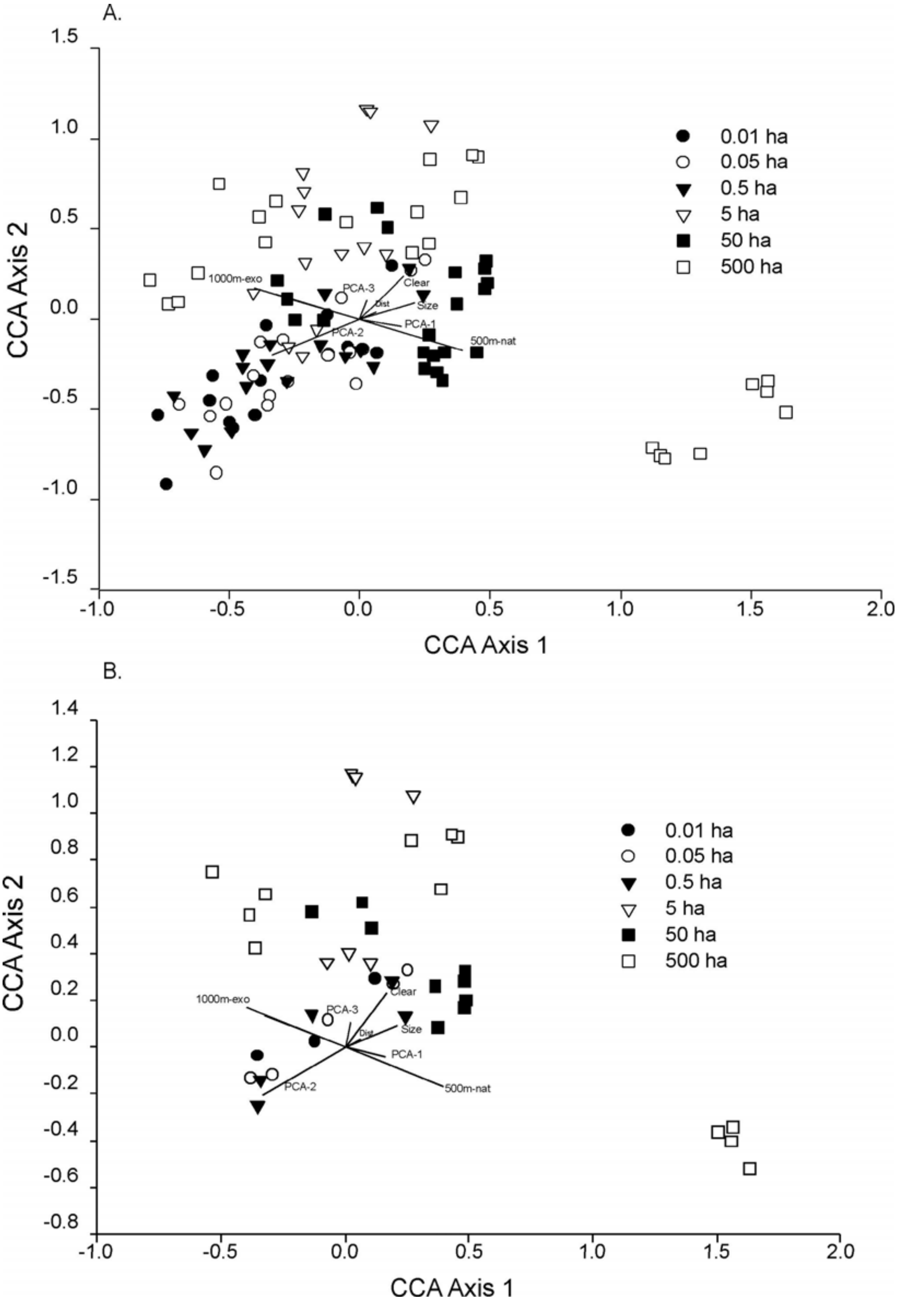

Figure 5.4. A) Partial CCA of all sites (forest and clearfell) with longitude and latitude removed as covariables. Significant environmental variables from a forward selection regression (Table 5.3) are given as lines from the origin, abbreviated environmental names are given in full in Table 5.2. B) Same pCCA showing only clearfell harvest sites. Comparisons show greater similarity between small clearfells and mature forest than with larger clearfell harvest areas.

5.4 Discussion

5.41 Effect of clearfell size on beetle species richness

The greater rarefied species richness in recent clearfells compared to adjacent mature *P. radiata* forest (Figure 5.2) is consistent with the post-harvest responses of carabid beetles in Europe (Niemela et al. 1993, Koivula et al. 2002). This increase has been attributed to the temporary retention of forest species augmented by colonisation by open-habitat species. Clearfells are often defined as harvest areas sufficient to cause a transition from a forest to an open-habitat microclimate (Kimmins 1992). As such, the observed trends in species richness across the forest boundary (Figure 5.2) suggest that post-harvest biodiversity within clearfells may change with harvest area. Why, because harvest area is a key factor in determining the degree of microclimatic change (Spittlehouse et al. 2004).

Microclimate studies indicate that the forest edge provides a moderating influence on the climate in open areas to a horizontal distance of one to two tree heights (Davies-Colley et al. 2000, Spittlehouse et al. 2004). Thus harvest areas of this size are a logical starting point to investigate potential threshold harvest areas that may result in significant change to species richness post-clearfelling. Based on stand records, the height of mature *P. radiata* in the study area was approximately 30-35 m at harvest indicating a potential harvest threshold of approximately 0.5 ha. The change in species richness between small 0.01 – 0.5 ha areas and slightly larger 5 ha areas is consistent with the notion of an ecological threshold; where small harvest areas retain microclimatic buffering from adjacent forest and larger harvest areas are transformed to an open habitat microclimate. However, based on our data such thresholds remain speculative, especially since the higher species richness in 50 ha sites is not significantly different from smaller harvest areas. Further sampling is required to determine if such threshold clearfell sizes are biological realities or an artefact of sampling.

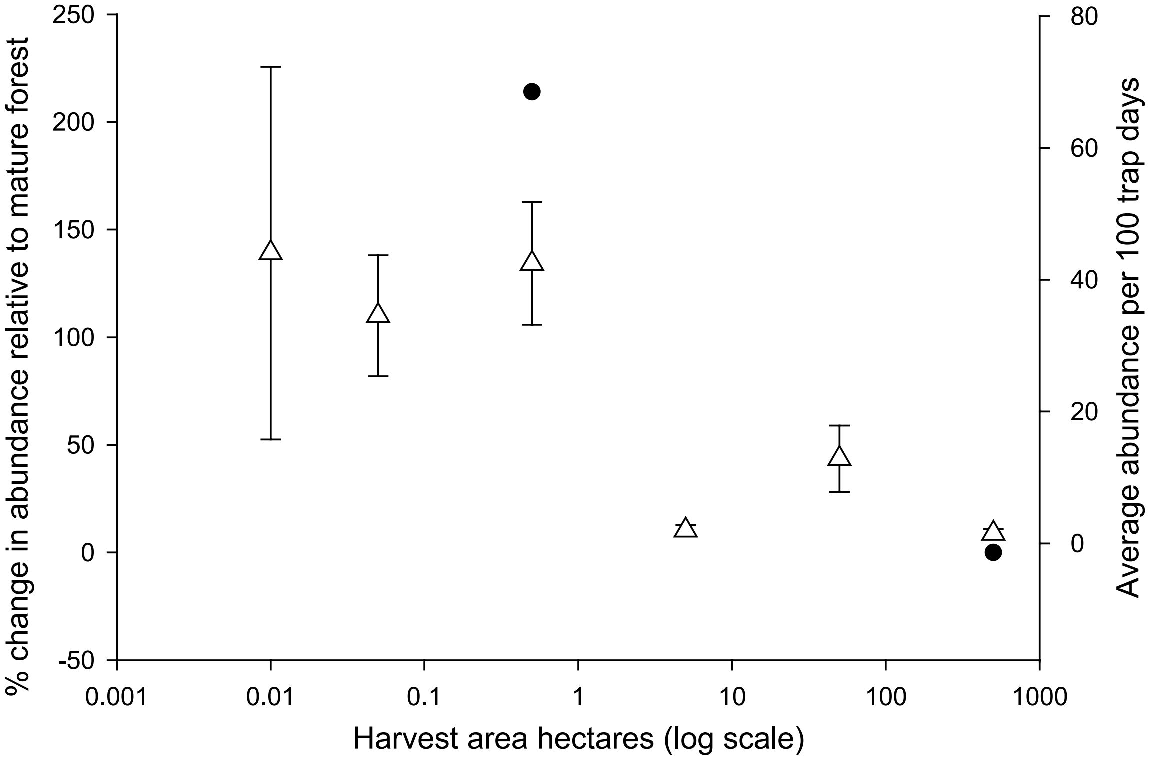

Figure 5.5. Difference in abundance of *Hylastes ater* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *H. ater* in clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale and when abundance in deep forest sites was zero differences could not be calculated and thus no value is given.

Determining the presence or absence of such a threshold size is important as it could have significant implications for forest management and future research into new silvicultural techniques. For example, many studies have compared the impact of alternative harvesting systems versus clearfelling on biodiversity (Beese and Arnott 1999, Beese and Bryant 1999, Huggard and Vyse 2002, Koivula 2002a, Knapp et al. 2003). These alternatives are in many cases small interspersed clearfells, but frequently research fails to account for the influence of harvest area.

Table 5.4. Abundance of individual species in mature *Pinus radiata* 125 m from the forest edge, average abundance at 0, 5, 25 and 125 m into clearfells and the change in abundance of taxa highly correlated with ordination axes 1-3 of a constrained analysis of principal coordinates (Anderson and Willis 2003) at different clearfell harvest sizes.

		0.01 ha			**0.05 ha**			**0.5 ha**			**5 ha**			**50 ha**			**500 ha**		
CAP Axis 1	**Correlation with CAP Axis**	**Forest**	**Clearfell**	**Change**	**Forest**	**Clearfell**	**Change**	**Forest**	**Clearfell**	**Change**	**Forest**	**Clearfell**	**Change**	**Forest**	**Clearfell**	**Change**	**Forest**	**Clearfell**	**Change**
?*Phrynixus* sp.	-0.413	0.83	2.08	150.60	0.00	2.19		2.46	19.68	700.00	0.00	2.61		0.00	16.51		0.00	0.45	
Ctenicera sp.	-0.416	5.83	13.70	134.99	6.57	3.65	-44.44	1.67	7.80	367.07	0.00	0.32		17.68	8.78	-50.34	0.00	0.00	
Sepedophilus sp.	-0.423	5.82	4.97	-14.60	3.25	5.01	54.15	4.13	4.78	15.74	1.32	1.64	24.24	0.83	1.88	126.51	1.52	0.76	-50.00
Odontria ?piciceps	-0.473	1.67	17.78	964.67	0.00	23.24		16.51	8.85	-46.40	0.00	0.97		1.67	19.64	1076.1	0.00	0.76	
?*Conoderus* sp.	-0.484	0.83	0.81	-2.41	0.83	5.82	601.20	2.50	21.88	775.20	6.58	3.62	-44.98	8.33	7.50	-9.96	0.00	0.00	
Parepierus sp.	-0.516	10.70	12.62	17.94	14.96	15.25	1.94	12.38	1.85	-85.06	1.32	2.29	73.48	0.83	2.30	177.11	0.00	0.00	
Hylastes ater	-0.590	0.00	44.06		0.00	34.54		13.53	42.48	213.97	0.00	1.97		0.00	12.84		1.52	1.52	0.00
Pycnomerus sophorae	-0.702	105.89	98.42	-7.05	47.47	95.13	100.40	47.30	27.83	-41.16	32.15	7.46	-76.80	137.94	12.18	-91.17	1.52	1.67	9.87
Thylycrodes australis	-0.796	73.86	44.56	-39.67	78.97	87.66	11.00	111.29	101.96	-8.38	7.76	39.07	403.48	36.36	20.99	-42.27	0.76	0.45	-40.79
CAP Axis 2																			
Paracatops phyllobius	0.596	67.44	22.32	-66.90	32.61	4.09	-87.46	118.30	7.55	-93.62	7.86	0.66	-91.60	0.83	0.00	-100.00	28.79	7.42	-74.23
Phrynixus astutus	0.459	14.99	15.41	2.80	12.53	17.16	36.95	17.56	13.50	-23.12	1.28	0.64	-50.00	3.33	10.93	228.23	12.88	8.94	-30.59
Eupuraea sp.1	0.436	9.69	11.38	17.44	24.15	3.75	-84.47	12.63	0.32	-97.47	0.00	0.65		3.38	1.06	-68.64	9.09	1.67	-81.63
Eupuraea sp.2	0.412	8.06	5.36	-33.50	16.67	0.62	-96.28	6.53	0.92	-85.91	7.73	0.64	-91.72	21.71	0.66	-96.96	34.85	1.82	-94.78

Brounthina aequalis	0.401	34.82	13.33	-61.72	20.54	1.85	-90.99	105.84	2.17	-97.95	0.00	0.66		0.00	0.00		0.00	0.00	
Cicindela tuberculata	-0.415	0.00	0.00		0.00	68.38		0.00	206.24		0.00	125.38		0.00	31.41		0.00	18.79	
Cotes sp.	-0.468	4.07	4.76	16.95	8.93	0.92	-89.70	4.92	4.32	-12.20	1.28	10.47	717.97	7.85	10.21	30.06	0.76	1.06	39.47
Gromilus sp.	-0.480	0.00	0.40		0.00	1.57		0.00	2.79		3.95	5.87	48.61	2.50	5.44	117.60	0.00	1.06	
CAP Axis 3																			
Sitona discoideus	0.525	0.00	1.28		0.00	3.78		0.00	15.11		1.32	0.96	-27.27	0.00	6.96		0.76	3.33	338.16

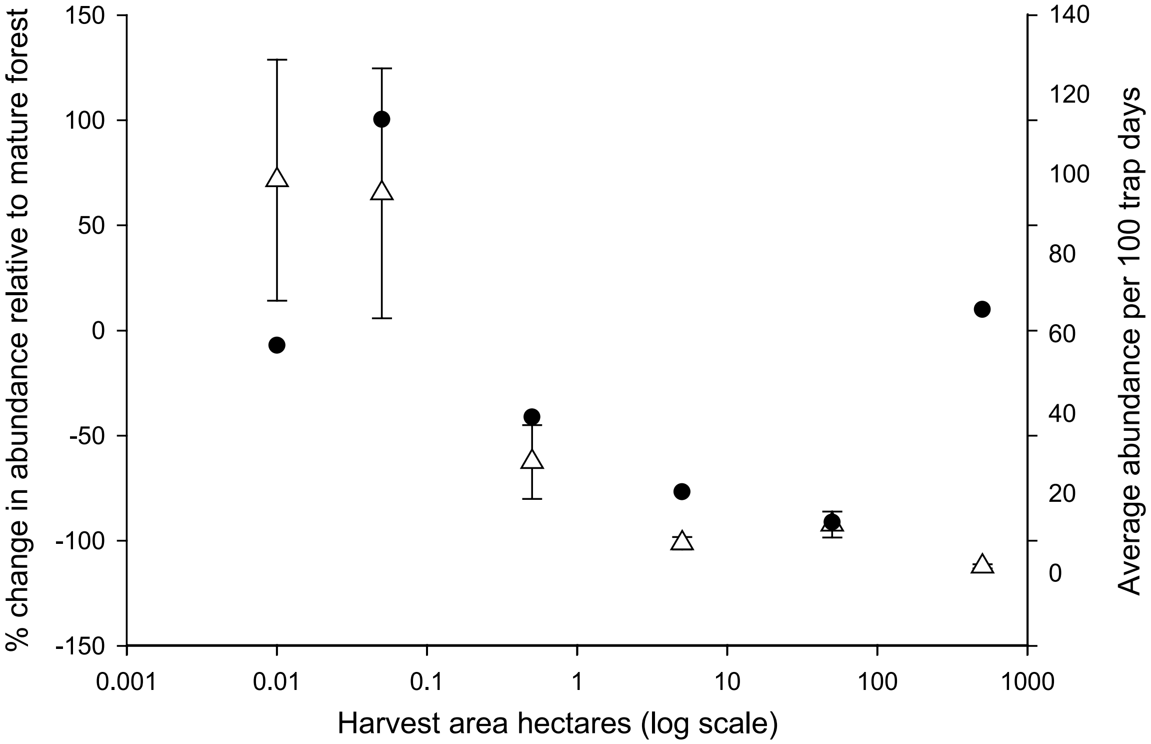

Figure 5.6. Difference in abundance of *Pycnomerus sophorae* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *P. sophorae* in clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale and when abundance in deep forest sites was zero differences could not be calculated and thus no value is given.

Species richness in the large (500 ha) areas was significantly greater than all other harvest areas sampled (Figure 5.1). However, harvest area is not the only important factor determining species richness as the mature forest stands adjacent to the 500 ha clearfells were also very species rich (Figure 5.1b). The reasons for this are unknown, although 500 ha sites were situated further north than other sites and had a greater proportion of native remnants within the immediate landscape. The use of adjacent mature *P. radiata* controls was important in this study as it identified the presence of site-specific factors that affected species richness, a result that may otherwise have been attributed solely to the clearfell harvest size treatment.

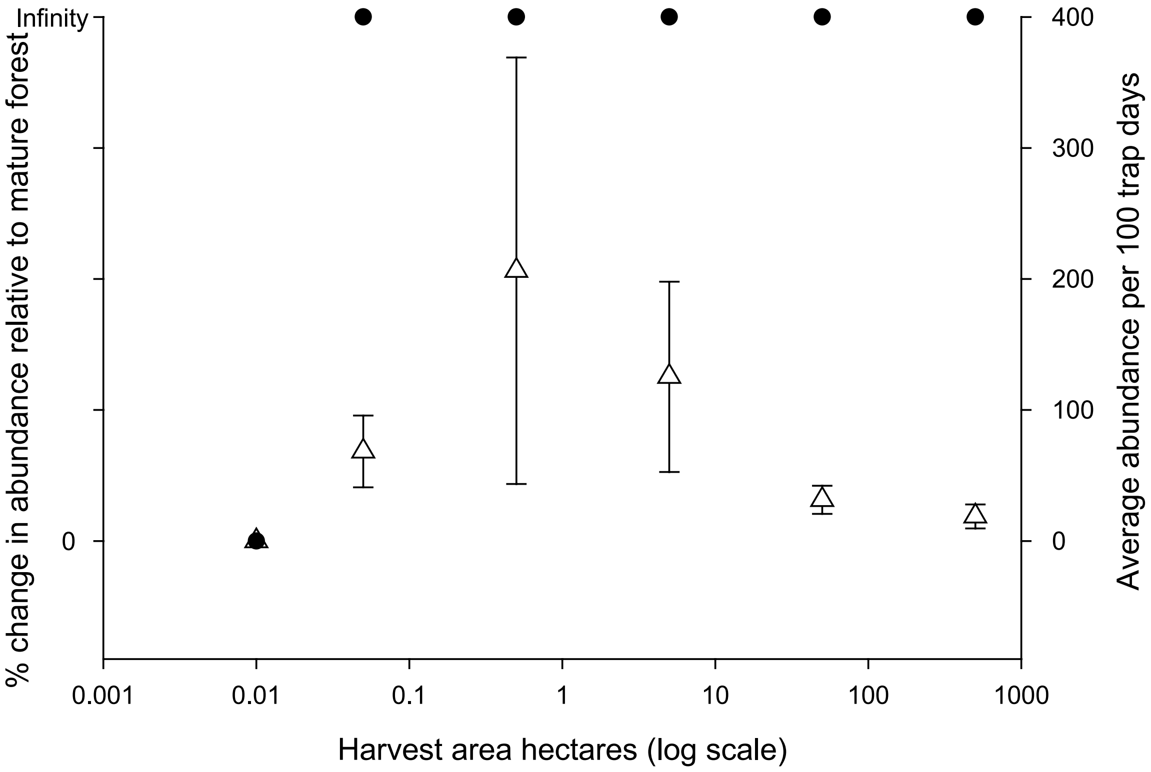

Figure 5.7. Difference in abundance of *Cicindela tuberculata* between clearfell and mature forest relative to the mature forest abundance (●) and the average abundance of *C. tuberculata* in clearfell areas (Δ) as a function of clearfell harvest size. Note: clearfell harvest size is expressed in hectares on a log scale, no *C. tuberculata* were caught in deep forest and thus the calculated values for the difference between clearfell and forest habitats when individuals were sampled from clearfells was infinity.

5.42 Effect of clearfell harvest size on beetle species composition

Given that beetle species richness appears to be influenced in part by harvest area and that other studies have documented changes in species composition related to clearfell harvesting (Niemela et al. 1993, Heliola et al. 2001, Koivula et al. 2002), I would expect to find changes in beetle species composition with changing harvest area. My results showed decreased similarity in the community composition of forest and clearfells with increasing harvest size (Figure 5.4). This may reflect the negligible change in some microclimatic variables in small harvest areas that are still buffered from open habitat conditions by the adjacent mature forest (Davies-Colley et al. 2000, Spittlehouse et al. 2004). The larger sites ranging from 5 – 500 ha have distinct open habitat microclimates that would in part be responsible for the greater difference in species composition between clearfell and forest portions of the sampling transect (Figure 5.4). However, the increasing distance from source populations at the forest edge may have contributed to the change in species composition in larger clearfell harvest sizes. Interestingly the 0 m traps placed on the drip line of the mature forest had a faunal composition most similar to forest traps despite habitat disturbance characteristic of clearfell areas.

Large clearfells have beetle assemblages that are different from those of small clearfells (Figure 5.4), and individual species in these larger clearfells can have significantly different abundances relative to those in adjacent mature forest (Table 5). However, it must be recognised that change in individual species abundance also occured at much finer spatial scales, e.g., 0.01-0.05 ha. The individual species responses to clearfell harvest size were variable, some species increased in abundance, e.g., *C. tuberculata* (Figure 5.7) whereas others decreased, e.g., *H. ater* (Figure 5.5) and *P. sophorae* (Figure 5.6). Species with strong negative correlations relative to CAP axis 1 favoured small 0.01-0.05 ha clearfell openings (Table 5). This infers a preference for a microclimate more similar to mature forest than to large clearcuts. However, the abundance of some species was sensitive to even the smallest clearfell harvest areas. For example, *Paracatops phyllobius*, *Brounthina aequalis* and *Pycnomerus sophorae* all had abundances greater than 30 per 100 trap days in the –125m mature forest control sites, yet in the adjacent 0.01 ha clearfells their abundance decreased, dropping -66.9 %, -61.72 % and -7.05 %, respectively, compared to adjacent mature forest. Meanwhile, *Hylastes ater* was abscent in –125 m mature forest controls and increased to 44.1 per 100 trap days. It is unlikely that the microclimate in small 0.01 ha harvest areas would have changed substantially (however this was not tested) therefore it is anticipated that other factors, such as individual biological traits of species or habitat disturbance, e.g., changes to leaf litter (Koivula et al. 1999, Magura et al. 2005) have significant influences on the abundance of species post clearfelling.

