An Investigation into the Simultaneous Impact of Climate Change and Land Use Modification on a Tri-Trophic Species Interaction

POPPY LAKEMAN-FRASER

Imperial College London

Division of Ecology & Evolution: Department of Life Sciences

Silwood Park Campus, Ascot, Berkshire, SL5 7PY, U.K.

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Supervisor: Dr Robert Ewers

The fragmented landscape of New Zealand

View from Maungatautari Ecological Island Reserve, Waikato, North Island

Photograph: Poppy Lakeman Fraser

Abstract

Nature is intrinsically complex; yet ecological research is steadily gaining insight into the relationships between abiotic and biotic conditions. This thesis seeks to examine these interactions; between the causal drivers of global environmental change (GEC) and between biotic units in which that change is manifested. Concern is mounting over the ecological surprises that multiple GEC drivers can exert on biota when they act simultaneously. Studying the greatest current threat to biodiversity, habitat modification, and the greatest potential future threat, climate change, I investigate the nature of these interactions. I determine whether they are of a synergistic nature, whereby one driver is exacerbated by another; or of an antagonistic nature, whereby the effect is reduced. These effects are quantified on two measures of biotic change: abundance and species interactions in a tri-trophic forest study system in New Zealand.

Taking a range of methodological approaches I utilise: field observation analysis, *in-situ* experiments and *ex-situ* experiments to investigate aspects of the umbrella research question. Throughout this research I study a tri-trophic biotic system in which to investigate broad ecological trends: an understory shrub, *Macropiper excelsum*; its herbivorous moth, *Cleora scriptaria*; and the herbivore's endoparasitoids, *Aleiodes declanae* and *Meteorus pulchricornis*.

Abstract

Three principal findings emerge from this investigation. Firstly, although climate and habitat fragmentation exhibit a mixture of effects on biota, when they interact, the net effects are all seemingly negative: abundance is reduced and the frequency of biotic interactions decrease. Secondly, these drivers combine in a non-additive fashion depending upon the trophic level and biotic measure assessed: antagonistically interacting to impact the *plant* species and species *interactions* and synergistically interacting to impact the *insect* species and *abundance*. Thirdly, the influence of interspecific relationships on dynamics within this study system is ostensibly comparable to the impact of anthropogenic pressures. This research suggests that, where possible, it is vitally important to investigate all known simultaneous drivers of change, to specify which taxonomic unit is being studied and to integrate biotic interactions when predicting the impacts on biodiversity in a changing world.

Thesis Declaration

I herewith certify that all material in this thesis is my original research; and collaborations with others are properly acknowledged. The experimental development was conceived in alliance with my supervisor, Dr Robert Ewers. Chapters 2 - 5 are co-authored with Dr Robert Ewers reflecting his input in the development of the concepts, advice on the methods, refinement of interpretations and in the editorial process. Dr Rudolph Schnitzler identified all parasitoid specimens, the results of which are discussed in Chapter 3. In all chapters I collected and analysed the data, produced the figures, wrote the first draft of manuscripts and edited subsequent drafts.

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Signed:

Poppy Lakeman-Fraser

Date: 28th June 2012

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1

An Introduction to Forest Fragmentation, Climate Change and Species Interactions in New Zealand

1 Introduction

1.1 Drivers of global environmental change

1.1.1 Interactions between drivers

Drivers of global environmental change impact natural and anthropogenic systems alike and exert influence across a gradient of ecological and geographical scales. Investigations into their effects span multiple fields of research. Direct impacts are well documented across a range of taxa, ecosystems and human environments, yet the simultaneous impacts of multiple drivers exert pervasive influences which are only beginning to be understood. Impacts not only influence species, populations and distributions but cascade through biotic interactions. This thesis seeks to investigate interactions on multiple levels: interactions between the causal drivers of change and interactions between the species impacted by that change.

Drivers of global environmental change (GEC) include nitrogen deposition, carbon dioxide enrichment, biotic invasions, climate change and land use change (Tylianakis *et al.* 2008). Alone, these drivers all impose considerable influence on biodiversity. For example, three of four climate and atmospheric variables exerted rapid changes on the diversity of Californian grasslands (Zavaleta *et al.* 2003). Carbon dioxide and nitrogen deposition diminished diversity after three years, precipitation increased it and warming had no effect. In this

system, when multiple drivers were analysed together, a simple additive effect on biodiversity was recorded. Additional concern is, however, mounting about the ability of environmental systems to absorb the simultaneous impacts that multiple anthropogenic stressors exert on ecosystems. Understanding how multiple drivers interact—do they simply add-up in a linear fashion or does one magnify the impact of another—is key to predicting their combined effects on biodiversity. A meta-analysis of the ecological literature revealed that three quarters of GEC studies show that species mortality rates cannot be explained by additive factors alone (Darling and Côté 2008).

Two types of non-additive outcomes are possible from interactions among GEC drivers: they either combine in a synergistic fashion (compounding effects are amplified), or they combine in an antagonistic way (compounding effects are minimised). In a review of the potential interactive and cumulative impacts on marine systems, Crain et al. (2008) found that of 171 studies, 36% found synergistic effects of multiple drivers, 38% found antagonistic effects and only 26% were simply additive. A different review found that the addition of a third stressor doubled the number of synergistic interactions (Mullan Crain *et al.* 2008), suggesting that the harder a researcher looks, the more likely they are to find non-additive impacts.

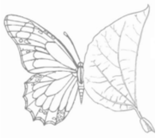
From a conservation biology perspective, synergies are the most worrisome. Synergistic interactions occur when GEC drivers magnify the impact of each other (Ewers *et al.* 2007; Darling and Côté 2008; Mullan Crain *et al.* 2008), ultimately exacerbating their combined impacts on biodiversity (Sala *et al.* 2000; Sala and Knowlton 2006). There is growing evidence that this extreme scenario occurs in nature (Hobbs 2001; Didham *et al.* 2009; Piessens *et al.* 2009). An investigation analysing the impact of three simultaneous drivers, found that declines in populations of rotifers occurred 50 times faster when fragmentation, temperature and overexploitation acted simultaneously than when fragmentation, warming and harvesting threats acted independently (Mora *et al.* 2007). The frequency with which synergies occur in nature however, may not be as prolific as the prevailing ecological paradigm suggests (Darling and Côté 2008). Antagonistic relationships have been frequently recorded affecting particular groups, for instance, autotrophs more than heterotrophs (Mullan Crain *et al.* 2008), producers more than consumers (Christensen *et al.* 2006) and communities as opposed to species (Mullan Crain *et al.* 2008). In addition, certain stressor pairs are commonly found to exert particular non-additive effects (Mullan Crain *et al.* 2008). Regularly regarded as the two dominant threats to biodiversity at global scale, habitat modification and climate change exert considerable influence on ecological systems (Sala *et al.* 2000; Piessens *et al.* 2009).

1.1.2. Habitat loss and fragmentation

Habitat loss and associated fragmentation are described as being the main global current (Wilcove *et al.* 1998) and future (Sala *et al.* 2000; Pereira *et al.* 2010) threats to biodiversity (Wilcove *et al.* 1986). Habitat fragmentation is a multifaceted concept described as a research panchreston by some (Lindenmayer and Fischer 2007) and a research paradigm by others (Ewers and Didham 2007b). The term is used to explain a variety of inter-correlated patterns and processes, each potentially a research subject on their own (Lindenmayer and Fischer 2007), yet all are related under the expedient framework of “habitat fragmentation” (Ewers and Didham 2007b). Distinct from habitat loss, in which the overall area of habitat is reduced, fragmentation implies a change in the spatial pattern of habitat. In the latter, continuous habitat is subdivided into smaller disconnected patches which are often altered in shape and isolated from each other by a matrix of dissimilar habitat (Lord and Norton 1990; Collinge 1996; Fahrig 2003; Lindenmayer and Fischer 2006; Ewers *et al.* 2006). A wealth of research has been undertaken into habitat fragmentation spanning datasets from landscapes (e.g. Watson et al. 2005), spatial scales (e.g. Lord and Norton 1990) and taxa (e.g. Debinski and Holt 2000). A variety of techniques (McGarigal and Cushman 2002) have been used to investigate a variety of attributes of fragmentation (reviewed by Ewers & Didham (2006)), leading to a diversity of conclusions about the impacts of habitat loss and fragmentation on biodiversity (Fahrig 2003). Although empirical studies to date have shown largely negative impacts of loss and fragmentation on biota, the magnitude and direction of trends is highly inconsistent. This may inherently be linked to differences in the responses of different taxa, but results are often not comparable because they work at different scales (Lord and Norton 1990; Doak *et al.* 1992; Donovan *et al.* 1997). For example, studies might collect data at the patch or landscape scale, and they may not distinguish between pure habitat loss and the fragmentation (i.e. subdivision) of that habitat (Fahrig 2003). Generalisations regarding the landscapes in which research is taking place can lead to a mismatch between the ecological theory driving research questions and the empirical research itself. In order to gain a realised insight into relative influences of for instance, fragmentation and loss, it is therefore imperative to detail the composition and structure of the communities in which research is being conducted (Schmiegelow and Monkkonen 2002).

Empirical studies identify five key features of habitat fragmentation that impact biodiversity: patch area, edge effects, isolation, fragment shape and matrix influences (Ewers and Didham 2006) (Fig. 1.1). These attributes directly (e.g. via reduced area to live in, causing barriers to movement etc.) and indirectly (e.g. via altered microclimatic conditions and novel biotic

interactions) shape the biota which persist within habitat remnants. In concert, they impact a diverse range of variables that reflect different aspects of biodiversity, including genetic diversity (e.g. Berry et al. 2005), the abundance of species (e.g. Esseen and Renhorn 1998; Fraser et al. 2008), species diversity (e.g. Holdaway N. 1990; Andrén 1997; Ewers and Didham 2008), species interactions (e.g. Burgess et al. 2006) and population distributions (e.g. With et al. 1997; Hill, Thomas, et al. 2001) (Fig. 1.1). Population dynamics will inevitably be influenced through altered mortality and fecundity rates and there is likely to be an increased frequency of novel species interactions and a reshuffling of functional roles as species from the native habitat interact with those from the novel matrix habitat. These influences on individuals may then cause knock-on impacts on other populations through domino effects and if key species go extinct, then cascade effects can ensue (Bascompte and Stouffer 2009). This battery of changes may render communities more vulnerable, or alternatively buffer against, natural and anthropogenic-induced biotic and abiotic fluctuations (e.g. demographic and environmental stochasticity), all of which will ultimately impact the health of an ecosystem (Fig. 1.1). It has been suggested that the two attributes particularly responsible for the negative impacts of habitat fragmentation *per se* are smaller patch sizes and proportionally greater edge environments (Fahrig 2003).



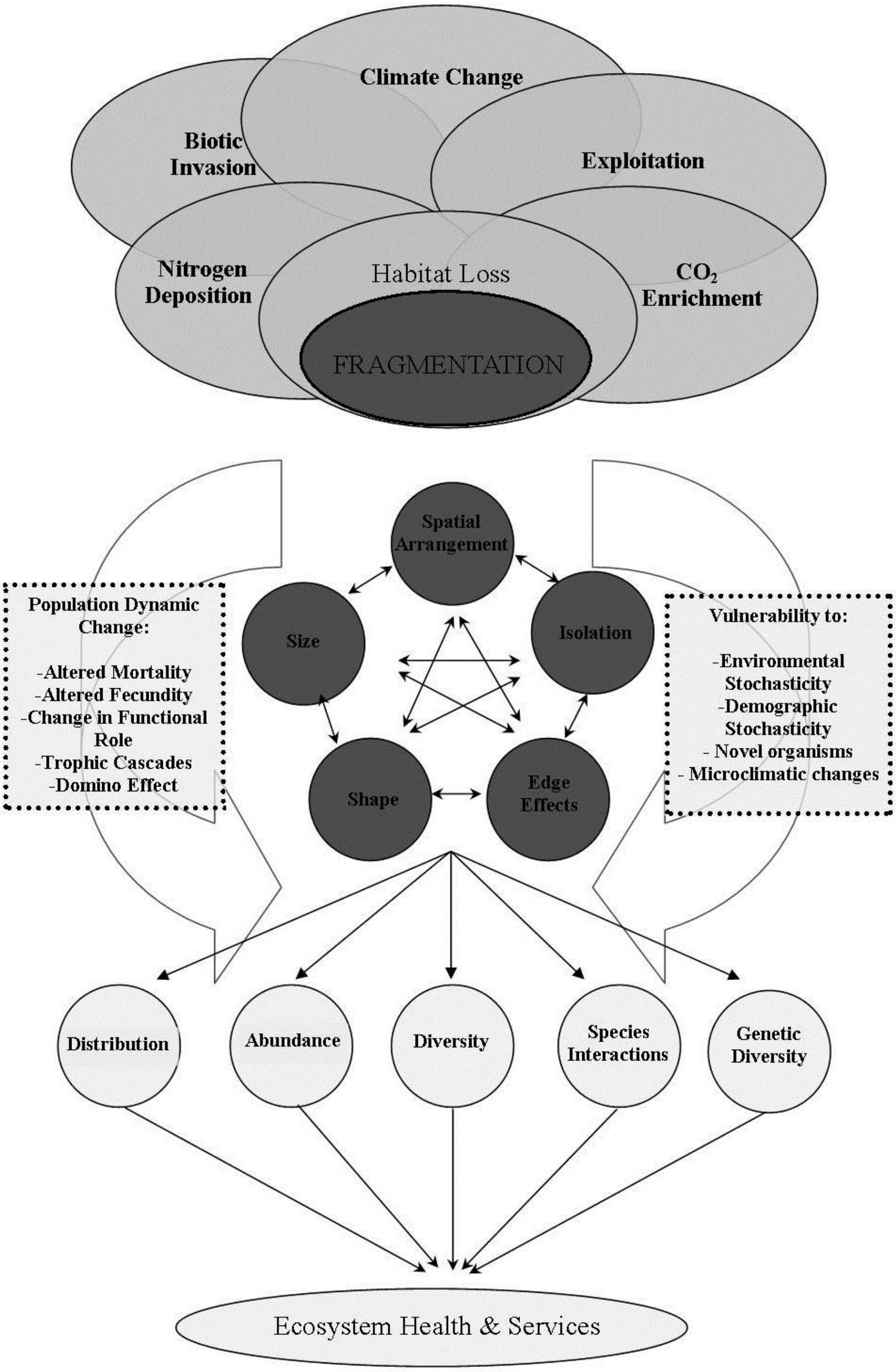


Figure 1.1. The interactions between habitat fragmentation and other global environmental change drivers (mid grey) linked to the key attributes of fragmented landscapes which have biological relevance (dark grey). Habitat loss and fragmentation, as well as other global environmental change drivers have been shown to impact a diverse range of variables that reflect different aspects of biodiversity which, together, combine to impact on the health of ecosystems (light grey). Those variables are influenced by changes to a large number of ecological and environmental processes (dotted boxes). Modified from Hobbs &Yates (2003).

1.1.2.1. Fragmentation Attribute: Area Effects

The theory of island biogeography (MacArthur and Wilson 1967) describes one of the most ‘ubiquitous patterns in nature’: the species-area relationship (SAR) (Collinge 2009). The theory has been extended from the analysis of oceanic islands to terrestrial remnant ‘islands’ of habitats surrounded by a matrix of inhospitable habitats, shaping much contemporary research into the ecological influence of fragmentation on biodiversity over the past forty years (Klein 1989; Soule *et al.* 1992; Saunders 1993). Immigration is predicted to decrease and extinction rates increase as fragment size diminishes, leading to a reduction in species richness and abundance (Arroyo-Rodriguez *et al.* 2009; Pollnac *et al.* 2009; Wilson *et al.* 2009). The species remaining in these small fragments are sometimes thought to be a nested subset of the species composition in larger (richer) assemblages (Hulten 1937; Darlington 1957; Daubenmire 1975; Ulrich *et al.* 2009) with the rare species being absent in smaller fragments (Golden and Crist 1999). The realised implications of this are that theoretically there will be an orderly sequence of species loss in progressively smaller habitat patches in fragmented landscapes (Patterson and Atmar 1986; Wright *et al.* 1998).

The species area relationship may be ‘the strongest empirical generalisation in community ecology’ (Holt *et al.* 1999), but the impact of reduced habitat size and fragmentation can be inconsistent among taxa, geographic study site and through time (Debinski and Holt 2000; Fahrig 2003; Drakare *et al.* 2006). However, if organisms are classified by life history traits or behavioural characteristics (such as feeding mechanisms or generation times) then clearer patterns have emerged. Golden & Crist (1999) found that parasitoids and feeding guilds of sucking herbivores showed decreased species richness in smaller fragments, whereas chewing herbivores and predators were largely unaffected. Moreover, Kruess & Tscharntke

(1994) reported that natural enemies (predators and parasitoids) were more sensitive to fragmentation than their prey. This trend, embodied in the trophic-level hypothesis (Holt *et al.* 1999), predicts that the slope of a species-area correlation will increase with trophic rank, such that top predators are likely be more negatively affected by fragmentation than plants.

1.1.2.2. Fragmentation Attribute: Edge Effect

Habitat fragments are intimately linked with the landscape in which they sit and it is at these boundaries where the surrounding habitat matrix influences the quality of habitat remnants (Ries *et al.* 2004; Collinge 2009). The habitat edge, ‘zone of transition’ (Ries *et al.* 2004) or ‘ecotone’ (Clements 1907) as it is otherwise known, is a relatively well studied attribute of fragmentation. By their very nature, edges exhibit conditions intermediate to environments which they span and typically manifest a gradient of microclimate across the boundary. Forest edges are associated with higher air and soil temperatures, more photosynthetically active radiation and higher vapour pressure deficits than the forest interior. The microclimatic differences can be extreme, with light levels and wind speed reduced by 99 % and 80 % respectively (Davies-Colley *et al.* 2000). Microclimatic changes generally penetrate a relatively short distance into the forest, with temperature and light gradients in *Nothofagus* spp. forests in New Zealand extending less than 10 m inside forest (Ewers and Didham 2008). Other microclimatic gradients can extend as far as 100 m inside forest (Denyer 2000), with penetration distances being greatest on the windward and northern aspects of fragments (Young and Mitchell 1994; Davies-Colley *et al.* 2000). These gradients are also greatly influenced by the structure of the surrounding matrix vegetation, with microclimatic edge effects penetrating forests five times further when forests are adjacent to pasture rather than pine plantation (Denyer 2000).

Biotic investigations of these zones were stimulated by game managers in the Midwestern United States who noticed enhanced abundance of wildlife such as deer, quail and grouse in landscapes rich in edges (Leopold 1933). Attitudes that edges are beneficial to biodiversity were later questioned as ecologists found these zones were not optimal for all species; indeed, many rare species are repelled from this dynamic zone. In a study into New Zealand beetles, almost 90 % of the 769 species that were recorded were significantly influenced by the habitat edge (Ewers and Didham 2008). Although many studies report microclimatic changes over distances of <100 m, Ewers & Didham (2008) found edge effects influenced species richness, beta diversity and composition up to 1 km into the forest. These conditions typically have the most pronounced negative effect on core dwelling species present in the original habitat whereas opportunistic species from the matrix habitat may do well in these areas (Tscharntke *et al.* 2002).

1.1.2.3. Interactive effects between fragmentation attributes

Most studies have dealt with the various attributes of fragmented landscapes independently, and some inadvertently confound distinctions between fragmentation attributes. Where recognised, researchers have found that multiple attributes of fragmentation (Ewers and Didham 2007a) can interact. In some cases (Davies *et al.* 2004) simultaneous impacts instigate a synergistic effect on biota (reviewed by Ewers and Didham (2006)). Ewers and Didham (2007) investigated this by using a novel technique to partition the variance following an ordination analysis, showing that a synergistic interaction between habitat area and edge effects exerted a stronger influence on beetle community composition than the individual attributes alone. They further showed that variation in the strength of edge effects

caused patterns that are more commonly associated with area effects, highlighting the potentially confounding nature of many fragmentation studies. Future studies may need to clarify which factor is the focus of research and which other factors need to be considered in the analysis (Fletcher *et al.* 2007).

All attributes of fragmentation indisputably influence biodiversity. However, different species and functional groups are impacted in different ways and to different extents depending upon the scale of measurement, the particular attribute and/or the combined effects of the various fragmentation attributes investigated. The impacts of this GEC driver on biodiversity are, however, likely to be further compounded by the impacts of additional drivers. Potentially, climate change is one such driver, being the greatest threat to future biodiversity.

1.1.3. Climate change

1.1.3.1. Global temperature changes

Global average temperatures have been rising at a rate of 0.2 ˚C per decade from 1990 to 2005, and mid-range estimates (A1B scenario) forecast ‘*likely*’ temperatures rising by 1.7 ˚C - 4.4 ˚C by 2090-2099 relative to 1980-1999 figures (IPCC 2007). Organism distribution, survival and reproduction are linked with surrounding environmental conditions, and as such will be inexorably impacted by climate change (Woodward 1987; Walther *et al.* 2002; Clarke 2003; Hiscock *et al.* 2004; Warren 2005).

Although rapid global temperature increases indicate that climatic change is occurring, it is not only these averages which will directly impact ecology but rather increases in climatic variability. Extinctions of populations of Checkerspot butterflies (*Euphydryas editha bayensis)* have been explicitly linked to precipitation variability (McLaughlin *et al.* 2002). The European summer heat wave of 2003 caused populations of host plant to decline with consequential impacts on the size of herbivore populations and fecundity levels (Piessens *et al.* 2009). In some cases it is thought that climate change is having (Franco *et al.* 2006), and will have in the future (Sala *et al.* 2000), an effect on biodiversity that is comparable in magnitude to that of land use modification. This biotic response will take a multitude of forms: from extinctions, to evolutionary adaptations, to shifts in behaviours, to altering biotic interactions (Walther *et al.* 2002; Callaghan *et al.* 2004; Gilman *et al.* 2010). Phenological and distributional shifts have been used 'biological fingerprints' to test the impacts of climate change on biota (Parmesan and Yohe 2003) and the latter is used extensively for analysing macroecological spatial changes .

1.1.3.2. Shifting climate envelopes and distributions

Temperature is not uniform across the globe, and by correlating the geographical distributions of species with these isoclines a species climate envelope can be generated. Most species envelope models assume that species will track their moving climate isocline — moving to higher latitudes and altitudes—in an attempt to stay within the geographical areas that encompass the temperature limits which allow them to function at their physiological optimum (Davis *et al.* 1998; Shaver *et al.* 2000). This ecological theory has been exemplified across a range of taxa (Parmesan *et al.* 1999; Root *et al.* 2003; Walther 2004; Ragupathy and James 2009). For example, 96 % of northern hemisphere butterflies that expanded their

ranges, did so in a predominantly poleward direction (Burton 2003) and even within Europe 63% of non-migratory butterflies have shifted north by 35-240 km, whereas only 3% shifted south over the past 100 years (Parmesan *et al.* 1999).

Assuming habitat and food resources are available, this geographical shift caused by climate change is thought to be driven by the retraction of populations at the trailing equatorial margins and expansion of populations at the leading edge (poleward) range margins where conditions become more favourable (Parmesan *et al.* 1999; Hampe and Petit 2005; Hellmann *et al.* 2008). Geographically, natural temperature gradients correspond to a 5 to 6.5 °C drop in temperature with 1000 m increase in elevation, or a decline of 6.9 °C every 1000 km of latitude (Colwell *et al.* 2008). This may allow predictions to be made about the average distances species may travel under various climate change scenarios. For example, species are predicted to retreat 10 m in altitude for every 10 km in latitude based upon the rate at which temperatures decline with increasing altitude and latitude (Jump *et al.* 2009) (Fig. 1.2). When investigated through empirical research, the rate of range change under current climates was summarised in a meta-analysis by Chen et al (2011) who found that the median rate of range shifts in terrestrial organisms was two to three times faster than previously thought. The median shift in elevation was 11m per decade and 16.9 km shift in latitude per decade.

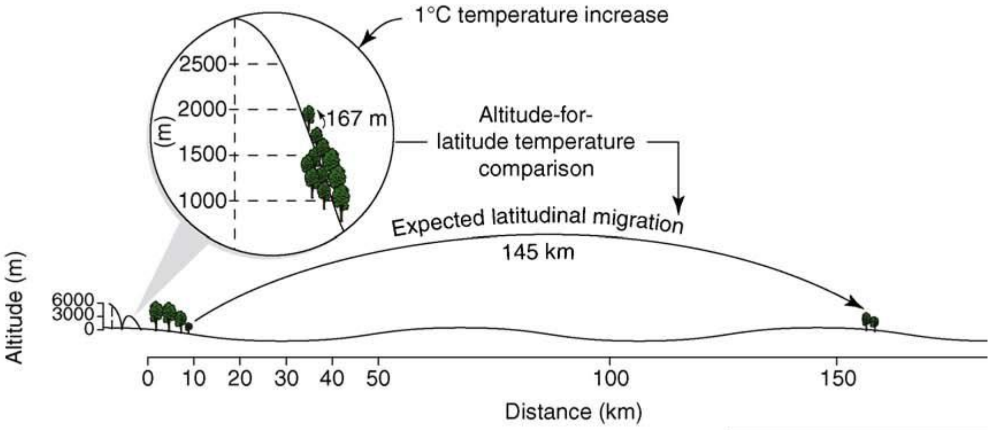


Figure 1.2. Species migrations under climate change based on an altitude-for-latitude model of temperature similarity (trees are not to scale). Reproduced from Jump (2009).