The biology of *Hylastes ater* is well known, largely due to its significance as a forest pest (Milligan 1978). The increased abundance of *H. ater* post-harvest, particularly in smaller harvest areas of 0.01-0.5 ha, is unlikely to reflect a preference for open habitat, but of an attraction to host volatiles from recently felled timber (Reay and Walsh 2002, Brockerhoff et al. Submitted a). Lower trap catches in larger harvest areas are potentially the result of a dilution effect, where a finite number of individuals in the surrounding environment have colonised a larger resource. Alternatively, the forest edge could be an attractor or barrier to dispersal out of the clearfells increasing trap catch of *H. ater* at the forest boundary. *P. phyllobius*, *B. aequalis* and *P. sophorae* all reacted negatively to habitat disturbance, however, little is known about the biology of these species that may explain the drop in abundance in small 0.01 ha harvest areas. These species are thought to be litter layer scavengers that may feed on subterranean fungi, however basic research is required on the biology of these species before the mechanisms driving these post-harvest changes in beetle assemblages can be inferred.

5.43 Species richness of plantation habitat

The total number of beetle species (355 species) identified was much greater than the 131 morphospecies recorded in samples from Hutcheson and Jones (1999) in their study of Coleoptera in New Zealand *P. radiata* plantations. Beetle species richness was also higher than studies of other New Zealand ecosystems dominated by exotic vegetation, e.g., gorse, 60 species (Harris et al. 2004), pasture, 30-70 species (Harris and Burns 2000). The high species richness observed here reflects, in part, a more extensive sampling strategy (that is known to influence species richness (Bunge and Fitzpatrick 1993, Gotelli and Colwell 2001)) including greater geographical range compared to other studies. However, the higher species richness is probably, in part, attributable to the different sampling techniques (pitfall versus Malaise). Such sampling differences were observed by Prentice *et al.* (2001) who found large differences in the species catch of spiders between malaise and pitfall traps. Irrespective of the sampling issues of comparing between studies, our results provide further support for the role of plantations in the conservation of biodiversity.

5.44 Edge gradients

Beetle species richness was greatest in clearfells and at edges (Figure 5.2), which is consistent with results from other studies that compared Carabidae in clearfells and forests in Europe (Niemela et al. 1993, Heliola et al. 2001, Magura 2002). This increased diversity in open habitats has been attributed to an influx of open-habitat, disturbance-adapted species and the short-term retention of forest species, which may, or may not be able to sustain breeding populations in the recently created clearfells (Niemela 1997, Fahy and Gormally 1998, Ings and Hartley 1999). Most of these studies took place in Europe and focus on the family Carabidae, whose ecological requirements are well known in the Northern Hemisphere. The extent of the open habitat effect is difficult to calculate in this study, as the taxonomy of the New Zealand insect fauna is not fully understood (Watt 1975), let alone their biology. However, the increased abundance of some known open habitat species of Carabidae in this study post-clearfelling, e.g., *Cicindela tuberculata* (and *Hypharpax* spp. and *Lecanomerus* spp. see chapter 3), suggests that similar processes are responsible.

5.45 Limitations of the study design

The greater species richness of 500 ha sites highlights one of the limitations of studying biodiversity by manipulative experiments in commercial forests at the landscape-scale. Greater control of experimental design can be achieved in large-scale experiments if the research is conducted on land owned by the research institute (Vyse 1999). I worked in a commercial forest and the economic value of commercial timber species within a 500 ha area was immense and experimental designs were not top priority in the decision of when and where such areas would be cut. In this study, 500 ha sites were concentrated in the northern area of Kaingaroa Forest, as I was constrained by the pre-defined harvesting plans of the participating forestry companies. An unconstrained CA analysis of beetle abundances showed distinct differences between uncut mature forest stands adjacent to 500 ha sites and all other harvest areas (Figure 5.3), which highlights the geographical variation in faunal composition. Furthermore, species richness was greater in the *P. radiata* stands surrounding the 500 ha samples (Figure 5.1b). There are many factors that could contribute to this, including the lower elevation, increased temperature and higher rainfall (Quayle 1983), which results in greater plant growth rates as measured by the *P. radiata* site index (Hunter and Gibson 1984). These physical characteristics that contribute to the growth of tree species also promote higher diversity of native plant species in indigenous forest (Leathwick et al. 1998). In addition northern study areas have an extensive network of native forest remnants that are absent from other areas of Kaingaroa Forest. The proportion of native forest within 500 m was the strongest environmental predictor of species assemblages (Figure 5.4), corroborating the findings of UK studies that have shown beetle species richness to be correlated with native vegetation proximity (Humphrey et al. 2004). The influence of remnant native habitat in these plantation dominated landscapes needs further investigation, as the role of landscape heterogeneity is increasingly acknowledged as a key determinant of biodiversity in managed forest landscapes (Humphrey et al. 2004, Lindenmayer and Hobbs 2004).

Environmental variables that were confounded with the 500 ha treatments can be partialled out using covariables in the ordination analyses. However, this is not possible for the rarefied species richness analysis, and these confounding factors should be considered when interpreting results from the largest harvest areas.

5.5 Conclusions

The impacts of clearfell harvesting on biodiversity have received considerable attention, however this study is the first attempt to quantify clearfell harvest impacts by experimental manipulation at a size relevant to current forestry practices in large-scale plantation forests. The degree of change in beetle species richness and community composition increased with clearfell harvest area. However, these results should be considered as the short-term context and long-term changes must be monitored, as the entire rotation response is critical to determine the full impacts of clearfelling as a silvicultural practice. Monitoring of invertebrate biodiversity is difficult due to the sampling of taxonomically diverse groups (Oliver and Beattie 1996), care should be taken of the selection of potential ‘indicator’ species for long-term monitoring projects as phylogenetic relatedness is not a reliable predictor of correlations (Oertli *et al.* 2005).

Given that beetle community assemblages change with clearfell harvest size it is important to include harvest area as a variable in comparisons between different silvicultural treatments. Results from the beetles sampled here suggest no significant ecological harvest size threshold to changes in species richness, but there is stronger evidence for a threshold change to species composition. Further work is required using other taxonomic groups, such as plants, lichens, fungi and birds, at spatial scales similar to this study, to examine the possibility of threshold changes in other groups that may be more sensitive to harvest impacts. However, the possibility exists that the most sensitive species are already locally extinct (prior to reforestation as a plantation), thus diminishing the observable effect of experimental manipulation of clearfell size. Significant environmental correlates to beetle species richness suggest that plantation managers should focus on broader landscape level issues, such as the isolation of forest stands from native habitat, as this appears to have a major effect on stand-level biodiversity.

Appendix 5.1 Raw species data of all 355 species and actual individual species catch in each habitat.

Family	**Genus/Species**	**Authority**	**0.01 ha**	**0.05 ha**	**0.50 ha**	**5 ha**	**50 ha**	**500 ha**	**Total**
Aderidae	*Xylophilus sp.126*		0	1	0	0	0	0	1
Anobiidae	*Megabregmus sp.234*		0	0	0	0	0	2	2
Anthicidae	*Anthicus sp.346*		0	0	0	0	0	22	22
Anthicidae	*Cotes sp.345*		39	31	29	36	74	13	222
Anthicidae	*Cotes crispi*	(Broun, 1880)	6	4	5	6	19	1	41
Anthicidae	*Sapintus pellucidipes*	(Broun, 1880)	7	29	43	35	486	46	646
Anthicidae	*Trichananca fulgida*	Werner and Chandler, 1995	1	0	5	0	12	0	18
Anthribidae	*Etnalis spinicollis*	Sharp, 1873	0	0	2	0	0	1	3
Anthribidae	*Phymatus sp.229*		0	0	0	0	1	0	1
Byrrhidae	*Microchaetes sp.72*		8	19	20	35	17	16	115
Byrrhidae	*Synorthus sp.71*		0	0	0	0	0	41	41
Byrrhidae	*Synorthus sp.68*		0	0	0	2	35	0	37
Byrrhidae	*Synorthus sp.73*		0	0	0	0	0	27	27
Byrrhidae	*Synorthus sp.69*		0	0	0	1	0	0	1
Carabidae	*Allocinopus sculpticollis*	Broun, 1903	0	0	0	0	0	2	2
Carabidae	*Amarotypus edwardsi*	Broun 1872	0	0	0	0	0	17	17
Carabidae	*Anomotarus variegatus*	Moore, 1967	0	0	0	0	0	3	3
Carabidae	*Aulacopodus calathoides*	(Broun, 1886)	0	0	9	19	6	41	75
Carabidae	*Cicindela tuberculata*	Fabricius, 1775	1	219	663	387	150	124	1544
Carabidae	*Cicindela parryi*	White 1846	16	57	11	3	192	9	288
Carabidae	*Ctenognathus adamsi*	(Broun, 1886)	19	2	12	32	7	8	80
Carabidae	*Ctenognathus bidens*	(Chaudoir, 1878)	0	0	0	0	0	5	5
Carabidae	*Demetrida nasuta*	White, 1846	0	0	0	0	1	0	1
Carabidae	*Dicrochile maura*	Broun, 1880	0	0	0	0	0	2	2
Carabidae	*Genus sp.89*		0	0	0	0	0	1	1
Carabidae	*Genus sp.90*		0	0	1	0	0	0	1
Carabidae	*Holcaspis mordax*	Broun, 1886	19	19	28	21	28	22	137
Carabidae	*Holcaspis ?mucronata*	Broun, 1886	0	0	0	0	0	7	7

Carabidae	*Hypharpax australis*	(Dejean, 1829)	0	0	1	0	0	0	1
Carabidae	*Lecanomerus vestigialis*	(Erichson, 1842)	1	1	0	2	4	3	11
Carabidae	*Lecanomerus sharpi*	(Csiki, 1932)	0	0	0	0	0	2	2
Carabidae	*Mecodema occiputale*	Broun, 1923	6	17	16	1	35	14	89
Carabidae	*Mecyclothorax rotundicollis*	(White, 1846)	2	4	3	0	1	1	11
Carabidae	*Pentagonica vittipennis*	Chaudoir,1877	0	0	0	3	0	0	3
Carabidae	*Platynus macropterus*	(Chaudoir, 1879)	0	4	1	10	4	7	26
Carabidae	*Rhytisternus miser*	(Chaudoir, 1865)	6	17	19	10	19	44	115
Carabidae	*Scopodes prasinus*	Bates, 1878	0	1	0	2	0	1	4
Carabidae	*Scopodes multipunctatus*	Bates, 1878	0	0	0	0	0	1	1
Carabidae	*Syllectus anomalus*	Bates, 1878	0	8	4	3	1	0	16
Cerambycidae	*Arhopalus tristis*	(Fabricius, 1787)	0	0	1	7	1	10	19
Cerambycidae	*Prionoplus reticularis*	White, 1843	2	4	2	5	4	1	18
Cerambycidae	*Ptinosoma sp.37*		0	2	0	6	2	0	10
Cerambycidae	*Ptinosoma sp. 37*		0	0	1	3	1	0	5
Cerambycidae	*Somatidia sp.29*		1	1	1	0	2	0	5
Cerambycidae	*Somatidia sp.34*		0	0	1	0	2	0	3
Cerambycidae	*Spilotrogia maculata*	Bates, 1874	0	0	0	0	0	1	1
Cerambycidae	*Tenebrosoma sp.40*		0	0	0	0	0	3	3
Cerambycidae	*Tenebrosoma sp.33*		0	0	0	0	0	1	1
Cerambycidae	*Xylotoles griseus*	(Fabricius, 1775)	0	0	0	0	0	8	8
Cerambycidae	*Xylotoles ?gratus*	Broun, 1880	0	0	0	0	0	1	1
Cerylonidae	*Hypodacnella rubripes*	*(Reit)*	0	0	0	0	0	1	1
Cerylonidae	*Philothermus sp.127*		0	1	0	1	1	0	3
Chrysomelidae	*Adoxia sp.244*		0	0	0	0	1	0	1
Chrysomelidae	*Aphilon sp.16*		0	0	0	0	0	4	4
Chrysomelidae	*Longitarsus ?jacobeae*	(Wat., 1858)	3	0	0	0	0	0	3
Chrysomelidae	*Trachytetra rugulosa*	(Broun, 1880)	0	0	0	0	0	1	1
Ciidae	*Cis sp.27*		0	0	0	0	0	12	12
Ciidae	*Cis sp.24*		0	1	0	0	1	1	3
Ciidae	*Cis sp.25*		0	0	0	0	0	2	2
Ciidae	*Cis sp.318*		0	0	0	0	0	2	2

Ciidae	*Cis sp.26*		1	0	0	0	0	0	1
Ciidae	*Cis sp.331*		1	0	0	0	0	0	1
Ciidae	*Scolytocis sp.319*		0	0	0	0	0	1	1
Clambidae	*Genus sp.272*		17	69	15	61	7	90	259
Clambidae	*Genus sp.1*		9	23	28	21	76	34	191
Clambidae	*Genus sp.3*		16	9	6	6	12	8	57
Coccinellidae	*Coccinella undecimpunctata*	Linnaeus, 1758	0	0	0	0	12	1	13
Coccinellidae	*Coccinella leonina*	Fabricius, 1775	0	0	0	0	1	0	1
Coccinellidae	*Diomus notescens*	(Blackburn, 1889)	0	0	2	0	5	3	10
Coccinellidae	*Genus sp.253*		0	0	0	0	0	3	3
Coccinellidae	*Rhyzobius sp.246*		0	0	0	0	0	3	3
Coccinellidae	*Rhyzobius sp.11*		1	0	0	0	0	0	1
Coccinellidae	*Rhyzobius sp.194*		0	0	0	0	0	1	1
Coccinellidae	*Rhyzobius ?consors*	Broun	0	0	0	0	0	1	1
Coccinellidae	*Scymnus loewi*	(Mulsant, 1850)	0	0	2	0	0	2	4
Corylophidae	*Arthrolips oblonga*	(Broun, 1893)	0	2	5	3	0	11	21
Corylophidae	*Clypeastrea pulchella*		1	3	3	2	1	4	14
Corylophidae	*Holopsis sp.274*		0	0	0	0	0	2	2
Corylophidae	*Holopsis sp.22*		0	0	0	0	0	1	1
Corylophidae	*Holopsis sp.275*		0	0	0	0	0	1	1
Corylophidae	*Holopsis sp.349*		1	0	0	0	0	0	1
Corylophidae	*Holopsis sp.5*		0	0	0	0	1	0	1
Corylophidae	*Holopsis sp.303*		0	0	0	0	0	0	0
Corylophidae	*Sericoderus sp.4*		2	10	6	12	17	97	144
Corylophidae	*Sericoderus sp.6*		0	0	0	0	1	21	22
Cryptophagidae	*?Micrambina sp.279*		0	0	1	1	0	0	2
Cryptophagidae	*Atomaria lewisi*	(Reitter, 1887)	1	1	1	28	0	2	33
Cryptophagidae	*Micrambina sp.122*		3	7	5	9	6	28	58
Cryptophagidae	*Micrambina sp.335*		0	0	0	0	0	1	1
Cryptophagidae	*Paratomaria sp.121*		0	2	12	0	1	0	15
Cryptophagidae	*Paratomaria crowsoni*	Leschen	0	0	2	2	1	0	5

Curculionidae	*?Athor sp.147*		1	0	0	0	1	0	2
Curculionidae	*?Bradypatae sp.151*		0	0	0	0	0	8	8
Curculionidae	*?Morronella sp.135 c*		0	0	0	0	0	1	1
Curculionidae	*?Notacalles sp.329*		0	0	0	0	0	4	4
Curculionidae	*?Notacalles sp.324*		0	0	0	0	0	3	3
Curculionidae	*?Notacalles sp.150*		0	0	0	0	0	2	2
Curculionidae	*?Notacalles sp.327*		0	0	0	0	0	1	1
Curculionidae	*?Notacalles sp.334*		0	0	0	0	0	1	1
Curculionidae	*?Phronira sp.160*		0	0	0	0	0	3	3
Curculionidae	*?Phronira sp.145*		0	0	0	0	0	1	1
Curculionidae	*?Phrynixus sp.144*		0	0	0	0	0	1	1
Curculionidae	*Agacalles formosus*	Broun, 1886	0	0	0	0	0	39	39
Curculionidae	*Agacalles sp.134 a*		0	0	0	0	0	1	1
Curculionidae	*Agacalles comptus*	(Broun, 1893)	0	0	0	0	0	1	1
Curculionidae	*Agatholobus waterhousei*	Broun, 1913	0	0	0	0	0	1	1
Curculionidae	*Allanalcis sp.167*		0	0	0	0	0	3	3
Curculionidae	*Allaorus sp.161*		0	0	0	0	0	2	2
Curculionidae	*Baeosomus amplus*		2	4	29	3	6	1	45
Curculionidae	*Baeosomus sp.330*		1	0	0	1	1	0	3
Curculionidae	*Camptoscapus planiusculus*	(Broun 1880)	0	0	0	0	1	0	1
Curculionidae	*Crisius sp.152*		0	0	0	1	0	0	1
Curculionidae	*Crooktacalles certus*	(Broun, 1880)	0	0	0	0	0	7	7
Curculionidae	*Dermothrius sp.333*		0	0	0	0	0	3	3
Curculionidae	*Euophryum sp.135 b*		0	0	0	2	0	0	2
Curculionidae	*Genus sp.143*		15	9	89	24	105	5	247
Curculionidae	*Genus sp.135*		0	1	0	3	1	1	6
Curculionidae	*Gromilus sp.139*		1	5	11	25	35	8	85
Curculionidae	*Gromilus setosus*		3	3	8	20	7	1	42
Curculionidae	*Gromilus sp.163*		0	0	1	0	3	1	5
Curculionidae	*Hylastes ater*	(Paykull, 1800)	111	110	158	9	79	12	479
Curculionidae	*Hylurgus ligniperda*	(Fabricius, 1787)	0	1	1	2	1	10	15
Curculionidae	*Listronotus bonariensis*	(Kuschel)	0	0	0	0	0	0	0
Curculionidae	*Mandalotus sp.136*		2	1	2	0	0	0	5

Curculionidae	*Mandalotus sp.155*		0	2	0	0	0	0	2
Curculionidae	*Mandalotus sp.328*		1	0	0	0	0	0	1
Curculionidae	*Megacolabus sp.157*		0	0	0	0	0	2	2
Curculionidae	*Megacolabus sp.159*		0	0	0	0	0	2	2
Curculionidae	*Metacalles sp.162*		0	0	0	0	0	39	39
Curculionidae	*Metacalles sp.332*		0	0	0	0	0	2	2
Curculionidae	*Metacalles sp.156*		0	0	0	0	0	1	1
Curculionidae	*Mitrastethus baridioides*	(Redtenbacher, 1868)	1	23	20	3	3	13	63
Curculionidae	*Pachycotes peregrinus*	(Chapuis, 1869)	2	15	4	5	5	3	34
Curculionidae	*Paromalia vestita*	Broun, 1880	0	0	0	0	0	3	3
Curculionidae	*Phrynixus astutus*	Pascoe	92	84	88	4	62	132	462
Curculionidae	*Phrynixus ?asper*		0	1	0	0	0	0	1
Curculionidae	*Praolepra sp.165*		12	4	7	0	15	1	39
Curculionidae	*Rhinocyllus conicus*		0	0	0	0	0	1	1
Curculionidae	*Rhopalomerus sp.153*		0	0	1	0	1	0	2
Curculionidae	*Scelodolichus sp.172*		0	0	0	0	0	6	6
Curculionidae	*Scelodolichus sp.170*		0	0	0	0	0	2	2
Curculionidae	*Scelodolichus sp.326*		0	0	0	0	0	1	1
Curculionidae	*Sericotrogus subaenescens*	Wollaston, 1873	0	0	0	0	1	3	4
Curculionidae	*Sitona discoidea*	Gyllenhal	10	19	53	6	34	30	152
Curculionidae	*Synacalles cingulatus*	(Broun, 1883)	0	0	0	0	0	5	5
Curculionidae	*Synacalles dorsalis*	(Broun, 1881)	0	0	0	0	0	1	1
Curculionidae	*Zeacalles picatus*		0	0	0	0	0	5	5
Curculionidae	*Zeacalles formosus*		0	0	0	0	0	2	2
Elateridae	*?Conoderus sp.190*		9	24	85	19	53	0	190
Elateridae	*Conoderus sp.183*		0	7	2	2	12	30	53
Elateridae	*Ctenicera sp.186*		157	27	33	3	157	0	377
Elateridae	*Ctenicera olivascens*	(White, 1846)	0	0	0	0	0	2	2
Elateridae	*Genus sp.266*		1	0	5	1	0	0	7
Elateridae	*Genus sp.184*		0	0	0	0	2	0	2
Elateridae	*Genus sp.265*		0	0	1	0	1	0	2
Elateridae	*Genus sp.178*		0	0	1	0	0	0	1

Elateridae	*Genus sp.182*		0	0	0	0	0	1	1
Elateridae	*Genus sp.189*		0	0	0	0	0	1	1
Elateridae	*Genus sp.262*		1	0	0	0	0	0	1
Elateridae	*Lomemus sp.314*		0	0	0	0	0	0	0
Elateridae	*Metablax acutipennis*	(White, 1846)	0	0	2	0	4	0	6
Elateridae	*Ochosternus zelandicus*	(White, 1846)	0	0	0	3	6	0	9
Elateridae	*Oxylasma sp.188*		0	0	0	0	0	8	8
Elateridae	*Panspoeus guttatus*	Sharp, 1877	3	8	18	7	10	2	48
Elateridae	*Panspoeus guttatus*	Sharp, 1877	0	0	0	0	0	1	1
Elateridae	*Protelater sp.249*		0	1	0	0	2	1	4
Elateridae	*Protelater sp.185*		0	0	0	0	1	0	1
Elateridae	*Sphaenelater collaris*	(Pascoe, 1876)	0	0	0	0	0	1	1
Elateridae	*Thoramus sp.180*		0	0	0	0	1	0	1
Endomychidae	*Holoparamecus sp.130*		0	0	0	4	0	0	4
Erotylidae	*Cryptodacne synthetica*	Sharp, 1878	9	5	8	5	1	14	42
Eucnemidae	*Genus sp.258*		20	10	10	16	8	2	66
Histeridae	*Parepierus sp.224*		83	89	24	20	13	0	229
Histeridae	*Saprinus detritus*	(Fabricius, 1775)	0	0	0	1	0	0	1
Hydrophilidae	*Adolopus sp.20*		0	0	0	2	0	0	2
Hydrophilidae	*Cyloma sp.356*		0	0	0	0	0	1	1
Latridiidae	*Aridius sp.105*		5	3	0	3	8	5	24
Latridiidae	*Aridius ?costatus*	(Erichson, 1842)	0	0	0	4	0	8	12
Latridiidae	*Aridius bifasciatus*	(Reitter, 1877)	0	0	0	1	1	6	8
Latridiidae	*Enicmus sp.106*		3	1	1	19	3	0	27
Latridiidae	*Enicmus sp.114*		0	0	0	0	0	0	0
Latridiidae	*Genus sp.108*		0	1	9	4	20	22	56
Latridiidae	*Genus sp.119*		0	0	0	1	0	0	1
Latridiidae	*Genus sp.120*		0	0	0	0	0	1	1
Latridiidae	*Lithostygnus sp.48*		0	0	0	1	0	9	10
Latridiidae	*Melanopthalma sp.117*		159	104	39	43	107	24	476
Latridiidae	*Melanopthalma sp.113*		0	0	5	1	1	5	12
Latridiidae	*Melanopthalma sp.109*		0	0	0	1	0	4	5
Latridiidae	*Melanopthalma sp.115*		0	0	0	1	1	0	2