1.1.3.3. Interactions between habitat fragmentation and climate change

Individually, land use modification and climate change pose the two greatest threats to biodiversity in the modern day, yet in combination the two have the potential to produce a ‘deadly anthropogenic cocktail’ (Travis 2003) with each exacerbating the impacts of the other. Mora et al. (2007) used experimental microcosm experiments to investigate these impacts. They found that restricting immigration (as a surrogate for fragmentation) in populations of marine rotifers caused the populations to decline at a rate 11.9 times faster than replenished control populations. Simultaneously, they mimicked climate change and found that population sizes at the high heating rate (0.6 °C) declined 1.4 times faster than populations with slower warming rates (0.3 °C). Combined, the interaction between fragmentation and climate change caused population declines 36.2 times faster than control populations and almost three times the rate that additive effects would exert.

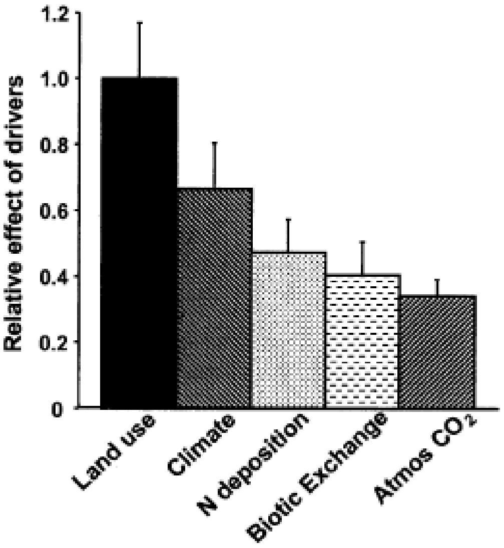


Figure 1.3. Relative effects of global environmental change drivers on biodiversity by the year 2100. Reproduced from Sala et al. (2000).

It has been suggested that climate change and habitat destruction are opposing forces, with climate acting to expand populations at leading edge range margins and fragmentation acting against expansion (Warren *et al.* 2001). Results from patch occupancy models (Travis 2003), however, suggest that when considering entire species ranges the two drivers act in the same direction and interactions between climate change and habitat destruction could be ‘disastrous’.

Altering the fundamental characteristics of the environment in which organisms reside will inevitably affect their basic life history traits: how they feed, move, interact and ultimately survive. Below certain critical threshold levels of both climate change and habitat availability, species occupancy of suitable habitat rapidly declines. The subdivision and isolation of habitats will, for example, inhibit the ability of less mobile organisms to shift distributions in line with their physiological optimum climate in a warmer world. Hill et al. (2001a) for example, combined climate models and empirical evidence, finding that range expansion in British butterflies is 42-45 % less in regions that had 24 % less woodlands. Particularly at risk are those species with poor dispersal abilities, with specialist habitat requirements, with a high degree of local adaptation and those species with narrow ranges (particularly equatorial species). Inherent differences in biotic responses will cause concomitant cascading effects on the interactions between species undergoing change, novel relationships will form, some existing relationships will be strengthened whereas others will be weakened.

1.2. Biotic interactions as a measure of global change

1.2.1. Importance of studying species interactions

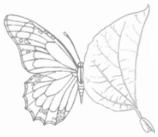
A large number of studies have measured the impacts of global change on ecological systems through changes in population abundance, organism physiology and distributional shifts. More recently, the role of complex biotic interactions—whether they be herbivorous, predatory, competitive, parasitic or relating to pollination—between networks of interacting species has been recognised as being fundamental in shaping and maintaining biodiversity (Bascompte *et al.* 2006).

The low frequency of studies into biotic interactions belies their importance. Species can respond very differently to different GEC drivers, which have differential impacts on the magnitude and direction of interspecific relationships (Tylianakis *et al.* 2008). Originally applied to climate change (but relevant for other GEC drivers) Gilman et al. (2010) formulate a framework for studying these interactions, and suggest that the fate of species is dependent

upon (i) direct effects of climate on the species, (ii) direct effects on interspecific interactions (iii) degree of specialisation of the species (iv) strength and climatic sensitivity of interactions (v) impacts of mobility and (vi) potential for novel community composition. Community responses are therefore the sum of these individual responses which ultimately complicate predictions of ecosystem resilience. Despite this, interactions are now being included in predictions of changing ecosystems, for example, inclusion of interactions in species distribution models has been shown to improve model accuracy (Heikkinen *et al.* 2007) and alter predicted areas suitable for species existence (Brooker et al. 2007; Araújo and Luoto 2007). Excluding these interactions from global change forecasts will limit the ability to accurately predict community responses (Heikkinen *et al.* 2007; Gilman *et al.* 2010).

1.2.2. Fragmentation impacting upon species interactions

Fragmentation studies which are based around IBT and metapopulations theory typically consider the effects on non-interacting species (Harrison and Bruna 1999). However, there has been a recent shift in studying these patterns, for example, through investigating mechanisms behind ecological processes i.e. “edge mediated effects” (Fagan *et al.* 1999). A synthesis by Fagan (1999) brings together the literature on how four classes of mechanisms influence species interactions at habitat edges: by altering dispersal and movement rates, by influencing mortality, by allowing or inhibiting spatial subsidies, and by generating novel species interactions. The former edge effect can either restrict or facilitate movement into fragments. The creation of additional edge environments by fragmentation effectively increases the accessibility. For example, populations of the endangered *Peraxilla tetrapetala* mistletoe species were higher in more fragmented *Nothofagus* forest patches of New Zealand (45 % seed set on isolated trees compared with 14 % in continuous forest) and this is thought

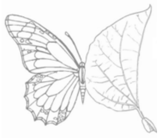


to be partially linked to increasing honeyeater bird visitation by tui (*Prosthemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*) (Ladley and Kelly 1995; Kelly *et al.* 2000). Mistletoe population levels, which were 40 % lower in single trees than in continuous forest, may also be influenced by herbivory, suggesting the bud herbivore, *Zelleria maculata,* was highly sensitive to fragmentation (Kelly *et al.* 2008). The third impact on interactions results from cross-boundary subsidies arising with certain species maintaining populations outside of patches and then moving into these areas to interact with patch residents. This was empirically demonstrated by Muller & Godfray (1997), who found that populations of aphids on nettles suffered early population decline (compared to controls) when grass pots were placed adjacent to nettles. This apparent competition caused by the presence of large concentrations of grass aphids attracting Coccinellidae predators effectively supported the numbers of predators that wouldn't have been as prevalent if there was less edge (or in this case exposure to grass environments). The fourth group of edge mediated change concerns the creation of a novel habitat and its role in instigating novel interactions. For example, the creation of edges in the Amazon stimulated prolific plant growth in the high light environment, which in turn attracted a wealth of insect species leading to increases in the numbers of insectivorous predators (Lovejoy *et al.* 1986).

1.2.3. Climate change impacting upon species interactions

It is thought that the largest uncertainty in predicting the impact of climate change on ecosystems is understanding how species will interact in novel conditions (Winder and Schindler 2004). Yet the fundamental importance of studying how species interactions are modified by this driver cannot be ignored. Changes to species interactions in response to climate change can take the form of interaction attrition or novel interaction associations. A weakening of trophic interactions can come about as species with differing levels of mobility move to track changing isothermic distributions, spatially decoupling interactions in some locations and creating new interactions in others (Araújo and Luoto 2007). Phenological studies of species interactions are relatively well documented (Sydeman and Bograd 2009; Yang and Rudolf 2010), often finding interaction attrition as differential rates of advance in spring and summer events among trophic levels are manifested (Thackeray *et al.* 2010). Secondary consumers showed the slowest rate of phenological advance, a trend that indicates a developing temporal trophic mismatch between predators and their prey (Thackeray *et al.* 2010). This was exemplified in a quad-trophic system of the host plant oak (*Quercus robus*), herbivorous caterpillars (frass samples), insectivorous passerines (three species of tit) and avian predators (*Accipiter nisus*) which found that the phenological response of consumers to climate change was weaker than the response of their food, and that the match between the passerine-caterpillar and avian predator- passerine decoupled over time (Both *et al.* 2009).

As species move at different rates a spatial mismatch can occur between trophic levels and in some cases ‘predator release’ ensues. The Brown Argus butterfly (*Aricia agestis)* for example, has travelled northwards in Britain during the past 30 years and Menéndez et al. (2008) recorded lower levels of parasitism on populations in the newly colonised areas over four consecutive generations. Climatic variability too was thought to cause a reduction in parasitism levels in Macrolepidoptera, suggesting that climatic changes interfere with parasitoids being able to track and locate their hosts (Stireman *et al.* 2005). In this context, the decoupling of a species interaction may allow populations of the prey species to exploit a wider range of environments, moving into areas becoming increasingly climatically suitable at a rate exceeding previous predictions (Menéndez *et al.* 2008). Such new associations will



inevitably be forged as populations move into new areas or move into temporal synchrony with novel species.

Pair-wise species interactions only explain the function of ecosystems to a limited degree and because of this more researchers are attempting to construct methodologies to analyse interaction networks and their dynamics under GEC drivers (Tylianakis *et al.* 2007; Tylianakis 2009; Gilman *et al.* 2010). Using an empirical network of 1420 pollinator species and 429 plant species in the USA, Memmott et al. (2007) found that phenological shifts in host plants reduced the availability of floral resources to 17-50% of pollinator species. This could be extended to interactions all the way up the food chain inducing ‘co-extinction cascades’ (Bascompte and Stouffer 2009), where the extinction of one species has incidental effects on the species with which it directly and indirectly interacts.

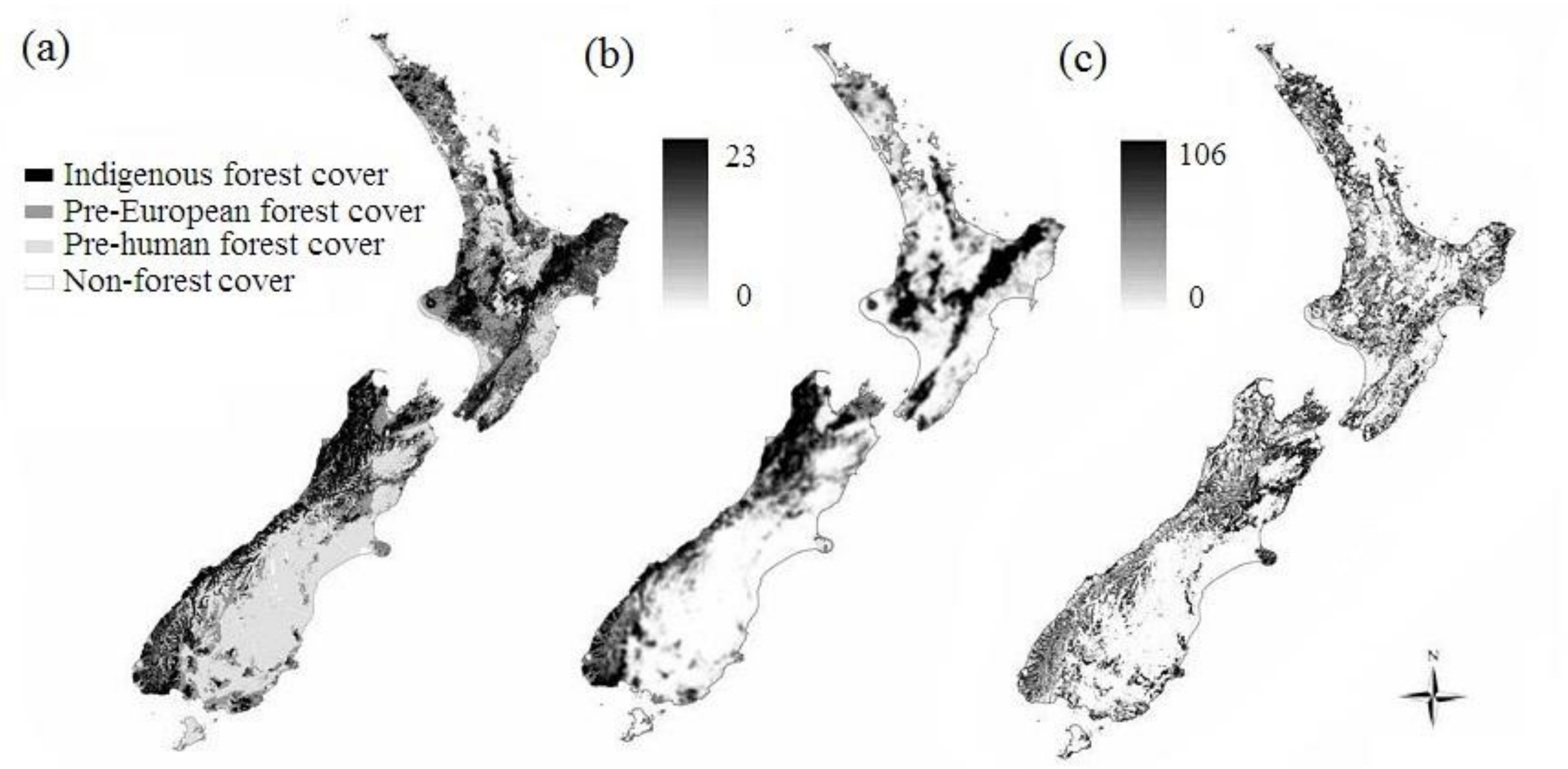
1.3. Study System: New Zealand and its native species

The two main Islands of New Zealand provide a contained experimental ground on which to carry out field observations and experiments on native flora and fauna. The New Zealand landscape has undergone considerable ecological change over the past 1000 years since human habitation and it is likely to undergo further rapid change under climate change scenarios.

1.3.1. Habitat modification in New Zealand

One thousand years of Polynesian and European colonisation in New Zealand has inevitably brought land use change (Anderson *et al.* 1984; McGlone 1989, 1995; Arnold 1994; McGlone and Wilmshurst 1999; Ecroyd and Brockerhoff 2005). National scale data on historical and present day landcover in New Zealand is among the finest in the world, with GIS data available for mapping the pre-human distribution of forest cover derived from species-environment models (Leathwick *et al.* 2004), indigenous forest cover patterns determined from aerial photographs taken mostly in the 1970s and 1980s (LINZ 2007), and remotely sensed landcover data from 1996/97 and 2001/02 in the Land Cover Database (Terralink 2004). Such detailed data lends itself to the calculation of fragmentation indices and allows patterns of fragmentation to be mapped across the country (Fig. 1.4).

Figure 1.4. Deforestation and forest fragmentation in New Zealand. The spatial distribution of deforestation over the past ~1000 years (a), data were obtained from: Land Cover Data Base (Terralink 2004) for current data, McGlone (McGlone 1989) and later digitised by Ewers et al. (2006b) for pre-European data and Leathwick et al. (2004) for pre-human data (~1000BP). Average patch size (m^2; colour ramp is min-max on a natural log scale) of indigenous forest remnants (b): indigenous forest (comprising of ‘broadleafed indigenous forest’, ‘manuka and/or kanuka’ and ‘indigenous forest’) 1km raster patch size information from LCDB2 averaged over an area of 10km using focal statistics. Average density of forest fragment (c), calculated using polyline forest perimeter values calculated from LCDB2 indigenous forest to create a surface of average edge (m) per 1km (colour ramp is min-max on a linear scale).



enhance human motility and potentially to aid Moa (Dinornithidae) hunting (Stevens 1988). In the 1800s, further deforestation accompanied the expansion of infrastructure and agricultural production by the increasing populations of European immigrants. Early landowners were legally obliged to improve their holdings and the most effective means to do this was through the clearance of forests (Salmon 1975). Initially the tendency was to target highly productive lowland areas for agricultural activities yet, today, the majority of these areas are occupied and the focus has shifted deforestation activities to locating exotic forestry plantations on marginal land (Walker, Price, *et al.* 2006).

Deforestation occurred in relatively equal proportions on the two main islands (Ewers *et al.* 2006), but the fragmentation and spatial arrangement differs between the North and South Islands (Fig. 1.4). Forest fragments are on average four times smaller in the North than South Island (61 *vs.* 244 ha respectively), and forest edge density is almost a third higher (0.93 *vs.* 0.72 km/km^2 respectively) (Ewers *et al.* 2006). The greater level of fragmentation on the North Island is due partially to a climate and landform that favoured the development of agriculture, with the associated growth in infrastructure dividing the remaining natural habitats. On the South Island, steep slopes and their unsuitability for farming safeguarded large swathes of land along the Southern Alps, some of which were protected as water catchments in the 1890s (Park 2000). Many of these areas were afforded official protection as nature reserves throughout the 20th century, with the first national park on the South Island being gazetted in Arthurs Pass in 1929. The relative wealth of forest along the Southern Alps masks an underlying imbalance of forest cover across the South Island. While the Gondwanan gymnosperm forests on the West Coast are among the ‘most extensive temperate rainforests on Earth’ (Conservation International 2007), forests in the drier and predominantly flat East Coast has been impacted by conversion to intensively cultivated land (Ewers *et al.* 2006).

Fifty seven percent of the country's land environments (LENZ categories derived from soil and climate data layers (Leathwick *et al.* 2002)) have suffered extreme loss (> 70 %) of indigenous cover (Walker, Price, *et al.* 2006). There may be a threshold level of forest cover below which fragmentation impacts may rapidly accrue (Andrén 1994) and the probability that populations will persist rapidly decreases (With and King 1999). This threshold value is likely to vary between species, however, a review of mammal and bird studies (Andrén 1994) found that the probability of an extinction threshold occurring greatly increases when forest cover decreases below 30 %. Native forest cover across the majority of New Zealand is, alarmingly, below this landscape 'extinction threshold' figure, and several districts that are currently above the threshold were predicted to fall below it by 2050 (Ewers *et al.* 2006). Quantifying the exact level of destruction caused by habitat fragmentation can be problematic, with researchers able to choose from hundreds of different indices that quantify different aspects of landscape structure (McGarigal and Marks 1995). Bridging the disconnect between landscape change and biodiversity change continuous biodiversity surfaces portraying spatial patterns of community composition change have been generated by combining point data observations (Ewers *et al.* 2009) and plant diversity data from the National Vegetation Survey Databank (Lafortezza *et al.* 2010) with remotely sensed landscape maps. Both studies display how the 'fine scale configuration of habitat loss sums across a landscape to influence changes in biodiversity at larger spatial scales' (Ewers *et al.* 2009) and are comparable among species, research approaches and biomes (Ewers *et al.* 2010).

1.3.2. Climate Change in New Zealand

There is a high degree of regional variation throughout the New Zealand archipelago, ranging from subtropical conditions in the north (average annual temperature of 16 ˚C) to cooler temperate conditions in the south (average annual temperature of 10 ˚C) (NIWA 2012). Temperatures in New Zealand have risen by 0.7 ˚C between 1900 and 1990 (Folland and Salinger 1995), slightly higher than the average global rise of 0.6 ˚C (Nicholls *et al.* 1996) and equating to a total rise of about 0.9 ˚C from 1908-2006 (Ministry for the Environment 2008) There is a reduced frequency in frosts over the majority of the country, with Marlborough and Canterbury experiencing an average of 20 fewer frosts per year than in 1970.

Future New Zealand climate projections adhere to the methods used in the IPCC Fourth Assessment Report comparing change to the period between 1980-1999 (abbreviated to 1990). Coarse scale information from General Circulation Models predicting global climate change were downscaled to 0.05 degrees latitude and longitude grid (5km by 4km) to cover the New Zealand landmass. Calculations are made for two periods 2030-2049 (‘2040’) and 2080-2099 (‘2090’). These downscaled models predict that temperatures will rise, there will be fewer frosts, more ‘hot’ days (above 25 °C), and there will be variations in localised rainfall. Predictions based on the average of 12 climate models and six emissions scenarios project a rise in temperature of between 0.2 - 2 °C by 2040 and between 0.7 - 5.1 °C by 2090. In all cases, the New Zealand projections in temperature increase are smaller than global SRES scenarios. Spatial differences will be present across the country, with warming slightly greater on the North Island compared to the South, and seasonal trends showing that in the summer and autumn the North Island and northwest of the South Island will experience the greatest warming whereas in the winter the South Island will exhibit the greatest warming. The number of frost days are projected to significantly decrease in the central North Island and South Island. Warm days are thought to show similarly dramatic changes, with areas such as Auckland set to experience triple the number of days above 25 °C. Rainfall is likely to decrease in the north of the North Island and the east coast, but increase along the west coast of the South Island and far south (Fig. 1.5).

Little has been documented on range shifts of New Zealand species in response to climate change. The small amount of literature on the ecological effects of climate change that does exist focuses on plant taxa (Whitehead *et al.* 1992). Whitehead et al. (1992) suggest that with temperature change there will be significant changes in the pattern of forest cover and that change will occur at the species (rather than community) level. Norton (1985) predicted that, with each one degree rise in temperature, species will migrate either 2.22° south (approximately 250 km) or 200 m upwards in altitude to keep within their optimum physiological conditions. This is slightly less distance than matching global predictions (Jump *et al.* 2009), yet nonetheless significant. As populations of species in New Zealand shift (or attempt to shift) in line with their climatic optimum, complex interactions between their hosts, competitors and predators are likely to alter in frequency and it is this change that I am interested in investigating by focussing on a tri-trophic forest feeding system in the remaining fragmented indigenous forests.

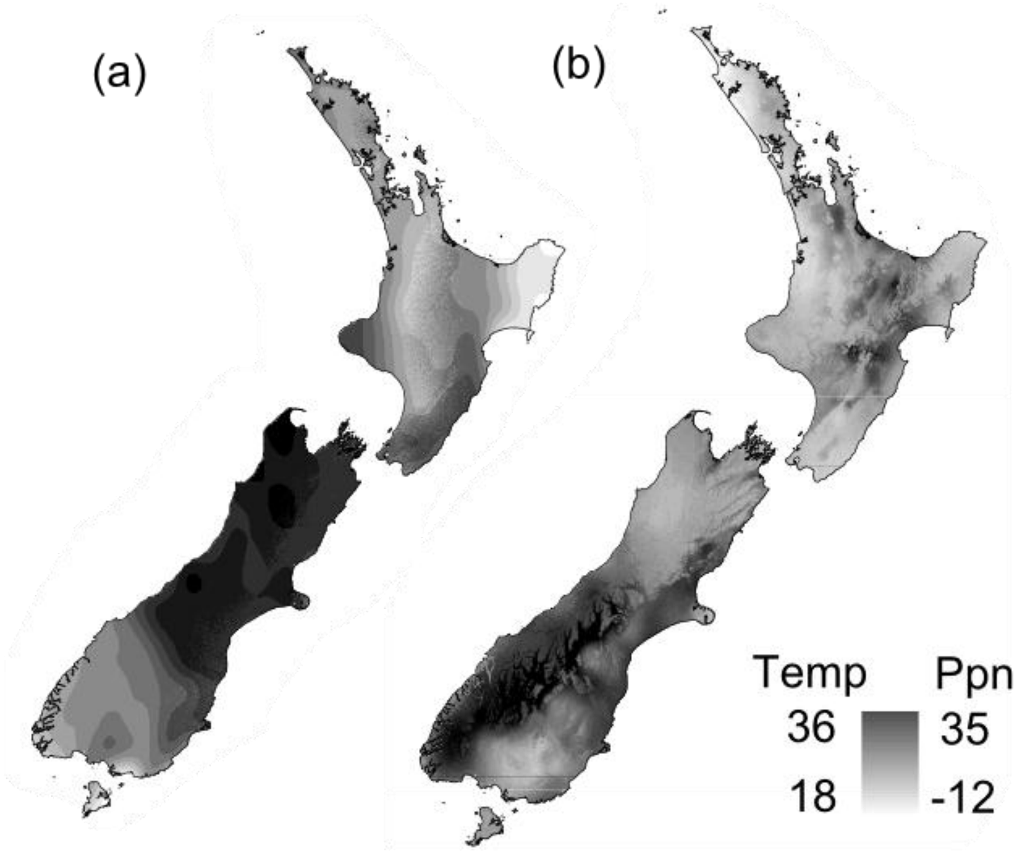


Figure 1.5. Projected climate change in New Zealand. Temperature increase of the warmest month (a) and change in precipitation seasonality (b) between current records and projected values for 2080. Bioclimate data (Bio 5 and Bio 15 respectively) from IPCC4 CIAT estimations were derived from a spatial downscaling Delta method (Hijmans *et al.* 2005) and A1B scenario under the CSIRO-MK model is displayed representing mid-level temperature and precipitation forecasts.

1.3.3. Tri-trophic species system

Arthropods, being the most diverse component of terrestrial ecosystems, can be used to investigate a wide array of information on ecological niches, ecosystem function and environmental change (Kremen *et al.* 1993). Their high rate of reproductive turnover, sensitivity to ambient conditions and short life span render them suitable to investigate multiple drivers of environmental change (Golden and Crist 1999).

The family Lepidoptera are used widely as biodiversity indicators (Burton 2003; Thomas *et al.* 2004; Hellmann *et al.* 2008). According to Brereton (2007), the order has the following qualities important for ecological investigations since they: (1) occupy a wide range of terrestrial habitats; (2) respond rapidly to environmental change; (3) are vulnerable to habitat fragmentation; (4) have relatively well documented distributions; (5) have long term data sets in different parts of the world; (6) allow for cost effective and policy relevant data to be produced; and (7) have high public appeal. Being ectotherms, moths and butterflies are particularly sensitive to climate change as there is a high correlation between their development rate and surrounding temperatures (Stamp and Casey 1993; Gotthard *et al.* 2000). The degree of temperature dependence, and therefore the optimum growth temperature, is however species specific (Taylor 1981).

Compared to knowledge of northern hemisphere arthropods, there is a relative lack of information available for New Zealand invertebrates (DOC 2000). Among the invertebrate taxa, moth species are particularly well-studied in New Zealand with more than 2000 species described (Parkinson and Patrick 2000). I will investigate a trophic system which is widespread across seven degrees of latitude in New Zealand, is present in remaining forest patches of different sizes, includes three trophic levels and involves species that have important cultural values.

1.3.3.1. Host plant

The native Kawakawa tree (*Macropiper excelsum*, Piperales: Piperaceae) is an important understory plant throughout the mixed native scrub environments of New Zealand (Smith

1975). *Macropiper* species predominantly exhibit shrub–like qualities, typically growing to a height between 1 to 3 m in shady gullies and producing new stems at the base of older ones, although *M. excelsum* can be single stemmed allowing the growth of a small tree up to 6 m and living for several decades (Gardner 1997). The genus *Macropiper*—of which Smith accepted nine species—has a distribution that is restricted to the central Pacific Ocean. The species *Macropiper excelsum* is confined to the coastal areas of the New Zealand mainland and a number of its offshore islands (Fig. 1.9). *M. excelsum* differs in the size and pigmentation of leaves in different regions, particularly on the northern offshore islands (Smith 1975). It produces axillary inflorescences in a pedunculate spike. Plants flower when mature which is around two years old, and Gardner (1997) speculated that the floral filaments of *M. excelsum* are relatively short to support a mixture of both wind and insect pollination. Photographic documentation has captured fruits being consumed by reptiles (personal communication with Debra Wotton, DOC), however, little research has been done into this area.

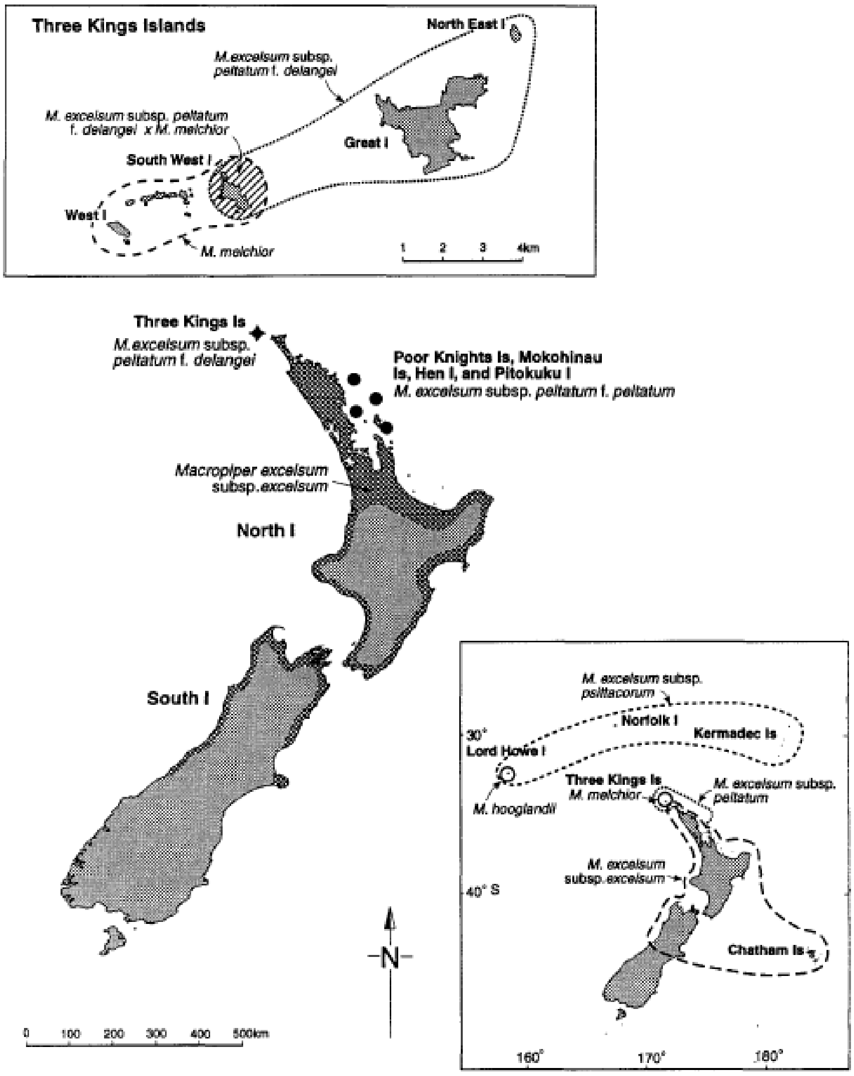


Figure 1.6. Distribution of *Macropiper* species across the south-western Pacific. Reproduced from Gardner (1997).

The family Piperaceae is known to contain a range of bioactive compounds which have been utilised in Maori medicine and as insecticides for over 160 years (TGA and Medsafe 2006). Leaves are consumed fresh (directly chewed), infused (to make tea), distilled or soaked in a bath to treat urinary complaints, stomach pains, skin conditions and circulatory issues (Brooker *et al.* 1987). The compound myristicin, thought to be accountable for antiseptic and insecticidal activity (Litchenstein and Casida 1963), is known to be the predominant component of the essential oil of *M. excelsum* leaves (Briggs 1941). Insecticidal effects are evident (Russell and Lane 1993); leaves are burnt to emit a toxin for crop protection against insect herbivores (Brooker *et al.* 1987) and it has been demonstrated that leaf material is toxic to house fly larvae (*Musca domestica* L.) (Russell and Fenemore 1973). Russell and Lane (1993) found that *M. excelsum* was in a group of plants displaying the highest level of defence to insects. Several insect-active constituents have been isolated (Russell and Fenemore 1973; Nishida *et al.* 1983). It is thought that novel ligans including juvadicine (Nishida *et al.* 1983) and a series of methylenedioxy ligans (Russell and Fenemore 1973) disrupt healthy development of larvae through mimicking the action of insect juvenile hormone (sesomolin). As myristicin did not seem to be responsible for inhibiting feeding (Russell and Lane 1993) the latter are responsible for the majority of herbivory defences.

The battery of defences deters widespread generalist feeding activity on *M. excelsum*, however despite the tree's range of anti-herbivory bio-compounds (Hodge *et al.* 2007) one particular species, *Cleora scriptaria* (Lepidoptera: Geometridae), is effective at sequestering these compounds and feeds extensively on the plant. *C. scriptaria* is responsible for the conspicuous shot hole appearance of herbivory scars which is highly distinguishable in this species (Fig 1.10).

Figure 1.7. *Macropiper excelsum* tree (left) and leaf exhibiting the shot-hole pattern of herbivory damage (right). Photographs by Poppy Lakeman Fraser.

A number of additional insects have been found on *M. excelsum*, including (*Cixius kermadecensis* (Homoptera: Cixiidae), *Ctenochiton piperis* (Hemiptera: Geometroidea), *Ctenopseustis obliquaria* (Lepidoptera: Tortricidae), *Epalxiphora axenana* (Lepidoptera: Tortricidae), *Pseudococcus glaucus* (Homoptera: Coccidae), *Rhapsa scotosialis* (Lepidoptera: Noctuidae) (Spiller and Wise 1982). However, the larvae of *C. scriptaria* is considered to be the primary herbivore (Hodge 1998).

1.3.3.2. Herbivore

Cleora scriptaria (Walker) (Fig. 1.11), commonly known as the kawakawa looper, is a native geometrid Lepidopteran which feeds predominantly on *M. excelsum*. Secondary host plant species have been recorded, such as *Dodonaea viscosa* (Sapindales: Sapindaceae) and *Pseudowintera* sp (Canellales: Winteraceae) (Spiller and Wise 1982) although their importance is thought to be comparably negligible. The larvae develop through five instars, growing to a size of approximately 20 mm and by the 5th instar have a head capsule width of 1.25 mm. The adult imago has a wingspan of 40 - 50 mm.

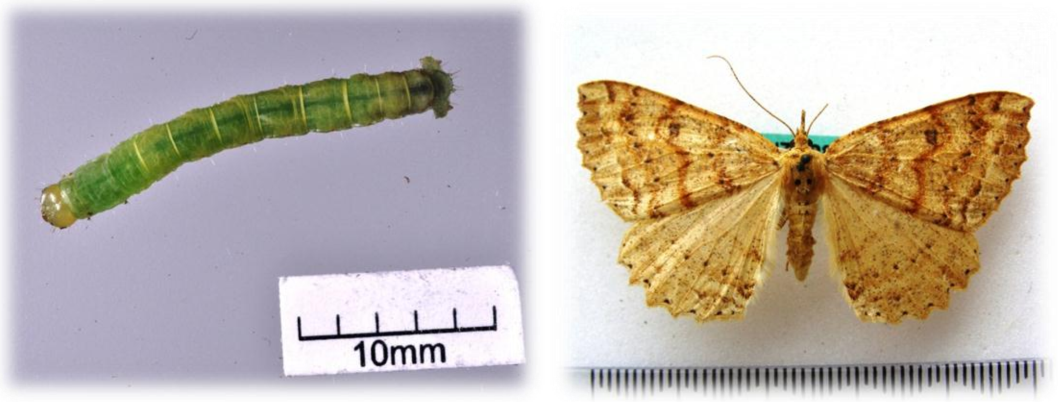


Figure 1.8. *Cleora scriptaria* larvae (left) collected by Poppy Lakeman Fraser and photographed by Matt Walters. *C. scriptaria* imago (right), specimen from Auckland museum photograph by Poppy Lakeman Fraser.

1.3.3.3. Parasitoids

Five species of solitary hymenopteran endoparasitoids have been reared from *Cleora scriptaria* (*Meterorus pulchricornis*, *Aleiodes declanae*, Microgastrinae sp, *Diadegma* sp, *Casinaria* sp), one tachnid (*Pales* sp), one nematode (Mermithidae sp.), two Roganidae (*Rogas* sp) and one Eulophidine hyperparasioid (*Zealachertus binarius)* has been associated with *Cleora scriptaria* (Schnitzler *et al.* 2004). The two most prevalent parasitoids are the introduced species *Meteorus pulchricornis* (Braconidae: Euphorinae) and the endemic species *Aleiodes declanaea* (Braconidae: Rogadinae).

Meteorus pulchricornis (Fig. 1.9) is a polyphagous koinobiont braconid endoparasitoid (Askari *et al.* 1977; Berry and Walker 2004). It has a broad global distribution (Shenefelt 1969) ranging from Western Europe to North Africa, Japan and it has been purposefully introduced into the US for biological control of the gypsy moth, *Lymantria dispar* (Fuester *et al.* 1993) and accidentally introduced into New Zealand in 1996 (Berry 1997). In New Zealand, only female specimens have been recorded suggesting it is thelytokous (females produced form unfertilised eggs) and originates from Asia, as opposed to Europe where this species is arrhenotokous (males produced form unfertilised eggs). Since its arrival, this parasitoid has become widespread in modified habitats and has been reared from 21 Lepidopteran species from eight families (Berry and Walker 2004). Stimulated by host movement activity (Yamamoto *et al.* 2009), *M. pulchricornis* attack larvae at the second instar, and emerge at the fourth. Upon emergence it suspends its pupal cocoon (oval 0.5-1 cm in length and pale-dark brown in colour) from silken threads usually attached to the underside of leaves (Berry 1997; Shirai and Maeto 2009). Development from egg to larva takes around 8-9 days (in the host *Pseudaletia separata*) and six days from pre-pupa to adult emergence with successful parasitism decreasing with age of host larva (Suzuki and Tanaka 2007). This is a solitary endoparasioid and as such only one egg per host can develop successfully. Superparasitism has been shown to occur, yet little is known about the superparasitism avoidance strategies in this species (Chau and Maeto 2008). It is widely accepted that the majority of parasitoids utilise supplementary sugar as a source of energy ultimately increasing reproductive capacity (Wu *et al.* 2008). As such, it has been collected predominantly from host larvae amongst vegetable crops spanning species in the families Geometridae, Lycaenidae, Noctuidae, Nymphalidae and Tortricidae in New Zealand (except *Pieris rapae*) (Berry 1997; Berry and Walker 2004). The exception to this pattern, however, are parasitoids reared from *Cleora scriptaria* larvae in native forest remnants of a suburban environment in Wellington (Schnitzler *et al.* 2004). The first record of *M. pulchricornis* (Berry 1997) suggests that this species was likely to become widespread. To date, no specimens have been collected in "true" native vegetation and Berry and Walker (2004)

suggest there may be potential barriers to movement into native habitats but that this question requires further investigation.

Figure 1.9. *Meterorus pulchricornis* specimen from Auckland museum, photographed by Poppy Lakeman Fraser.

Aleoides declanae (van Achterberg, 2004; Fig. 1.10) is one of two rogadine braconids native to New Zealand. *Aleoides* spp are koinobiont endoparasitoids which mummify their Macrolepidopteran hosts (van Achterberg *et al.* 2004). This species is known to be confined to the North and South Islands of New Zealand, and has four known Geometridae-Ennoniminae hosts: *Cleora scriptaria*, *Pseudocoremia suavis*, *P. fenerata* and *Declana floccosa* (van Achterberg *et al.* 2004). It is thought to attack larvae at the first to second instar and mummify host in the fourth/fifth instar, emerging though a circular hole at the dorsal apex (van Achterberg *et al.* 2004). Two species of hyperparasitoids have been reared from *A. declanae* mummies, *Mesochorus* sp (Ichneumonidae: Mesochorinae) (van Achterberg *et al.* 2004) and *Gelis tenellus* (Say) (Berndt *et al.* 2006). *A. delclanae* was recorded in Eyrewell forest Canterbury from 1960-1962, although the parasitoid exerted no demonstrable impact on populations of its hosts (Dugdale 1964).

Figure 1.10. *Aleoides declanae*, identified by Rudolph Schnitzler and photographed by Matt Walters.

1.3.3.4. Trophic interactions in the kawakawa feeding system

Previous research into this tri-trophic feeding relationship, although relatively limited, has investigated a range of biochemical, behavioural and ecological approaches. As discussed, *M. excelsum* contains a number of bioactive compounds which inhibit insect activity. The extensive herbivore damage to leaves has prompted researchers to investigate consequential botanical impacts in leaf phenology and chemistry. Hodge et al. (2000) found that herbivory in fact did not stimulate the production of increased levels of chlorophyll to compensate for area loss, nor did it induce increased shedding of damaged leaves (even when up to 90% of leaf are removed) (Hodge *et al.* 1998). The patchy configuration of ‘shot holed’ feeding damage—so distinctive of *M. excelsum* leaves—suggests that caterpillars feed in discontinuous bouts, perhaps indicating that *M. excelsum* has a system of induced chemical defence. Caterpillars, however, demonstrated no preference for non-wounded leaves (Hodge, Keesing, *et al.* 2000) despite bioassays showing that mechanical wounding does induce a change in *M. excelsum* leaves which stunts the growth of *C. scriptaria* larvae (Hodge *et al.* 2007). This defence strategy may have evolved to reduce the size of larvae (and hence the size of pupae), ultimately reducing the fecundity and therefore reducing the population size of herbivores. Additional tri-trophic influences may assist in this process through the slowed development which renders herbivores more susceptible to parasitoid attack (Hodge *et al.* 2001). Relatively little is known about the top-down influences on this herbivore-host system, although Baird (1983) and Schnitzler et al. (2004) provide initial information on larval parasitism rates. Using this tri-trophic system as a model to investigate the effects of habitat fragmentation at different spatial scales, Schnitzler et al. (2011) found that *Aleoides declanae* parasitism rates were significantly higher in more isolated patches and were negatively correlated with populations of other species. By contrast, *M. pulchricornis* parasitism rates were not impacted by fragmentation, but were positively related to *C. scriptaria* density. Similarly, herbivory rates were related to host plant abundance but not to indices of fragmentation (Schnitzler *et al.* 2011).

Little is known about how climatic gradients affect the Kawakawa tri-trophic feeding relationships, nor whether synergies between climate and habitat fragmentation will magnify the impacts of these global environmental change drivers on the feeding relationship. Using this system across multiple spatial scales (Fig. 1.11), I will address globally relevant questions about the degree to which fragmentation and climatic conditions interact additively or non-additively to destabilise the species interactions that are crucial for the maintenance of biodiversity.

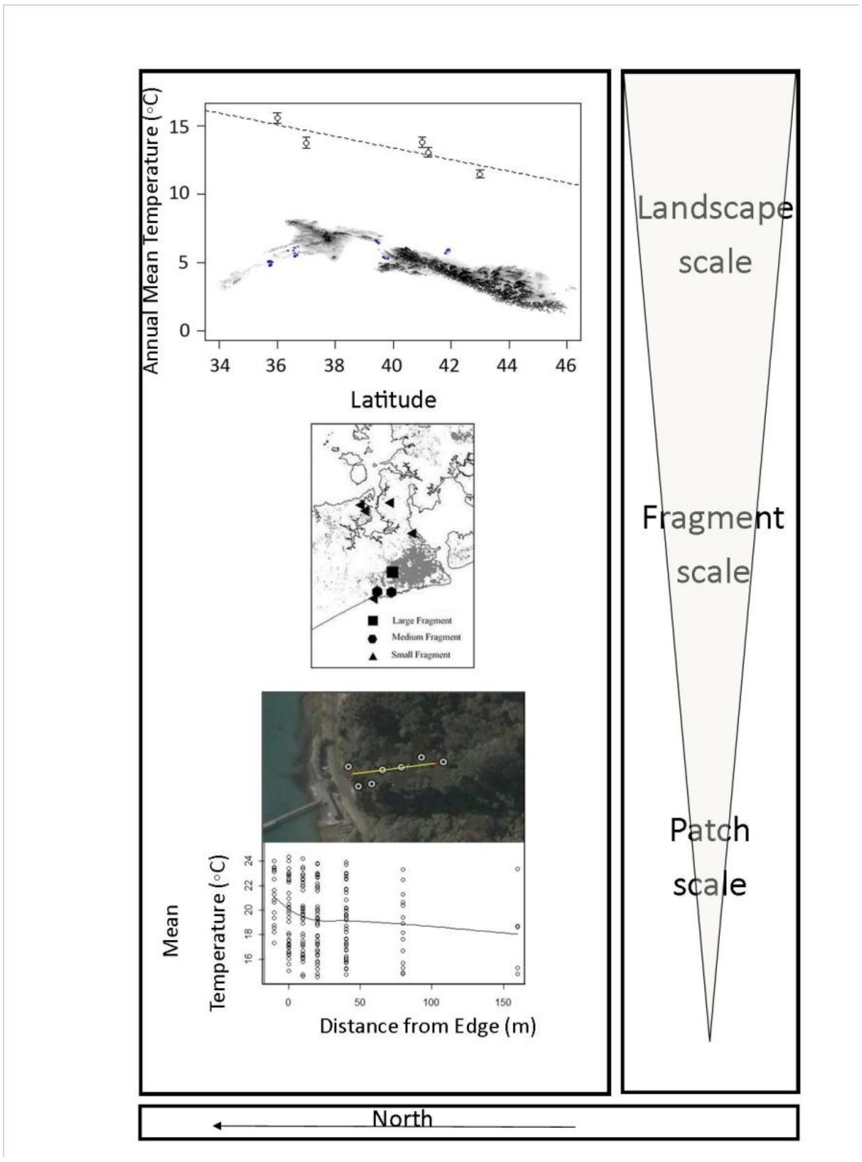


Figure 1.11. The multiple spatial scales over which this research is conducted.

1.4. Thesis Outline

This research investigates the complexities of environmental interactions between two prevalent drivers of global environmental change, habitat modification and climate change through determining the impact that these drivers are having across a tri-trophic feeding system. This thesis is structured into four main chapters each corresponding to a methodological approach: a literature review, field observation research, an *in-situ* experiment, and an *ex-situ* experiment,; and are written in the format of manuscripts for submission to international peer-reviewed journals.

1.4.1. Chapter 2: The ecological consequences of habitat loss and fragmentation in New Zealand

Poppy Lakeman-Fraser & Robert Ewers

Submitted to: *The New Zealand Journal of Ecology* on the 11th April 2011

Resubmitted with amendments: 20th June 2012.

Assimilating the wealth of research that has been conducted on the ecological consequences of habitat loss and fragmentation in New Zealand this chapter draws trends and effective management suggestions from these findings. The abiotic consequences of habitat subdivision are discussed before reviewing impacts on genetic diversity, the abundance of individuals, species diversity, species interactions and the movement of species between patches. I then discuss the confounding influence of habitat modification with other GEC drivers before suggesting three conservation recommendations that arise from the ecological patterns earlier described. Findings from this review later aid and inform interpretation into my own findings.

1.4.2. Chapter 3: Untangling Interactions: Do climate gradients and habitat fragmentation simultaneously impact species interactions?

Poppy Lakeman-Fraser & Robert Ewers

Submitted to: *Global Change Biology* on the 27th June 2012

Resubmitted: 11th December 2012

Concerned with the crux of the project research question this chapter presents the findings from field observations to determine the simultaneous impact of habitat fragmentation and warmer environments on tri-trophic species interactions. Using a latitudinal gradient as a surrogate for climate change and a forest patch size and edge gradient to measure habitat fragmentation, I investigate: firstly whether interactions between drivers are additive or non-additive (synergistically or antagonistically); and secondly whether these interactions differ across trophic levels and biotic measures.

1.4.3. Chapter 4: Enemy release promotes range expansion in a host plant

Poppy Lakeman-Fraser & Rob Ewers
Submitted to: *Oecologia* on the 7th November 2011
Resubmitted with amendments: 24th June 2012
Revised submission: 13th November 2012
Accepted: 27th November 2012
Proofs Submitted: 7th December 2012

Simulating a polewards latitudinal shift this chapter reports the findings from a translocation study designed to investigate whether *M. excelsum* can survive south of its current range and if so, how species interactions influence the successful persistence in a novel location. This chapter highlights the importance of integrating biotic interactions alongside abiotic variables when predicting future species ranges under climate change.

1.4.4. Chapter 5: Trophic destabilisation in a dynamic world: will a preference for natal host plant topodemes inhibit herbivore range shifts?

Poppy Lakeman-Fraser & Robert Ewers

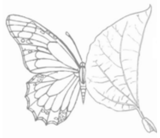
Submitted to: *The New Zealand Journal of Ecology* on the 7th November 2011

Resubmitted with amendments: 14th June 2012

Designed to investigate how biotic interactions will change under potential species distribution shifts this chapter presents findings from an *ex-situ* glasshouse experiment. Using the plant-herbivore interaction I experimentally translocated caterpillars collected from three distinct geographic regions onto plants originating from a natal and novel origin (different topodemes). These findings comment upon biotic attrition under environment-induced distribution shifts and add to the findings in Chapter 4 which highlight the importance of including biotic influences when predicting the impact of environmental change on populations and distributions.

1.4.5. Chapter 6: Discussion

Here I assimilate the findings from all three of my data chapters plus my literature reviews drawing interpretation on the general patterns found across projects and discusses how each contributes to the investigation of my original research question.