Latridiidae	*Melanopthalma sp.118*		0	0	0	2	0	0	2
Latridiidae	*Melanopthalma sp.123*		0	0	0	2	0	0	2
Latridiidae	*Melanopthalma sp.110*		0	0	1	0	0	0	1
Latridiidae	*Melanopthalma sp.23*		1	0	0	0	0	0	1
Latridiidae	*Melanopthalma sp.280*		0	0	0	0	0	1	1
Latridiidae	*Melanopthalma sp.315*		0	0	0	0	1	0	1
Leiodidae	*Agyrtodes nebulosus*	(Broun, 1880)	1	0	0	0	1	0	2
Leiodidae	*Camiarus estriatus*	Broun, 1912	0	0	0	0	0	1	1
Leiodidae	*Inocatops sp.267*		0	0	0	0	0	1	1
Leiodidae	*n.g. sp.76*		0	0	0	2	6	0	8
Leiodidae	*n.g. sp.18*		0	0	0	0	2	2	4
Leiodidae	*Paracatops phyllobius*		231	78	266	16	5	194	790
Leiodidae	*Zeadolopus ?maoricus*	Daffner, 1985	0	0	0	0	1	30	31
Leiodidae	*Zeadolopus sp.364*		0	0	0	2	0	1	3
Leiodidae	*Zeadolopus sp.320*		0	0	0	0	1	0	1
Lucanidae	*Dendroblax earlii*	White, 1846	1	0	0	0	0	0	1
Lycidae	*Porrostoma rufipennis*	(Fabricius)	1	3	3	2	3	1	13
Melandryidae	*Axylita sp.129*		0	1	0	0	0	0	1
Melandryidae	*Genus sp.257*		0	0	0	1	0	4	5
Melandryidae	*Genus sp.132*		0	0	0	3	0	0	3
Melandryidae	*Genus sp.241*		0	0	0	0	0	1	1
Mordellidae	*Mordella jucunda*	(Broun, 1880)	0	0	0	0	0	1	1
Mycetophagidae	*Triphyllus sp.125*		47	35	15	3	18	28	146
Mycetophagidae	*Triphyllus ?punctulatus*	Broun, 1880	0	4	4	5	3	0	16
Mycetophagidae	*Triphyllus serratus*	(Broun, 1880)	1	0	0	0	1	0	2
Nitidulidae	*Brounthina aequalis*	Kirejtshuk, 1997	153	69	157	6	0	0	385
Nitidulidae	*Epuraea sp.357*		43	27	15	21	31	90	227
Nitidulidae	*Epuraea sp.354*		65	62	20	2	17	28	194
Nitidulidae	*Epuraea sp.359*		1	0	1	0	0	15	17
Nitidulidae	*Epuraea sp.358*		0	0	0	0	0	7	7
Nitidulidae	*Epuraea sp.360*		0	0	0	0	0	3	3
Nitidulidae	*Priateles optandus*	Broun, 1881	1	5	0	0	1	0	7
Nitidulidae	*Thalycrodes australis*	Germor	390	424	607	160	208	4	1793

Oedemeridae	*Baculipalpus strigipennis*	(White, 1846)	68	71	189	58	138	221	745
Oedemeridae	*Genus sp.197*		0	0	0	0	0	1	1
Oedemeridae	*Selenopalpus sp.193*		1	38	14	4	14	0	71
Phloeostichidae	*Priasilpha obscura*	Broun, 1893	0	0	0	0	0	1	1
Prostomidae	*Dryocora howitti*	Pascoe	1	0	1	0	0	0	2
Ptiliidae	*?Notoptenidium ?lawsoni*		1	1	2	0	4	34	42
Ptiliidae	*Genus sp.264*		1	0	0	0	0	5	6
Ptiliidae	*Genus sp.271*		0	0	0	1	2	0	3
Ptiliidae	*Genus sp.10*		0	0	0	1	0	1	2
Ptiliidae	*Genus sp.263*		0	2	0	0	0	0	2
Ptiliidae	*Genus sp.268*		0	0	0	0	0	0	0
Ptiliidae	*Genus sp.270*		0	0	0	0	0	0	0
Rhysodidae	*Kupeus arcuatus*	(Chevrolat, 1873)	0	1	0	3	0	0	4
Salpingidae	*Genus sp.225*		0	0	0	0	0	2	2
Salpingidae	*Genus sp.256*		0	0	0	0	0	1	1
Salpingidae	*Genus sp.317*		0	0	0	0	0	1	1
Scarabaeidae	*Ataenius brouni*	(Sharp, 1876)	0	0	0	0	1	0	1
Scarabaeidae	*Costelytra ?zelandica*	White, 1846	1	0	0	1	1	0	3
Scarabaeidae	*Odontria ?piciceps*	Broun, 1893	78	87	68	4	107	12	356
Scarabaeidae	*Odontria sylvatica*	Broun, 1880	3	7	5	3	29	7	54
Scarabaeidae	*Odontria magnum*	Given, 1952	0	1	0	0	0	3	4
Scarabaeidae	*Pyronota sp.58*		0	0	0	0	0	5	5
Scarabaeidae	*Pyronota sp.83*		0	0	0	0	1	0	1
Scarabaeidae	*Saphobius squamulosus*	Broun, 1886	0	0	0	0	0	3	3
Scraptiidae	*Nothotelus sp.316*		0	1	0	0	0	0	1
Silvanidae	*Brontopriscus pleuralis*	(Sharp, 1877)	0	0	0	0	0	2	2
Silvanidae	*Cryptamorpha brevicornis*	(White, 1846)	0	0	2	1	3	0	6
Silvanidae	*Cryptamorpha desjardinsi*	(Guerin, 1844)	0	0	0	0	0	3	3
Staphylinidae	*?Quedius sp.352*		2	2	2	0	3	4	13
Staphylinidae	*Agnosthaetus sp.341*		0	0	0	0	0	1	1
Staphylinidae	*Anabaxis foveolata*	(Broun, 1880)	39	28	37	22	46	12	184
Staphylinidae	*Anotylus sp.371*		29	47	33	22	15	354	500
Staphylinidae	*Anotylus sp.374*		9	17	16	11	2	158	213

Staphylinidae	*Anotylus sp.373*		0	0	0	0	22	0	22
Staphylinidae	*Anotylus sp.370*		0	0	0	0	0	3	3
Staphylinidae	*Anotylus sp.372*		0	0	0	0	0	1	1
Staphylinidae	*Astenus guttula*	Fauvel, 1877	0	0	0	0	2	10	12
Staphylinidae	*Baeocera sp.13*		5	1	4	3	25	2	40
Staphylinidae	*Brachynopus sp.14*		0	1	2	3	6	27	39
Staphylinidae	*Eupines sp.216*		0	0	1	0	0	28	29
Staphylinidae	*Eupines sp.208*		0	0	0	0	0	1	1
Staphylinidae	*Eupines sp.209*		0	0	0	0	0	1	1
Staphylinidae	*Eupinolus sp.214*		0	0	0	0	0	1	1
Staphylinidae	*Falagria sp.*		136	161	292	28	111	27	755
Staphylinidae	*Falagria sp.348*		1	1	3	0	0	0	5
Staphylinidae	*Genus sp.375*		6	7	202	3	2	15	235
Staphylinidae	*Genus sp.*		16	21	32	14	27	66	176
Staphylinidae	*Genus sp.308*		22	18	29	16	40	31	156
Staphylinidae	*Genus sp.292*		0	0	0	0	0	39	39
Staphylinidae	*Genus sp.218*		2	2	1	4	4	18	31
Staphylinidae	*Genus sp.211*		0	1	0	0	1	20	22
Staphylinidae	*Genus sp.217*		4	5	1	3	2	4	19
Staphylinidae	*Genus sp.284*		0	8	0	0	5	4	17
Staphylinidae	*Genus sp.300*		8	0	0	0	1	1	10
Staphylinidae	*Genus sp.212*		0	0	0	3	4	2	9
Staphylinidae	*Genus sp.310*		0	2	3	0	1	1	7
Staphylinidae	*Genus sp.204*		0	1	0	0	2	3	6
Staphylinidae	*Genus sp.219*		0	0	0	1	0	2	3
Staphylinidae	*Genus sp.287*		1	0	0	0	1	1	3
Staphylinidae	*Genus sp.296*		0	0	1	0	1	1	3
Staphylinidae	*Genus sp.313*		1	0	2	0	0	0	3
Staphylinidae	*Genus sp.343*		2	0	1	0	0	0	3
Staphylinidae	*Genus sp.291*		0	0	0	1	0	1	2
Staphylinidae	*Genus sp.207*		0	0	0	0	0	1	1
Staphylinidae	*Genus sp.215*		0	0	0	0	0	1	1
Staphylinidae	*Genus sp.286*		0	0	0	0	0	1	1

Staphylinidae	*Genus sp.290*		0	1	0	0	0	0	1
Staphylinidae	*Genus sp.298*		0	0	0	0	0	1	1
Staphylinidae	*Genus sp.304*		0	0	0	1	0	0	1
Staphylinidae	*Genus sp.305*		1	0	0	0	0	0	1
Staphylinidae	*Genus sp.311*		1	0	0	0	0	0	1
Staphylinidae	*Genus sp.353*		0	0	0	0	0	1	1
Staphylinidae	*Genus sp.363*		1	0	0	0	0	0	1
Staphylinidae	*Genus sp.369*		0	0	0	1	0	0	1
Staphylinidae	*Genus sp.289*		0	0	0	0	0	0	0
Staphylinidae	*Hyperomma sp.293*		0	0	0	0	0	2	2
Staphylinidae	*Metacorneolabium sp.309*		0	8	0	1	0	0	9
Staphylinidae	*n.g. sp.240*		0	2	0	0	0	2	4
Staphylinidae	*Nototorchus ferrugineus*	(Broun, 1893)	9	33	63	0	0	2	107
Staphylinidae	*Paratorchus sp.339*		0	0	0	0	0	10	10
Staphylinidae	*Phanophilus comptus*	(Broun, 1880)	2	0	1	8	5	0	16
Staphylinidae	*Physobryaxis inflata*	(Sharp, 1874)	0	0	0	0	2	21	23
Staphylinidae	*Quedius sp.294*		12	9	8	2	1	1	33
Staphylinidae	*Quedius sp.295*		2	0	0	0	0	0	2
Staphylinidae	*Quedius sp.306*		0	0	1	0	0	0	1
Staphylinidae	*Sagola genalis*	Broun, 1881	0	0	0	0	3	3	6
Staphylinidae	*Scaphisoma funereum*	Loebl, 1977	1	0	0	1	11	17	30
Staphylinidae	*Sepedophilus sp.82*		34	34	30	10	17	7	132
Staphylinidae	*Sepedophilus sp.80*		0	1	0	0	1	31	33
Staphylinidae	*Sepedophilus sp.77*		3	3	0	3	4	18	31
Staphylinidae	*Sepedophilus sp.78*		0	2	0	3	5	16	26
Staphylinidae	*Sepedophilus sp.81*		2	2	2	0	0	1	7
Staphylinidae	*Sepedophilus sp.307*		0	0	1	0	0	2	3
Staphylinidae	*Sepedophilus sp.84*		0	0	0	0	0	1	1
Staphylinidae	*Silphotelus nitidus*	Broun, 1895	2	1	3	6	4	32	48
Staphylinidae	*Tachyporus nitidus*	(Fabricius, 1781)	0	0	0	0	3	2	5
Staphylinidae	*Thyreocephalus sp.297*		0	0	1	7	5	51	64
Staphylinidae	*Tychotyrus sp.206*		1	0	1	8	11	4	25
Staphylinidae	*Zeoleusis virgula*	(Fauvel, 1889)	0	2	0	0	0	2	4

Tenebrionidae	*Amarygmus sp.238*		0	0	0	0	0	1	1
Tenebrionidae	*Archaeoglenes costipennis*	Broun, 1893	0	0	0	0	0	8	8
Tenebrionidae	*Artystona sp.237*		0	0	0	0	0	6	6
Tenebrionidae	*Kaszabadelium aucklandicum*	(Broun, 1880)	2	6	1	0	5	17	31
Tenebrionidae	*Menimus sp.228*		0	0	0	0	0	2	2
Tenebrionidae	*Menimus sp.247*		0	0	0	0	0	2	2
Tenebrionidae	*Uloma tenebrionoides*	White, 1846	2	1	0	0	2	1	6
Trogossitidae	*Australiodes vestitus*	(Broun, 1882)	1	1	2	0	0	13	17
Trogossitidae	*Australiodes sp.28*		1	0	0	0	0	0	1
Trogossitidae	*Genus sp.9*		0	0	0	0	0	4	4
Trogossitidae	*Genus sp.365*		0	0	1	0	0	2	3
Trogossitidae	*Genus sp.367*		1	0	1	0	0	0	2
Trogossitidae	*Genus sp.131*		0	0	0	0	1	0	1
Trogossitidae	*Genus sp.273*		0	0	0	0	0	1	1
Trogossitidae	*Genus sp.366*		0	0	0	0	0	1	1
Zopheridae	*?Ablabus sp.54*		0	0	0	0	0	2	2
Zopheridae	*Ablabus sp.47*		26	27	12	4	14	21	104
Zopheridae	*Bitoma distans*	Sharp	0	0	9	0	8	1	18
Zopheridae	*Bitoma insularis*	White, 1846	0	0	1	0	1	1	3
Zopheridae	*Bitoma ?rugosa*	Sharp	0	1	0	0	0	0	1
Zopheridae	*Chorasus sp.43*		0	0	0	0	0	5	5
Zopheridae	*Epistranus sp.55*		0	0	0	1	0	16	17
Zopheridae	*Notocoxelus sp.51*		0	0	0	0	0	1	1
Zopheridae	*Pristoderus bakewellii*	(Pascoe, 1866)	7	51	15	2	34	72	181
Zopheridae	*Pristoderus antarcticus*	(White, 1846)	0	3	0	0	0	1	4
Zopheridae	*Pristoderus tuberculatus*	Broun	0	0	0	0	0	7	7
Zopheridae	*Pristoderus scaber*	Fabricius	0	0	0	0	1	1	2
Zopheridae	*Pristoderus antarcticus*	(White, 1846)	0	0	0	0	0	1	1
Zopheridae	*Pycnomerus sophorae*	Sharp	543	381	180	76	277	19	1476
Zopheridae	*Rytinotus squamulosus*	Broun, 1880	0	0	0	0	0	1	1
Zopheridae	*Syncalus sp.351 d*		0	0	0	0	0	8	8
Zopheridae	*Tarphiomimus indentatus*	Wollaston, 1873	2	1	0	3	0	17	23

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Chapter 6 - A space-for-time substitution experiment to test long-term changes in the abundance of beetle species throughout an entire 26 year forest rotation.

6.1 Introduction

Despite the considerable loss of native habitats worldwide (FAO 2001), the area of plantation forests is increasing rapidly in many countries and has the potential to mitigate the effects of habitat loss (Carnus et al. 2006). Exotic plantations are generally perceived to support low biodiversity (Hartley 2002), however managed forests of *Pinus radiata* provide suitable low-contrast alternative habitat to native forest for many indigenous species (Clout 1984, Clout and Gaze 1984, Kleinpaste 1990, Bonham et al. 2002, Mesibov 2005, Carnus et al. 2006). Species composition and abundance of native understorey plants in New Zealand plantations changes dramatically throughout a rotation (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003). However, knowledge about invertebrate biodiversity in such ecosystems is limited (Hutcheson and Jones 1999, Berndt et al. Submitted). Despite this, insects are essential to most ecosystem functions, e.g., pollination (Murren 2002), nutrient cycling and litter decomposition (McCullough et al. 1998, Chapman et al. 2003) and are key components in food-webs, providing food for more charismatic species such as birds and mammals (Clout 1984, Clout and Gaze 1984). Because of their ecological importance greater knowledge of invertebrates and their long-term ecological responses to clearfelling will allow forest managers to enhance the biodiversity value of plantation stands.

International desire to preserve biodiversity is growing steadily alongside recognition that the production landscape matrix can provide suitable habitat for native species (Meurk and Swaffield 2000, Novacek and Cleland 2001, Kupfer et al. 2006). Plantation forest managers have in many cases responded to concerns about sustainable management by voluntarily adopting one of a range of management certification schemes such as the Forest Stewardship Council (FSC). One of the goals of these sustainable forest management schemes is to increase the capacity of plantations to support non-commercial species, thus contributing to the maintenance of regional biodiversity.

Clearfell harvesting is one of the most visible and controversial forestry practices. It invokes strong negative public reactions (Hansis 1995) and has been a key contention in some forest certification applications (Hock and Hay 2003). Short-term impacts of clearfelling on biodiversity are comparatively well studied (Beaudry et al. 1997, Roberts and Zhu 2002, Knapp et al. 2003, Saint-Germain et al. 2005), however post-harvest recovery of populations, recolonisation of regenerating stands, and the recovery of ecosystem processes may take many years, if not decades (Spence et al. 1996). This has serious implications for biodiversity preservation particularly in short-rotation forestry and a greater understanding is required of these long-term post-harvest impacts.

Despite the 100-year history of large-scale short-rotation plantation forest management in New Zealand (Roche 1990), the short-term impacts of clearfell harvesting on plants (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003) and invertebrate taxa (Chapter 5) have only been studied in the last 10 years. Our current understanding of long-term changes in invertebrate populations is poor, with only a single published mensurative study comparing the beetle fauna of three different-aged *Pinus radiata* stands (Hutcheson and Jones 1999). Previous studies of understorey plant diversity have sampled across a wider range of stand ages, because it is a simpler, less resource-intensive process than sampling invertebrate diversity. Hutcheson and Jones (1999) is still the most comprehensive multi-aged (5, 14 and 30 year-old stands) invertebrate study in New Zealand plantation forests. From their data they could distinguish between different aged stands on the basis of Malaise-trapped beetle species composition. However, the restricted sampling of plantation age classes and unequal distribution of sampling effort between treatments limits the ability to infer whether the differences in abundance of individual species between sites translates into long-term changes in abundance over time.

Plantations can be viewed as pre-existing large-scale fully replicated study areas suitable for space-for-time experiments capable of documenting the process of succession from a disturbance-adapted community to a forest dominated ecosystem over time. Detailed management records, including stocking rates, pruning and thinning schedules and most importantly the time of harvest exist for the extensive *Pinus radiata* plantations of the central

North Island of New Zealand. An accurate account of the time since disturbance and subsequent management actions provides excellent opportunities to establish trials that assess forest succession processes by spatial substitution of replicates, i.e., a chronosequence (mensurative approach (McGarigal and Cushman 2002)). Population and community recovery of forest ecosystems post-disturbance can be assessed in different-aged stands simultaneously, which circumvents the process of following individual stands through time. Space-for-time substitution studies make the study of long-term effects more viable as resource and logistical issues are simpler to overcome, and results are more quickly realised to guide future management. However, space-for-time studies can be affected by confounding variables, such as spatial heterogeneity, which may be ameliorated to some extent by adequate site replication.

This chapter evaluates the population responses of selected individual invertebrate species and plant species richness at different distances into regenerating stands and adjacent mature forest. The short-term responses of the invertebrate species are already known (Chapter 5), and this study aims to establish the similarity of long-term responses with early successional post-harvest processes.

6.2 Methods

6.21 Study sites and experimental design

The study was conducted in the extensive *Pinus radiata* plantation forests of New Zealand's central North Island. Stands of six different age class treatments (1, 2, 4, 8, 16 and 26 yrs) were selected from available forest compartments of the correct age. To mitigate unwanted size effects stands were restricted to those within 20% of a desired 50 ha in size. Treatment stands also had to meet the constraint that they were surrounded by *P. radiata* of at least 20 years of age (in order to assure full canopy closure) with one stand boundary being at least 25 years. The 25 year-old boundary represents a mature forest reference point to compare with the abundance of beetles in adjacent regenerating stands.

Beetles were sampled in pitfall traps placed along a gradient between the different aged regenerating stands and the adjacent mature 25 year-old forest stand. Traps were placed at

$\log_5$ distances from the drip-line of the mature forest and subsequently at 5, 25, 125 and 290 m in either direction perpendicular to the stand boundary (Figure 6.1). The end of each transect thus represented the rough mid-point of the approximately square 50 ha stands evaluated. Two replicates of 4, 8, 16, and 26 year-old-stands were sampled monthly between November 2002-February 2003 and two additional independent replicates of each age class were sampled between January and February 2004. Three replicates of year 1 stands were sampled monthly from November 2002-February 2003 and in their second year post harvest, January 2004-February 2004. For an in-depth description of other methodology including the collection of vegetation data, study sites and pitfall trap design consult chapter 2.

Sampling across gradients between age treatments and their adjacent mature forest reference point provides a localised ‘control’ site that allows the change in abundance post-harvest to be compared with the closest available mature plantation stands. Traditionally, studies that have compared harvest treatments only have one or a limited number of control sites that can be at considerable distances from treatment areas. The concept of pairing treatment and mature forest sites is an attempt to reduce random spatial variability and thus increase the statistical power of testing differences between mature and regenerating stands.

6.22 Selection of beetle taxa and analysis of data

A comprehensive study analysing the change in abundance of all beetle taxa was not feasible due to the processing time required to sort the large quantity of material collected and the taxonomic impediment of correctly assigning individual specimens to valid species. As such we decided to choose a suite of indicator taxa. It is important that the selection of indicator taxa is robust and justifiable, preferably from some initial sampling (McGeoch 1998). I selected seven beetle taxa on the basis of results from earlier research into short-term responses to clearfell harvesting (Chapter 5). The abundances of these seven species were known to change significantly in the first two years post-harvest, either increasing or decreasing in response to clearfell harvest disturbance (Table 6.1).

Beetles were sorted from samples preserved in alcohol and counts were converted to catch per 100 trap days to account for the unequal sampling time between traps. As such all references to abundance in this chapter are actually a relative measure of capture rate, expressed as catch per 100 trap days.