2

The ecological consequences of habitat loss and fragmentation in New Zealand

2 Fragmentation in NZ

The ecological consequences of habitat loss and fragmentation in New Zealand

Poppy LAKEMAN FRASER[1*] & Robert. M. EWERS[1]

[1] Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

[*] Author for correspondence: Email poppy.lakeman-fraser08@imperial.ac.uk; Tel. +44(0)20 7594 2231

Running header: Habitat fragmentation in New Zealand

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2 Fragmentation in NZ

2.1 Abstract

Extensive loss of New Zealand’s indigenous habitats has shaped the contemporary landscape and caused concomitant impacts on the archipelago’s flora and fauna. The New Zealand scientific literature documents the historical transformation of vegetation cover across an increasingly modified landscape, presents extensive empirical data on the ecological impacts of habitat loss and fragmentation, and details appropriate conservation strategies for the archipelago’s threatened biodiversity. To date however, there has been no comprehensive review which assimilates these findings. Here, we discuss the ecological changes to New Zealand ecosystems which have directly caused and indirectly accompanied the loss and fragmentation of indigenous habitats. Moreover, confounding the impact of land use change introduced species play an integral role of changes to flora and fauna in a fragmented landscape, we go on to consider the interactions between these drivers. Derived from the literature discussed in this review, we conclude by providing evidence-based recommendations for managers seeking to conserve New Zealand’s unique biodiversity.

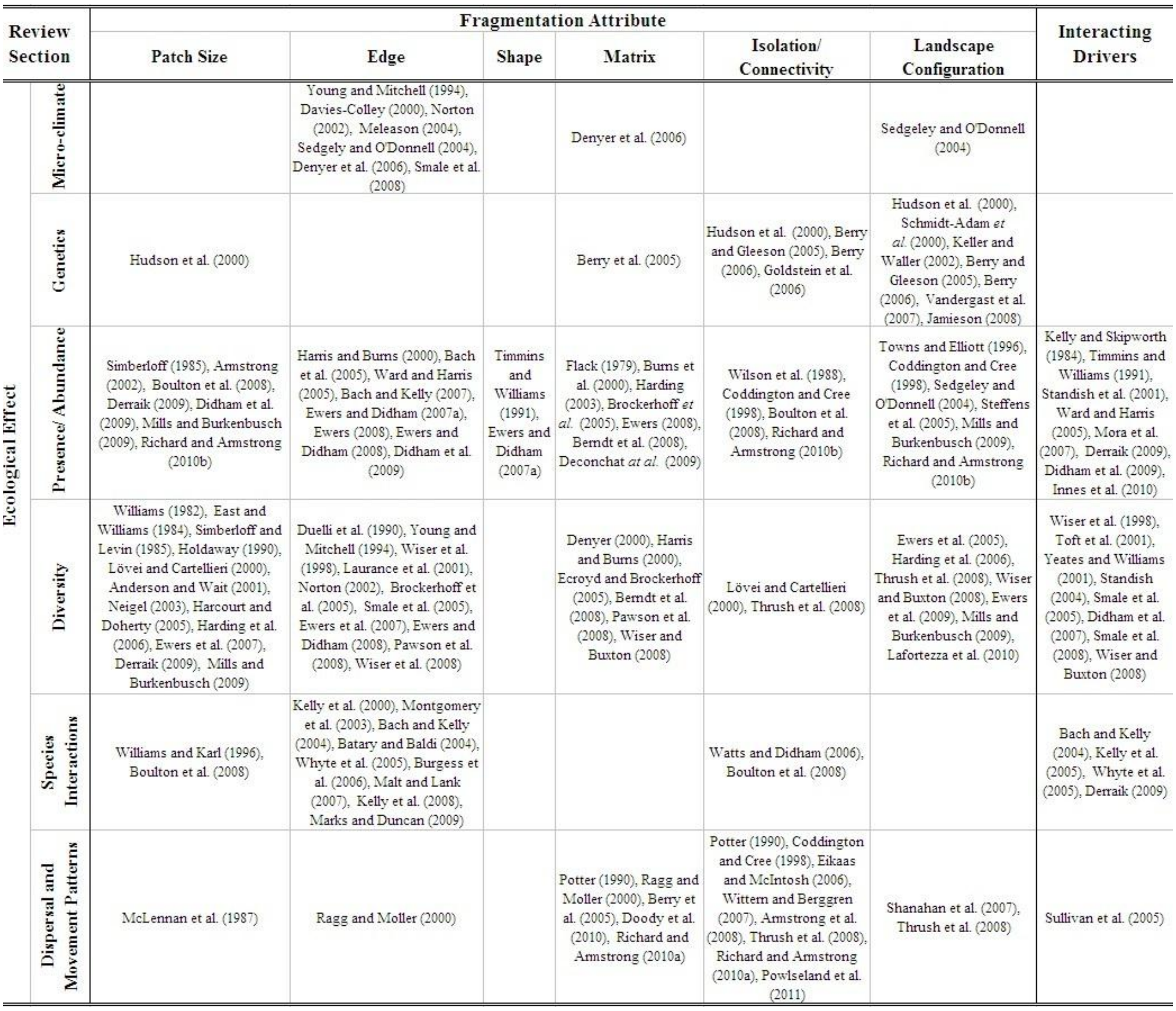
2.2. Introduction

New Zealand’s landscape has undergone a vast transformation since human colonisation (Leathwick 2001; Leathwick *et al.* 2004; McGlone *et al.* 2004). With at least three quarters of the archipelago’s natural environment significantly modified by human activities (Department of Conservation 2000), much of the remaining lowland forest is characterised by small remnant patches isolated by extensive pasture (Smale *et al.* 2008). Application of comprehensive National scale historical and current landcover in New Zealand (Leathwick *et al.* 2004; Terralink 2004) has tracked this loss and subdivision (Ewers *et al.* 2006) and is beginning to be combined with ecological data to understand impacts of landscape change on the archipelago’s communities (Ewers *et al.* 2009; Lafortezza *et al.* 2010). Habitat loss and fragmentation match invasive species as a dominant force driving the decline of biodiversity in New Zealand (Saunders and Norton 2001).

Habitat fragmentation is a multi-faceted concept that is used to explain a variety of inter-correlated patterns and processes, each potentially a research subject on their own, yet all are related under the collective expedient framework of ‘habitat fragmentation’. Distinct from habitat loss, whereby the overall area of habitat is reduced, fragmentation implies a change in the spatial pattern of habitat. In the latter, continuous habitat is subdivided into smaller disconnected patches which are often altered in shape and isolated from each other by a matrix of dissimilar habitat (Lord and Norton 1990; Collinge 1996; Fahrig 2003; Lindenmayer and Fischer 2006; Ewers *et al.* 2006). Worldwide, habitat fragmentation has become the single largest topic of research in conservation biology (Fazey *et al.* 2005), while habitat loss is recognised as the most immediate threat to global biodiversity (Wilson 1992; Gonzalez *et al.* 2011). Whilst other reviews and research manuscripts have discussed forest

loss (Ewers *et al.* 2006) and conservation issues (Craig *et al.* 2000) and management of forest fragmentation in New Zealand (Burns *et al.* 2011); here, we review literature on the ecological consequences of habitat loss and fragmentation that are relevant to New Zealand. The Web of Knowledge search engine were surveyed for papers using the terms “habitat fragmentation” and “New Zealand” along with additional terms relevant to each section of this paper. For fragmentation attributes these terms included: “patch size”, “edge”, “shape”, “matrix”, “isolation” and “landscape configuration”; and for ecological impacts this included: “microclimate”, “genetics”, “abundance”, “diversity”, “species interactions” and “dispersal” (Table 2.1). We summarise the relevant findings that have come from New Zealand, and place them into the international literature with a view to aiding the interpretation and understanding of those findings.

Table 2.1 The diversity of research into the ecological consequences of habitat fragmentation in New Zealand.



Review Section		Fragmentation Attribute						Interacting Drivers
		Patch Size	Edge	Shape	Matrix	Isolation/ Connectivity	Landscape Configuration	
Ecological Effect	Micro-climate		Young and Mitchell (1994), Davies-Colley (2000), Norton (2002), Meleason (2004), Sedgely and O'Donnell (2004), Denyer et al. (2006), Smale et al. (2008)		Denyer et al. (2006)		Sedgeley and O'Donnell (2004)	
	Genetics	Hudson et al. (2000)			Berry et al. (2005)	Hudson et al. (2000), Berry and Gleeson (2005), Berry (2006), Goldstein et al. (2006)	Hudson et al. (2000), Schmidt-Adam *et al.* (2000), Keller and Waller (2002), Berry and Gleeson (2005), Berry (2006), Vandergast et al. (2007), Jamieson (2008)	
	Presence/ Abundance	Simberloff (1985), Armstrong (2002), Boulton et al. (2008), Derraik (2009), Didham et al. (2009), Mills and Burkenbusch (2009), Richard and Armstrong (2010b)	Harris and Burns (2000), Bach et al. (2005), Ward and Harris (2005), Bach and Kelly (2007), Ewers and Didham (2007a), Ewers (2008), Ewers and Didham (2008), Didham et al. (2009)	Timmins and Williams (1991), Ewers and Didham (2007a)	Flack (1979), Burns et al. (2000), Harding (2003), Brockerhoff *et al.* (2005), Ewers (2008), Berndt et al. (2008), Deconchat *at al.* (2009)	Wilson et al. (1988), Coddington and Cree (1998), Boulton et al. (2008), Richard and Armstrong (2010b)	Towns and Elliott (1996), Coddington and Cree (1998), Sedgeley and O'Donnell (2004), Steffens et al. (2005), Mills and Burkenbusch (2009), Richard and Armstrong (2010b)	Kelly and Skipworth (1984), Timmins and Williams (1991), Standish et al. (2001), Ward and Harris (2005), Mora et al. (2007), Derraik (2009), Didham et al. (2009), Innes et al. (2010)
	Diversity	Williams (1982), East and Williams (1984), Simberloff and Levin (1985), Holdaway (1990), Lövei and Cartellieri (2000), Anderson and Wait (2001), Neigel (2003), Harcourt and Doherty (2005), Harding et al. (2006), Ewers et al. (2007), Derraik (2009), Mills and Burkenbusch (2009)	Duelli et al. (1990), Young and Mitchell (1994), Wiser et al. (1998), Laurance et al. (2001), Norton (2002), Brockerhoff et al. (2005), Smale et al. (2005), Ewers et al. (2007), Ewers and Didham (2008), Pawson et al. (2008), Wiser et al. (2008)		Denyer (2000), Harris and Burns (2000), Ecroyd and Brockerhoff (2005), Berndt et al. (2008), Pawson et al. (2008), Wiser and Buxton (2008)	Lövei and Cartellieri (2000), Thrush et al. (2008)	Ewers et al. (2005), Harding et al. (2006), Thrush et al. (2008), Wiser and Buxton (2008), Ewers et al. (2009), Mills and Burkenbusch (2009), Lafortezza et al. (2010)	Wiser et al. (1998), Toft et al. (2001), Yeates and Williams (2001), Standish (2004), Smale et al. (2005), Didham et al. (2007), Smale et al. (2008), Wiser and Buxton (2008)
	Species Interactions	Williams and Karl (1996), Boulton et al. (2008)	Kelly et al. (2000), Montgomery et al. (2003), Bach and Kelly (2004), Batary and Baldi (2004), Whyte et al. (2005), Burgess et al. (2006), Malt and Lank (2007), Kelly et al. (2008), Marks and Duncan (2009)			Watts and Didham (2006), Boulton et al. (2008)		Bach and Kelly (2004), Kelly et al. (2005), Whyte et al. (2005), Derraik (2009)
	Dispersal and Movement Patterns	McLennan et al. (1987)	Ragg and Moller (2000)		Potter (1990), Ragg and Moller (2000), Berry et al. (2005), Doody et al. (2010), Richard and Armstrong (2010a)	Potter (1990), Coddington and Cree (1998), Eikaas and McIntosh (2006), Wittern and Berggren (2007), Armstrong et al. (2008), Thrush et al. (2008), Richard and Armstrong (2010a), Powlseland et al. (2011)	Shanahan et al. (2007), Thrush et al. (2008)	Sullivan et al. (2005)

2.2.1. Ecological impacts of habitat loss and fragmentation

In this section, we first explore how the physical fragmentation of habitat alters the abiotic conditions of the environment, before reviewing the known impacts of fragmentation on genetic diversity, the abundance of individuals, species diversity, species interactions and the movement of species between patches. We conclude by examining evidence for how habitat

loss and fragmentation might interact with introduced species to exert combined impacts on native biodiversity.

2.2.1.1. Abiotic impacts

Small scale microclimatic gradients occur within habitat fragments, with habitat loss exposing the remaining habitat to altered environmental conditions that influence ecological processes as diverse as germination and early growth of the Kohekohe tree *Dysoxylum spectabile* (Young & Mitchell 1994), reproductive fitness of long-tailed bats, *Chalinolobus tuberculatus* (Sedgeley & O’Donnell 2004), and penetration of invasive Argentinian ants *Linepithema humile* into native forest, scrub and mangrove habitats (Ward & Harris 2005). Studies conducted in the podocarp-broadleaf forests of Northland (Young and Mitchell 1994), *Nothofagus* forests in Canterbury (Sedgeley & O’Donnell 2004), broadleaf forests in the Waikato (Davies-Colley *et al.* 2000; Denyer *et al.* 2006), and in the lowland rainforests of Westland (Norton 2002) found generally consistent impacts of forest edges on microclimatic conditions. Forest edges are associated with higher air and soil temperatures, more photosynthetically active radiation and higher vapour pressure deficits than the forest interior, impacting humidity-sensitive species such as the epiphytic filmy ferns such as *Cyathea smithii* and *Dicksonia squarrosa* (Norton 2002; Smale *et al.* 2008). The microclimatic differences can be extreme, with light levels and wind speed reduced by 99 % and 80 % respectively in forest interiors compared with open conditions (Davies-Colley *et al.* 2000). Microclimatic changes generally penetrate a relatively short distance into the forest, with elevated temperature and light gradients in North Island podocarp-broadleafed forests extending 50 m inside forests (Young & Mitchell 1994). This distance, however, is influenced by the adjacent matrix habitat, with edge effects infiltrating New Zealand forests

five times further when forests are adjacent to pasture rather than pine plantation (Denyer 2000).

2.2.1.2. Biotic impacts

2.2.1.2.1. Extinction and the species-area relationship

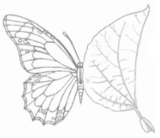
New Zealand has experienced an ‘extinction event’ over the last century, losing 40-50 % of its avifauna, 50 % of herpetofauna and unknown proportions of other taxa (Holdaway 1989) including species unknown to science (Harding 2003). Pioneer studies into species area relationships (SAR), commonly used to predict extinction rates arising from habitat loss (Simberloff 1992a; b; Lozano-Zambrano *et al.* 2009), found that patterns of avifaunal species loss matched ‘remarkably predictably’ with predicted values (Simberloff & Levin 1985). Brooks et al. (2002) later suggested that SAR extinction models based on habitat loss underestimate the number of bird extinctions in New Zealand, and correlations with introduced species strongly suggest that invasive mammalian predators may explain the relatively high rates of avifaunal extinction (Blackburn 2005). However, further analyses showed that invasion rates are closely correlated with rates of habitat modification (Didham, Ewers, *et al.* 2005), suggesting it is not possible to absolutely attribute extinctions to either driver alone. Habitat loss can promote the invasion of species (Craig *et al.* 2000; Didham *et al.* 2007), meaning there may seldom be a simple, single-factor explanation for extinction threats (Didham, Ewers, *et al.* 2005), and that habitat loss may make an unnoticed contribution towards extinctions attributed to other causes such as introduced species.

2.2.1.2.2. Genetic diversity and inbreeding

Habitat loss leads to direct reductions in the size of populations, and fragmentation further isolates and subdivides those populations. A reduction in both genetic diversity and gene flow caused by factors such as fragmentation can lead to inbreeding depression, consequent reductions in the reproductive ability of individuals and higher risk of extinction of populations (Keller & Waller 2002, Jamieson et al. 2008). Furthermore, reduced genetic diversity may limit the potential of populations to be resilient to future perturbations in the environment (Vandergast *et al.* 2007) such as changing climates or species invasions (Jamieson *et al.* 2008).

There are relatively few studies from New Zealand that have shown changes in genetic diversity that can unequivocally be equated with the effects of habitat loss and fragmentation. We do know that small populations of species such as the North Island kokako (*Callaeas cinerea wilsoni*) in Rotoehu forest and Mapara Wildlife Reserve had lower levels of microsatellite variability than larger populations in the nearby Te Urewera National Park (Hudson *et al.* 2000). However, although the initial decrease in kokako distributions was recognised as being caused by forest clearance, declines have also been recorded in extant forests (Rasch 1992). The recent losses are thought to be the spread of introduced mammals over the past century (Rasch 1992; Innes *et al.* 1999).

Impacts of habitat loss and fragmentation have been detected in Grand skinks (*Oligosoma grande*), a species that has a naturally fragmented distribution restricted to rock outcrops. Berry and Gleeson (2005) presented mitochondrial and microsatellite DNA data that suggested there was probably always a strong genetic pattern of isolation-by-distance within this species that has very limited dispersal, but that this isolation has been exacerbated by



habitat loss in the region (Berry and Gleeson 2005; Berry *et al.* 2005). At fine spatial scales, the loss of native habitat between rock outcrops has reduced dispersal rates (Berry et al. 2005). This species exhibited no inbreeding avoidance in small populations (18 % of matings occurred between full siblings), yet Berry (2006) found that this had no effect on the first year survival of offspring and as such fragmented populations of this species may remain viable at low numbers.

For plants, genetic effects of habitat fragmentation can be mediated by changes to the pollinator community. This hypothesis was tested by Schmidt-Adam et al. (2000) who compared outcrossing rates in isolated stands of Pohutukawa (*Metrosideros excelsa*) on the mainland with those on islands. Mainland pollinator communities were dominated by introduced species whereas island pollinators were predominantly endemic species, but this difference did not result in any clear changes to outcrossing rates, which were very low in all populations (Schmidt-Adam *et al.* 2000). In all populations the low level of outcrossing resulted in large numbers of inbred seedlings, but levels of gene fixation in the adults were much lower than in seedlings suggesting there is strong selection against the survival and reproduction of homozygote individuals (Schmidt-Adam et al. 2000).

2.2.1.2.3. Abundance and population size

Abundance is arguably one of the most responsive means of gauging the magnitude of human impacts on native organisms at small spatial scales (Pereira *et al.* 2010). Concern over extinction risk is the key factor driving many of these abundance studies, with a number of authors asserting a belief that habitat loss and fragmentation is a key factor threatening populations of particular species such as endangered carabid beetle species (Brockerhoff *et* *al.* 2005) and grand skinks (Coddington & Cree 1998). It should be considered that other threats may be contributing to the decline of populations and it is often difficult to estimate the exact level of the impact of habitat loss on the size of surviving populations of endemic and native species, although newly developed statistical methods provide avenues to do this (Ewers *et al.* 2010).

In the absence of direct quantification, however, some information can be inferred from studies examining seasonal and altitudinal movements in locations with continuous forest cover extending from the coast to the mountains. For example, a number of bird species, including the tui (*Prosthemadera novaeseelandiae*) and the bellbird (*Anthornis melanura*), migrate seasonally in and out of the Ohikanui Valley to winter habitats in warmer, floristically rich lowland forests (Wilson *et al.* 1988). The non-random pattern of deforestation in New Zealand, which has removed much lowland forest (Ewers et al. 2006), indicates that the populations of seasonally migrating birds that still persist in montane forests may have been reduced.

One approach to estimating the potential impact of habitat loss on population sizes is to estimate the number of breeding individuals required for a population to be self-supporting (Frankel and Soulé 1981) and the subsequent amount of habitat needed to support these numbers (Mclennan *et al.* 1987). For example, McLennan et al. (1987) found that the North Island brown kiwi (*Apteryx australis mantelli*) in the Hawke's Bay region had an average range size of 30 ha and therefore there is a requirement for reserves to have 7500-15000 ha of continuous forest to support a minimum viable population (calculated by Frankel & Soulé (1981) to be 500-1000 breeding individuals). Computer simulations of brown kiwi dispersal suggest similar minimum areas (10 000 ha) and stress these figures are based on forested

areas which are not only protected but have active predator management (Basse & McLennan 2003) as kiwi chick survival is only 5% in areas without control of predators such as the stoat *Mustela erminea* (Basse *et al.* 1999). In Hawke's Bay no patches of continuous primary indigenous vegetation of this size remain (majority of forest patches are < 100 ha). However, the total area utilised for movement and foraging of kiwis should be considered. For example, kiwis have been observed venturing over farmland outside the Paerata reserve on the North Island (Potter 1990) suggesting that if gaps are not greater than 300 m (Bennett 1998) then alternative habitats under pest management such hospitable matrix, mixed native forest, scrub, plantation could be included in calculations estimating areas of suitable conditions for self-sustaining kiwi populations.

Smaller and irregular shaped patches are more dominated by edge effects which can have either positive, negative or neutral impacts on the abundance of species that reside within these patches (Ries *et al.* 2004). In New Zealand beetle communities, almost 90% of species were significantly impacted by edges in the Lewis Pass region of the Southern Alps, with edge effects typically penetrating 20 - 250 m inside forest fragments, and one in eight of the common species having edge effects that extended at least 1 km into the interior of temperate beech (*Nothofagus* spp.) forest (Ewers and Didham 2008). These effects do not, however, always result in population reductions, with many indigenous species of Coleoptera exhibiting elevated abundance at the edge of Kahikatea-pasture boundaries in Waikato (Harris & Burns 2000), suggesting their total population sizes of edge species may have increased due to elevated edge habitat caused by fragmentation (Ewers & Didham 2007).

The type of matrix habitat surrounding forest fragments will greatly influence the impact of habitat loss and fragmentation on species' populations. Deconchat et al. (2009) demonstrated this for native forest birds, showing that the abundance of all but one of nine bird species were negatively correlated with the amount of farmland environment surrounding native forest (including regenerating manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*)). However, populations of three species were enhanced in fragments surrounded by an exotic plantation matrix: the brown creeper *(Mohoua novaeseelandiae)*, New Zealand pigeon (*Hemiphaga novaeseelandiae*) and the rifleman (*Acanthisitta chloris*). Trends are highly species specific, with birds such as the shining cuckoo (*Chrysococcyx lucidus lucidus*) and silvereye (*Zosterops lateralis lateralis*) exhibiting low abundance in regions with high levels of exotic forest cover (Deconchat *et al.* 2009). Research into invertebrates suggests that plantations of the Monterey pine (*Pinus radiata)* can support beetle populations adjacent to native fragments, changing the strength of edge effects (Campbell *et al.* 2011) and even providing alternative habitats when native habitats are reduced below critical levels (Berndt *et al.* 2008; Pawson *et al.* 2008). Although only limited samples, it appears pine plantations have provided alternative food, lodging opportunities and movement channels for the critically endangered beetle *Holocaspis brevicula* in the Canterbury plains where its native habitat has been reduced below 2 % of the original cover (Brockerhoff *et al.* 2005).

2.2.1.2.4. Diversity and community composition

The SAR, commonly used to predict extinction from habitat loss at large scales, is also often used to predict species richness at small scales within individual habitat patches (Neigel 2003, Harcourt & Doherty 2005, Tikkanen et al. 2009). Virtually all New Zealand studies that have investigated SARs for terrestrial habitat fragments have detected them, including for plants (e.g. Williams 1982), invertebrates (e.g. Derraik 2009) and birds (e.g. East et al. 1984). The detection and strength of SARs are, however, dependent on the design of studies.

Ewers et al. (2007) found that SARs constructed on data from 893 species of beetle were highly dependent on the distance from the edge at which sampling took place, with positive SARs found at forest edges and interiors, but negative SARs found at intermediate edge distances. The authors suggested this pattern arose because of differential responses to forest edges in fragments of increasing area by forest specialist species and species adapted to the surrounding matrix habitat.

A number of studies have reported increased species diversity of plants and invertebrates at habitat edges (Young & Mitchell 1994, Ewers et al. 2007). Edges may support higher diversity for a wide variety of reasons, including the prevalence of pioneering species able to cope with these dynamic environments (Laurance *et al.* 2001), an increase in generalist species which can utilise many environments (Webb *et al.* 1984; Webb 1989), spill-over of species from adjacent habitats (Duelli *et al.* 1990), or the presence of an enhanced food sources such as rich invertebrate communities supporting rich bird communities (Helle & Muona 1985).

Species exhibit a wide array of responses to the same patterns of habitat fragmentation, and this variation in response may be due to species traits. For example, working in kahikatea forests in an agricultural matrix, Harris & Burns (2000) found that indigenous species dominated the forest beetle community whereas adventive species were prevalent in the pasture. Changes in the relative abundance of different feeding groups of beetle communities across forest edges has been reported, with detrivores, fungivores and saprophages having increased abundance in forest interiors (Ewers & Didham 2008), whereas herbivores were more prevalent in the surrounding pasture (Ewers & Didham 2008).

2.2.1.2.5. Species interactions

A number of New Zealand studies have found an altered frequency of species interactions at habitat edges. The red mistletoe, *Peraxilla tetrapetala*, had higher fruit set at forest edges than in the forest interior as a result of higher bee visitation (Burgess *et al.* 2006) and bird pollination (Montgomery *et al.* 2003) rates in the summer months of December 2001 at Lake Ohau and January 2002 at Craigieburn. Leaf herbivory by the possum (*Trichosurus vulpecula*) on these mistletoes was also significantly greater at edges, but this negative effect was partially offset by reduced flower predation by the native moth *Zelleria maculata* at edges (Bach & Kelly 2004).

Elevated predation rates at forest edges have been shown in many studies outside New Zealand, with most studies focussed on nest predation rates (Gates & Gysel 1978, Ries & Fagan 2003, Piper & Catterall 2004, Batary & Baldi 2004, Malt & Lank 2007, Marks & Duncan 2009). In the New Zealand context, however, Whyte et al. (2005) found that rates of attack on artificial wax eggs were highly variable across edge gradients and found no strong evidence for increased predation rates near habitat edges.

Isolation of habitat fragments can disrupt species interactions in fragmented landscapes. An experimental manipulation of potted *Sporodanthus ferrugineus* (Restionaceae) host plants in the Hauraki plains found that colonisation and damage rates by the Lepidopteran herbivore, *Batrachedra* spp. was reduced with increasing isolation of the plants (Watts & Didham 2006). A moderate degree of isolation (400 m) caused a near complete breakdown of the plant-insect interaction, although the interaction on restored ‘plant islands’ recovered within

196 and 308 weeks, showing that habitat restoration can reinstate interactions within a moderate time frame (Watts & Didham 2006).

2.2.1.2.6. Dispersal and movement patterns

The loss of forest cover and the spatial distribution of forest remnants are known to impact the dispersal patterns of several New Zealand species. Some species, such as the brown kiwi, are able to move relatively freely through matrix environments, travelling up to 330 m across pastoral farmland between their preferred native forests (Potter 1990). When making longer movements, however, brown kiwi preferentially followed forest corridors or ‘stepping stones’ of remnant forest fragments to reach destinations up to 1200 m from their original location (Potter 1990). This suggests that although the main limitation on kiwis is predation in a fragmented habitat rather than fragmentation itself, individual behaviour may be impacted by the spatial pattern of habitat fragmentation. There are other species, such as the New Zealand pigeon, which are strong dispersers and are known to have flown more than 480 km in a 100 day period (Powlesland *et al.* 2011). This strong flight ability suggests that this species is unlikely to be impacted by the isolation of forest patches. By contrast, juvenile North Island robins (*Petroica longpipes*) show a marked reluctance to fly over pasture. Most juvenile robins disperse among patches separated by less than 20 m (Wittern & Berggren 2007), and were not observed crossing forest gaps greater than 110 m (Richard & Armstrong 2010).

2.2.1.3. Synergistic interactions between habitat fragmentation and introduced species

Understanding interactions between multiple drivers of global environmental change (GEC)—i.e. land use change, climate change, nitrogen deposition and biotic exchange—is paramount if we are to accurately predict future anthropogenic driven changes in biodiversity (Didham *et al.* 2007; Tylianakis *et al.* 2008). Land use change, including habitat loss and fragmentation, has been identified as being the greatest threat to biodiversity in the coming century (Sala *et al.* 2000; Pereira *et al.* 2010), but an increasing body of research is illuminating the combined actions of multiple GEC drivers interacting to magnify the impacts of fragmentation (Ewers & Didham 2006, Mora et al. 2007).

In New Zealand, the greatest contemporary threat to biodiversity is widely considered to be biotic exchange, i.e. the introduction of exotic species (Craig *et al.* 2000; Department of Conservation 2000; Clout 2001). Didham et al. (2005b) suggested, however, that the prevalence of exotic species can be an indirect effect of habitat modification. For example, increasingly modified matrix habitats in the tussock grasslands of Banks Peninsula are associated with increased invasion of exotic grass species into native outcrop habitats (Wiser & Buxton 2008), and habitat edges represent the focal point for weed invasion into forests (Wiser *et al.* 1998). The invasion of weeds can alter the frequency of feeding interactions between herbivores and their herbaceous food plants following a scrub invasion of grassland (Hobbs & Mooney 1986), and resource availability for native plant species when an exotic species creates a surrounding deficit of nutrients or moisture (Boswell & Espie 1998). It has been shown, however, that lowland forest areas simultaneously impacted by the detrimental

impacts of fragmentation, introduced mammalian predators and livestock grazing can structurally recover when fencing and pest control management is applied (Dodd *et al.* 2011).

Although most weeds are unable to invade intact forest (Craig *et al.* 2000), habitat fragmentation can degrade forests and thereby promote weed invasion in forest fragments and lead to strong impacts on native species. Small patches, and patches with high perimeter to edge ratios, are particularly vulnerable to weed invasion as demonstrated in Auckland reserves (Timmins & Williams 1991, Smale & Gardner 1999), an alluvial forest remnant in the Bay of Plenty (Smale 1984) and an urban remnant of alluvial forest in Hamilton (Whaley *et al.* 1997). The South American invasive weed *Tradescantia fluminensis* is capable of smothering emerging native seedlings where it is found in fragmented patches in New Zealand (Timmins & Williams 1991, Whaley et al. 1997, Smale & Gardner 1999, Smale et al. 2005). It grows most vigorously in areas with high light levels and low canopy cover such as along the edges of native forest fragments. Being a horticultural escape species, however, its survival depends upon successional trajectories, being present for instance, in areas close to urban propagule sources (Sullivan *et al.* 2007). *T. fluminensis* radically alters native forest ecosystems by increasing litter decomposition rates (Kelly & Skipworth 1984, Standish et al. 2004), is associated with reductions in the survival rates, abundance and species richness of native forest seedlings (Standish *et al.* 2001), and alters the composition, and reduces the diversity, of invertebrate communities (Toft et al. 2001, Yeates & Williams 2001, Standish 2004).

In addition to weeds, more than 80 species of alien animal species have established in New Zealand (King 1990), a number of which have known associations with habitat loss and fragmentation. Invasive Argentinian ants, for example, penetrate indigenous habitats up to 20

m into indigenous forests, 30 m into mangroves and 60 m into scrub (Ward & Harris 2005). Derraik (2009) found that as fragment size decreased, the abundance of the native mosquito species *Culex pervigilans* steadily reduced as abundance of the exotic mosquito *Aedes notoscriptus* increased.

Predatory mammals such ferrets (*Mustela furo*), have been found to frequently use forest-pasture edges (Ragg & Moller 2000), although this pattern did not translate into an increase in the predation rates of bird nests along forest edges (Whyte *et al.* 2005). Possums were responsible for greater amounts of foliage damage at forest edges than in the interior of patches (Bach & Kelly 2004), meaning that the increasing densities of forest edges in New Zealand landscapes (Ewers *et al.* 2006) may be enhancing the impact that these introduced species are having on native species such as mistletoes (Bach & Kelly 2004).

Many New Zealand forest fragments are embedded in pasture, leaving them susceptible to grazing by non-native domesticated animals. Although domesticated animals are largely controlled by humans, and hence do not typically fall under the category of biotic exchange, these species are non-natives, and individuals can still cause considerable damage to indigenous species in forest remnants. For example, populations of indigenous understory shrubs such as the highly palatable *Alseuosmia quercifolia* are reduced or exterminated directly by domestic sheep (*Ovis aries*) and cattle (*Bos Taurus*) (Smale *et al.* 2008). Smale et al. (2005) recommend that fencing of patches to prevent stock grazing is the single greatest factor that will ensure the viability of indigenous fragments. Didham et al. (2009) expanded upon this by simultaneously investigating the impacts of management treatments (pest eradication and livestock exclusion) and patch size on invertebrate communities in forest fragments in Waikato. They found that patch area had indirect effects on invertebrate

community composition, but that this fragmentation effect was relatively weak when compared to the effects of management actions or the interaction between livestock exclusion and pest management. Similarly, Dodd et al. (2011) found that livestock grazing and predation both had direct effects on forest fragment communities in the Waikato region, but concluded that, with fencing and pest control, fragments can become partially resilient to these pressures. They found evidence for engineering resilience in forest fragments (a term used to describe structural recovery), yet suggested more research is needed into deciphering whether forests exhibit ecological resilience (whereby ecosystems have multiple stable states under management).

2.3. Conservation management in fragmented landscapes

Maximising conservation gains is a fundamental goal for much ecological research. New Zealand boasts one of the highest proportions of protected land of any nation (Ministry for the Environment 1997), actively protects remnant fragments in ‘Mainland Island’ initiatives (Saunders & Norton 2001), hosts a government department committed to conservation (Department of Conservation 2007), has pioneered several largely successful species recovery programmes (Merton 1992, Clout & Craig 1995, O’Donnell & Sedgeley 2007), and maintains public support for environmental preservation (Craig et al. 1995; Ministry for the Environment 1997). Yet despite all this, the loss of species and degradation of native environments is ongoing (Craig *et al.* 2000; Department of Conservation 2000; Norton 2000; Walker, Price, *et al.* 2006; Ewers *et al.* 2006). Management options in fragmented landscapes that account for geometric design principals in wildlife conservation (Diamond 1975) or issues such as private vs. public land property rights (Porteous 1993, Kareiva & Wennergren

1995, Department of Conservation 2000, Norton 2000, Saunders & Norton 2001, Hitchmough 2002, Wehi & Wehi 2010, Burns et al. 2011) have been covered extensively elsewhere, so here we restrict our conservation recommendations to those arising directly from the ecological patterns described in this review.

2.3.1. Optimising the shape of habitat fragments

Fragments that are compact in shape, such as squares or circles, have lower edge to area ratios than more convoluted fragments, meaning the interior of the fragment is better protected from the influences of the surrounding habitat matrix (Ewers & Didham 2007). It follows, then, that a good way to protect fragments from the surrounding environment is to reduce the complexity of fragment shape by widening those areas where habitat fragments are narrow. This will simultaneously increase the amount of ‘core’ habitat that is shielded from the matrix, and connect disjunct sections of core habitat within the same fragment (Ewers & Didham 2007). Where this is not possible, a potential mechanism to enhance the quality of habitat fragments is to surround them with low contrast matrix habitats (Denyer *et al.* 2006; Brockerhoff *et al.* 2008; Deconchat *et al.* 2009; Campbell *et al.* 2011). Creating buffer zones of habitat such as plantation forests that support some of the species found in native environments may limit the degree to which edge effects penetrate, and reduce the extent of, the core area of habitat fragments.

2.3.2. Connecting fragments with corridors

The use of corridors to connect remnant fragments together has been widely advocated in the conservation literature (Wilson & Willis 1975, International Union for the Conservation of Nature and Natural Resources 1980, Viles & Rosier 2001), and have been proven to aid the persistence of biodiversity in large-scale experiments (Damschen *et al.* 2006). The use of corridors must be carefully planned with regard to the landscape in which they may be situated, accounting for the habitats intended to be connected and the species which are expected to benefit. For instance, few kiwis (30 %) cross distances between fragments isolated by more than 120 m, suggesting that about 10 regularly spaced ‘stepping stones’ should be restored between patches of forest up to 1.2 km apart (Potter 1990). However, most juvenile North Island robins will only move among patches separated by less than 20 m (Wittern & Berggren 2007), suggesting that a near-continuous corridor of habitat would be required to promote the landscape-scale movement of this species.

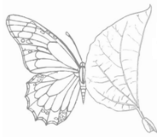
The integration of transport network management with environmental objectives represents a practical method to developing networks of corridors. The ‘greenway’ concept uses linear terrain features, either natural (ridge contours or rivers) or artificial (railways, canals and roads), to link patches of habitat across jurisdictional boundaries, private and public property to improve connectivity within landscapes. Although road safety standards need to be considered, planting alongside roadside verges has the potential to facilitate the extension of ecological corridors, thereby negating some of the negative habitat subdivision effects that road construction typically creates (Viles & Rosier 2001).

2.3.3. Landscape thresholds

There may be a threshold level of forest cover below which fragmentation impacts may rapidly accrue (Andrén 1994) and the probability that populations will persist rapidly decreases (Rutledge 2003; Ewers *et al.* 2006). Although this threshold value is likely to vary between species, a review of mammal and bird studies (Andrén 1994) found that the probability of an extinction threshold occurring greatly increases when forest cover decreases below 30 %. Native forest cover across the majority of New Zealand is, alarmingly, below this landscape 'extinction threshold' figure (Walker, Price, *et al.* 2006; Ewers *et al.* 2006) and as such, connectivity between remnant patches is likely to be heavily compromised. Without functional connectivity between habitats, local extinction events are unlikely to be balanced by recolonisation and metapopulations may collapse (Kareiva & Wennergren 1995), with even small additional losses of habitat able to greatly reduce the probability of species persisting (With & King 1999). Priority setting for habitat restoration could take advantage of modelling approaches that quantify the metapopulation capacity of a landscape (Hanski & Ovaskainen 2000, 2002), thereby identifying specific regions in which small amounts of restored habitat may prevent, or even reverse, the passing of landscape and extinction thresholds. Similarly, empirically based statistical models of species and communities across fragmented landscapes (Ewers *et al.* 2009, 2010; Lafortezza *et al.* 2010) can be used to explore the potential impact of changes to landscape configuration arising from habitat restoration, helping to identify optimal landscape configurations that might benefit either targeted species or entire communities.

2.4. Conclusion

The loss and fragmentation of habitats has had pervasive impacts on biodiversity in New Zealand. The unique species and landscapes which characterise New Zealand not only enrich the country's identity, but are fundamental to the islands' tourism industry, resource supplies and ecosystem services. As many of the papers in this review have demonstrated, there are ongoing advances in our understanding, and ability to manage the impacts, of habitat fragmentation. There are, however, still gaps in our knowledge. Notably, these knowledge gaps lie in our understanding of how fragmentation interacts with other anthropogenic drivers of biodiversity change such as invasive species. The fact that habitat loss and rates of biotic exchange are spatially and temporally correlated make it difficult to tease apart their relative effects, yet understanding the potential interactions among these drivers of biodiversity change remains crucial to accurately inform conservation decisions. This will require cleverly designed field studies that are able to independently vary gradients of habitat fragmentation with the presence or absence of invasive species. This might be achieved by taking advantage of previous conservation successes in New Zealand. For instance, fragmentation studies conducted on islands freed of mustelids such as Great Barrier Island and Stewart Island could be compared to matching fragmentation studies conducted on the mainland and in the presence of these predatory mammals to separate the relative and combined impacts. Filling knowledge gaps like these will be crucial for the effective management of the remaining indigenous habitat in a changing environment, and will help us to further marry contemporary research from ecologists and landscape biologists with effective decision making by conservation practitioners in order to support the persistence of native species and ecosystems in New Zealand's fragmented landscape.



2.5. Acknowledgments

We would like to acknowledge the Grantham Institute for Climate Change and the Gilchrist Educational Trust for funding this research.

3

Untangling Interactions: Do climate and habitat fragmentation gradients simultaneously impact biotic relationships?

3 Untangling Interactions

Untangling interactions: Do climate and habitat fragmentation gradients simultaneously impact biotic relationships?

Poppy LAKEMAN-FRASER[1]* and Robert M. EWERS[1]

[1] Imperial College London, Silwood Park Campus, Ascot, Berkshire,

SL5 7PY, UK

* Author for correspondence: Email poppy.lakeman-fraser08@imperial.ac.uk; Tel. +44(0)20 7594 2231

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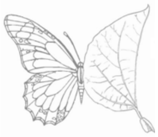
Keywords: *Alieodes declanae*, Antagonistic, Biotic interactions, *Cleora scriptaria*, Climate change, Habitat fragmentation, *Macropiper excelsum*, *Meteorus pulchricornis*, New Zealand, Synergistic.

Type of Paper: Primary Research Article

3.1. Abstract

Gaining insight into the impact of anthropogenic change on ecosystems requires investigation into interdependencies between multiple drivers of ecological change and multiple biotic responses. Previous studies have found that multiple global environmental change drivers can act simultaneously to impact the abundance and diversity of biota, but few of these studies also measure the impact across trophic levels. We firstly investigated whether climate (studying locations across a latitudinal gradient as a surrogate) interacts with habitat fragmentation (measured according to fragment size and distance to habitat edges) to impact a New Zealand tri-trophic food chain (plant, herbivore and natural enemy). Secondly we examined how these interactions might differentially impact both the abundance and biotic processes of species at each of the three trophic levels. We found evidence to suggest that these drivers act non-additively across trophic levels. The nature of these interactions however varied: with location synergistically interacting with fragmentation measures to exacerbate the detrimental effects on insect abundance; and antagonistically interacting to ameliorate the impact on plants and on the interactions between species (i.e. herbivory and parasitoid attack rate). The findings from this research indicate that the ecological consequences of environmental modification will vary depending upon the driver pair analysed, the trophic level studied and the biotic unit measured. In any case, interactions between both the causal drivers of change and the biotic manifestations of that change have highly pervasive impacts on ecology in a changing world.



3.2. Introduction

Concern has been mounting for over a decade about the ability of environmental systems to absorb multiple anthropogenic pressures (Breitburg *et al.* 1999; Mullan Crain *et al.* 2008). Despite this, the global environmental change research is a young branch of ecological knowledge (Didham *et al.* 2007), and only a few studies have empirically investigated (e.g. Mora *et al.* 2007; Forister *et al.* 2010), conceptually modelled (e.g. Vinebrooke, Cottingham, Norberg, *et al.* 2004) or reviewed (e.g. Darling and Côté 2008; Mullan Crain *et al.* 2008; Mantyka-pringle *et al.* 2012) simultaneous pressures explicitly.

Drivers of global change include nitrogen deposition, CO2 enrichment, biotic invasions, climate change and land use change (Tylianakis *et al.* 2008). Alone, these drivers each impose considerable influence on biodiversity around the world. For example, Zavaleta *et al*. (2003) found that three (elevated CO2, nitrogen deposition and precipitation) of four (warming) global change variables exerted a rapid impact on the diversity of Californian grasslands. Carbon dioxide (ambient plus 300 ppm) and nitrogen deposition (increased by 7 g.m-2.yr-1) diminished diversity after three years, precipitation (increase of 50%, including a growing-season extension of 20 days) increased it and warming (soil-surface warming 0.8–1°C) had no effect. Understanding how multiple drivers interact—do they simply add-up in a linear fashion or does one non-additively interact with the other-—is perhaps increasingly imperative given the challenges facing contemporary conservation science (Sala *et al.* 2000; Zeidberg and Robison 2007).

Two types of non-additive outcomes are possible from interactions among global change drivers: they either combine in a synergistic fashion (total effect is amplified), or they combine in an antagonistic way (total effect is reduced) (Folt *et al.* 1999). The former, synergistic interactions, was exemplified by Mora *et al.* (2007), who found that declines in experimental populations of rotifers occurred 50 times faster when fragmentation, environmental warming and overexploitation acted simultaneously than when these same threats occurred in isolation. The latter, antagonistic interactions, was exemplified by Zvereva and Kozlov (2006), who found that the adverse impact of carbon dioxide elevation on herbivore performance was offset by the favourable impact of increased temperature. Systems subjected to multiple, usually sequential stressors such as imposed by global change, may therefore enter alternative abnormal stable states, and hence “ecological surprises” can be expected when attempting to predict effects (Paine *et al.* 1998).

Climate change and land use modification are the two dominant drivers of global environmental change (hereafter referred to as ‘global change’ drivers) (Sala *et al.* 2000; Pereira *et al.* 2010), altering population dynamics (e.g. Franco *et al.* 2006; Lemoine *et al.* 2007), restricting species distributions (e.g. Warren *et al.* 2001; Honnay *et al.* 2002), and influencing food web dynamics (e.g. Tylianakis *et al.* 2008; Piessens *et al.* 2009). While these drivers have globally recognised impacts on the persistence of biodiversity, relatively few studies have empirically investigated their simultaneous impacts (Mullan Crain *et al.* 2008; Mantyka-Pringle *et al.* 2012) and have instead focussed on one or the other driver (e.g. Valladares *et al.* 2006; Andrew and Hughes 2007). Initial studies into their interactive impact do however suggest that climate change and habitat destruction have potential to produce a ‘deadly anthropogenic cocktail’ (Travis 2003). Here, we investigate the impact of these two

global change drivers in New Zealand, the last major land mass to be colonised by humans (Duncan and Young 2000). In the ~ 730 years of human occupation (Wilmshurst *et al.* 2008), the clearance of native habitat for food provisions and transport networks (Ewers *et al.* 2006) has reduced indigenous forest cover from 82 % (Leathwick *et al.* 2004) to 24 % of the total land area leaving the remnants heavily fragmented (Ewers *et al.* 2006). These environments are simultaneously undergoing the additional pressure of rapid climate change. Temperatures in New Zealand have risen by about 0.9 ˚C from 1908-2006 (Ministry for the Environment 2008), slightly higher than the average global rise of 0.4 – 0.8 ˚C over the past 100 years (IPCC 2002). This trend is projected to continue with an additional national average rise in temperature of between 0.2 - 2 °C expected by 2040, and 0.7 - 5.1 °C temperature rises expected by 2090 (Ministry for the Environment 2008).

A large number of studies have measured the impacts of global change on ecological systems through changes in population abundance (e.g. Bowen *et al.* 2009), diversity (e.g. Fahrig 2003), organism physiology (e.g. Chown *et al.* 2010), and distributional shifts of suites of species (e.g. Pearson and Dawson 2003). More recently, the role of biotic interactions—whether they be pollination, competition, herbivory, predation, parasitism—between networks of interacting species has been recognised as being fundamental in shaping and maintaining biodiversity (Bascompte *et al.* 2006) and in determining response to multiple drivers (Breitburg *et al.* 1999; Mullan Crain *et al.* 2008). Biotic interactions may be more susceptible to global change drivers than abundance or diversity measures alone due to the compounding impacts of multiple phenological, physiological and behavioural responses of those interacting species (Tylianakis *et al.* 2007, 2008; Suttle *et al.* 2007). Differential responses of species at varying trophic levels to global changes have resulted in differential adaptation (Atkins and Travis 2010; North *et al.* 2011), distributional shifts (Coope 1978; Parmesan *et al.* 1999; Warren *et al.* 2001), phenological mismatch (Memmott *et al.* 2007; Thackeray *et al.* 2010; Rafferty and Ives 2011; Li *et al.* 2011) and spatial mismatch (Post *et al.* 2008; Schweiger *et al.* 2008) between the species that interact in biotic networks. Habitat fragmentation, for example, has been found to truncate food chains (Kruess and Tscharntke 1994; Komonen *et al.* 2000). In addition to recording measures such as abundance or density, incorporating process-based measures into ecological change research is likely to enhance the accuracy of predictions on the response of species to global change (Gilman *et al.* 2010).

Here, we monitor a New Zealand tri-trophic system in order to examine how different levels of the food chain respond (abundance measures) and how the frequency of interactions (process measures) alters under multiple drivers of environmental change. Specifically, the study seeks to investigate whether two drivers of global environmental change—habitat fragmentation and climate change (latitudinal surrogate)—exert an additive or interactive effect on the various components of this tri-trophic system, and whether simultaneous global change impacts are experienced uniformly across trophic levels and species interactions.

3.3. Methods

3.3.1. Study species

The native Kawakawa tree (*Macropiper excelsum*, Piperales: Piperaceae) is a common understory plant throughout the mixed native scrub environments of New Zealand (Smith 1975). The species is confined to coastal areas of the New Zealand mainland and a number of its offshore islands, and reaches its southern limit at a latitude of 43º 46’ S (Banks Peninsula) on the Pacific coast of New Zealand. A range of biochemical defences stored within *M. excelsum* leaves deters widespread generalist feeding activity. However, despite the tree’s range of anti-herbivory bio-compounds (Hodge *et al.* 2007) it has a primary herbivore, *Cleora scriptaria* (Lepidoptera: Geometridae). This moth is effective at sequestering these compounds and feeds extensively on the plant. *C. scriptaria* is responsible for the conspicuous shot hole appearance of herbivory scars which is highly distinguishable in *M. excelsum*. The two most commonly associated parasitoid species, which feed on this geometrid moth, are *Aleiodes declanae* (Brachonidae: Rogadinae) and *Meteorus pulchricornis* (Brachonidae: Euphorinae). The former is a native koinobiont endoparasitoid which attacks the moth larvae at the first and second instars and mummifies at the fourth and fifth instars. The latter is a globally widespread generalist endoparasitoid accidentally introduced into New Zealand in 1996 (Berry and Walker 2004). This invasive koinobiont species also attack larvae at the second instar and emerge at the fourth.