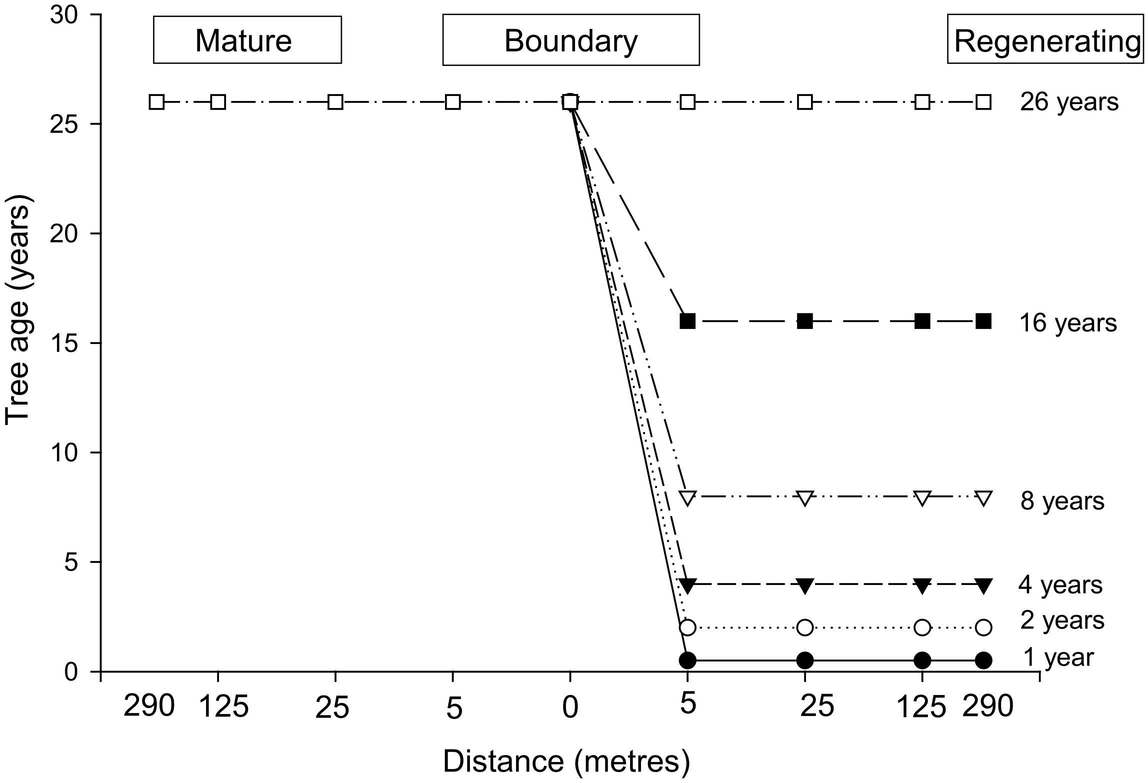


Figure 6.1 Concept graph illustrating the experimental design of transects between mature forest control sites and adjacent regenerating stands of *P. radiata*. Transects were 580 m in length and were sampled from 290 m into mature *P. radiata* to 290 m into different-aged regenerating stands. In all graphs where the full transect is shown (Appendix 6.1) the mature forest control is given on the left and the regenerating stand on the right. Distances are measured in metres and presented on a $\log_5$ scale.

Table 6.1. Observed patterns in the abundance of selected beetle taxa as a function of clearfell size (data presented in detail in Chapter 5). Exotic species are denoted by an-asterisk.

Species	**Change in abundance with respect to increasing clearfell size**
Pycnomerus sophorae	Negative
Paracatops phyllobius	Negative
Latridiidae sp 117	Negative
Hylastes ater[*]	Negative
Cicindela tuberculata	Positive
Odontria sp. 56	Bimodal, high at small and large clearfell sizes.
Sitona discoideus[*]	Positive

Individual 'proc-mixed' models (SAS V8) for each species were used to analyse the significance of both fixed (age, distance, distance^2 and the age*distance and age*distance^2 interactions) and random effects (forest compartment, compartment*age interaction). Squared terms are to account for potential curvilinear responses in the data. Distance was coded as a continuous variable in the analysis and species data were tested for normality prior to the application of square root, log or inverse transformations, as appropriate, to correct for skewness and ensure that the assumptions of normality for the 'proc mixed' model were met. Interaction terms across the entire gradient were complex and to distil trends from only the regenerating stands the difference between mature and regenerating stands was analysed rather than the raw abundance data. The difference between mature and regenerating stands was calculated by subtracting the combined mean abundance of 5, 25, 125 and 290 m traps in mature forest from the abundance at each individual distance (including the 0 m) in the adjacent regenerating stand. The mean mature forest value was calculated separately for each age comparison and curves were fitted by linear regressions using the standard linear curve fitting function of Sigmaplot (Version 7, SPSS Inc 2001).

Species with no significant change in abundance with respect to distance across transects within a single age treatment are presented as a scatterplot of the mean difference in abundance per age class, with associated confidence intervals. Species with significant linear regression slope coefficients in one or more age classes can not be plotted as an average difference per age class, as the mean would not provide a suitable estimate of abundance due to its dependence on distance. In such cases the slope coefficient is compared at different ages.

6.3 Results

6.31 Understorey plant diversity

The average species richness of native vascular dicotyledonous plants (excluding grasses, sedges and rushes) per quadrat surrounding the pitfall traps was greater than the number of adventive species in all age classes (Table 6.2). Average species richness of native understorey plant species per quadrat decreased significantly with increasing distance from the mature forest edge in 1 year-old and 4 year-old stands (Figure 6.2a & 6.2b). However, the similarity in native plant species richness between mature forest and regenerating stands increased with stand age as shown by the reduced slope of the linear regression analysis of species richness as regeneration proceeded (Figure 6.2a-e).

Table 6.2. Average species richness of native (N) and adventive (A) plants (excluding grasses, herbs and mosses) per 2 x 2m quadrat surrounding pitfall traps at different distances along an edge gradient sampled between mature 26 year *P. radiata* and regenerating stands of different ages.

		Age of regenerating stand (years)									
		1		**4**		**8**		**16**		**26**	
	Distance from edge (m)	**N**	**A**	**N**	**A**	**N**	**A**	**N**	**A**	**N**	**A**
Mature	-290 m	5.0	0.3	4.0	0.8	4.7	1.0	4.0	1.0	5.5	0.5
	-125 m	7.0	0.3	3.6	0.8	5.7	0.7	4.8	1.0	2.3	0.5
	-25 m	5.7	0.3	3.4	1.0	6.0	0.7	5.0	1.0	3.3	0.5
	-5 m	3.3	1.0	5.6	0.6	7.3	1.3	6.5	0.5	4.8	0.5
	Boundary 0 m	4.0	1.0	4.4	0.6	3.7	1.3	5.0	1.5	4.8	0.3
Regenerating	+5 m	2.3	1.0	3.2	1.2	5.3	1.5	4.0	1.0	4.5	0.3
	+25 m	2.7	0.7	2.2	0.4	4.3	0.3	4.8	0.8	4.5	0.8
	+125 m	2.7	0.0	1.8	0.4	3.3	0.3	4.8	0.8	3.3	0.5
	290 m	2.0	0.0	2.2	0.8	4.0	0.3	5.5	0.8	5.8	0.3

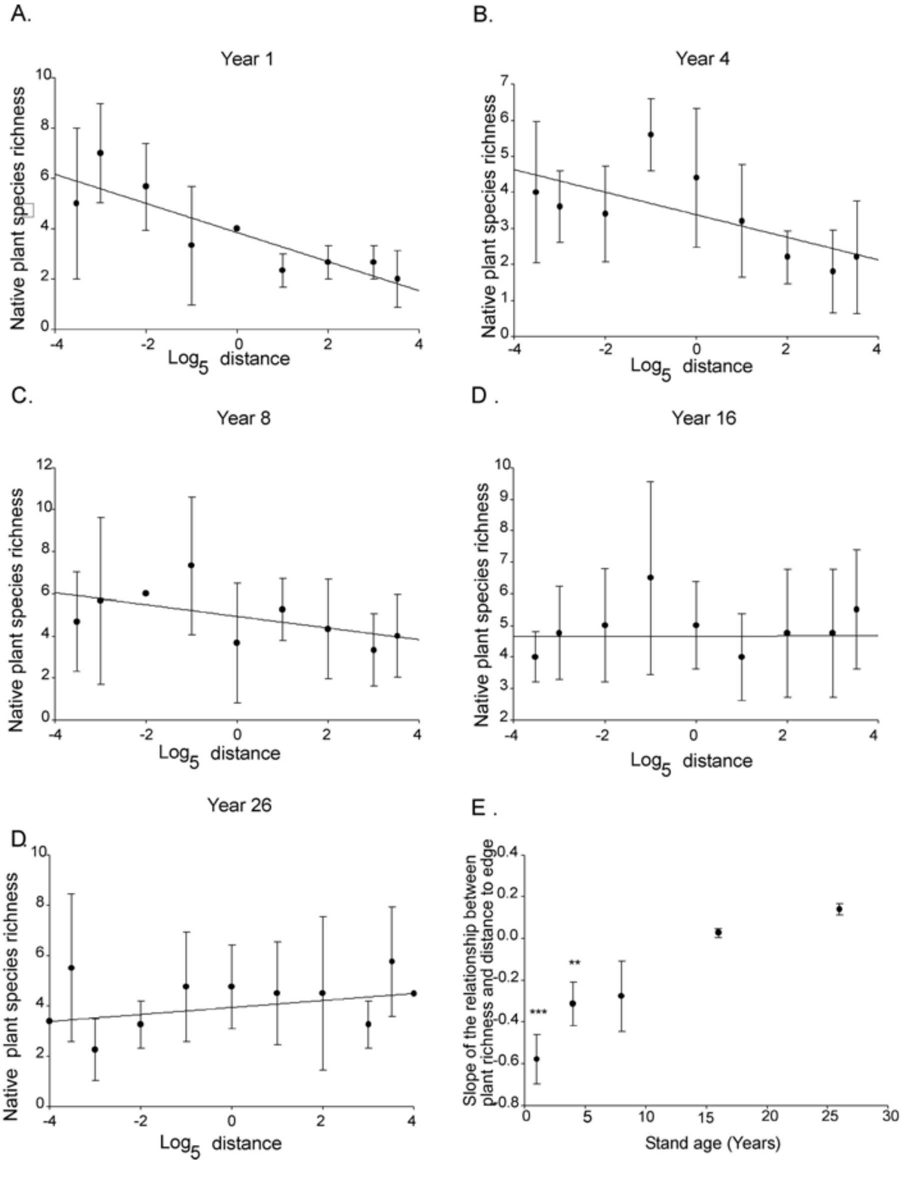


Figure 6.2. Average species richness of understorey vegetation decreased significantly with distance from mature forest in 1 and 4 year-old regenerating stands. a) year 1 ($Y= -0.58x + 3.85$ $R^2 = 0.49$, $P = 0.0001$), b) year 4 ($Y= -0.31x + 3.38$ $R^2 = 0.17$, $P < 0.0049$), c) year 8 ($R^2 = 0.10$, $P < 0.11$), d) year 16 ($R^2 = 0.001$, $P < 0.82$), and e) year 26 ($R^2 = 0.03$, $P < 0.29$) stands. Negative distances indicate sites in mature forest and positive into regenerating stands. Error bars are 95% confidence intervals of the sample based rarefied species richness; E) Similarity of understorey vegetation diversity increases with stand age, i.e., tends to zero. Significant of regression slopes is indicated by the use of alphabetical superscripts * = $P<0.05$, ** = $P<0.01$ and *** $P< 0.001$.

6.32 Beetle abundance

A total of 25,065 individuals of the seven selected were species extracted from pitfall samples; this comprised 10,193 *Cicindela tuberculata*, 9,605 *Pycnomerus sophorae*, 2,113 Latridiidae sp 117, 1,545 *Paracatops phyllobius*, 626 *Hylastes ater*, 608 *Odontria ?piciceps* and 375 *Sitona discoideus*. Average catch per 100 trap days across the mature forest-regenerating stand gradient is given for each species in Appendix 6.1.

6.33 Changes in abundance as a function of stand age and distance from forest edge

Separate mixed model ANOVAs for individual species showed that *C. tuberculata* was the only species to exhibit significant changes in abundance as a function of stand age post-harvest (Table 6.3). The abundance of *C. tuberculata* was very low in mature forest compared to extremely high catches in 1 and 2 year-old stands (Appendix 6.1).

Table 6.3. F-values and associated significance (<0.05 *, <0.01 ** and <0.001 ***) of a mixed model, random effects ANOVA to test for changes in species abundance by stand age, distance along transect (both linear and curvilinear) and the age*distance age*dist^2 (curvilinear) interaction. Random effects in the model were the age and age (compartment).

Species	**Age**	**Dist**	**Dist^2**	**Age*Dist**	**Age*Dist^2**
d.f.:	**(5, 2)**	**(1, 537)**	**(1, 537)**	**(5, 537)**	**(5, 537)**
Odontria ?piciceps	7.01	4.26*	13.49***	0.43	7.07***
Pycnomerus sophorae	3.44	23.94***	5.13*	4.93***	1.51
Paracatops phyllobius	0.88	41.06***	0.14	2.99*	1.66
Sitona discoideus	1.84	18.03***	0.18	2.29*	0.21
Cicindela tuberculata	25.57*	238.46***	0.57	58.51***	4.00**
Hylastes ater	18.19	9.44**	14.01***	4.76***	3.67**
Latridiidae sp. 117	3.79	58.40***	3.76	10.53***	3.79**

However, as with plant species richness, the abundance of all seven beetle species differed significantly with distance (main effect in model) across the mature forest-regenerating stand gradient (Table 6.3). These changes were not always linear, e.g., *Odontria ?piciceps*, *Hylastes ater* and *Pycnomerus sophorae* showed significant Distance^2 terms indicating a curvilinear response in abundance as a function of distance along the gradient. The strong curvilinear responses of *O. ?piciceps* is shown clearly by the preference for edge habitat in younger stands (Appendix 6.1).

6.34 Interaction terms

The response of all species to distance from the regenerating stand edge changed significantly with increasing stand age (despite *C. tuberculata* being the only species to show a significant main effect of stand age). Analysis of the difference in abundance between mature and regenerating stands at each distance showed that the abundance of *Odontria ?piciceps*, *Cicindela tuberculata* and *Hylastes ater* changed significantly with distance into the regenerating stand for at least one age treatment. Abundance of *Odontria ?piciceps* decreased significantly with distance into 1 and 2 year-old stands (strong negative regression slopes that were a product of two of the three replicates: year 1: R = 0.59, n = 15, P=0.018; year 2: R = 0.77, n = 15, P = 0.0008 (Figure 6.3 a & b)), however there was no significant differences in older 4, 8, 16 and 26 year-old stands (Figure 6.3c-f). The difference in abundance of *C. tuberculata* between mature and regenerating stands increased significantly with distance into 2 year-old stands (R = 0.68, n = 15, P = 0.005 (Figure 6.4a & b)), and *H. ater* decreased into 1 year-old stands (R = 0.476, n = 20, P = 0.034 (Figure 6.4c & d)). As abundance is dependent on distance across the gradient for these species, an average ‘difference’ value could not be calculated for each age class and thus comparisons must be made using the regression lines as in Figures 6.4b & d). In contrast, Latridiidae sp. 117, *Pycnomerus sophorae*, *Paracatops phyllobius* and *Sitona discoideus* did not vary in abundance with distance and average values can be calculated for the difference between mature forest and regenerating stands in each age class (Figures 6.5a-d)

The immediate post-harvest change in the abundance of individual beetle species in regenerating stands compared to adjacent mature forest was variable. *C. tuberculata* (Figure 6.4b), *H. ater* (Figure 6.4d), *O. ?piciceps* (Figure 6.3 a-f) and *Sitona discoideus* (Figure 6.5d) increased in abundance immediately post-harvest and declined as regeneration proceeded; note the changes in *C. tuberculata*, *H. ater* and *O. ?piciceps* abundance were dependent on distance in some age classes. This distance effect varied between species with *C. tuberculata* increasing in abundance with greater distance into young regenerating stands, whereas *O. ?piciceps* and *H. ater* decreased in abundance along the same gradient.

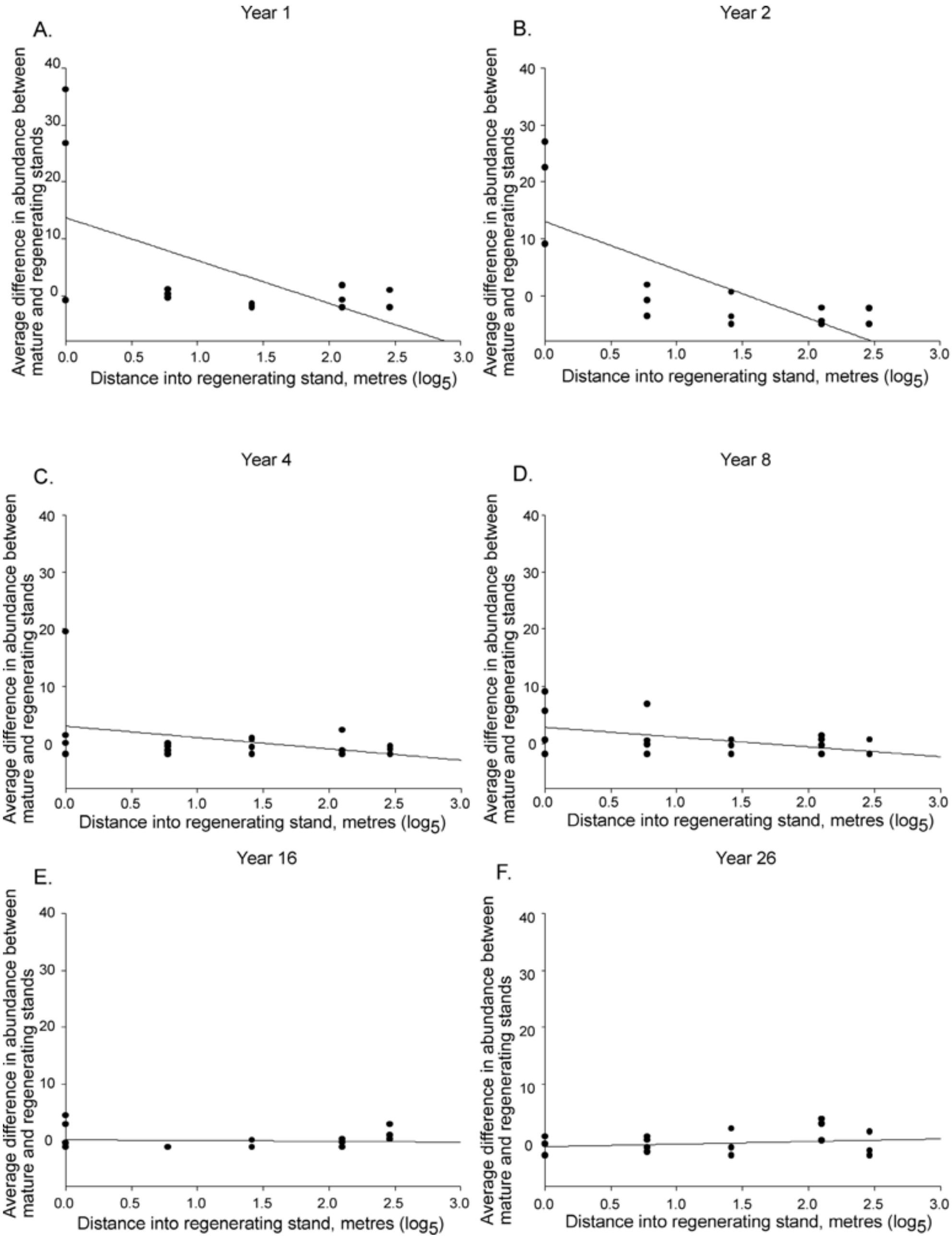


Figure 6.3. Scatter-plot with linear regressions of the difference in abundance of *Odontria ?piciceps* between regenerating stands and their adjacent mature forest control at a) year 1, b) year 2, c) year 4, d) year 8, e) year 16 and f) year 26. Slopes of the linear regression were significantly different from zero in year 1 and 2, where trap catch was greatest at the forest edge. Harvesting did not have a positive impact on all species.

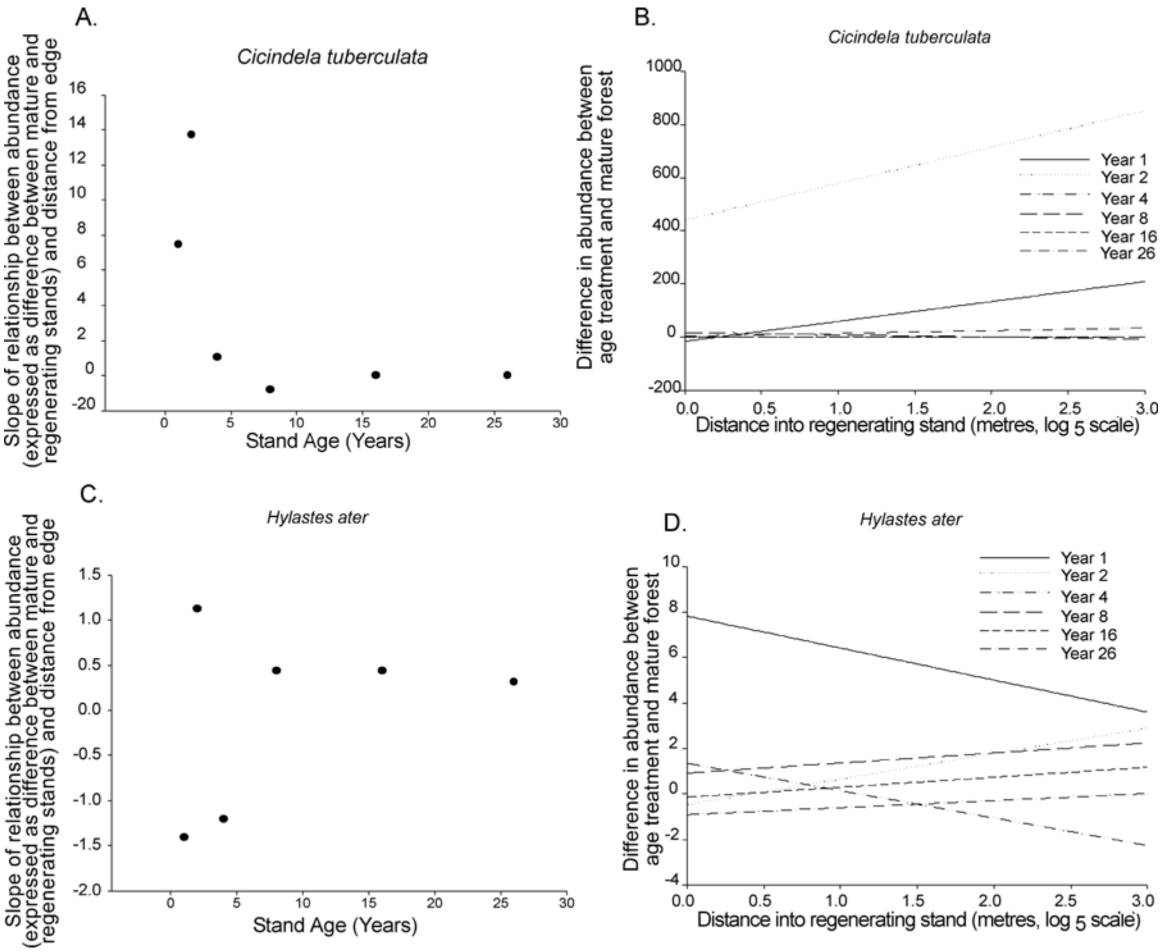


Figure 6.4. Slope of relationship between abundance and distance was approximately zero in stands older than 8 years, indicating no difference in abundance along the habitat gradient. However, **a)** *Cicindela tuberculata* and **c)** *Hylastes ater* showed disparate responses in younger stands. *C. tuberculata* increased in abundance with distance into clearfell harvest areas, whereas *H. ater* decreased. Regression lines of the difference in abundance between mature and regenerating stands show that **b)** *C. tuberculata* and **d)** *H. ater* had greater abundance in young stands compared to adjacent mature controls.