3.3.2. Sampling design

We collected data on the tri-trophic system across a fragmentation and climatic gradient, using latitude as a surrogate for a gradient of climate change. We selected five field locations spanning seven degrees of latitude from Banks Peninsula on the South Island (43º 46’ S) up to Auckland on the North Island (36º 51’ S) (Fig. 3.1). This corresponds to a 4.1 ˚C average temperature gradient, this value is within the range of temperature increases projected for each region by 2090 (average across region ranging from 0.6 – 5.3 ˚C; Fig. 3.2). Three additional locations were selected at intervals between the experimental extremes, located in the Waikato district (37° 54’ S), Wellington district (41° 12’ S), and the Nelson district (41° 15’ S). Two of these locations (Wellington and Nelson) lie at similar latitudes, but are sited on different land masses (North and South Island respectively). Although elevation differed significantly between sites ($F_{4,516} = 34.84$, $p < 0.001$), Tukey HSD tests revealed one site, Hamilton, was significantly higher than the other four which had relatively consistent elevations across the two main islands (mean m.a.s.l; Auckland: 71, Hamilton: 185, Wellington: 100, Nelson; 96 and Christchurch: 93). Indigenous forest cover (in 2002) in the five regions varied between 6 % and 31 % (Auckland: 13 %, Waikato: 22 %, Wellington: 20 %. Nelson: 31 % and Canterbury: 6 %; Ewers et al. (2006)).

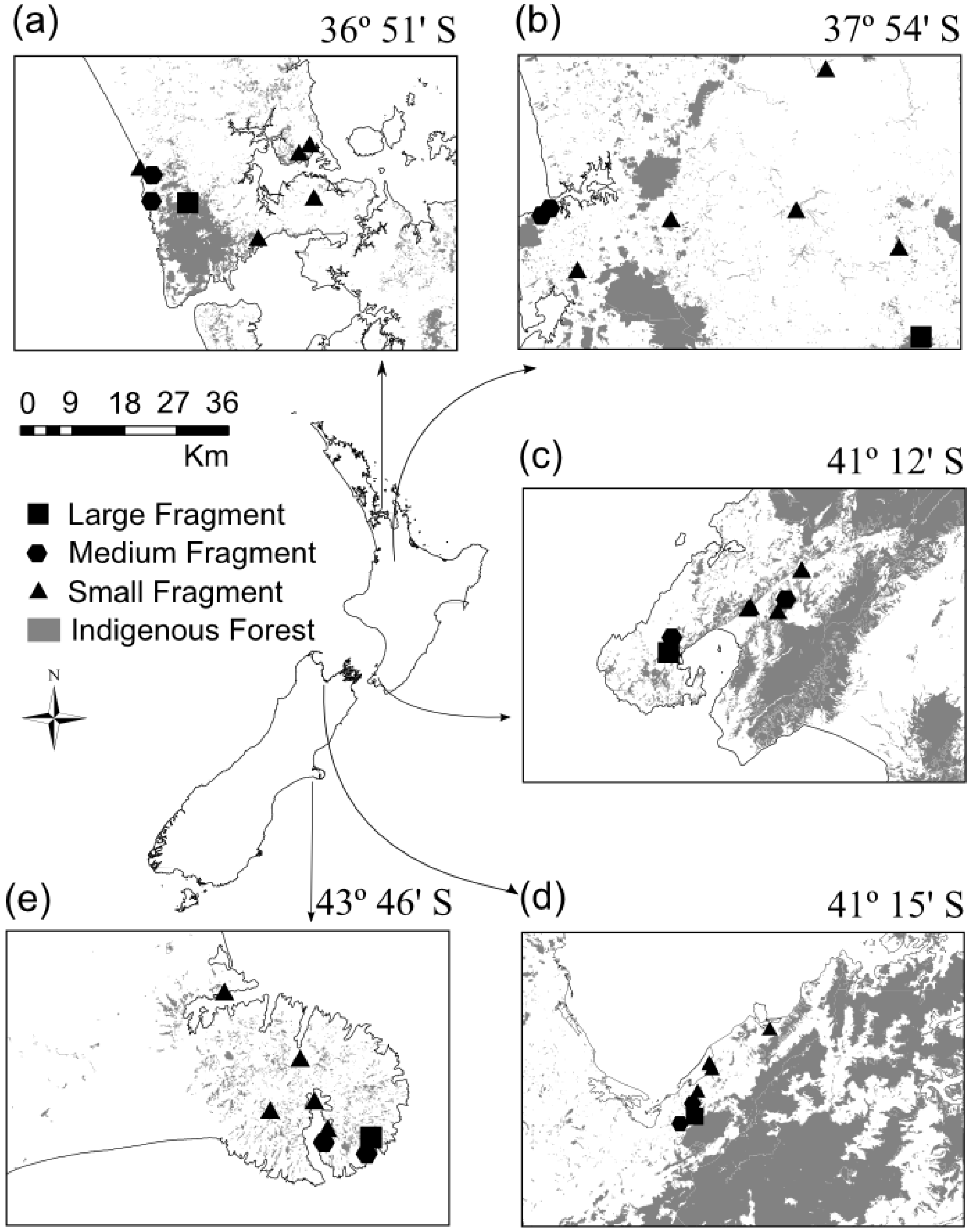


Figure 3.1. Field site localities. Five sites span the distribution of *Macropiper excelsum* (light grey on national map, modified from Gardner (1997)) and extend across a latitudinal gradient of ~7 ° over the North and South Island of New Zealand: Auckland (a), Waikato (b), Wellington (c), Nelson (d) and Banks Peninsula (e). Grey shading in panels A-E shows the distribution of indigenous forest in the five study localities. At each locality, eight forest fragments (average latitude given above insets) were sampled, with the fragments categorised according to area: large >100 ha (squares), medium 10-100 ha (circles) and small < 10 ha (triangles)

At each of the five *locations* (~ latitude), eight forest *fragments* were selected on the basis of *M. excelsum* presence, landowner permission, accessibility and size. To reflect the size distribution of fragments in real landscapes (the abundance of small patches of forest in comparison to large) we surveyed more small than large fragments and surveyed an equal number of small, medium and large fragments at each location. This comprised one large fragment (> 100 ha), two medium fragments (10 – 100 ha), and five small (< 10 ha) fragments. A single transect in each forest fragment was established, extending from the edge (denoted by the dripline marking the extent of overhanging branches) to the interior of the forest fragment along a north to south trajectory. Sampling *plots* (i.e. individual plants) were situated every 10 m along transects. The length of a transect was dependent upon the size of fragment: transects were 300 m in large fragments (N = 31 plots x 1 fragment), 150 m in medium fragments (N = 16 plots x 2 fragments) and 60 m long in small fragments (N = 7 plots x 5 fragments). This sampling design ensured that the total number of sample plots in each of the three fragment size categories were approximately equal in each region ($31 \leq N \leq 35$).

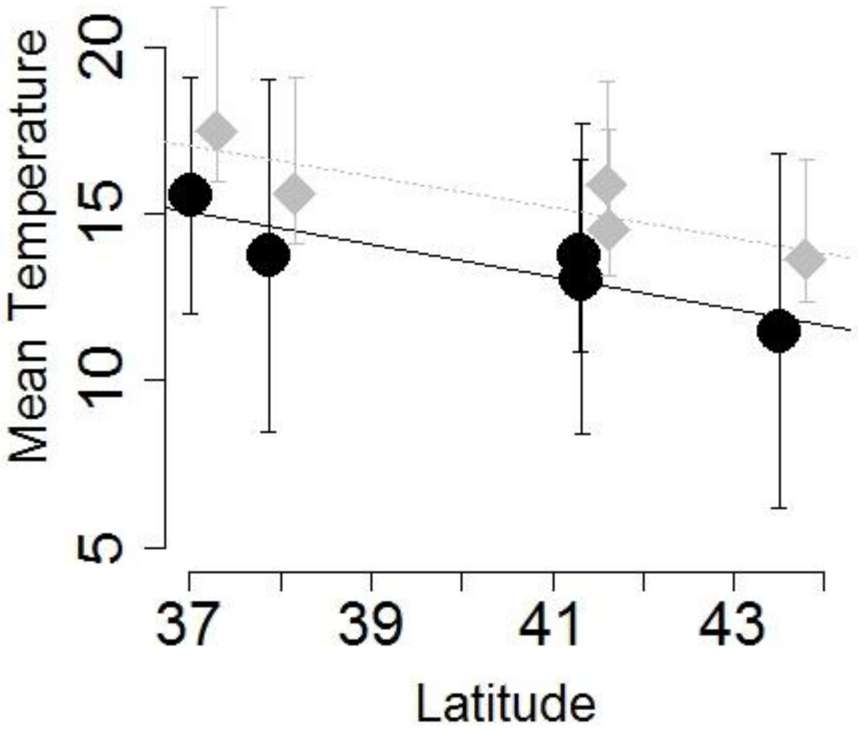


Figure 3.2. Temperature variation across latitude in New Zealand. Current mean air temperature (black circles) averaged over the previous 10 year period (2002-2011), whiskers represent the average minimum and average maximum daily air temperatures over this period (The National Climate Database; NIWA 2012). Future temperature changes derived from 12 model projections of A1B scenario 2090 mean temperature (Ministry for the Environment 2008). These values are added to the mean value of average annual air temperatures from 1980-1999 for each region (The National Climate Database; NIWA 2012) to display average projected mean annual temperature for each latitude in 2090 (grey diamonds), whiskers represent the minimum and maximum model variation in predicting average temperature range

3.3.3. Field data collection

Data collection took place in the austral summer of 2009/10. One *M. excelsum* tree was sampled per plot, with the tree selected being the one that was nearest the centre of the plot. All trees selected were located within 2 m of the transect. For each tree, we recorded the density of surrounding *M. excelsum* individuals (number of individuals in a 2 m radius centred on the target tree) and plant growth (number of young leaves visible at time of sampling, with young leaves identified by their light green colouration and small size). Density of the caterpillar *C. scriptaria* was determined by beating each tree for 10 seconds (approximately one beat per second) and counting the number of larvae collected on a 1 m^2 beating tray extended beneath the tree. Herbivory levels were estimated by quantifying the percentage of the leaves exhibiting evidence of feeding. From each tree, we live-collected a maximum of ten larvae which were reared in the laboratory to determine parasitism rates. If < 5 larvae were sourced from the target tree, we collected additional larvae from the tree's nearest neighbours until we had collected five caterpillars in total. In some cases, we were unable to collect five caterpillars from trees within the specified distance from the forest edge, so we reduced sample size at these sample plots (mean = 2.9 caterpillars per plot; range 0-10). In the laboratory, caterpillars were fed a diet of *M. excelsum* and raised in transparent plastic containers through to either adult development or parasitoid emergence in controlled conditions of 20 ºC and 65 % relative humidity (following Hodge *et al.* (2000), Schnitzler *et al.* (2004)). The parasitoids that emerged from *C. scriptaria* were then identified and parasitism rates calculated by comparing the number of caterpillars that were found to be attacked against the number that were not attacked.

3.3.4. Analysis

To analyse (i) whether two drivers of global change—habitat fragmentation and climate change (latitudinal surrogate)—exert an additive or interactive effect on forest ecosystems and (ii) whether simultaneous global change impacts are experienced uniformly across trophic levels and interactions, we use generalised linear mixed effect models (GLMM) performed using the *lmer* function in the *lme4*-library (Bates *et al.* 2011) of the R 2.11.1

statistical environment (R Development Core Team 2010). Due to the hierarchical nature of this experimental design, the random effect of *fragment* (8 fragments at each of 5 locations, $N = 40$) was included in the model to account for the close proximity of fragments surveyed at the same latitude. As we were interested in investigating the impact of latitude (a surrogate for climate) and fragmentation, we included *location* (categorical), fragment *size* ($\log_e$-transformed, continuous) and distance from *edge* (continuous) as main effects. We treated *location* as a categorical variable, and relied on post-hoc interpretation to identify trends across the latitudinal temperature gradient. Model assessments followed Zuur *et al.* (2009), beginning with a full model and simplified using Akaike’s Information Criterion (AICc) adjusted for small sample size (Ritz and Spiess 2008). The effects of multiple drivers were considered non-additive if models including interaction terms had the lowest AICc values, or conversely, were considered additive if the additive models had lower AICc values.

The nature of interactions was determined by comparing effect sizes between additive and non-additive interactions. Although detection of higher order interactions typically precludes the requirement to analyse lower order interactions (Zar 1999), here, similar to Christensen *et al.* (2006), we utilised these models comprising individual effects and lower order interactions to help interpret higher order interaction models. Interaction effect sizes (F values) were subtracted from the sum of main effect sizes (F values) producing values representing the difference between additive and interactive effects. If the value was positive (i.e. additive effect was greater than the interactive) then the relationship was considered to be *antagonistic* (the impact of the drivers was reduced when acting interactively); if however, the value was negative (i.e. additive effect was less than the interactive) then the relationship

was considered to be *synergistic* (the impact of the drivers was increased when acting interactively).

To measure the effect of location and fragmentation on the tri-trophic feeding system, we analysed data within and among multiple trophic levels, with data collected on a measure of both abundance variables and process variables at each level. At trophic level one, we recorded plant density (count of abundance per unit area) and plant growth (growth process: quantified as the number of new leaves present at time of observation); at trophic level two, the caterpillar density (count of abundance per tree) and herbivory (feeding process: quantified as the percentage of leaves exhibiting signs of attack) were recorded; and at the third trophic level, the parasitoid density (count of the abundance: quantified as the total number of parasitoids that emerged from caterpillars collected at each plot, with the number of caterpillars collected at that plot included as an offset in the model) and the parasitoid attack rate (predation process: quantified as the proportion of caterpillars with parasitoids). All abundance response variables were count data, and as such a Poisson link function was applied to the GLMMs. We also used a Poisson error when analysing plant growth. By contrast, herbivory rates were percentage data and as such arc sine square root transformations were applied and data analysed using Gaussian errors, and the parasitism rate represented the number of attacked caterpillars *vs.* number not attacked and, as such, was analysed using a binomial link function.

3.4. Results

For all dependent variables (except herbivory) the optimal model with lowest AICc included an interaction term between at least two of the independent variables (edge, area and location), suggesting that location and fragmentation exert non-additive influences on this tri-trophic system (Appendix 3.1). For all but one of those dependent variables, the optimal model included interaction terms between all three main effects, and for the other (caterpillar density), the optimal model included interactions between edge and location (Appendix 3.1). Habitat fragmentation and latitudinal differences both exerted considerable influence over the abundance of species and the frequency of interactions between those species (Table 3.1; Fig. 3.3). Location tended to exert larger effects on the abundance of organisms than fragmentation, whereas the opposite was generally true of the ecological processes (Table 3.1). Interactions between location and fragmentation were stronger than interactions between the two attributes of fragmentation (edge and area) for all response variables except caterpillar herbivory (Table 3.1).

Table 3.1. Individual and interactive impacts of habitat fragmentation (edge and area effects) and climate (using location across a latitudinal gradient as a surrogate) on interacting New Zealand forest species: the host plant *Macropiper excelsum*, the herbivore *Cleora scriptaria* and the parasitoid *Aleiodes declanae*. Abundance variables (dark grey shading) give a measure of density (per 2 x 2 m for plants, per plant for caterpillars, and per plant for parasitoids emerging from caterpillars). Process variables (light grey shading) give a measure of ecosystem functioning (number of new leaves present at time of sampling for plants, percentage of leaves exhibiting signs of herbivory, and number of caterpillars attacked by parasitoids). Linear mixed effect model *F* values reported, significance denoted by *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Trophic Level	Biotic Measure	Independent Effects			Two Way Interaction Effects			Three Way Interaction Effects
		Edge (E)	Area (A)	Loc (L)	E x A	A x L	E x L	E x A x L
First	**Plant Density**	0.549	7.772**	23.242***	0.006	4.129**	4.939***	0.307
	Plant Growth	14.888***	20.287***	5.641***	0.321	0.856	0.612	1.453
Second	**Caterpillar Density**	0.181	0.232	0.706	1.419	13.684***	12.389***	5.425***
	Caterpillar Herbivory	11.555***	10.899**	3.769**	29.435***	16.934***	10.953***	2.729*
Third	**Parasitoid Density**	0.765	0.119	1.182	1.265	13.904***	12.518***	4.608**
	Parasitoid Attack Rate	4.225*	15.889***	7.485***	0.206	0.411	1.897	5.886***
Degrees of Freedom		1,488	1,488	4,485	1,486	4,480	4,480	4,470

Significant effects of individual driver attributes (edge effects, small patch size and locations with higher temperatures) were found on all process variables (Table 3.1; light grey shading). When non-additive effects of multiple drivers were included, we detected significant two-way interaction between fragmentation and location for both area x location and edge x location in all density variables (Table 3.1; dark grey shading). The two measures of fragmentation significantly interacted in only one dependent variable, exacerbating the negative effect on herbivory (Table 3.1; Fig. 3.4). Significant three-way interactions were detected between location, size and edge for both abundance and process variables in all but the lowest trophic level (Table 3.1).

For all three trophic levels, densities and biotic processes increased in fragmented environments (near the edge) at the warm location (Auckland), but this effect either disappeared or was reversed in cool locations (Fig. 3.3). Overall however the greatest densities and process frequencies were in most cases, recorded in cool locations (Fig. 3.3). There were, however, important differences in species responses to the individual and interactive effects of the global change drivers.

The first trophic level appeared to be significantly impacted by independent measures of both fragmentation and location, but only plant density was impacted by these two drivers simultaneously (Table 3.1). The reduced density in smaller fragment size in cooler locations was offset by higher densities in smaller fragments in warmer locations (Fig. 3.3), thereby producing antagonistic responses in plant abundance (Fig. 3.4a).

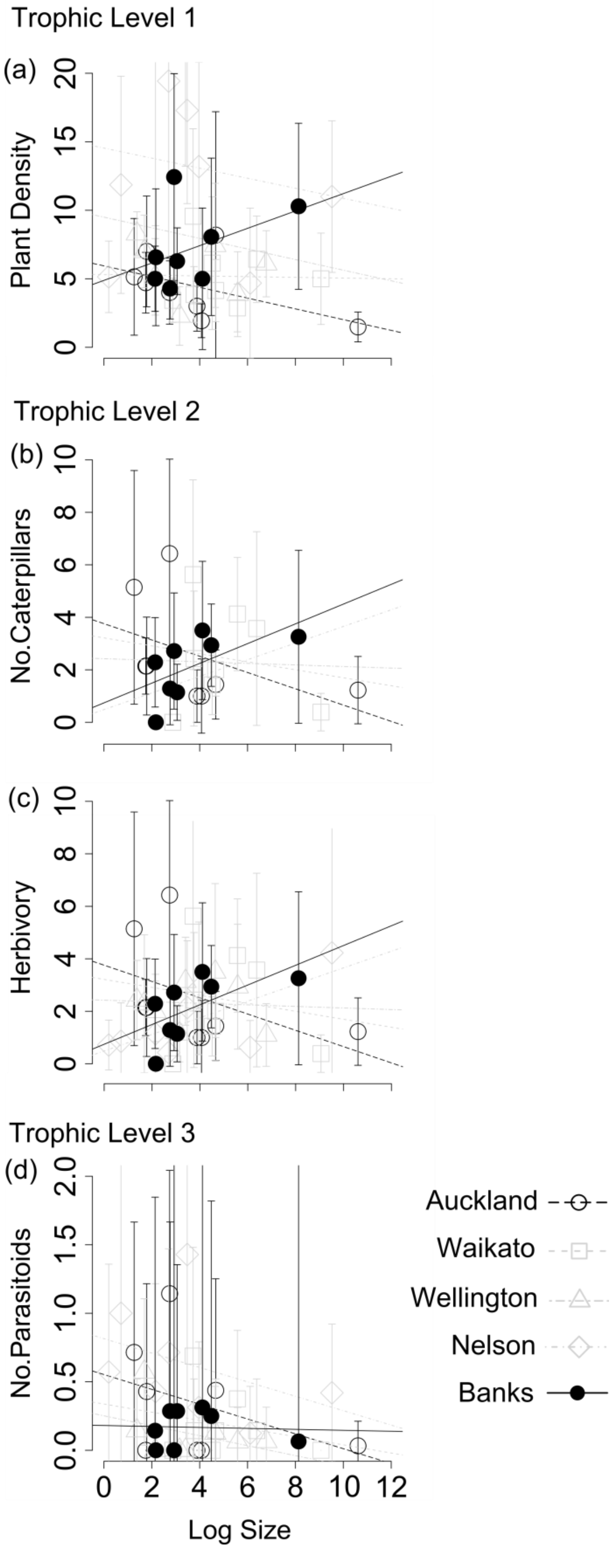


Figure 3.3. Effects of habitat fragmentation (fragment size) and climate (location surrogate for temperature differences) on three trophic levels (1: a, 2: b-c, 3: d) across two biotic measures (density: a, b, d and process: c). Graphs display mean values (± 95% CI) for all locations ranging from the warmest (Auckland; hollow circles and dashed line) to the coolest (Banks Peninsula; filled circles and solid line) and represent examples of significant two-way interactions between global change drivers.

At the second trophic level, only herbivory was significantly impacted by individual drivers. There were, however, significant interaction effects that influenced both herbivore density and herbivory rates (Table 3.1; Fig. 3.3). The nature of this interaction differed: caterpillar density had synergistic two and three-way interactions among fragmentation and location variables, whereas herbivory principally (except for Area x Location) exhibited antagonistic interactions (Fig. 3.4b). The one exception was that fragment area appeared to synergistically combine with location to depress herbivory rates relative to large fragments in cool locations.

At the third trophic level, effect sizes suggest parasitoid attack rates were significantly influenced by individual drivers, but parasitoid density was not (Table 3.1). By contrast, parasitoid density was impacted by two-way interactions between fragmentation and location variables but parasitoid attack rates were not. Both variables, had significant three-way interactions (Table 3.1), with the interaction effect on parasitoid density being synergistic but the effect being antagonistic on parasitoid attack rates (Fig. 3.4c).

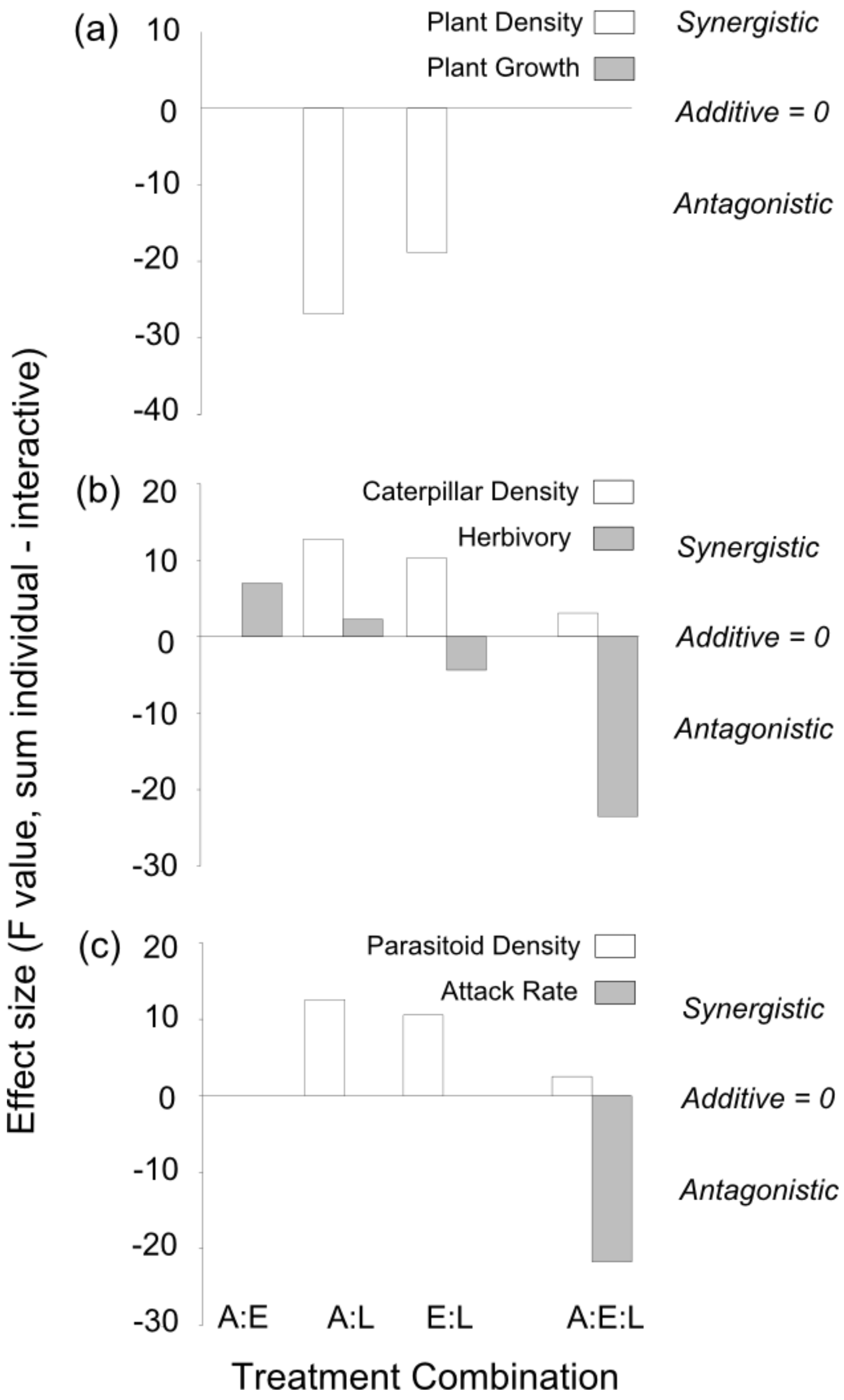


Figure 3.4. The nature and magnitude of interaction effects among fragment area (A), distance to habitat edges (E) and climate as represented by a latitudinal gradient of study locations (L) on three trophic levels: (a) the host plant *Macropiper excelsum* (b) the herbivore *Cleora scriptaria* and (c) the parasitoid *Aleoides declanae*. Effects were classified by calculating the difference between the sum of individual effect sizes and the interactive effect sizes, with positive values representing synergistic effects and negative values representing antagonistic effects. Only treatment combinations that exhibited significant interactions ($p < 0.05$) in linear mixed effect models are displayed

3.5. Discussion

Contemporary ecological research recognises the importance of studying the simultaneous impact of multiple drivers of global environmental change (Vinebrooke *et al.* 2004; Darling and Côté 2008; Tylianakis *et al.* 2008; Mantyka-Pringle *et al.* 2012), and our results suggest that focussing on a single driver will provide only restricted insight into the impacts of global changes on species and their interactions. Here, we found evidence that climate (using location as a surrogate) and the degree of habitat fragmentation (represented simultaneously by proximity to fragment edges and the size of forest fragments) both exerted influences on the abundance and trophic interactions of all levels of a tri-trophic food chain in New Zealand. The two drivers of environmental change interacted non-additively across all trophic levels. The nature of these interactions however, depended upon the biotic measure and the trophic level.

3.5.1. Simultaneous GEC drivers

In the majority of cases, the optimal model analysing habitat fragmentation and location included a three-way interaction term and in many cases significant two-way interactions were found. This suggests that non-additive interactions are the norm rather than the exception in this study system. In the wider literature, non-additive impacts of multiple drivers are also considered to dominate studies that have investigated the simultaneous impacts of multiple drivers (Darling and Côté 2008; Mullan Crain *et al.* 2008). Although these non-additive interactions are often assumed to be synergistic in nature (Myers 1995; Sala *et al.* 2000), several meta-analyses have found similar numbers of studies displaying antagonistic interactions between drivers (Darling and Côté 2008; Mullan Crain *et al.* 2008).

In one of these reviews, community level studies (where interspecific interactions buffer the negative impacts of multiple stressors) largely exhibited antagonistic interactions whereas studies at population level largely exhibited synergistic responses (Mullan Crain *et al.* 2008). Our results parallel these general findings, with fragmentation and location mostly exerting antagonistic interactions on the ecological processes we examined, yet exerting synergistic interactions on the abundance of consumers.

3.5.2. Trophic level responses

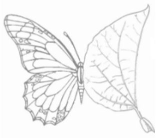
Altered dynamics of biotic interactions are an "insidious and functionally important hidden effect" of anthropogenic environmental modification (Tylianakis *et al.* 2007). Non-additive effects have been analysed with respect to differential effects on trophic levels and reviewed by Mullen Crain *et al.* (2008). They found that autotrophs exhibited antagonistic responses whereas heterotrophs exhibited synergistic responses. Here, we found this was also the case: multiple drivers did exert antagonistic impacts on plant density and growth; and synergistic responses were found for insect densities (Fig. 3.4b, c). This may perhaps be related to the trophic level hypothesis (Holt *et al.* 1999) which suggests that populations at top trophic levels should be more vulnerable to extinction than those lower down the food chain (Lawton 1995; Steffan-Dewenter and Tscharntke 2002). It has been suggested that there is a loss of biological insurance (i.e. the capacity for diverse communities to be more resilient to perturbations (sensuYachi and Loreau 1999)) as taxonomic, physiological and genetic diversity is lost towards apex populations (Christensen *et al.* 2006) and as such multiple drivers have also been found to exert more negative impacts on these top trophic level organisms (Mullan Crain *et al.* 2008).

Another possible explanation is that the nature of an interactive response may be explained by the physiological tolerances of that organism (Vinebrooke *et al.* 2004). For example, the antagonistic responses in our host plant (Fig. 3.4a) may be explained by the fact that *M. excelsum* in New Zealand is known to be frost sensitive and hence limited by low rather than high temperatures. Consequently, in the cooler locations, it is less abundant in positions which expose the plant to low temperatures such smaller fragments as opposed to larger forest fragments which may buffer the impact of frost (Fig. 3.3a). In warmer climates, however, (corresponding to lower latitudes), forest edges are less likely to experience frosts and conditions are more suitable for plant growth, meaning that increasing temperatures may ameliorate the negative influences of habitat fragmentation. This positive effect of increasing temperature on *M. excelsum* in fragmented landscapes may be misleading, however, as the overall density of the plant in warmer locations is lower than in cooler locations, and hence the species should not be expected to benefit from climate change.

For the higher trophic levels, the synergistic nature of global change impacts on the herbivore and parasitoid may be explained by a combination of factors: a potential aversion to the warmer microclimates created by both habitat fragmentation and warmer locations; and a potential cascade of impacts filtering up from lower trophic levels. Firstly, as fragmentation occurs, the proportion of habitat near edges increases geometrically (Temple and Cary 1988) and environmental conditions in the remaining habitat are altered (such as air temperature and moisture, vapour pressure deficit, soil moisture, and light intensity) (Murcia 1995). This is commonly hypothesised to impact species that require habitat interior microclimate conditions (Murcia 1995; Ewers and Didham 2006). For example, it was suggested that unfavourable microclimates were responsible for reduced leaf-miner herbivory and parasitoid

abundance near fragment edges and in small habitat fragments in Argentina (Valladares *et al.* 2006). *Cleora scriptaria* is known to typically inhabit forested areas (Hassell 1986; Schnitzler 2008) where conditions are cool and moist. A change in the quantity of core habitat will result in microclimatic alterations, and it has therefore been suggested (Schnitzler 2008) that herbivory rates may be negatively impacted by degradation of this habitat. If *C. scriptaria* do not fare well in the more extreme temperatures that are typical of matrix environments, then it is likely that they will suffer from habitat fragmentation associated with microclimates that are warmer and less humid, and from the warmer and more extreme environmental conditions expected under climate change (Ministry for the Environment 2008). Secondly, any ecological effect that reduces the abundance of the herbivore is likely to have a cascading effect on the abundance of the parasitoids. This is likely to be the case for *M. pulchricornis*, as this species responds positively to increased larval densities of *C. scriptaria* as a result of frequency dependent prey searching behaviour (Schnitzler *et al.* 2011). As such, the synergistic interaction between habitat fragmentation and location on the herbivore *C. scriptaria* (Fig. 3.4) is likely to pre-define a similar synergistic interaction for the parasitoid *M. pulchricornis*, assuming this species does not switch between hosts. Our data suggest this trophic interaction between the herbivore and parasitoid is more heavily controlled by bottom-up, rather than top-down, processes because the pattern of global change interactions on the two trophic levels is consistent. If the process was top-town, a strong negative impact on the parasitoid would be expected to cause either alternating or cascading influences down the food chain.

Our data have shown that non-additive interactions more effectively explain the simultaneous impacts of habitat fragmentation and climate (location surrogate) on biota than the additive



effects of single drivers, in line with the majority of global change studies that have investigated multiple drivers (Darling and Côté 2008). Furthermore, our data lend support to more traditional concerns that the detrimental effects of global change drivers are exacerbated in higher trophic levels. What remains uncertain, however, is whether these synergistic effects at high trophic levels may be ameliorated by the antagonistic nature of global change drivers acting on species interactions. Bringing this into a global context, whether investigating individuals, species, functional groups or communities there will always be relative ‘winners’ and ‘losers’ with global change. With human activities exerting increasing and more numerous pressures on ecosystems, the overall magnitude of change is likely to be considerable; and if this study provides insights into widespread trends, the impacts on biota are likely to be predominantly detrimental. As Paine (1998) describes, and as we empirically demonstrate, ecological surprises are likely to be commonplace. This research highlights the requirement to consider multiple drivers of global environmental change and multiple biotic measures when predicting the effects of, and solutions to, reducing anthropogenic impacts on biodiversity.

3.6. Acknowledgements

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3.7. Appendix

Appendix 3.1: Comparisons of models for impacts of global change drivers on biota. Small sample size of Akaike’s information criterion (AICc), delta AICc and the model weight are given for three trophic levels (producer, herbivore and parasitoid respectively) and two biotic measures within those levels (density and process). Main effects, additive and interaction models are fit to independent variables (rows) as AIC values for generalised linear mixed effect models. The optimal model is presented in bold

	Trophic Level One						Trophic Level Two						Trophic Level Three					
	Plant Density			Growth			Caterpillar Density			Herbivory			Parasitoid Density			Attack Rate		
	AICc	ΔAICc	Weight	AICc	ΔAICc	Weight	AICc	ΔAICc	Weight	AICc	ΔAICc	Weight	AICc	ΔAICc	Weight	AICc	ΔAICc	Weight
Area (A)	1404.399	35.1996	1.23E-08	8613.141	407.741	2.88E-89	1023.75	16.5019	2.36E-04	**-250.2**	**0**	**9.60E-01**	1232.82	292.827	2.59E-64	366.611	24.7893	4.08E-06
Edge (E)	1404.31	35.1099	1.28E-08	8507.809	302.409	2.15E-66	1021.88	14.6287	6.02E-04	-243.34	6.89402	3.06E-02	1188.9	248.911	8.90E-55	370.281	28.4597	6.51E-07
Location (L)	1394.785	25.5853	1.50E-06	8616.288	410.888	5.98E-90	1027.79	20.5433	3.13E-05	-238.54	11.6862	2.78E-03	1241.69	301.702	3.06E-66	356.572	14.7504	6.18E-04
A + E	1404.12	34.9203	1.41E-08	8520.464	315.064	3.84E-69	1023.87	16.6264	2.22E-04	-236.03	14.2004	7.92E-04	1189.43	249.439	6.84E-55	368.095	26.2731	1.94E-06
A + L	1395.204	26.0041	1.22E-06	8610.937	405.537	8.69E-89	1029.68	22.433	1.22E-05	-231.8	18.4265	9.57E-05	1238.29	298.305	1.67E-65	350.588	8.76617	1.23E-02
E + L	1395.085	25.8855	1.29E-06	8506.251	300.851	4.69E-66	1027.84	20.5894	3.06E-05	-225.57	24.6555	4.25E-06	1191.3	251.314	2.68E-55	358.563	16.7412	2.28E-04
A * E	1404.167	34.9669	1.38E-08	8342.328	136.928	1.85E-30	1025.81	18.5645	8.41E-05	-240.07	10.1602	5.97E-03	2322.46	1382.47	6.31E-301	366.395	24.5734	4.55E-06
A * L	1398.651	29.4517	2.18E-07	8617.089	411.689	4.01E-90	1029.42	22.174	1.38E-05	-210.59	39.6431	2.36E-09	1227.21	287.218	4.28E-63	357.462	15.6407	3.96E-04
E * L	1369.526	0.32583	4.59E-01	8476.174	270.774	1.59E-59	**1007.2**	**0**	**9.04E-01**	-174.07	76.1573	2.79E-17	1053.11	113.117	2.73E-25	356.538	14.7164	6.28E-04
A + E + L	1394.992	25.7924	1.36E-06	8509.911	304.511	7.52E-67	1029.83	22.5774	1.13E-05	-217.75	32.4774	8.51E-08	1192.09	252.098	1.81E-55	1192.09	850.265	2.30E-185
A * E * L	**1369.2**	**0**	**5.41E-01**	**8205.4**	**0**	**1.00E+00**	1011.75	4.50063	9.52E-02	-93.23	157	7.76E-35	**939.99**	**0**	**1.00E+00**	**341.82**	**0**	**9.86E-01**

4

Enemy release promotes range expansion in a host plant

4 Enemy Release

Enemy release promotes range expansion in a host plant

Poppy LAKEMAN-FRASER* and Robert M. EWERS[1]

Imperial College London, Silwood Park Campus, Ascot, Berkshire,

SL5 7PY, UK

* Author for correspondence: Email poppy.lakeman-fraser08@imperial.ac.uk; Tel. +44(0)20 7594 2231

Keywords: Biotic interactions; Climate change; Predator release; Range margin;

Translocation

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[1] Author Contributions: PLF and RE conceived and designed the experiments and analysed the data. PLF performed the experiments and wrote the manuscript and RE provided editorial advice.

4 Enemy Release

4.1. Abstract

Climate is considered to be the predominant driver shaping species distributions at macroecological scales, yet the importance of incorporating biotic interactions in predicting future range margins under climate change scenarios is increasingly being recognised. We used translocation studies to investigate how survival and growth patterns of an understory shrub planted at latitudes within its range, at its range limit and beyond its polewards boundary (in areas it may colonise as a result of shifting climate envelopes) are affected by the presence of a primary herbivore. Specifically, we tested the null hypotheses that: (1) biotic interactions do not exert a significant role in limiting survival and growth rates across the limits of a host plants' latitudinal range; and at smaller spatial scales that: (2) biotic interactions do not exert a significant role in determining survival and growth rates at edge *vs.* interior position within a forest fragment. We found that the understory shrub *Macropiper excelsum* is able to survive polewards of its current latitudinal limit within the first year after transplant; in fact, growth is higher outside the plant's current natural range than within its present-day distribution. This trend is particularly pronounced in forest core environments and corresponds closely to patterns of reduced herbivory outside the plants' range. The absence of the primary herbivore, *Cleora scriptaria*, and concomitant reduction in the suppressive effects of herbivory outside of the plants' range appear to be supporting enhanced growth and survival. If host plants are able to successfully track their climatic niche and disperse into novel areas prior to the arrival of their natural predators, it is possible that 'enemy-release' may facilitate the establishment of plant species. These findings highlight the importance of considering biotic interactions alongside abiotic variables when predicting future species ranges under climate change.

4.2. Introduction

Climate exerts a fundamental influence on the global distribution of plant populations (Holdridge 1947; Box 1981), while a number of additional factors—including other abiotic conditions, dispersal capabilities and biotic interactions—can also influence the successful persistence and prevalence of plants in their existing range. Gaining an insight into the interaction between climate and biology is fundamental if we are to improve accuracy in predicting changes to species ranges with future climate changes (Brooker et al. 2007; van der Putten et al. 2010).

Global average temperatures have warmed by 0.7 ºC between 1906-2005 and are expected (under the A1B scenarios) to increase by 1.7- 4.4 ºC by 2090-2099 relative to 1980-1999 temperatures (IPCC 2007). Predicting how species respond to global changes is a major goal for biologists and there is a wide spectrum of literature documenting the impacts of climate change on phenology (e.g. Yang and Rudolf 2010), population density (e.g. Best et al. 2007), community composition (e.g. Wahl et al. 2011), phenotypic plasticity (e.g. Matesanz et al. 2010) and species interactions (e.g. Tylianakis et al. 2008). Perhaps the response yielding the greatest attention is the shifting of species range margins as populations respond to moving climate envelopes with advancing latitudinal and altitudinal isotherms (Thomas and Lennon 1999; Davis and Shaw 2001; Beaugrand *et al.* 2002; Walther 2004; Thomas 2010). This pattern is found across a range of taxa and geographical localities, with 84 % of British vertebrate and invertebrate taxa that were tested having expanded polewards in response to a warming climate (Hickling *et al.* 2006). These findings are roughly equivalent to an earlier study conducted over a larger study area, which found that 81 % of populations of British

birds, Swedish butterflies and Swiss herbs at poleward or high altitude range margins were expanding 6.1 km northwards or 6.1 m upwards per decade (Parmesan and Yohe 2003). This research adds to a plethora of empirical studies documenting a spatial expansion in populations at polewards range margins where abiotic conditions become increasingly favourable under climate change (Parmesan 1996; Parmesan *et al.* 1999, 2005; Chen *et al.* 2011). Species distribution models (SDMs) are being developed to track and predict these future ranges under various climate scenarios (Guisan and Thuiller 2005; Elith and Leathwick 2009). Although SDMs are seen as valuable tools for analysing the potential dynamics of species ranges under specific climate scenarios, many models assume that species movements are in equilibrium with shifting climate envelopes and disregard the constraints of historical and biotic factors such as barriers/facilitators to dispersal and species interactions (Morin and Lechowicz 2008; Jiménez-Valverde *et al.* 2008). A high degree of land use conversion in recent history has left many habitats patchy and isolated causing potential barriers to dispersal of populations at the range boundaries of distribution (Gaston 2003). In addition to this, biotic influences alter a species' fundamental niche through competition (e.g. Connell 2011), mutualisms (e.g. van der Heijden et al. 2003), enemy pressure or bottom up limitations (e.g. Lapointe et al. 2011). As shown by the fossil record (e.g. Davis and Shaw 2001) and empirical studies (e.g. Davis et al. 1998), species respond individually to climate change and, as a result of varying dispersal rates, interactions between those species may be eroded and new ones formulated (Urban *et al.* 2012). Biotic interactions shape the spatial arrangement of species within their habitats and may also limit the expansion of species distributions under climate change (Brooker *et al.* 2007; van der Putten *et al.* 2010). Competition limits the range distribution in *Ulex* species for example (Bullock *et al.* 2000), and predation on an invasive crab limits the expansion of its range in eastern North America (DeRivera *et al.* 2005). Stimulated by the importance of biotic interactions in empirical findings, these interactions are now being more commonly considered in SDMs. Araújo and Luoto (2007) found that incorporating *Corydalis* host plant occurrence alongside climate variables distribution improved the performance of models predicting the distribution of the Clouded Apollo butterfly (*Parnassius mnemosyne*) at macro scales in Europe. Integrating land use patterns and biotic interactions with SDMs might therefore improve predictions of species ranges under climate change (Hampe 2004; Pearson and Dawson 2005; Araujo and Guisan 2006; Moore et al. 2007; Heikkinen et al. 2007; Ibáñez et al. 2009a,b; Meier et al. 2010; van der Putten et al. 2010).

Gaining an understanding into the complex responses of species to climate change will not only require large scale modelling approaches but crucially fine scale investigations into how species interactions are modified by temperature, precipitation and frost gradients (Poloczanska *et al.* 2008; Marsico and Hellmann 2009). The response of plants to climate changes can be studied through artificial manipulation of microclimates (Walker, Wahren, *et al.* 2006), investigation of local plants along environmental gradients (DeFrenne *et al.* 2009) or translocations from common garden experiments (Clausen *et al.* 1940; Kollmann *et al.* 2004). Although each have benefits, translocations allow plant ecotypes to be transferred into regions with different annual temperatures under natural conditions (Niedrist *et al.* 2011), whilst distinguishing between phenotypic plasticity and local adaptation across a species' range (Macel *et al.* 2007; Magnani 2009; DeFrenne *et al.* 2009). Assuming there is no dispersal limitation, a plant species will occur in a location which confers conditions which are suitable for its survival, growth and reproduction, with performance declining along a gradient of climatic severity as its reaches its range boundary (Prince and Carter 1985). If moved outside of its current range one may expect performance to rapidly decline, unless climate is not the sole or even the major determinant of range limitation (Willis *et al.* 2009). Translocation experiments therefore have the potential to identify key limiting factors on plant survival and growth, and this approach has been successfully utilised to study species at multiple trophic levels beyond their natural distributions (Marsico and Hellmann 2009; Willis et al. 2009).

Here, we use translocation experiments to test the capacity of an understory plant to persist polewards of its current geographic range and determine whether biotic interactions with its primary herbivore have a role in limiting distributions. We test the null hypotheses that: (1) biotic interactions do not exert a significant role in limiting survival and growth rates across the limits of a host plants range, and (2) biotic interactions do not exert a significant role in determining survival and growth rates at edge *vs.* interior positions within forest fragments.

4.3. Methods

4.3.1. The study species and system

The New Zealand native Kawakawa tree (*Macropiper excelsum*, Piperales: Piperaceae) is a common understory plant throughout the mixed native scrub environments of New Zealand (Smith 1975). The species is confined to the coastal areas of the New Zealand mainland and a number of its offshore islands, reaching its southern limit at a latitude of ~43˚5’S (Fig. 4.1). The battery of defences stored within *M. excelsum* leaves deters widespread generalist feeding activity, however despite the tree’s range of defensive bio-compounds it still suffers herbivory. Although seven insects are known to feed on *M. excelsum* (Spiller and Wise 1982) it has one primary herbivore, *Cleora scriptaria* (Lepidoptera: Geometridae), which is effective at sequestering these compounds and feeds extensively on the plant (Hodge 1998).

4.3.2. Experimental design

We conducted this experiment in lowland mixed indigenous forests on the South Island of New Zealand. We selected five experimental regions along a gradient of five degrees of latitude (between 41º and 46º S) that extended across the southern range margin of the study species (Fig. 4.1). We focus on the poleward margin of this species range as (considering global poleward latitudinal shifts) this is the margin which is most likely to experience population expansion under climate change and the equatorial margin of this species on mainland New Zealand (disregarding presence on offshore islands) is inhibited by coastal geography (as opposed to an apparent climate gradient). Average annual temperatures decrease by 1 ºC every 1.59º of latitude towards the poles on the South Island (Fig. 4.2). This suggests that for every degree rise in temperature under climate change, species will have to migrate 200 km to keep within their optimum physiological conditions. Our study location where therefore spaced accordingly: at the southern (polewards) range limit (Banks Peninsula), up to two degrees south of this latitude and beyond the current distribution of the species (polewards treatments at Timaru and Dunedin), and up to two degrees north of this latitude and within the current species range (the control treatments at Kaikoura and Nelson).

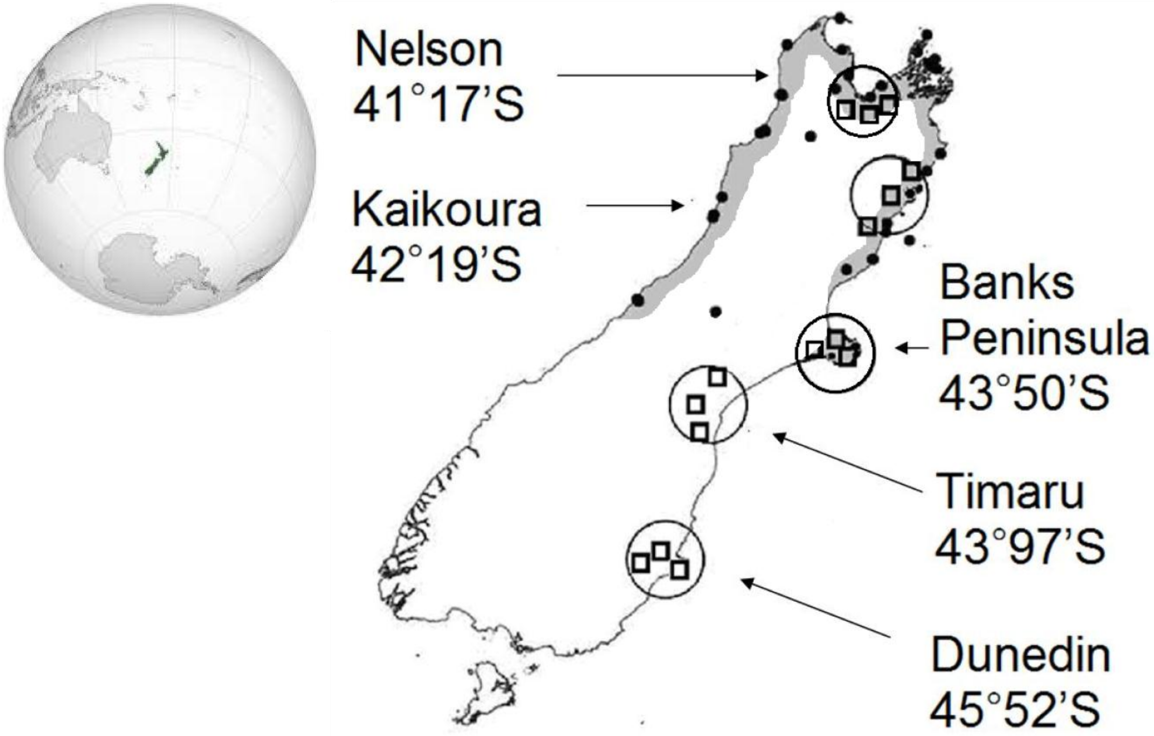

Fig. 4.1 Map showing survey locations of forest fragments (open squares) in relation to the present-day distribution of *Macropiper excelsum* on the South Island of New Zealand. Grey shading the extent of the species current distribution (Gardner 1997). Black dots represent locality records from museum specimens or direct field observations recorded by the authors

The experimental locations at the extremes of the latitudinal gradient were separated from the present-day range margin by about 300 km equate to roughly 1.5 ºC temperature difference (Fig. 4.2). This is equivalent to a mid-range climate projection scenario of the likely increase in average annual temperature in New Zealand by 2040 (1 ºC; range of 0.2 - 2 ºC derived from a full range of projections across emission scenarios (Ministry for the Environment 2008). Therefore assuming no dispersal limitation, the location of our polewards experimental site lies within the potential climatically suitable region for *M. excelsum* colonisation over the next three decades.