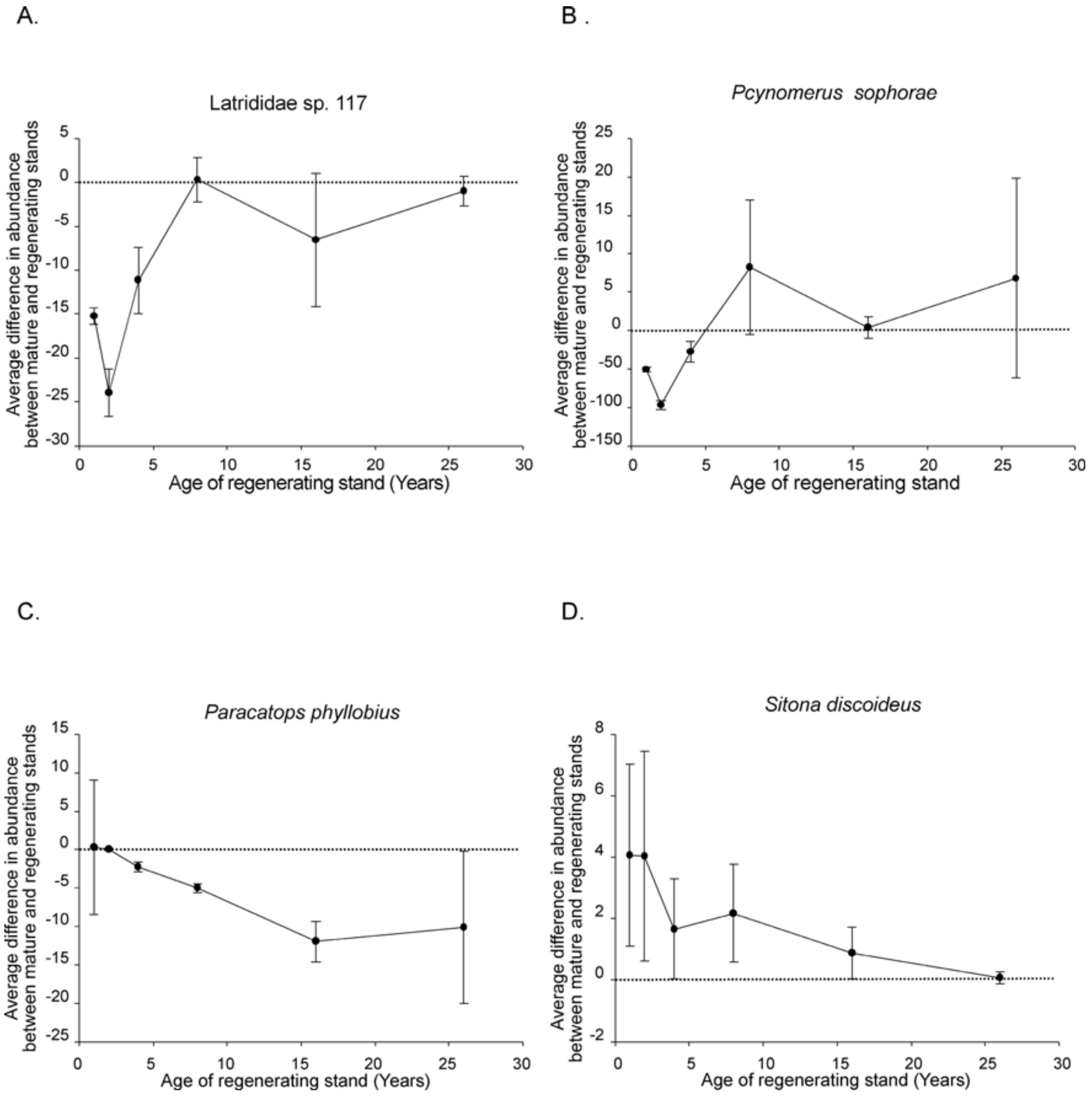


Figure 6.5. Average difference in abundance between regenerating stands and adjacent mature forest controls of **a)** Latridiidae sp. 117 and **b)** *Pycnomerus sophorae* decreased immediately post-harvest and recovered as stands regenerated. **c)** *Paracatops phyllobius* showed a similar response with a time lag of 4 years, but did not appear to fully recover after 26 years. In contrast **d)** *Sitona discoideus* had higher abundance in young stands compared to the adjacent mature forest that decreased with stand age. Dashed lines indicate zero difference between mature *P. radiata* and adjacent regenerating stands.

The difference in abundance of *Pycnomerus sophorae* and Latridiidae sp. 117 across the habitat gradient exhibited an immediate negative response to harvesting. However, populations recovered to pre-harvest levels within 26 years (Figures 6.5a & b). *Paracatops phyllobius* was also negatively affected but there was a delayed response (significant decrease at 4 years post-harvest) but the species appears to recover within the 26-year time frame sampled when the variance around the mean is acknowledged (Figure 6.5c).

6.4 Discussion

This study is the most comprehensive analysis of changes in beetle abundance as a function of stand age to be attempted in a New Zealand *P. radiata* plantation. Data support the notion that 50 ha clearfells are not significant barriers to stand recolonisation by these beetles, as six of the seven species sampled were collected from all distances along the habitat gradient, irrespective of the age class comparison. *Cicindela tuberculata*, which is a strongly-flighted heliophilous predatory species (Savill 1999, Larochelle and Larivière 2001), was the only species not present in deep mature *P. radiata* habitat, but it was clearly capable of rapidly colonising clearfells post-harvest, as shown by the high abundance in recent clearfells (Appendix 6.1).

6.41 Dispersal into regenerating stands

Transition zones between different habitats (ecotones) have been the focus of intense research, particularly with respect to changes in the abundance of organisms and the effects of edges on dispersal probability (Ries et al. 2004). New Zealand plantation forests have few avian frugivores and are dominated by insectivorous bird species (Clout 1984) resulting in a largely wind-assisted mode of dispersal for most plant species. Plant species richness decreased significantly with distance from forest edge in 1 and 4 year-old regenerating stands, which is consistent with many other studies of seed dispersal (Cubina and Aide 2001, Clark et al. 2005, Devlaeminck et al. 2005, Lavi et al. 2005). Short-distance wind dispersal of seeds further highlights the importance of proximity to native vegetation (see chapter 5) and the role of landscape level habitat attributes to the retention of diversity.

Dispersal into regenerating stands is not always passive, insects can disperse actively and their abundance in a particular location may, in part, reflect habitat suitability, rather than proximity of source populations in highly mobile groups (Hughes et al. 2000). Abundance of *Hylastes ater* and *Cicindela tuberculata* changed significantly with distance from the forest edge in 1 and 2 year-old regenerating stands. *Hylastes ater* is a bark beetle and would be attracted to recent harvest areas by suitable host volatiles (Reay and Walsh 2002). *Cicindela tuberculata* is an open habitat species (Savill 1999) that would be attracted to, and is easily capable of dispersing into, recently created clearfells. The two species responded differently to distance from forest edge (Figure 6.4b & 6.4d), *H. ater* was most abundant at forest edges, whereas *C. tuberculata* was most numerous in the centre of clearfells. The reasons for such differential responses are poorly understood, however structural contrast between adjacent habitats, microclimatic changes at forest edges, and individual behavioural responses are known to play a role in edge permeability to dispersal (Ries and Debinski 2001, Schtickzelle and Baguette 2003).

Two scenarios may explain the high abundance of *H. ater* at recently clearfelled stand boundaries: (i) a source-sink effect where a finite population in surrounding forest disperses into recently harvested areas and abundance decreases with distance from the source; or alternatively, (ii) individuals migrating from within clearfells accumulate at the stand edge as it presents a barrier to outward dispersal (changes in dispersal behaviour at habitat boundaries have also been recorded for Lepidoptera (Schultz and Crone 2001)). A detailed tracking study would be necessary to assess the relative influence of these two alternatives.

The larvae of *C. tuberculata* inhabit shallow (10-15cm) burrows in exposed mineral soil (Larochelle and Larivière 2001), which is abundant in freshly clearfelled stands. The large increase in trap catch during the second year post-harvest is probably due to the emergence of the adult progeny of the previous year’s overwintering larvae (Appendix 6.1). However, this does not explain the change in abundance relative to habitat edge. Adventive grasses and herbaceous species have been shown to rapidly colonise harvested stands (Brockerhoff et al. 2003). In this study, native plant species richness was highest at the edge of regenerating stands (Figure 6.2a & b). Bare ground is a key resource for *C. tuberculata* and high abundance in the centre of clearfells may have been the result of more rapid regrowth of vegetation close to the boundary (seed source) of regenerating stands.

Apart from understorey plant species richness, and *C. tuberculata* and *H. ater* abundance, the difference in abundance between mature and regenerating stands of the other five beetle species sampled did not vary with distance from source populations (mature forest). However, the average difference in abundance of these five species did change with the age of regenerating stands. This indicates alternative life-history strategies (forest, open habitat and edge preference) that allow these species to maintain populations in a mosaic of different stand ages. The biology of these five species is poorly understood. Given that so little is known about these species generalising results to other taxa should be done judiciously, as phylogenetic relatedness is not a reliable criterion for extrapolation (Ricketts et al. 2002, Oertli et al. 2005).

6.42 Forest habitat species

Pycnomerus sophorae and Latridiidae sp 117 had significantly reduced abundance in young regenerating stands suggesting a preference for mature forest (Figure 6.5a & b). However, the effect of harvesting on species abundance is not always immediate (Niemela et al. 1993). In this study *Paracatops phyllobius* seemed relatively unaffected immediately post-harvest, but had low abundance in 4 year-old stands. Forest species require suitable source habitat within the range of their dispersal capabilities to initiate habitat recolonisation (Cunningham 2000, Murren 2002). The dispersal distances of the three forest species studied are unknown, however dispersal is an important determinant of how these species would experience connectivity between different aged forest stands, and is critical for maintaining and enhancing biodiversity in managed forest ecosystems (Lindenmayer and Hobbs 2004, Barbaro et al. 2005).

6.43 Open habitat species

Sitona discoideus is an open habitat species with high abundance in young regenerating stands, however it was also present at low densities in older stands (unlike *C. tuberculata*). The high abundance of *Sitona* in the 1, 2 and 8-year stands is unlikely to reflect the proportion of bare ground (as in the case of *C. tuberculata*) as *Sitona* is herbivorous and its distribution is probably more dependent on the availability of its principal host (Lucerne (*Medicago sativa*), although it does feed on other introduced *Medicago* spp. that are very uncommon). Mature stands with full canopy cover have a low abundance of Lucerne and consequently low incidence of *Sitona*. The high abundance in open, recently clearfelled sites, may not be solely dependent on host plant availability, as coarse woody debris created during harvesting may also be attractive as summer aestivation sites, which are important for *Sitona* (Goldson et al. 1984).

6.44 Edge species

The existence of edge-specialist species has been shown in many studies of Carabidae (Magura et al. 2001, Molnar et al. 2001, Magura 2002) and butterflies (Schultz and Crone 2001). However the concept is controversial, as their existence is not universal (Heliola et al. 2001), and is thought to be restricted to human modified habitat boundaries (Imbeau et al. 2003). *O. ?piciceps* was chosen for this study as previous sampling indicated that it had an unusual preference for extreme clearfell sizes, both large and small (Chapter 5). Detailed sampling across different age stands showed that *O. ?piciceps* had a strong preference for edge habitat at the boundary of mature forest and young 1-2 year-old regenerating stands (Appendix 6.1). This edge effect is less defined in 4 and 8 year old stands where regenerating trees can be over 10 m tall (Carson et al. 1999). Modifications to flight behaviour have been observed in other flying insects with respect to habitat edges, e.g., butterflies (Ries and Debinski 2001, Schultz and Crone 2001), but the interaction between insects and habitat edges are often species-specific, and can vary temporally and micro-climatically (Ewers et al. In Press).

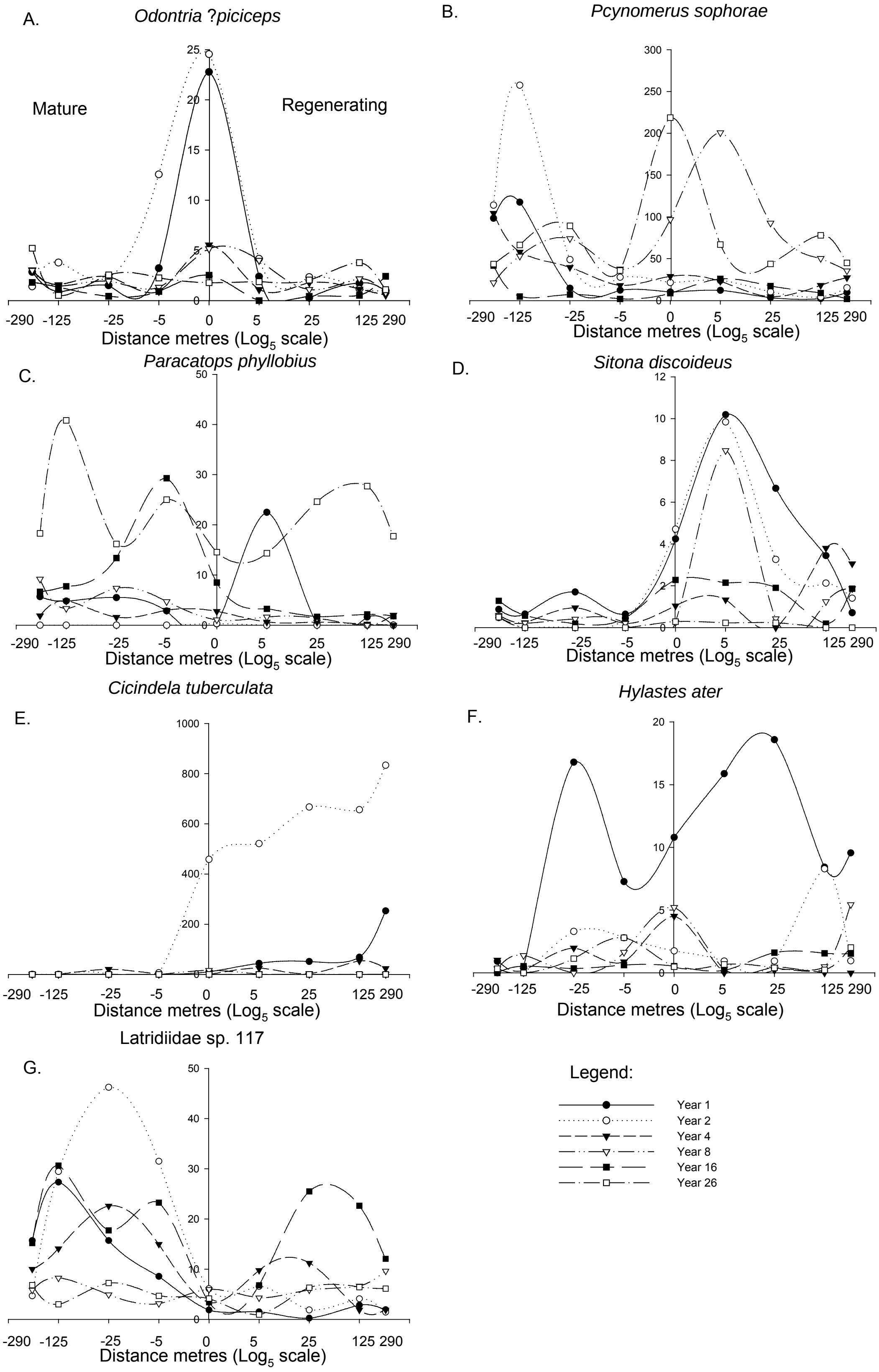
6.45 Exceptions to general abundance trends and their implications for forest management

There were some exceptions to the broad patterns in abundance that were exhibited by the seven species sampled. For example, *Pycnomerus sophorae* was highly abundant in the 5 and 25 m traps of one replicate of the 8 year-old stands (Appendix 6.1). Spatially variable resources such as coarse woody debris are known to have an influence on the abundance of litter dwelling invertebrates (Evans et al. 2003), and the peaks in the individual trap data of *P. sophorae* were associated with high trap catches at two sites that had large piles of adjacent pruning slash. Pruning slash may act as a reservoir or attractor for this species in the young regenerating stands, as I found them living in large numbers under the bark of recently dead trees. The abundance spikes are a sampling effect and their overall significance should be considered in that context, however their existence raises important questions about the role of spatially variable resources in biodiversity retention, e.g., legacy management, where key biological resources such as standing dead trees are retained in harvested areas to provide habitat for biodiversity whilst stands regenerate (Lindenmayer and Hobbs 2004, Keeton and Franklin 2005). Mechanical site preparation is known to affect biota both above and below ground (Miller et al. 1999, Peltzer et al. 2000, Bird et al. 2004), however species responses are inconsistent and subject to spatial variation (Bird et al. 2004). The sharp peaks in abundance of *P. sophorae* indicate fine scale spatial clustering, which is one of the goals of legacy management. Legacy management aims to leave high-biodiversity value, spatially variable resources such as standing dead trees after harvest (Lindenmayer and Franklin 2002, Mazurek and Zielinski 2004). The question remains as to whether these peak spots of insect abundance can be replicated by post-harvest site preparation and whether these peaks in individual species are a reflection of high overall invertebrate biodiversity. Further research into the over-all community response to the presence of these biological legacies may identify simple modifications of current silvicultural practices that can enhance biodiversity.

6.5 Conclusions

Species show disparate responses to clearfell harvesting, and distance from forest edge can be an important factor determining the abundance of species. Beetle species utilised the forest stands at different stages in forest regeneration, which highlights the need to provide a level of connectivity between stands of different ages that match the dispersal capabilities of the species. There is a clear lack of basic biological information on dispersal capabilities, habitat requirements of non-pest species and the factors mediating movement across patch and matrix boundaries. Future work should focus on species groups with life-history strategies that are known to make them vulnerable to habitat change, e.g., large flightless habitat specialist species with poor dispersal abilities (Gibbs and Stanton 2001, Fahrig 2003, Driscoll and Weir 2005), as their dispersal success is likely to decrease dramatically with increasing distance between suitable forest stands.

Appendix 6.1. Average catch per 100 trap days of selected beetle taxa across pitfall trap gradients between mature forest and regenerating stands (positive distances) is presented. **A)** *Odontria ?piciceps* was attracted to edge habitat in young stands, where as **B)** *Pycnomerus sophorae*, **C)** *Paracatops phyllobius* and **G)** Latridiidae sp. 117 preferred mature forest stands. In contrast **D)** *Sitona discoideus*, **E)** *Cicindela tuberculata* and **F)** *Hylastes ater* were most abundant in the open habitat of young clearfells. Lines in all graphs are splines created using the curve fitting function of Sigma Plot (Version 7.0, SPSS Inc).


A.
Odontria ?piciceps
Mature
Regenerating
25
20
15
10
5
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
B.
Pcynomerus sophorae
300
250
200
150
100
50
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
C.
Paracatops phyllobius
50
40
30
20
10
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
D.
Sitona discoideus
12
10
8
6
4
2
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
E.
Cicindela tuberculata
1000
800
600
400
200
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
F.
Hylastes ater
20
15
10
5
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
G.
Latridiidae sp. 117
50
40
30
20
10
0
-290 -125 -25 -5 0 5 25 125 290
Distance metres (Log5 scale)
Legend:
Year 1
Year 2
Year 4
Year 8
Year 16
Year 26

Chapter 7 - Synthesis

7.1 Introduction

It is universally recognised that deforestation is a key driver of global biodiversity loss (Sala et al. 2000). Deforestation is closely linked with national wealth (Meyer et al. 2003, Rudel et al. 2005, Ewers et al. In Press), and some wealthy countries are experiencing net afforestation (Ewers et al. In Press). Most of New Zealand's lowland and coastal regions have suffered extensive historic deforestation by both Polynesian and European settlers (McGlone 1989), and in some ecological districts deforestation continued to the point where less than 1 % native forest cover remains, e.g., Canterbury and Waikato (data from LCDB2, (Terralink 2004) , Walker et al. 2005). It was only in the early 1800s that New Zealand went through the initial stages of a developing nation, with an economy that was heavily reliant on natural capital, e.g., native forests. It was recognised as early as 1911 that extractive forestry was unsustainable, and a comprehensive government-driven operation was begun to develop plantation forests (Roche 1990). Today New Zealand's publicly-owned native forests are totally protected and it is the large plantation forest estate of nearly 2 million hectares of exotic species that supports the now privatised forest industry. Overseas studies of the long-term clearfell harvesting impacts have focussed on managed native forests (Spence et al. 1996, Williams et al. 2001, Koivula et al. 2002, Ferguson and Elkie 2003), not fast-growth plantations of exotic species. As such, overseas research is often not applicable and it is important to undertake clearfell harvest research in New Zealand.

7.2 Non-native forests as reservoirs for native biodiversity in a fragmented New Zealand landscape

Plantation forests have the potential to provide alternative habitat for biodiversity, particularly in highly fragmented landscapes that retain little of their indigenous forest cover (Carnus et al. 2006). This implies that plantation forest, as a 'matrix' habitat, provides a suitable low-contrast extension of native habitat (Kupfer et al. 2006), that also improves connectivity between native remnants and the populations present therein (Norton 1998). Empirical studies have shown that plantations in New Zealand and Australia can support significant populations of native plants (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003), birds (Clout

1984, Lindenmayer et al. 2002, Spurr and Coleman 2002) and invertebrates (Bonham et al. 2002, Mesibov 2005, Berndt et al. Submitted), including a number of threatened or rare species (Kleinpaste 1990, Brockerhoff et al. 2005). My studies of selected beetle taxa found no difference in rarefied beetle species richness between native forest, mature *P. radiata* or pasture (Chapter 4) in the central North Island of New Zealand. Furthermore, over 350 species of beetles were collected during an assessment of clearfell harvest size impacts on biodiversity (Chapter 5). Most beetle species were native and only a few exotic species were present. Exotic species were not a feature of the native forest, which suggests that the increased frequency of disturbance in plantation forests, and the tree species composition may present opportunities for the establishment of non-native beetle species. Despite the presence of exotic species in mature *P. radiata* stands, the beetle assemblages in this production habitat were the most similar to native forest. These results show that New Zealand plantation forests are a suitable habitat extension to remaining native forest, even though they could never fully replace them as habitat for all native species. Native habitat and its proximity will remain pivotal to many species that require specialist resources that are not available in managed plantations of exotic tree species.

Although there was no difference in the species richness of pasture sites compared to other habitats sampled, sampling did not extend more than 125 m into grassland habitat. In contrast *P. radiata* sites sampled within the middle of Kaingaroa forest were several kilometres from the nearest native habitat, yet they retained high beetle biodiversity. Further study is required to understand the influence of the proximity of remnant native forest and plantation stands on biodiversity in adjacent pasture. The high diversity of native beetle taxa recorded in our pasture sites may be the result of short-distance dispersal from adjacent forest, and thus not represent self-sustaining populations. This point is critical given that the dominant matrix habitat throughout New Zealand is pasture and native remnants in some ecological regions are highly isolated.

7.3 Impact of forest harvesting

Forest harvesting, especially clearfelling, is a controversial process (Noon and McKelvey 1996), and clearfelling unquestionably results in severe and immediate changes to forest ecosystems (see review in Chapter 3; and references therein). There has been a slow transition to alternative harvesting regimes that avoid the large-scale, even-aged forest management approach of clearfelling, particularly in North America and Europe. These new silvicultural techniques have been the focus of several long-term, large-scale research projects, e.g., at Sicamous Creek (Vyse 1999) and MASS (Beese and Arnott 1999) in British Columbia. However, the work presented in this thesis is the only attempt to measure biodiversity in experimentally created clearfell harvest areas of different sizes that are relevant to current plantation forestry practices in New Zealand.

7.31 Short-term impacts

The expected rarefied species richness of native beetles in clearfell habitat was greater than that found in mature *P. radiata* stands (Chapter 4). Furthermore, there was a significant increase in rarefied beetle species richness in recent clearfells relative to adjacent mature *P. radiata* stands (Chapter 5). This is consistent with overseas studies of clearfell harvesting were species richness of certain taxonomic groups increased post-harvest, e.g., Carabidae (Niemela et al. 1993), although individual species responses are inconsistent (Atlegrim et al. 1997). The cause of these short-term changes in species richness is not fully understood. European studies of Carabidae have shown an initial survival of forest species, which is augmented by the rapid colonisation of clearfells by open-habitat species (Niemela et al. 1993, Atlegrim et al. 1997, Koivula et al. 2002). My work supports the notion of rapid colonisation of open habitat species, such as *C. tuberculata*, and the resultant post-harvest increase in overall species richness. However the persistence of ‘forest’ species is difficult to assess as the ecological requirements of New Zealand Carabidae, like those of other southern hemisphere countries, e.g., Australia (New 1998), are poorly understood.

Rarefied species richness of native beetles was significantly higher in the largest 500 ha clearfells, but unfortunately there was significant spatial autocorrelation in the analysis of this treatment level, so the significance of the high species richness in these large harvest areas should be treated with caution. In contrast to large clearfell areas there was little change in beetle species richness in 0.01 ha to 50 ha clearfell harvest areas. However, significant changes in the beetle species composition between different-sized clearfell harvest areas and adjacent mature forest stands did occur. Small 0.01 ha harvest areas showed very little change in species composition, whereas larger clearfells had a very different fauna compared to adjacent mature *P. radiata* stands. A central theme to this thesis has been the concept of a threshold clearfell size (See Chapter 3). My analysis of beetle diversity across a range of clearfell harvest sizes did not indicate the presence of a threshold clearfell size where the rate of change in ecological impacts was disproportionate to the change in clearfell harvest size. Perhaps the theoretical concept of an ecological threshold is not valid, or alternatively I was unable to detect it due to my experimental design. The taxa studied or the size range sampled may not have been suitable to document an effect. Furthermore, the effect of historical land-use may have had a stronger influence on biotic communities than the size of different harvest areas. The study was undertaken in second and third rotation plantation forests and many of the clearfell harvest area sensitive species may already have been lost; or alternatively they did not survive the transition from native forest to a production ecosystem.

Proximity of native forest and clearfell harvest size were the most significant environmental factors explaining this short-term change in species composition between harvest size treatments (see also Humphrey *et al.* 2004). As such, landscape scale management of habitat heterogeneity may indeed be crucial for enhancing biodiversity in managed forests, as suggested by Lindenmayer *et al.* (2004).

Short-term disruption to the visual appearance of forests post-harvest can be severe, and such aesthetic changes are the focus of intense public opposition to clearfelling (Ribe and Robert 1999). Aesthetic change is undoubtedly one factor that influences the public perception of harvest impacts on biodiversity, although this appears not to have been studied. Empirical research presented in this thesis has shown that clearfelling is not necessarily detrimental for biodiversity (and can be beneficial for some species). Unfortunately, such research may never counter-balance the current strength of public opinion. As such, forest managers should seriously consider a coordinated education programme to inform the general populous of the potential biodiversity benefits of plantation forests. Irrespective of the negative consequences of clearfell harvesting (both real and perceived) and the potential short-term benefits for some disturbance-adapted species, it is the long-term impact (over the entire forest rotation) that determines the sustainability of current clearfell harvesting practices.

7.32 Long-term implications

Biodiversity in overseas plantations is often lower than that in managed native forests (Magura et al. 2003), however my results show that plantations can have similar or greater rarefied beetle species richness than adjacent native forest. Biodiversity has been shown to recover to pre-harvest levels in some managed native forests, although this may take many years, e.g., 70 years for birds in an Australian eucalypt forest (Williams et al. 2001). Although, sensitive groups, such as saproxylic beetles are known to suffer from clearfell harvesting and do not recover under current management techniques (Grove 2002a, 2002b). Prior to my study the only evidence for differences in beetle community assemblages between different-aged *P. radiata* plantation stands in New Zealand was a limited three-age-class study by Hutcheson and Jones (1999). Results from my study (Chapter 6) indicate that the beetle species sampled recover from the short-term effects of clearfell harvest within 8 years. Despite the high-intensity disturbance to the forest ecosystem during harvesting, insect species still colonise regenerating stands as they mature. Furthermore, individuals of the seven species sampled were distributed throughout the entire gradient between 50 ha clearfells and different aged stands sampled, which indicates that harvest areas of this size are not detrimental to the long-term retention of these species, as suitable habitat is within the scope of individual dispersal distances of these species.

Understorey plant diversity decreased significantly with distance into harvested stands (Chapter 6), but like beetles, a long-term space-for-time chronosequence study showed that plant species recovered quickly to pre-harvest levels (Chapter 6). Recovery of understorey plant species in New Zealand plantations can also be inferred from studies by Allen *et al.* (1995), Ogden *et al.* (1997) and Brockerhoff *et al.* (2003), as they recorded high understorey diversity in second rotation plantation stands indicating recolonisation post-harvest.

7.4 New Zealand forestry: modern biodiversity challenges, their implications and potential solutions.

Approximately one-third of New Zealand's plantations are currently certified as sustainably managed forests and adhere to the criteria of the Forest Stewardship Council (FSC). Since 1995 FSC principle 10, which comprises 9 criteria specific to the management of plantation forests (that must be adhered to in addition to the other 9 principles), has been a key element of the FSC process. However a draft discussion document (Synnott 2002) that attempted to clarify policies within principle 10 was rejected in November 2002 by the FSC general assembly as 'too ambiguous' and in need of clarification. In response principle 10 is currently under review (see FSC website, http://www.fsc.org/en/work_in_progress /plantations_review), and some environmental NGOs have made attempts to exclude exotic species plantations from FSC on the basis that they are not 'forests' in the natural sense (Rosoman 2004). Will this affect forestry in New Zealand and why is it relevant to my thesis?

New Zealand currently has 1.8 million hectares of plantation forest (Anon 2005) and approximately 112,000 ha of native forest managed for timber production. Depending on the outcome of the FSC review, the New Zealand plantation forest industry could be severely affected, as many important export markets demand FSC certification of their wood products. There are several key points of contention; the use of chemicals, clearfell harvesting and the biodiversity capacity of plantations versus natural forests. Results from this thesis provide one of the largest single studies about clearfell harvest impacts and stand regeneration on invertebrate biodiversity in New Zealand. The knowledge that plantation forests are suitable low-contrast alternative forest habitat for Coleoptera, and that they compare favourably with other habitats elements within the landscape can be used, in part, to argue for the inclusion of plantations within the scope of FSC. New Zealand plantations are no longer established by replacing native forest, in fact there is a higher probability, given current economic conditions, that plantations will be converted to pasture. Unfortunately pastoral areas are incapable of supporting native plants and probably most forest insect species (although further sampling is required). As such, increases in the proportion of pastoral farming could potentially lead to significant reductions in regional biodiversity. Regardless of this argument, plantations will never provide all of the necessary habitat requirements for specialist invertebrate species (and nor should they), thus remaining native habitat in the landscape is extremely important and should be protected and enhanced through active management. This can be achieved by plantation initiatives such as FSC Principle 10.5 that requires a portion of the estate to be managed as natural forest cover, currently no similar standards exist for pastoral farming. Furthermore utilising plantation resources alleviates pressure on remaining native forest resources, thus protecting native ecosystems.

Clearfelling is one of the most controversial issues addressed by the FSC review of principle 10. Clearfell harvesting clearly has significant impacts on the invertebrate fauna (Chapter 4 & 5), but there is no indication that larger clearfell sizes detrimentally affect short-term beetle species richness at the scales sampled in this study. However, larger harvest areas cause greater change in beetle community composition. My study has not detected any clear ecological threshold size to clearfell harvesting impacts that could potentially guide the creation of clearfell harvest size policies in New Zealand. Nevertheless, there is some indication that rarefied beetle species richness may change significantly between 0.5 ha and 5 ha, although this requires further investigation.

What is clear from my work is that the proportion of native habitat in the landscape has a significant effect on the composition of the beetle fauna in clearfelled stands (Chapter 4 & 5), and that native plant understorey influences beetle species composition in different habitats (*P. radiata*, native forest and pasture, Chapter 4). The proximity of native forest remnants and their influence on nearby plantation stands has been recorded before (Humphrey et al. 2004), and landscape heterogeneity is increasingly acknowledged as an important determinant of biodiversity in managed forest ecosystems (Lindenmayer and Hobbs 2004, Barbaro et al. 2005, Loehle et al. 2005). As such, FSC should move away from stand-level management issues and place further emphasis on larger landscape-level issues within plantations and how they influence biodiversity. By increasing landscape scale heterogeneity in stand ages and decreasing the isolation of stands from native remnants, native biodiversity within plantation forests may benefit more than specific changes to stand-level clearfell harvest policies. Biodiversity in New Zealand forestry is not an issue of “plantation forests versus native forests”. Plantations in New Zealand should be seen as a complimentary habitat and efforts should concentrate on how best to integrate this resource into the landscape to enhance biodiversity preservation at a landscape level.

7.5 Future research directions

As with most research projects many questions arise from a set of initial experiments. These questions then provide the basis for future research directions, which are listed below.

- What is the influence of landscape and stand structural heterogeneity on invertebrate biodiversity? Clearfelling is a stand-level attribute, however important landscape level issues (Lindenmayer and McCarthy 2002, Barbaro et al. 2005) are yet to be studied in New Zealand plantation forests. Overseas research has concentrated on the influence of native habitat proximity on biodiversity in managed native forests, but it is important to answer this question in a New Zealand plantation context. Our forest industry is unique in that we rely, almost solely, on fast-rotation exotic plantation forests. Furthermore the New Zealand fauna has evolved on a large, isolated archipelago, which was recently colonised by humans and has been subjected to an extraordinary complement of exotic plant and animal invasions. Because of these differences with Northern Hemisphere continental habitats, e.g., Boreal forests, the interaction between New Zealand's plantation and native habitats may vary considerably from that of other countries.

- Individual species respond differently to post-harvest environmental changes. Some species increase in abundance and others decline relative to levels in adjacent mature forest. At present our species-level ecological knowledge is limited and we do not know the mechanisms that drive these species response. By designing specific experiments to test abiotic and biotic factors that may influence the abundance of individual species we can potentially reduce the impact of forest harvesting on these species.

- Invertebrates are a key food source for many other species, and are present in much higher abundances in recent clearfells compared to other habitat (Chapter 4). Recent clearfells are also popular breeding sites for the New Zealand flacon (*Falco novaeseelandiae*) that preys on small passerine birds. As yet we do not know if there is a link between harvested areas, invertebrate populations, small bird abundance and predatory species such as the New Zealand falcon. Future research on the ecological links between trophic levels in plantations may allow forest managers to increase the populations of threatened New Zealand fauna, such as falcons or kiwi on their estates.

- How does clearfelling affect the small-scale, farm forester? During the latter stages of my PhD I was asked to write a small article for 'The Tree Grower' (Appendix 7c) outlining how my results may be of relevance to farm foresters. Large-scale plantation forest stands nearly always have remaining mature stands to provide source populations for the regenerating stands. Farm foresters in New Zealand manage a total of over 100,000 ha of plantation forest but in most cases these are small isolated stands that are harvested in their entirety at once. As such, the question remains, do invertebrates manage to successfully recolonise these harvested stands given their potential isolation from source populations of forest invertebrates.

- By sampling across gradients between different landscape elements it became apparent that there was a 'spill-over' effect caused by the dispersal of species from adjacent habitat (Chapter 4). Because pasture was only sampled at a maximum isolated distance of 125 m we cannot be certain that the biodiversity recorded in this study is independent of such dispersal effects. Further sampling is necessary to determine the effect of habitat isolation on biodiversity within pasture, especially since it is the dominant matrix habitat in most modified New Zealand landscapes.

"You cannot see the forest for the trees? I assure you it is there, beneath the green plantation canopy lives a thriving forest community of native species"

Paper produced from 84% FSC certified forest resources

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Appendix A – Other publications produced during my PhD

This chapter includes four publications that were completed during the course of this study:

A) Pawson, S. M., and Brockerhoff, E. G. 2005. Natives in a pine forest. *New Zealand Geographic* 72:78-93.

B) Pawson, S. M., Brockerhoff, E. G., Didham, R. K., and Norton, D. A. 2005. Clearfell harvest size: A key issue for biodiversity conservation in New Zealand's plantation forests. *New Zealand Journal of Forestry* 50:29-32.

C) Pawson, S.M. (In Press). Native biodiversity and the impact of forest harvesting on small-scale farm forests. *The Tree Grower*.

D) Brockerhoff, E.G., Pawson, S.M. and Ecroyd, C. 2005. Is there a role for plantation forests in the conservation of biodiversity? *Indigena* December 25-27.

KENNEDY WARNE

Natives in a Pine Forest

By Steve Pawson

with contributions by
Eckehard Brockerhoff

Plantations of exotic timber trees, especially pines, are looked on with disdain by many as alien monocultures, an unpleasant accommodation necessary to protect precious indigenous forests from the logger's chainsaw. Yet a good range of native organisms, untroubled by the trees' pariah status, are quietly enjoying life beneath the rain of pine needles.

The uncommon New Zealand falcon is a species that seems happy to move into even quite freshly milled exotic forest areas, nesting successfully among the debris and feeding on newly-exposed birds and insects.

DEBBIE STEWART, WINGSPAN BIRDS OF PREY TRUST

It’s another warm, sunny summer day, ideal for tree growth. Just south of the Waiotapu pub, on the Rotorua-to-Taupo highway, I head into one of New Zealand’s largest pine forests, Kaingaroa Forest, to check my pitfall traps and see how many insects I’ve caught.

After parking the dusty ute and donning the usual high-vis reflective clothing, it’s into the blackberry and gorse that seem to protect the edge of many pine plantations from all but the most curious of people. In the open it’s already hot, but inside the forest it’s cool and damp, with a lush carpet of mosses and ferns underfoot. The first of my insect traps is only a few hundred metres inside; however, along the way there are several diversions. A fantail flitters behind me as I push through increasingly dense tree ferns and small native shrubs. Rotten tree stumps have been heavily damaged by a pig that has spent a recent evening feasting on the huhu grubs within. The remains of last night’s work by the local spiders sparkle with morning dew, and webs strung between trees catch my face.

My first pitfall trap is placed next to a grove of tree ferns. It consists of a plastic cup sunk to ground level with a rain cover and panels that guide ground-dwelling invertebrates to the central collecting pottles. A robin hops along to have a look at my haul of weta, millipedes, beetles, flies and a myriad other creatures. I transfer these to a jar of alcohol for later examination and move on, as I have only five days to check over 400 such traps spread throughout Kaingaroa and Tarawera Forests and some smaller neighbouring plantations. Besides which, Ecki, who is attending to the other half of the trap line in the adjacent compartment, will soon be waiting at the truck, and we still have another 11 trap lines to check before the end of the day.

How rich are our exotic pine plantations in native flora and fauna? It was Ecki who brought the biodiversity value of pine forests to my attention at the start of my studies. In his work in Rotoehu and Kaingaroa Forests (near Rotorua), Hochstetter Forest (on the West Coast) and Eyrewell Forest (in North Canterbury) he found a total of 202 native and 70 introduced plant species in only 60 small study plots. This number of native plants represents almost 10 per cent of New Zealand’s total, a very respectable figure indeed considering the small size of the area assessed. Plant diversity is pretty much confined to the understorey, however, the upper canopy in older stands consisting entirely of pine. So far my insect traps, part of a large-scale project investigating the impact of the size of clearfell harvest areas on invertebrate biodiversity in pine forests, are showing similar results. I’ve found over 350 species of native beetle alone, and the number keeps climbing.

Pine forests are a mosaic of stands of different ages, with recently harvested areas, young trees and mature pines in relatively close proximity. This provides a wide range of habitats, and also helps me to navigate. A forest-establishment map and an eye for different tree heights (and thus ages) allow me to find my way to various sites, despite the maze of unnamed roads that leave first-time visitors disoriented.

Introduced plant species such as buddleia, gorse, broom and grasses tend to dominate in the open—in harvested areas and skid sites (where timber is collected for transportation) and along roadsides—although many natives are also present in these places. This tends to be all that the average passing motorist sees of the country’s pine plantations, which does little for an appreciation of the diversity of native plants in the understorey.

As a plantation ages and successional processes kick in, the proportion of native species begins to increase. By the time the pines are 20 years of age a dense understorey of native shrubs, tree ferns and, in some cases, sub-canopy trees is likely to have developed. As long as moisture is adequate, the low light levels associated with canopy closure give native plants an advantage over exotics such as gorse, which demand more light. As the pines approach maturity the understorey is often very similar to that of nearby native-forest remnants. The dry Canterbury Plains forests, however, such as

KENNEDY WARNE

About a quarter of New Zealand’s forests consist of exotic plantations, 90 per cent of them radiata pine. On the pumice lands of the central volcanic plateau, Kaingaroa Forest (seen here) covers hundreds of kilometres—a vast resource for the myriad native plants and animals that have taken up residence within it.

This 20 mm long native chafer beetle ***Stethaspis suturalis*** is common in both native and exotic forests, where its larvae feed on tree roots.

BRIAN CHUDLEIGH

Eyrewell, have much lower understorey diversity than the wetter forests around Rotorua and on the West Coast.

Probably the most conspicuous native plants in pine plantations are ferns, which regularly reach levels of diversity similar to those in adjacent native forest. The large mamaku, or black tree fern (*Cyathea medullaris*), and our national emblem, the silver fern (*Cyathea dealbata*), are common in the sub-canopy of many low-altitude North Island pine forests. I regularly do battle with their fronds as I push through to my more distant pitfall traps, although bracken is worse, growing to a height of 2 m at some of my sites.

The densest groves of tree ferns develop in moist gullies, while smaller ferns are ubiquitous. Studies by John Ogden of Auckland University have shown that tree ferns commonly reach densities of 2000–2500 per hectare in the mature pine plantations of the central North Island. Such proliferation is largely a reflection of tree ferns' dispersal capabilities. Fern spores are readily blown through the landscape, and the canopy of a radiata forest provides an ideal environment for their germination and subsequent growth. Even stands as young as 6 years may have healthy fern populations derived from the regrowth of plants that survived the harvesting process.

Not only are pine forests a haven for common New Zealand native plants, they are home to a number of endangered or threatened species. For example, the native woodrose (*Dactylanthus taylorii*), a bat-pollinated parasitic plant that grows on the roots of sub-canopy trees (see *NZ Geographic*, Issue 6), has been found in a pine forest in north Taranaki. An undescribed species of *Pomaderris*, a genus of indigenous shrubs uncommon in the South Island, is found in relative abundance in Eyrewell Forest. Probably the most fascinating plants to be found in New Zealand's pine forests, however, are the native orchids.

The Iwitahi Orchid Reserve, established in a corner of Kaingaroa Forest in August 1987, is a small piece of paradise for orchid lovers. Only a few hectares in size, this old-growth *Pinus nigra* forest, with its deep litter layer and rich fungal flora, supports a staggering 36 species of native orchid, including the only known North Island population of *Chiloglottis valida*. Not to be outdone, a larch and Corsican and Austrian pine forest near Hanmer Springs, in North Canterbury, is also rich in native orchids. Controversy has recently arisen as a result of large areas of this forest being harvested. Despite the dramatic changes to the landscape, the orchids and other wildlife should return in time. To facilitate recovery, however, foresty companies need to draw up sensible harvesting plans. Thoughtful logging allows indigenous flora to survive in the remaining mature compartments of a forest while regeneration takes place in the younger stands. A chequerboard pattern of stand ages can maximise ecological opportunities and facilitate dispersal between habitats, thereby maintaining (even enhancing) forest biodiversity on a landscape scale.

New Zealand's unique bird fauna is without doubt a main focus of the country's conservation efforts. On the whole New Zealanders prefer to watch and listen to birds than to observe other animals. If past research is anything to go by, one of the best places to see birds is in your local pine forest.

The earliest records of native birds colonising pine forests were made in the 1940s. By the 1960s, Kaingaroa Forest boasted the highest densities of birds recorded on the New Zealand mainland, with 1203 pairs per 100 ha, 652 of which were native. Such abundance is still noticeable. On warm, fine afternoons, as I walk through Kaingaroa Forest to check my pitfall traps, the chorus of birdsong is unlike anything I've heard in other mainland forests. Although the avifauna of pine forests is not as diverse as that of thriving native ecosystems, forest biologist R.W. Jackson recorded 54 native and 26 exotic species in pine forests. Insectivo-

ECKEHARD BROCKERHOFF

As pine forests mature and the canopy closes after 10 or 15 years, the heavy shade beneath the trees is perfect for the growth of not only native ferns, but a whole range of understorey species such as five finger, various coprosmas, putaputaweta, pate, and hangehange.

WARREN JUDD

A year after a logged forest at Riverhead north of Auckland has been replanted, introduced weeds such as fireweed, gorse and pampas abound, but a few natives that like high light levels, such as this kumaraho, have also established. Once the growing pines produce shadier conditions, these species will only survive on the margins of the forest.

rous birds dominate owing to the abundance of suitable food and the general lack of fruit and nectar as required by other birds, such as tui, bellbirds and kereru. Whiteheads, tomtits, robins and brown creepers are all abundant within their respective ranges, as are a number of introduced species.

Lunchtime in a pine forest is always a good time to observe these birds and presents me with an opportunity to feed the local population of inquisitive robins the odd crumb from my cheese sandwich. However, a couple of my study sites are rather more dangerous places in which to dawdle, being home to breeding pairs of the endangered New Zealand falcon. These birds don't take kindly to visitors and have been known to force this humble entomologist to run between traps to keep out of their way. Many falcon families have taken up residence in pine plantations, and the species is currently flourishing in the large clearfell areas and young stands of radiata in the central North Island forests. The precise reasons for this success are not known; however, there is an abundance of prey due to the high densities of insect- and seed-feeding songbirds in pine plantations. Falcons are also present in exotic forests elsewhere in the country.

Don Cooper, a retired New Zealand Forest Service technical officer and long-time amateur ornithologist from Nelson, has had a long association with the falcons in nearby Golden Downs forest. Brief glimpses of falcons chasing prey through the trees was about as much as he saw of the birds while working in the forests over 40 years ago. Yet his long-term observations indicate that birds from the finch family make up a large proportion of the falcon diet in Nelson's exotic forests, and that nearby streams are important preening and bathing sites.

Since spring 2003, Nelson forest owners Weyerhaeuser have discovered numerous falcon nests in recently harvested areas. With a little help from logging crews and plastic tape to keep machinery away from their nests (which are on the ground, among harvesting debris), the falcons have been flourishing. Cooper has witnessed the fledging of numerous chicks from these areas, sometimes as many as three at once, when two is more usual. The falcons' hunting ground of open scrubland expands as the crews remove yet more trees. If you venture into such an area, don't forget to wear a hard hat or you might just get a slap on the head from a swooping bird.

Other rare or threatened New Zealand birds are either resident in pine forests or occasionally visit them. These include the rifleman, fernbird and long-tailed cuckoo. Kaka in the Whirinaki region derive a considerable portion of their diet from exotic trees, in particular Douglas fir, from which they strip and eat the bark of the terminal leaders as well as the seeds. Wetlands and streams within plantations also provide habitat for species such as blue duck, Australasian bittern, brown teal, dabchick, banded rail, spotless crake and, perhaps surprisingly, kakapo, kiwi and kokako. Yes, three of our most iconic bird species are quite happy about spending time in pine forests, odd as this may seem.

Kakapo deserve a special mention with respect to pines. It is thought that plant hormones present in green rimu fruit—in the relatively occasional years in which this is abundant—trigger kakapo breeding. These hormones are also present in other developing fruits and plant materials. On Maud Island/Te Hoiere, in the Marlborough Sounds, where some kakapo were kept for a time, one of the birds' favorite foods was *Pinus radiata*. Foliage, stems, pollen cones, small green cones, bark—they loved everything. In 1998 two Maud Island kakapo, Flossie and Richard Henry, bred successfully on this

Insect-eaters, such as the native robin, are often to be found in plantations where decaying prunings and the carpet of needles provide shelter and sustenance for a great range of arthropods.

KENNEDY WARNE

KENNEDY WARNE (BOTH PHOTOS)

Ecki Brockerhoff shakes a kanuka tree to dislodge insects onto a collecting sheet. Ecki leads a team studying biodiversity and conservation in plantation forests at the Forest Research's Centre for Sustainable Forest Management. Steve Pawson (right) checks the critters that have had the misfortune to stumble into his preservative-containing collecting jar.

diet. From early November 2004 to February 2005, 13 female and 4 male kakapo on Codfish Island/Whenua Hou were fed green pine conelets in an attempt to stimulate breeding. Preliminary results suggest possible success.

Birds are the noisiest contributors to the biodiversity in plantations; however, the majority of native organisms in pine forests remain unseen by most visitors. Many invertebrates are active only at night, and the prolific fungal communities are, for the most part, underground. Fungi are for long periods present only as masses of white and yellow hyphae that grow slowly through the deep layers of pine-needle litter and woody debris on the forest floor. However, every year they burst forth with the fruiting bodies we know as toadstools and mushrooms. Brown, red, purple, orange and white, they sprout following periods of rain. Thousands of red- and white-spotted *Amanita muscaria* can pop up seemingly overnight, imbuing the forest with a magical fairytale quality.

Apart from their attractive—and, in some cases, deadly—fruiting bodies, fungi play a vital role in the health and growth of pine trees. Chemical decomposition of organic matter by the enzymes produced by fungi is integral to the recycling of nutrients in a forest. Some fungi have a symbiotic relationship with trees. These are the so-called mycorrhizal fungi, which live among the tree roots, where they receive shelter from the soil environment and enjoy a ready source of carbon as food. In return, mycorrhizae help trees garner nutrients such as nitrogen and phosphorous, which are essential for growth but often in limited supply.

The prolific growth of fungi and the abundant supply of decaying wood provide ideal habitat and food for many insects. Insect diversity in an individual pine forest could well top 1000 species when beetles, flies, wasps, true bugs and all other insect groups are taken into account.

The huhu beetle is a very common and gastronomically popular denizen of pine forests. As the sun sets and the light fades on warm summer evenings, the drone of their wings as they cruise the forest in search of freshly felled timber is clearly audible. Females lay eggs in recently dead radiata logs or stumps. Once hatched, the grubs proceed to turn the wood into dust before emerging as adults two years later. However, hungry wild pigs, which use their powerful tusks to rip apart such logs in search of a high-protein snack, often interrupt this process.

Weta is the common name for several families of native flightless grasshopper. A number of species of ground weta and cave weta are common in pine forests. Cave weta are perfectly at home there, thriving in the damp environment of rotting logs or piles of waste wood produced during pruning or thinning.

Caterpillars of the ghost moth (family Hepialidae, members of which grow up to 10 cm long) spend the nocturnal hours ambling across the forest floor looking for food while trying to avoid becoming food for others. By day they shelter in deep burrows in the litter, protected from predators and the drying sun. As they roam at night, feeding on fallen leaves, they create little swirls in the pine needles surrounding their homes. However, you have to tread very carefully if you want to see one, as they are incredibly sensitive to vibration and quickly retreat underground.

Unlike many countries New Zealand has a relatively impoverished native mammal and frog fauna. What few species it boasts are endemic and of international importance. Neither group is commonly represented in plantation forest but specimens from both have been found there. Long-tailed bats have been seen roosting in the decaying boles of old pines, and populations of the scarce Hochstetter's frog (see

STEVE PAWSON

KENNEDY WARNE

Up to 1000 species of insect—and that wouldn't include spiders such as *Hemicloea rogenhoferi* (above)—are likely to live in individual pine forests. Since the species found will vary around the country, the total number of native insect species that use pine forests will be considerably higher. The beetle with the fine jaws is a 3.5 cm *Placumostethus planiusculus*, from Marlborough.

ROGAN COLBOURNE

Kiwi, being eaters of grubs, slugs, worms and insects, can probably reach higher densities in pines than in native bush. This bird was photographed in Waitangi Forest where some 1000 kiwi are thought to live in the midst of normal forestry operations.

NZ Geographic, Issue 38) survive in a number of Northland pine forests, where suitable habitat exists along the margins of streams.

Lorna Douglas, at Northern Poytechnic, began studying Hochstetter's frogs in 1997 and has been returning to some sites in the pine plantations for the last six years. She has found the majority of frogs are resident in steep gullies that retain some native forest and are buffered from the surrounding agricultural landscape by an encircling pine forest. The gullies provide an ideal habitat, with small waterfalls and cascades and abundant shelter under rocks. Douglas's research has shown that the frogs are reliant on good shelter and water quality. In most areas water quality is assured by the riparian margin of undisturbed native forest bordering the streams. However, wind-throw events are common due to the underlying soil types in the area, and canopy disturbance from forest harvesting occurs every 25–30 years. These can have an impact on water quality, resulting in periods of stream sedimentation. The good news is that recent monitoring in Carter Holt Harvey's forests has shown that some frogs survive both wind throw and harvesting and have been found in regenerating stands after logging.

Native frogs are not the only interesting animals associated with the streams of plantation forests. Compared with some other productive land uses, such as pastoral farming, plantation foresty doesn't contribute much sediment to streams. Good forestry practices protect riparian vegetation, which stabilises riverbanks and, most importantly, provides shade, preventing an increase in water temperatures. This combination of

Exotic habitats are known to support some of New Zealand's more threatened organisms. For example, the large and endangered Mahoenui giant weta, thought to have lived originally in the epiphytes of formerly abundant tawa forest, now thrives in a large patch of King Country gorse. Among insect samples recently collected from Kaingaroa and Tarawera Forests were six specimens of an as yet undescribed and little-known species of rove beetle—doubling the number of known specimens.

Another unusual find was recently made in a pine plantation on the Canterbury Plains, a region that has lost 98 per cent of its natural vegetation: seven specimens of the ground beetle *Holcaspis brevicula*, a species unknown outside the plains.

Few areas remain that resemble the forest habitat it occupied before people modified the landscape and, because of its rarity and localised occurrence, it is near the top of New Zealand's red list of threatened species, being categorised as critically endangered. All seven specimens originated from Eyrewell Forest, which may be the only habitat remaining to it. The fact that the trees are not native doesn't seem to bother the beetle, which does, however, shun open grassland.

North Island brown kiwi are quite common in North Island pine plantations, especially in Northland. Waitangi Forest, near Kerikeri, is estimated to be home to 800–1000 kiwi—despite normal forestry activities and the killing of several hundred birds by a single stray dog in 1987. The kiwi in this forest are well known because they have been studied intensively, first by Harold Corbett, a forestry student, and then by TV personality Ruud "Bugman" Kleinpaste and Rogan Colbourne. Their research showed that many of the kiwi territories were located entirely within areas planted with pines, indicating that the birds did not necessarily require indigenous forest. This surprised some conservationists, who assumed that exotic plantation forests couldn't possibly be good kiwi habitat. However, if the birds' basic requirements are met—sufficient food (in the form of soil-dwelling invertebrates), shelter and a scarcity of predators—it doesn't seem to matter too much whether the trees are kauri or radiata pine.

The story of the kiwi in Waitangi Forest has helped to alleviate some of the negative perceptions of plantation forests. If their value to native organisms was better appreciated, more could be done to protect birds in particular. Prohibiting dogs would be a good start. The way in which harvesting is conducted is also important. For example, if smaller, scattered compartments could be harvested, rather than large, contiguous areas, kiwi populations wouldn't lose all their territories at once, and could disperse gradually and recolonise new areas.

Alternatively, if small areas of scrub were left after harvesting, at least some kiwi might be able to remain in their existing territories. It would also be advantageous to reduce harvesting during the breeding season.

Where threatened species are found, forest managers are increasingly trying to manage their forests more sympathetically, although low log prices currently make anything that requires extra expenditure tricky. In the near future, the management of endangered species resident in pine forests will be given a boost by publication of the *Guide to the Management of Rare and Endangered Species in Plantation Forests* by the New Zealand Forest Owners Association, an initiative led by Colin Maunder of Kaingaroa Timberlands. The guide will be an excellent source of information for forest owners interested in enhancing the biodiversity in their forests.

STEVE PAWSON, KENNEDY WARNE (INSET)

stabilised banks and shade makes good habitat for many native fish. Several endangered species, such as the giant kokopu and short-jawed kokopu, have been found in streams running through plantations.

Prehuman New Zealand was predominantly a forest landscape; however, much of the original forest has been cleared. In the past plantations were sometimes established on the clear-felled remains of native forest. The New Zealand Forest Accord, signed by most forest owners in the early 1990s, has ensured that new pine plantations are now created by the afforestation of non-forest land, such as marginal agricultural areas. Thus, new plantations now provide a forest habitat and associated microclimate not present under the previous regime of pastoral or arable farming.

For many native species of bird, fungus, insect and plant this is sufficient, as they do not discriminate between native and plantation forest. They benefit greatly from the reforestation of large areas of the country, and as plantations have expanded, so has the habitat available to them. Unfortunately the recent boom in the dairy industry, in combination with a slowdown in the forestry sector, has resulted in commitments to return some large plantations to pasture and other non-forest habitats once the trees have matured and been harvested.

The average rotation of a pine plantation allows insufficient time for most native canopy tree species to mature. Neither do plantations provide the right conditions for some specialist forest dwellers, such as hole-nesting birds. Many native plants and animals depend for their survival on other natives—as hosts (in the case of parasitic species), food sources or pollinators. A lack of these in radiata forests means that some species will never be able to live there.

Many people consider these facts a negative aspect of New Zealand's pine forests. But while plantations are not native forests and can never be more than a next-best substitute, they do represent a significant proportion of the country's forest cover and provide many native species with suitable habitat that other productive land uses do not. When assessing the value of pine forests in terms of native biodiversity, we should not base our judgements solely on traditional comparisons of pine plantations with unmodified forests of native species. When plantations are compared with other kinds of productive land use, such as pastoral or arable farming, which allow few indigenous species to thrive, it is clear they have their merits. ■

KENNEDY WARNE

Huhu grubs (opposite)—larvae of the largest brown beetles in Stephen Pawson's top tray (above)—being prepared by Uwe Braun for a recent entomology conference. The grubs are just one of many native species to find conditions congenial in the new forests.

B)

Technical Note: New Zealand Journal of Forestry 2005 - 50(2): 29-32

Clearfell harvest size: A key issue for biodiversity conservation in New Zealand's plantation forests

S. M. Pawson[1, 2, 3], E.G. Brockerhoff[3], R.K. Didham[1] and D.A. Norton[2]

The New Zealand forest industry and biodiversity

In recent years the concept of biodiversity has increasingly been integrated into land management issues (Brockerhoff *et al.* 2001). Biodiversity is now a key component of national policy statements and strategies, such as the New Zealand Biodiversity Strategy, as well as a number of international agreements, such as the Montreal Process. The forest industry itself has developed a number of policies, including the Biodiversity Position Statement, from the New Zealand Institute of Forestry (NZIF) (Shaw 1997).

By definition, "*"Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*" (Convention on Biological Diversity, 1992).

The forest industry has always valued the within species component of biodiversity for the potential breeding opportunities it represents and the potential for crop enhancement. By contrast, a more general appreciation for the broader concept of native species biodiversity in New Zealand's plantation forests has been limited, to a large extent, by the perception that plantations are biological deserts. A number of recent articles have challenged this perception. Brockerhoff et al. (2003) have shown that plantation forests can support a wide range of indigenous vegetation. Maunder et al. (2005) produced an excellent review of the contribution that plantation forests make to the protection of biodiversity and this was promoted to a broader non-scientific audience in the New Zealand Geographic (Pawson and Brockerhoff 2005).

As a productive land use forestry does provide certain conservation benefits. However, there remain some serious issues and major information gaps that need addressing (Maunder *et al.* 2005). Hock & Hay (2003) in their review of forest certification systems in New Zealand point out the need to give greater attention to rare, threatened and endangered species and representative ecosystems. Less obvious from their review, but of equal concern, was the number of corrective action requests (CARs, from Forest Stewardship Council) requiring a policy on maximum clearfell size.

In this article, I briefly discuss some of the known impacts of clearfelling and synthesise the few studies that have investigated the influence of clearfell harvest size on biodiversity. I then outline the Ecological Impacts of Harvest Area (EIHA) study initiated in 2002 by ForestResearch and Tenon Ltd (at that time Fletcher Challenge Forests). EIHA was designed to investigate clearfell harvest size impacts in a New Zealand context. Some preliminary results are provided.

Effects of clearfell harvesting

Clearfelling (and subsequent reestablishment) causes the greatest single disturbance that any plantation ecosystem will undergo. Clearfelling alters microclimatic conditions, including temperature, wind speed, relative humidity, evaporation and solar radiation (Chen *et al.* 1995). These combined changes then have effects on catchment-level and regional water balance (Davie & Fahey 2005), erosion and subsequent sedimentation of streams (France 1997). Clearfelling also has significant impacts on the biological communities in forests. Post-clearfelling, species composition and species richness of native plants and animals can change dramatically. For example, in New Zealand the flora of recently harvested and regenerating stands are dominated by exotic weedy species, whereas mature stands have a greater proportion of indigenous shrub species (Brockerhoff *et al.* 2003).

Recent work in New Zealand (Pawson, Unpub. data) corroborates overseas studies, which show that clearfelling induces a transient increase in the species richness of invertebrates (Niemelä *et al.* 1993). This phenomenon is caused by the short-term survival of forest species combined with colonisation by open-habitat species. The survival of old-growth specialist forest invertebrates after clearfell harvesting is a significant issue, particularly for short-rotation forestry (Spence *et al.* 1996) that dominates the New Zealand industry.

Despite the obvious impacts of clearfelling, scientists internationally have not focused on addressing issues related specifically to whether there is an optimal size of harvest areas that might maintain greater levels of biodiversity. Instead, most recent research has focussed on alternative harvesting strategies and comparisons between these and traditional clearfelling (Schowalter 1995, Beese & Arnott 1999, Beese & Bryant 1999, Koivula 2002). Why is this so? It appears that public pressure by individuals and environmental organisations (Potton 1994, Rosoman 1994) have largely circumvented research focused on sustainable clearfell harvesting options and promoted the use of alternatives. Public perception is driven largely by the negative aesthetic image of clearfelling and is a powerful force for change (McCool *et al.* 1986, Bliss 2000) that can have strong indirect effects on silvicultural activities by controlling consumer demand (Wilson & Wilson 2001). Alternative harvesting systems have been promoted as 'better' than clearfelling, but many of these are merely small clearfells (e.g., group selection or patch cutting), although the definition of terms is often country specific, complex and confusing (Bradshaw 1992)

To date around the world only a handful of studies have attempted to quantify the impact of different sized clearfells, and none of these were conducted at scales relevant to New Zealand forestry practices (Pawson *et al.* 2002). The limited studies of areas up to 10ha in extent do suggest that there are changes in species composition and abundance following clearfelling, however the magnitude and direction of changes shown so far is dependent on taxonomic groups (Shure & Phillips 1991, Huggard & Vyse 2002).

What are we doing about it in New Zealand?

The Ecological Impacts of Harvest Area (EIHA) study was designed to address five key questions related to clearfell harvest size:

- What is the relationship between clearfell harvest size and invertebrate species richness?
- Does clearfell harvest size alter the magnitude of edge effects into remaining forest?
- Do the abundance of individual species change with clearfell size?

- Is there a threshold size above which clearfelling has more severe ecological impacts?
- What is the value of plantation habitat for native biodiversity protection compared with other land uses?

The EIHA study encompasses a large area of central North Island forests. Specific study sites were located in stands throughout Kaingaroa, Tarawera, Matahina, Putuaki and Broadlands forests. Customised experimental clearfells were created measuring 0.01, 0.05, 0.5 and 5ha (assisted initially by Fletcher Challenge Forests and subsequently by Kaingaroa Timberlands), whilst larger 50 and 500ha clearfells were selected from existing harvest plans. This study is unique worldwide as comparisons of the ecological impacts of clearfell harvesting have never been attempted over such a large spatial scale before. As well as determining clearfell harvest size impacts the, EIHA study also compares the invertebrate biodiversity between different productive and non-productive landuses: plantations, pasture and native forest.

Pitfall traps were installed in transects between mature *Pinus radiata* stands and recent (<1 yr) clearfells to collect invertebrates at distances of 0, 5, 25, 125 and 625m into clearfells and to 5, 25 and 125m into mature forest (Figure 1). Sampling distances were truncated in harvest treatments where the diameter of the harvest area was smaller than the transect length. Additional traps were also placed at the same series of distances away from clearfells into the adjacent forest to analyse edge-effect impacts that harvesting may have on remaining stands. The traps were sampled continuously over two summer periods from November 2002 to February 2003 and from December 2003 to February 2004.

To date over 86,000 specimens of beetles have been sorted from traps established. A full list of beetle species identified from all aspects of the study is near completion and so far exceeds 380 species, including 21 adventive species. Such high species richness provides further empirical support that plantation forests do contribute to the maintenance of regional biodiversity. The families Curculionidae (weevils), Carabidae (ground beetles), Elateridae (click beetles) and the staphylinid sub-family Pselaphinae (rove beetles) dominate overall beetle biodiversity (Table 1). The weevils and click beetles include many wood-feeding species, which take advantage of a resource that is present in large quantities post-clearfelling.

In some cases species have shown distinct changes in their abundance with increasing clearfell size. For example, the abundance of *Pycnomerus sophorae* (Family: Zopheridae, false-darkling beetles) was higher in small clearfell sizes relative to populations in adjacent mature forest stands. However, in larger 5 and 50ha clearfells the abundance of *P. sophorae* dropped relative to mature stands (Figure 2). *P. sophorae* abundance increased slightly in 500 ha clearfells, however, average catch per 100 trap days was extremely low at the 500 ha sizes compared to the other sites. There are a number of possible explanations for the low abundance at 500ha clearfell sizes. Most likely it was a geographical site effect. Alternatively, it could represent an edge effect, where the influence of large 500 ha clearfells penetrated deep into surrounding mature forest and influenced the population dynamics of *P. sophorae* in remaining forest stands. Such potential edge effects need further study.

Where to from here?

The final pitfall traps were recently sorted and the vast quantities of data are currently being databased and analysed. In-depth analyses will concentrate on determining the response of species richness and total abundance to clearfell size, individual responses of key indicator species and their interaction with remaining adjacent mature stands, and comparing the species composition of different habitat types, e.g., mature forest, clearfell, regenerating forest, pasture and native remnants.

Answers to the five key questions will have practical benefits to New Zealand foresters. Information gained will be useful for guiding policies on an optimal clearfell size that minimises ecological impacts. It has already provided evidence that plantation forests can make a significant contribution to the protection of invertebrate biodiversity. Such policies and the protection of biodiversity will become more significant as the increasing influence of forest certification regulates market access for timber products around the world.

Acknowledgements

This study would not have been possible without the generous in kind assistance of the participating forestry companies, Tenon Ltd (formerly Fletcher Challenge Forests) and Kaingaroa Timberlands. Funding for this study was provided by Tenon Ltd, ForestResearch and the Tertiary Education Commission (TEC).

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Tables and Figures

Table 1. Species richness of beetle families sorted from a sub-sample of pitfalls established to determine the ecological impacts of clearfell size impacts. Note that Staphylinidae and have broken into sub-family groupings and are distinguished by the suffix –inae.

Aderidae	1	Euaesthetinae	1	Phloeostichidae	1
Aleocharinae	?	Eucnemidae	1	Prostomidae	1
Anobiidae	1	Histeridae	2	Proteininae	3
Anthicidae	5	Hydrophilidae	2	Pselaphinae	19
Anthribidae	2	Latridiidae	18	Ptiliidae	8
Byrrhidae	5	Leiodidae	9	Rhysodidae	1
Carabidae	26	Lucanidae	1	Salpingidae	3

Cerambycidae	11
Cerylonidae	2
Chrysomelidae	4
Ciidae	7
Clambidae	3
Coccinellidae	9
Corylophidae	9
Cryptophagidae	6
Curculionidae	55
Elateridae	22
Endomychidae	1
Erotylidae	1
Lycidae	1
Melandryidae	4
Mordellidae	1
Mycetophagidae	3
Nitidulidae	9
Oedemeridae	3
Omaliinae	6
Osoriinae	3
Oxytelinae	5
Paederinae	5
Scaphidiinae	3
Scarabaeidae	8
Scraptiidae	1
Scydmaenidae	6
Silvanidae	3
Staphylininae	11
Tachyporinae	8
Tenebrionidae	7
Trogossitidae	8
Zopheridae	18

Figure Captions

Figure 1. Illustration of a pitfall trap transect to capture invertebrates. The 0m trap is placed on the drip-line of remaining trees and transects extend in either direction. The insert provides a close-up of pitfall trap illustrating plastic guides that channel ground-dwelling invertebrates to a central covered collecting pottles sunk to ground level and partially filled with preservative.

Figure 2. Abundance of the beetle P*ycnomerus sophorae* expressed as a percentage relative to that caught in control traps placed in adjacent mature forest stands (left hand y-axis). Values greater than zero indicate higher abundance in clearfell areas compared to forest. Average catch per 100 trap days of *P. sophorae* caught in clearfell areas as a function of harvest area (right hand y-axis).

Figure 1.

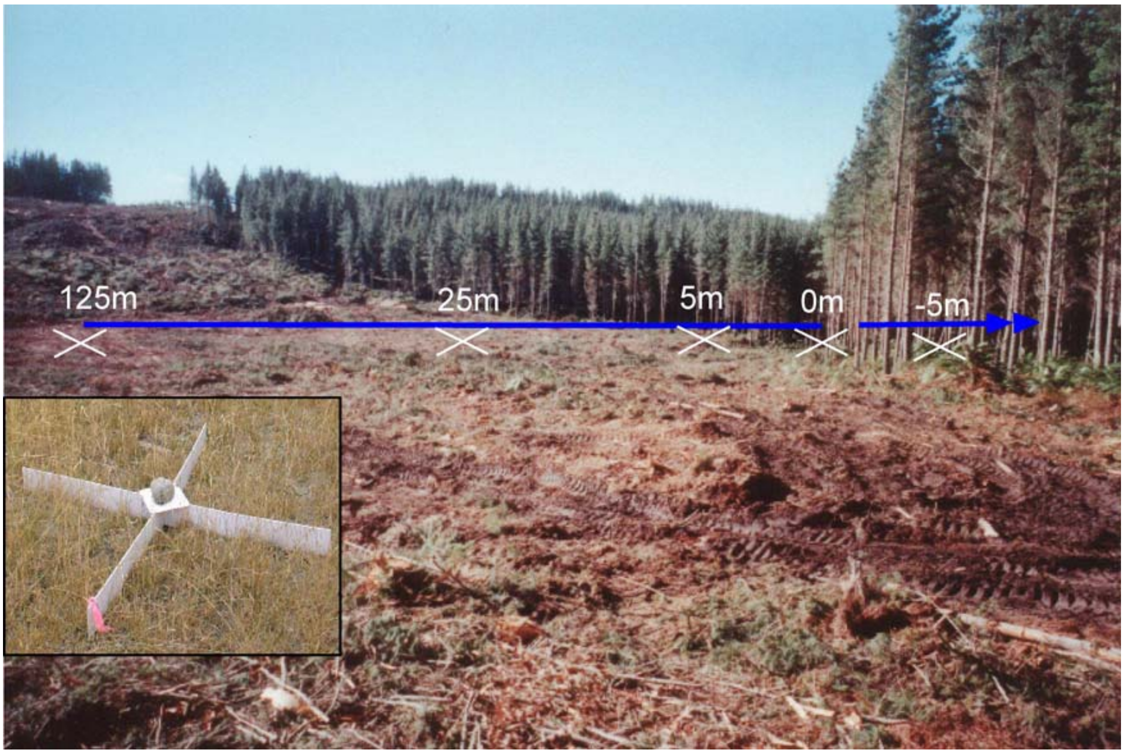
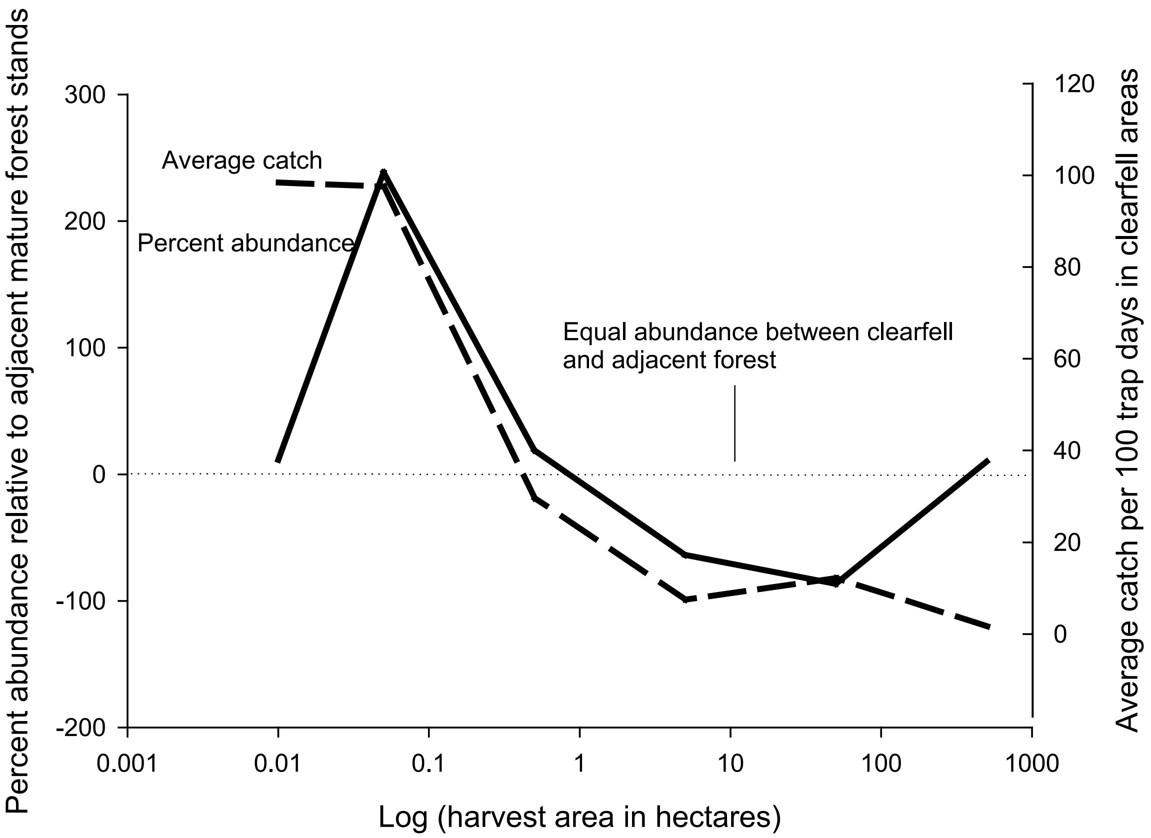


Figure 2.


Percent abundance relative to adjacent mature forest stands
300
200
100
0
-100
-200
Average catch
Percent abundance
Equal abundance between clearfell and adjacent forest
120
100
80
60
40
20
0
Average catch per 100 trap days in clearfell areas
0.001
0.01
0.1
1
10
100
1000
Log (harvest area in hectares)

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C)

Native biodiversity and the impact of forest harvesting on small-scale farm forests.

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As a tree grower the small forest stands on your farm have numerous positive effects – many of which are not obvious. They are not only stabilising hill slopes, reducing global CO_2 levels and making financial ends meet, but they are also providing forest habitat for important native plants, birds and insects that don't survive in high-productivity pastoral grasslands. Farm forest stands are quite different to the large tracts of forest land publicly owned for the purposes of conserving nature. Most of these indigenous forests are in the mountainous regions, while the few native forest patches that remain in many lowland agricultural dominated landscapes are small and heavily fragmented. For example the Canterbury Plains has less than 1% of its remaining indigenous habitat intact. It is in such landscapes that small-scale farm forestry can make a significant contribution by providing substitute forest habitat for native flora and fauna – and this, in turn, could well enhance the market acceptability of your produce.

As stands mature they develop a distinct forest microclimate of increased shade, reduced temperatures, and deep litter layers (with their abundance of fungal communities) that can be a haven for forest dwelling species of plants, insects and birds. Increased abundance and diversity of native plant species with increasing stand age is well documented in New Zealand plantations, as is the abundance of insectivorous birds. Despite this, the diversity and abundance of invertebrates that sustain these birds is poorly understood, particularly when it comes to the one inevitable consequence of plantation forestry: harvest! At some point in time the trees will be harvested, be this at 28 years for radiata pine or 40-50 years for Douglas-fir and results in immediate and drastic ecosystem changes that have impacts on all species living in those stands.

Over the past 3 years, I have been researching the impact of clearfell harvesting on the beetle communities in the large plantation estates of the central North Island. More recently, I was asked to comment on how relevant my findings might be to small-scale farm foresters, who wish to maximise biodiversity preservation in their forest stands.

The dominant harvesting system in New Zealand is clearfelling, which immediately changes the microclimate from a protected cool shady forest interior to an open habitat subject to the extremes of temperature and wind. The most noticeable change in this disturbed post-harvest landscape is the rapid colonisation of by exotic species of herbs, forbs and grasses that are adapted to harsh environments. Less noticeable but just as important is the influx of insect species adapted to these open habitats. Some of these insects are associated with the breakdown of harvesting debris and they can also provide food for a number of bird species. Recent research of three families of beetles, the *Carabidae* (ground beetles), *Scarabaeidae* (chafers) and *Scolytinae* (bark-beetles) have shown a massive increase in abundance immediately post-harvest (Figure 1), particularly of a few key species, e.g., the tiger beetle (*Cicindela tuberculata*). While the diversity of species was not affected as strongly as abundance, it may increase slightly, due to an influx of open habitat species, which augment remnant populations of forest dwelling species that survive for the first few years post-harvest. However, species diversity drops sharply a few years after harvest as the forest-adapted species cannot maintain successful breeding populations (Figure 1) - although, as long as a suitable source populations exist, species can potentially re-establish as regeneration proceeds and forest stands once again begin to mature. Reestablishment in the case of my study sites in Kaingaroa was not difficult as other forest stands were merely ‘across the road’ - however for small scale foresters the post-harvest biodiversity considerations are likely to present other challenges.

Unlike large plantation companies, small wood-lot owners are more likely to harvest their entire stand in one event. This has a number of potential ramifications that have yet to be studied. Although populations of forest invertebrates are likely to remain in recent clearfells in the short-term, long-term replacement from adjacent habitat becomes limited for poorly dispersing non-flighted species, particularly if the regenerating stand is in a largely pastoral dominated landscape and isolated from other forest habitat. Most common understorey plant species in plantations have wind or bird-dispersed seeds allowing dispersal across larger distances, however there are limits to the dispersal ability between forest fragments. Having stated that, it could be argued that all the resident biodiversity (i.e., birds, plants and insects) in small forests established on pre-existing pasture arrived at these developing stands without assistance. If so, then the conclusion must be that no future help will be necessary post-harvest, as the cycle of colonisation will merely repeat itself. This concept treats the matrix habitat within the landscape as an ecological sieve where plant and animal communities accumulate ‘naturally’, mainly from species with good dispersal characteristics, but also from a few chance arrivals that subsequently colonised these habitats. A more beneficial approach (that is less subject to the vagaries of chance dispersal events) is to provide some form of continuity to forest cover, thus enhancing reestablishment opportunities such that biodiversity is maintained at the farm and ultimately the landscape level.

Continuity in mature forest habitat can be achieved in a number of ways; the easiest is by planting adjacent to an existing remnant of native forest or shrubland. For example, that steep gully (fenced to prevent stock access) at the back of the property can provide a reservoir for recolonisation of harvested stands planted on its boundary. The native remnant also benefits, as the planted trees buffer its habitat edge from external influences such as strong and/or cold winds. Alternatively, one could plant two stands of different species side by side. Different maturation times will result in a semi-mature stand adjacent to your harvest area that can provide refugia for forest species until subsequent regeneration allows recolonisation of the clearfelled area.

In conclusion, the majority of the indigenous biodiversity present in your average farm-forestry situation is going to be within your native remnants (including forest, shrubland and wetlands) and your plantation forests. Native plants struggle to survive in improved pastoral grasslands, although a few native insects do thrive, e.g., grass grub and porina. It only takes a little considered thought during the planning stages and perhaps some small concessions (such as mixing species and the location of forest stands) to make a big difference to the continuity of biodiversity within your landscape come harvest time. Given the increasing interest in biodiversity protection on private land, and the growing environmental sensitivity of consumers, the presence of species-rich plantation forests on your farm could make a significant difference in the acceptability of your produce in the market-places of the future.

Further Reading

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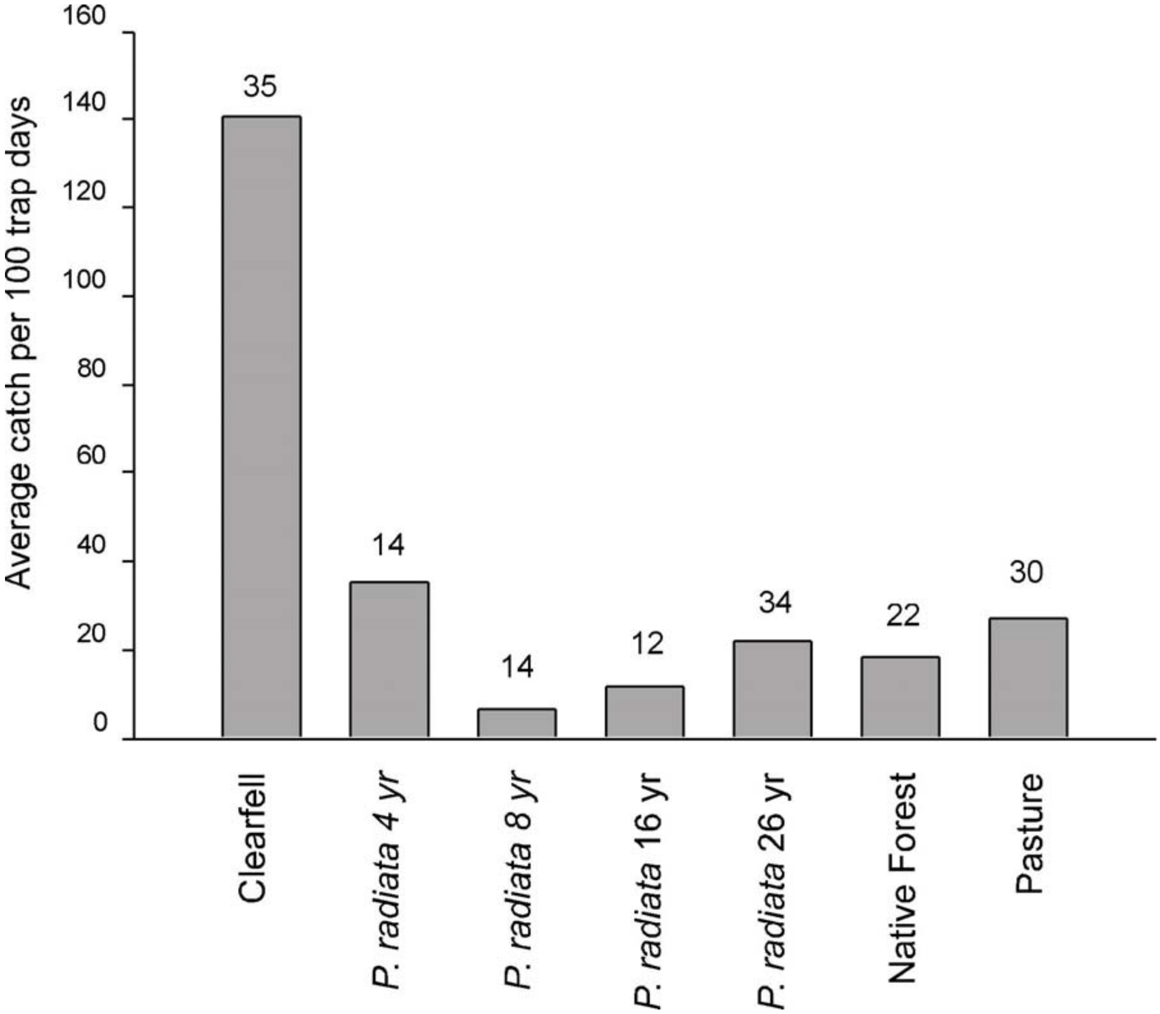
Figure 1. Average catch per 100 trap days of effort of all ground beetles, chafer beetles and bark beetles in different habitats, including different ages *P. radiata*, clearfells, native forest and pasture. Numbers above the bars are the actual number of species caught in each habitat. Note: That samples were obtained by running transects between habitat pairs and the actual species number and abundance in each habitat is influenced to some degree by dispersal from adjacent habitat types. For example the abundance of beetles in pasture would have been considerably lower if the contribution of dispersing tiger beetles (*Cicindela tuberculata*) from the 5 metre pasture samples adjacent to recent clearfell habitat was discounted as this species (like others) was not recorded further than 5m into pasture. However, the data clearly shows an increase in invertebrate abundance in recently clearfelled forest stands and a reduction in species richness in young regenerating forest stands compared to other habitat types.



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D)

Is there a role for plantation forests in the conservation of biodiversity?

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Introduction

To the casual observer it seems difficult to associate our 'monocultures' of pines or other exotic trees with native biodiversity. The biodiversity values of our plantation forests are often judged solely by the planted tree species despite the common occurrence of many native inhabitants in these forests. Some plantations have little undergrowth and this can indeed give the impression that there is no other life. Furthermore, the routine clearfelling of such forests causes concerns from an aesthetic point of view and also for the 'welfare' of the plants and animals that may live there. But, it's not that simple! In fact, many studies have shown that despite this, plantation forests are very valuable as habitat for native species, including some threatened species. After several years of intensive research of plantations in many corners of New Zealand and in other countries, we have often been surprised by our findings, and it is becoming clear that we need to take a more considered view of the value of plantations for biodiversity.

The understorey of plantation forests

The flora of plantation forests undergoes considerable changes during a rotation from planting to a mature forest, following a pattern of natural succession (Allen et al. 1995, Brockerhoff et al. 2003). Typically, the open areas created by clearfelling are colonised by light-demanding pioneer species, mostly exotic grasses and forbs. Over time the canopy becomes denser, the availability of light decreases, and the conditions become more suitable for shade-tolerant species such as the ferns and shrubs that are common in the understorey of native forests. But how exactly this 'succession' of the understorey proceeds, and which species dominate each stage, depends on a number of factors such as climate, the flora of the surrounding area, and the density of the canopy (Brockerhoff et al. 2003).

Plantations in regions with high rainfall tend to have a much more lush understorey than those in relatively 'dry' regions where low soil moisture levels may not sustain much undergrowth. There is also a strong influence from the surrounding vegetation. When there is some native forest nearby, plantations generally have a much higher diversity of native forest species than those that are in regions with little or no native forest. Accordingly, Eyrewell Forest on the Canterbury Plains has a poor understorey in terms of native biodiversity with comparatively many exotic species and with similarities to the equally poor understorey of the few native forest remnants in the area. By contrast, plantations in the central North Island and Westland, regions with larger areas of remaining native forest, are much more species rich and dominated by native species (Allen et al. 1995, Brockerhoff et al. 2003).

Although the closing canopy of a stand creates shady conditions that favour native understorey plants, there can be too much shade. This is seen in densely planted, unpruned stands of radiata or Douglas-fir where there may not be enough light even for the more shade-tolerant plants. However, light is not a limiting factor in the more typical stands that are thinned and pruned.

Plantation forests as 'nurse crops' for native species

The native understorey of a plantation does not depend on species that were present at the site before planting. We studied a plantation on the Paeroa Range near Taupo that was established in 1973 into typical pasture of mostly exotic species. By 2000, the afforested site had developed a rich understorey with over 100, mostly native, plant species (Ecroyd and Brockerhoff, unpublished), despite an earlier harvesting disturbance. In our plots in the adjacent pasture we recorded 13 exotic pasture species and only two species of native herbs. The 65 species of native plants that were found in the plantation had all arrived naturally, primarily from a native forest about 1 km away which served as a source of seeds and the main dispersal agents – birds. Projecting this development into the future, it becomes obvious that the site has the potential to revert back to native forest, all by itself. Interestingly, this capacity of plantation forests to act as a nurse crop has been described in a QE II National Trust book on 'Native Forest Restoration' where it is stated that "Radiata pine provides a fast-growing nurse crop for the establishment of native species" (Porteus 1993). However, this positive biodiversity effect of plantations is not widely recognised.

Plantations as habitat for native animals

As with plants, the fauna of plantations can also be dominated by native species, particularly in older stands. Most birds with a diet of insects and other invertebrates can be found in plantations (Clout and

Gaze 1984), including some rare or threatened species such as kiwi (Kleinpaste 1990) and North Island robin (Pawson and Brockerhoff 2005). A recent study of bush falcon revealed a very healthy population in Kaingaroa Forest, with the surprise finding that the birds liked to feed and nest in clearfell areas (Richard Seaton, pers. comm.).

The range of insect species in plantations is surprisingly similar to those of native forests nearby. For example, a recent study at Mt. Oxford in North Canterbury found that the ground beetle assemblage of older radiata stands was a close match to that of the adjacent black beech forest (Berndt et al., unpublished). Our study in the central North Island gave similar results (below).

A remarkable case is that of the critically endangered ground beetle *Holcaspis brevicula*. Eyrewell Forest on the Canterbury Plains is the only known habitat of this species that appears to be endemic to the Eyrewell region in North Canterbury (Brockerhoff et al. 2005). This is perhaps the only example of a native species that now only lives in the habitat provided by an exotic plantation forest.

Landscape perspectives

The case of the critically endangered ground beetle mentioned above highlights how plantations can be important substitute habitat for native forest species in regions where little native forest remains. The Canterbury Plains are a classic example of this situation because although the Plains used to be covered by forest in pre-human times, today less than 0.5% is covered in native forest. Eyrewell Forest is not particularly rich in native plants and animals (see above), but the fact that it is the only remaining forest of substantial area does make it particularly important as habitat. Other noteworthy occurrences of native species in this forest are the only South Island population of *Pomaderris* aff. *phylicifolia* and the abundance of kanuka in the understorey (Fig. 1) (Ecroyd and Brockerhoff 2005).

The effects of clearfelling on forest beetles

In a recent study of biodiversity and the impacts of clearfell harvesting over 350 species of beetles, mostly natives, were sampled from radiata pine plantations in Kaingaroa Forest (Pawson, 2005). This clearly illustrates the value of plantation habitat as a reservoir of native biodiversity. Somewhat surprisingly, clearfell harvesting did result in a temporary increase in species richness and abundance due in part to changes in beetle community assemblages, such as colonisation by open habitat species in conjunction with short-term retention of forest species, which is consistent with other European research (Niemelä, 1993).

Three groups of beetles; Carabidae (ground-beetles), Scarabaeidae (chafer beetles) and Scolytidae (bark and ambrosia beetles) were sampled in detail in different-aged forest stands and other adjacent habitats including pasture and native forest. There were distinct differences in the community structure between the insects sampled in radiata stands (4, 8, 16 and 26 years), recent clearfells, pasture and native forest. Radiata pine stands adjacent to alternative habitat such as native forest and pasture did have beetle community assemblages similar to the non-plantation habitat. This would be expected given their geographic proximity and provide preliminary evidence for dispersal across at least the 125 m between habitats The overall combined rarefied species richness (corrected for differential sampling effort) of these three groups did not vary significantly between pasture, native forest and radiata pine stands. However, recent clearfells did have significantly lower species richness than 8-year-old radiata pine stands. Interestingly, individual species did make use of plantation stands at different periods throughout the rotation. For example, *Cicindela tuberculata* (a native tiger beetle) was super-abundant in recent clearfells and 4 year-old stands but almost absent from older forest (native and plantation) and pasture. In contrast *Mecodema occiputale* (a ground beetle) was more abundant in mature radiata pine and native forest than young pine stands. The effects of clearfelling appear only temporary and even the larger clearfells are successfully re-colonised by forest species during a 25-year rotation.

Concluding remarks

The recent studies we summarised in this paper show conclusively that plantation forests can in fact play an important role in the conservation of forest biodiversity. Although in the past some plantations have been established at the expense of native forest, today that is not likely to happen. Most plantation managers realise that they are also stewards of the flora and fauna of their forests. Assessments of the flora and fauna in plantations and in the native forests, wetlands and other habitats within plantations are standard practise for those interested in environmental certification for their operations. Pest control is often being carried out with obvious benefits for many native species. Unfortunately, the current trend of conversion of plantations to dairy farming renders many of these areas unsuitable for the native species that have lived there. This is especially critical in regions such as the Canterbury Plains where most native forest has been lost and where plantation forests harbour much of the remaining diversity of native forest species.

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