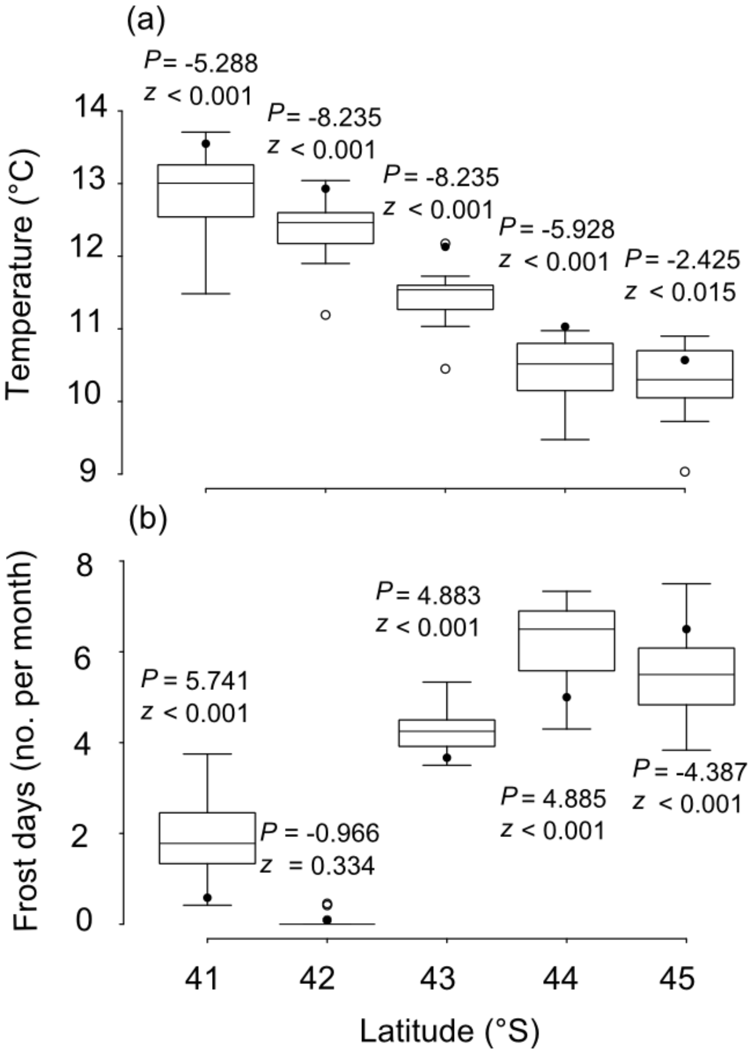

Fig. 4.2 Variation in a) air temperature and b) number of frost days per month across five experimental locations between March1992 and March 2010. Boxes are the interquartile range, whiskers are 1.5 times the interquartile range; hollow points the outliers over the previous 18 years; and filled points the average for the experimental period (March 2010 - March 2011). Values represent the *z*-statistic and *P*-value from Z tests comparing the experimental period average value to historical averages. Data were collected at the nearest airport or automatic (AWS) weather station to the experimental sites (all within 50 km proximity), and were obtained from the National Climate Database (NIWA 2012)

4.3.3. Data collection

A translocation experiment was conducted using seeds collected in March 2009 from the ripe fruit of a population at the southern range limit of *M. excelsum* (Stony Bay, Banks Peninsula

43° 51' 10 " S, 173° 2' 26" E). Although marginal populations do not always reflect the attributes of core populations (Kawecki 2008), we selected this location for seed collection on the expectation that if this species' range moves polewards, in line with the majority of other species range movements observed around the world, it is this southern population that would be expected to expand. Seeds were germinated in mixed purpose compost covered with a layer of gravel and successively re-potted and placed under growth lamps at the University of Canterbury. Seedlings were grown to a height of ~50 cm in a glasshouse environment before being moved outside in February 2010, exposing the plants to ambient conditions before experimental translocation. Since all plants were less than two years old, no reproductive catkins would be produced to spread genetic material in the timeframe of this experiment. It was therefore possible to gain permission to transplant these *M. excelsum* plants on private land, local Council reserves and Trust owned land for the purposes of this experiment.

At each of the five locations along the latitudinal gradient, we selected three lowland indigenous forest fragments for experimental translocations. We transplanted 10 shrubs into each of the forest fragments (*N* = 150 shrubs) in February-March 2010. Five of the shrubs were planted at the edge of each forest fragment (hereafter referred to as 'edge' position), and the other five were planted 50 m inside the forest (hereafter referred to as 'interior' position). Shrubs were tethered to a single bamboo cane for support, watered and left in place over the austral winter of 2010.

Experimental sites were revisited in March/April 2011 to record plant *survival* over the one-year period. Plants were recorded as alive or dead, with individuals having a brown cambium

assumed to have died. We assessed the presence or absence of *non-insect damage* to the plants (e.g. caused from frost, wind or pathogen damage), with presence indicated by evidence of browning or yellowing of leaves. In addition to these two health variables we recorded plant *growth* over the year by recording the number of leaves on each shrub on planting and on removal. To measure *herbivory* levels, we recorded the number of leaves showing evidence of insect attack and those unaffected by insects. Presence of the primary herbivore, *C. scriptaria* was determined by beating each tree for 10 seconds (approximately one beat per second) and counting the number of larvae collected on a 1 m^2 beating tray extended beneath the tree. Upon completion of data collection, all shrubs were cut down, their root masses dug up, and all vegetative material was removed from the forest fragment to avoid any potential for establishing *M. excelsum* populations outside of its current distributional range.

We used Z-tests to compare the climatic conditions during the experiment with historical averages. The average temperature during the experiment (March 2010- March 2011) at each location was significantly higher than the annual temperature in the 18 years prior to the experiment (Fig. 4.2a). In addition, the average number of frost days per month over the experimental period were significantly lower across many of the experimental locations (Fig. 4.2b). This is with the exception of the polewards site, Dunedin, which had 6.5 frost days per month during the experimental period compared to an average of 5.5 frost days per year between March 1992 - March 2010.

4.3.4. Analysis

Generalised linear models were implemented in the R 2.11.1 statistical environment (R Development Core Team 2010). Interactions between the main effects: *latitude* (continuous variable) and *position* (discrete edge/interior variable) were analysed as it was hypothesised that there would be a difference between the response variables across the natural range of *M. excelsum*, and that there would also be a difference between the edge and interior of forest fragments.

Survival levels were calculated as the number of dead *vs.* alive plants at each edge position and *non-insect damage* was recorded as the number of plants with evidence of damage *vs.* un-damaged at each *site* (N=30, edge and interior of each of the 15 fragments). Similarly, *herbivory* was recorded as the number of attacked leaves *vs.* non-attacked on each plant (N=145 plants) and as such binomial models were used on these three analyses. *Caterpillar presence* was measured as the number of caterpillars per plant and analysed using Poisson errors. *Growth* was measured as the change in the numbers of leaves for each plant (N=145 plants) over the 2010 season and analysed using Gaussian errors. The height of plants was added as an offset to this model to account for the variation between individuals. The direct impact of herbivory (percentage of leaves attacked) on growth levels (change in the numbers of leaves for each plant) was analysed using a general linear model with Gaussian errors, again adding plant height as an offset.

4.4. Results

Of the 150 transplanted *M. exceslum*, 5 were lost due to human damage and a further 19 died over the 12 month period of the experiment. Of the surviving plants, 79 appeared to be in full health and 47 showed evidence of non-insect damage.

4.4.1. Survival potential & growth

Survival rate showed little variation across the range of *M. excelsum* (Fig. 4.3a; Table 4.1). There was little variation in non-insect plant damage and this was reflected by the lack of significant main effects of latitude and the interaction between latitude and position for this variable (Table 4.1). Significant interactions were detected between latitude and edge position for plant growth (Table 4.1), with the surprising pattern that plants transplanted outside of the species natural range tended to increase the number of leaves, whereas those inside the range tended to lose leaves. This pattern was stronger for plants in the forest interior than those at forest edges (Fig. 4.3b).

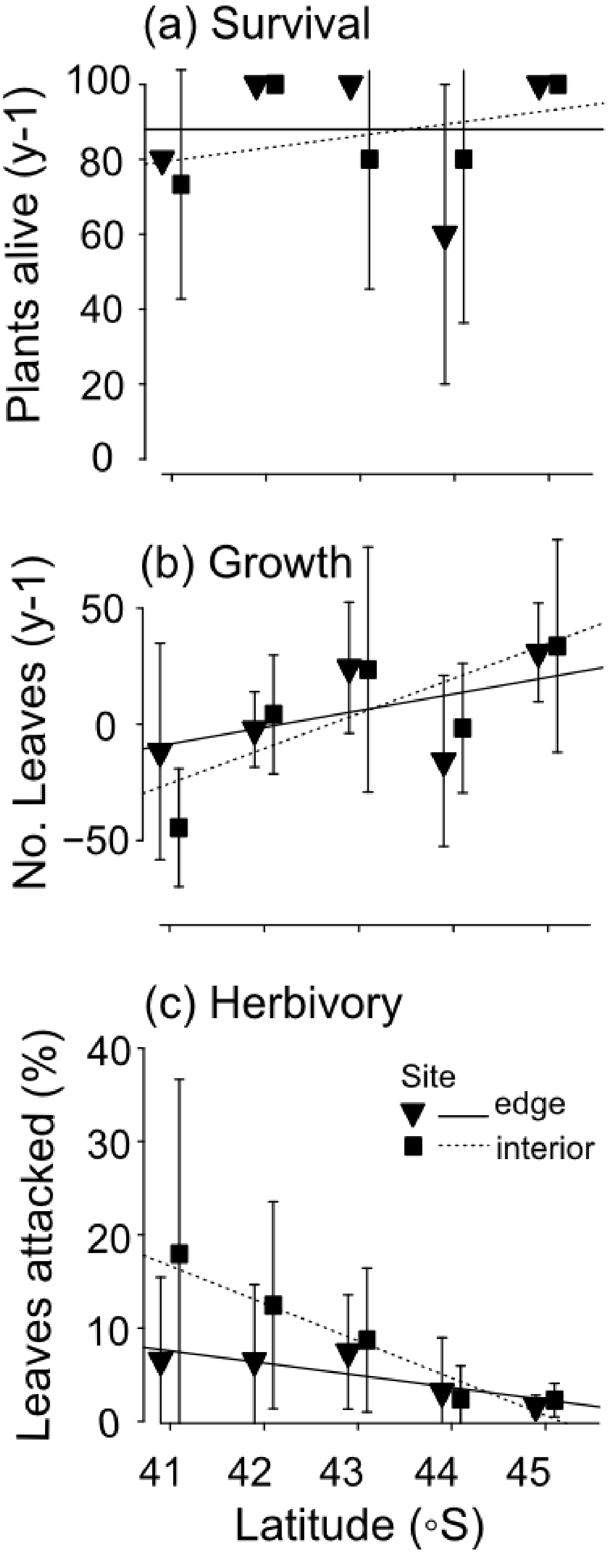

Fig. 4.3 Responses of *M. excelsum* plants transplanted across a latitudinal gradient following a 12 month transplant period. (a) Survival: percent of plants still alive, b) Growth: change in leaves number on surviving plants, c) Herbivory: percentage of leaves attacked on each individual. Values are means (± 95% CI) for plants located at the edge (triangles) and interior (squares). Linear models are shown for each location, solid lines across latitudinal range at fragment edges and short dashed line across latitudinal range at fragment interior

4.4.2. Impact on species interactions

There was a highly significant interaction between latitude and edge position on herbivory levels (Table 4.1). Herbivory rates were highest within the species range and declined outside of it, but that trend was much stronger at the interior than edges of fragments where significantly more leaves were attacked. Outside of the species range, there was no difference in herbivory rates among edge and interior positions (Fig. 4.3c). There was also, predictably, a significant effect of latitude on the presence of the primary herbivore (Table 4.1) with *C. scriptaria* only being recorded inside the plants' natural range at Kaikoura and Nelson. Enhanced growth rates appeared to be manifested through a direct impact of herbivory: the higher the percentage of leaves attacked, the lower the amount of leaf growth over the season ($t_{1,129} = -2.194$, $p < 0.05$).

Table 4.1. Results from generalised linear models for the influence of latitude and position on the biotic processes of translocated *M. excelsum* and on the presence of *Cleora scriptaria*

	Survival		**Non-insect damage**		**Growth**		**Herbivory**		**Caterpillar Presence**	
	z value	*P* value	*z* value	*P* value	t value	*P* value	*z* value	*P* value	*z* value	*P* value
Latitude	0.094	0.925	0.126	0.900	1.197	>0.05	-13.44	**<0.001**	**-2.013**	**0.044**
Position	-0.818	0.414	0.231	0.818	-2.170	**<0.05**	15.73	**<0.001**	-0.705	0.481
Interaction	0.811	0.417	-0.130	0.897	2.156	**<0.05**	-15.32	**<0.001**	0.710	0.478

4.5. Discussion

Biotic interactions are fundamental in determining the ability of plants to survive and prosper in novel environments. Here, we conducted an *in-situ* experiment, translocating a native plant species polewards of its present-day distribution. Our findings suggest that *M. excelsum* survives equally well—indeed exhibits accelerated growth rates—outside of its natural distribution compared with locations inside the range. These accelerated growth rates appear to be due to significantly decreased levels of herbivory from its specialised insect herbivore in polewards locations. This may indicate that *M. excelsum* is benefiting from suppressed insect attack at latitudes outside of the primary herbivores range. The pattern is probably a signal of 'predator release' and may initially augment the polewards range expansion of *M. excelsum*, adding to the increasing body of evidence that suggests biotic interactions may modulate species responses to climate change (Araújo and Luoto 2007; Poloczanska *et al.* 2008; van der Putten *et al.* 2010).

Contrary to results expected under a scenario of climate limitation, *M. excelsum* did not exhibit reduced survival rates outside of its natural range. Indeed, plants in the interior of forest fragments, where ambient microclimate conditions would theoretically be buffered from the more extreme climatic conditions outside the forest (Young and Mitchell 1994; Davies-Colley *et al.* 2000), appeared to have slightly elevated survival levels and enhanced growth rates at sites outside of the plants range as compared to sites within the species range (Fig. 4.3a,b). This species is particularly sensitive to frost (The Native Plant Centre 2007), yet despite frosts being more frequent than average in the southernmost location with just two (1992, 2003) out of the past 18 years having more frost days than 2010, survival rates at the

southernmost location were still very high (Fig. 4.3a). If, as many models assume, climate envelopes are the predominant factor determining species ranges (Pearson and Dawson 2003), the high survivorship levels in regions polewards of *M. excelsum*'s natural distribution in this investigation indicate that the climate here is suitable for adult survival and therefore that some other factor must limit the geographic range of the species. However, it is still premature to entirely rule out the possibility of climatic controls on the geographic range of *M. excelsum*, as other parts of the species' life history such as germination or propagation may limit its ability to successfully form breeding populations. In addition, due to the pragmatic limitations on introducing fertile novel species outside their range, this study was conducted over a comparatively short time for investigations into survival capabilities of transplanted organisms, with most researchers discounting the first year of measurements due to initial vigour of plant growth even in unsuitable sites (Ibáñez *et al.* 2008). However, studies that did undertake transplants under shorter time frames have found that initial mortalities occurred within a week of transplantation with little or no deaths occurring after this period (Silander and Klepeis 1999), suggesting that our findings may still provide insights into patterns of plant survival in polewards locations. Further investigation into the germination capacity and reproductive output of *M. excelsum* seeds in polewards regions, as well as an extension of the study duration to account for more extreme weather events and any potentially delayed mortalities, are necessary to confirm if, as this study would suggest, climate in this novel area is suitable for the plants long-term survival and persistence.

A number of studies have found that dispersal can be equally or even more important than climate in limiting the expansion of species ranges towards the poles (Grashof-Bokdam and Geertsema 1998; Norton *et al.* 2005; Svenning and Skov 2007; Marsico and Hellmann 2009).

For those plant species that are able to expand into novel geographic areas in which their primary herbivores do not exist or are reduced in numbers, a release from high levels of herbivory suppression may facilitate the successful colonisation, successful growth and range expansion (Keane and Crawley 2002). A similar translocation experiment on Vancouver Island found that survivorship of *Lomantium nudicaule* (Apiaceae) was equal to, or improved, outside relative to inside the present-day range (Marsico and Hellmann 2009). The authors reported that the climate outside the range of *Lomantium* spp. had been suitable for the previous 100 years, and suggested that a more likely factor limiting the range extent of *Lomantium* spp. was the fragmented nature of habitat at the range margin (Marsico and Hellmann 2009). In the context of our experiment, models of potential vegetation patterns suggest there was continuous native forest extending along the east coast of the South Island prior to human habitation (Leathwick *et al.* 2004). *M. excelsum* often grows in the understory of many of the canopy species thought to have been present, and as such there would have been the potential for *M. excelsum* populations to spread south of its present-day range. However in the ~ 730 years since human colonisation of New Zealand (Wilmshurst *et al.* 2008), indigenous forest cover has been reduced from 81 % to 23 % of the total land area (Rutledge 2003), and the Canterbury plains – the present-day southern limit of *M. excelsum* – was particularly rapidly and heavily affected (Ewers *et al.* 2006). Dispersal limitation in this fragmented landscape may, therefore, be one mechanism responsible for the lack of naturalised *M. excelsum* south of Banks Peninsula.

The key influence of biotic interactions on plant growth rates is evident from this study, and these findings contribute to an increasing body of evidence that biotic limitations play a fundamental role in determining current distributions of plants and in the responses of species to climate change (Suttle *et al.* 2007; Araújo and Luoto 2007; van der Putten *et al.* 2010). *C. scriptaria* herbivory is positively related to *M. excelsum* abundance (Schnitzler *et al.* 2011) and this herbivore shows a preference for 'core' forest conditions (Schnitzler 2008). We found firstly, and at small spatial scales, herbivory is higher on trees in forest fragment interiors than at forest edges. Outside the species range, where no *C. scriptaria* larvae were recorded, herbivory still occurred at low levels yet the difference between interior and edge disappeared. The loss of this trend outside the range may be an indication of altered community interactions. With the absence of *C. scriptaria*, other less dominant herbivores have access to this novel food resource. We suggest that these generalist herbivores (Spiller and Wise 1982) have no clear preference for 'core conditions' and as such the edge/interior trend disappears. Secondly, and at larger spatial scales, we found a strong trend indicating enhanced growth (particularly inside forest fragments) at latitudes outside the species range (Fig. 4.3b). Interestingly, these trends were almost the exact opposite of the trends in herbivory levels, which were higher inside the species range (particularly at forest interior positions) and diminished in latitudes outside the range (Fig. 4.3c). These results suggest a causal link between biotic activity and plant health and as such, this experiment may emulate the erosion of trophic interactions when species become geographically separated.

Temporal phenological mismatch is frequently being recorded when the timings of vital life history events of predators and prey drift apart (Post and Forchhammer 2008), a situation that can be precipitated by climate change (Schweiger *et al.* 2008). Also important, yet less frequently recorded, are spatial mismatches in which species with differing levels of mobility move (or don't) to track changing isothermic distributions, resulting in geographically decoupled species interactions (Araújo and Luoto 2007). Such a situation has been predicted from SDMs for lepidopteran species that exhibit a pronounced loss of range when their host plant is not able to fill its projected ecological niche (e.g. in the case of *Boloria titania* (Schweiger *et al.* 2008)), and in empirical studies where hosts experience lower levels of parasitoid attack after colonising a novel area (e.g. the butterfly *Aricia agestis* (Menéndez *et al.* 2008)). This ‘predator release’ phenomenon is more commonly discussed in the context of the invasive potential of exotic species. The enemy release hypothesis predicts that as plant species move into novel regions, their establishment will be enhanced by the lack of natural predators that exert herbivory stress on the plant (Keane and Crawley 2002). Our data provide empirical support for this hypothesis. We recorded no *C. scriptaria* larvae south of the current *M. excelsum* distribution limit (as a result caterpillar numbers significantly reduced with increased latitude; Table 4.1), and we found that plants established beyond the range of the specialised herbivore appeared to gain an advantage in terms of growth (Fig. 4.3). Applied to the context of distribution shifts under climate change, the enemy release hypothesis may provide further insights into how plants may respond at the polewards range if they move beyond the distribution of their specialised herbivores. It is possible, therefore, that the spatial distribution of herbivores may facilitate the expansion of plant species ranges under climate change (Maron and Vila 2001). However, this expectation must in turn be balanced by the expectation that, in the absence of a direct climatic control on their distribution, mobile insect herbivores such as *C. scriptaria* will likely expand their range to keep pace with that of their host plant. In addition, although unlikely due to the range of defensive compounds in this plant, there is the potential for herbivores in polewards locations to overcome these chemical barriers and for herbivory to gradually increase over time. Under these scenarios, predator release and the subsequent growth advantage experienced by a polewards expansion of *M. excelsum* will likely be short-lived.

It is thought that the largest uncertainty in predicting the impact of climate change on ecosystems is understanding how species will interact in novel conditions (Winder and Schindler 2004). Therefore, the fundamental importance of studying how species interactions are modified by climate change, must not be ignored (Suttle *et al.* 2007). We have shown that *M. excelsum* can survive polewards of its natural distribution and it is likely that the improved growth rate is due to a release from the suppressive influence of high levels of herbivory in forest outside of the range of its primary herbivore. However, this does not explain the current southern range limit of the species, which we hypothesise is caused either by historical dispersal limitation or from undetected climatic limitations to the ability of the species to germinate or reproduce. Further work would be needed to separate these hypotheses. Predator release can only benefit a plant species if it has first overcome dispersal limitation to reach a new location, and then successfully germinated and formed a reproducing population. Such work in this domain is important if we are to understand more fully how species will respond to climate change at their range margins.

4.6. Acknowledgements

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5

Trophic destabilisation in a dynamic world: will a preference for natal host plant topodemes inhibit herbivore range shifts?

5 Trophic Destabilisation

Trophic destabilisation in a dynamic world: will a preference for natal host plant topodemes inhibit herbivore range shifts?

Poppy LAKEMAN-FRASER[1*] and Robert M. EWERS[1]

[1] Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

[*] Author for correspondence: Email poppy.lakeman-fraser08@imperial.ac.uk; Tel. +44(0)20 7594 2231

Running head: Population origin determines trophic attrition

Keywords: *Cleora scriptaria;* Endemic Species; Geographic Distribution; *Macropiper excelsum;* New Zealand; Poleward-Margin Population; Species Interactions.

5 Trophic Destabilisation

5.1. Abstract

Species shift their distribution to track environmental conditions which support their physiological optimum, yet differences in plant biochemistry in novel areas may hinder the successful movement of herbivores. Here, we examined the extent to which altered feeding on novel host plant topodemes might inhibit range shifts in a mobile herbivore. Using a plant-herbivore interaction in New Zealand, we experimentally translocated Geometrid caterpillars, *Cleora scriptaria,* collected from three regions along a latitudinal gradient onto *Macropiper excelsum* host plants of a natal and novel origin. Contrary to our expectation, we found no overall significant tendency for caterpillars to exhibit different herbivory levels on plants that originate from their natal region. However, we found evidence to support our hypothesis that caterpillars in a population at the polewards edge of the host plant distribution fed differently to those elsewhere in the range. We found the polewards population fed equally prolifically, or removed more leaf matter, on novel host plants, whereas central and equatorial populations fed more effectively (although non-significantly) on natal host plants. Herbivory levels were reduced when northern caterpillars were placed on plants from an increasingly southerly origin. Our findings indicate that potential distribution shifts under climate change may result in the attrition of the plant-herbivore interaction across much of the *C. scriptaria* geographic range, but the ability of the population at the poleward range edge to feed successfully on novel topodemes indicates that range expansion under climate change may not be limited by feeding capabilities in novel geographic regions.

5.2. Introduction

One of the most frequently cited influences of climate change on biota is the movement of species distributions towards the poles as they track their moving isothermal ranges (Parmesan et al. 1999; Warren et al. 2001; Ragupathy and James 2009; Thomas 2010). The ability of herbivore species to shift their range in response to environmental change depends on their level of mobility, their ability to adapt to novel conditions, the degree to which their habitat is fragmented and their dependency on particular food plants (Pearson and Dawson 2003, 2005). Biotic interactions, including food plant dependency, are a fundamental yet relatively understudied factor shaping the distribution of species (Schmitz et al. 2003; Suttle 2007), and exert a strong influence on current and predicted future distribution shifts (Araujo and Luoto 2007; Pelini et al. 2010).

Specialist herbivores appear to be dominant amongst phytophagous insects (Joy and Crespi 2007). For example, from a number of herbivory studies, Bernays and Graham (1988) suggested that <10% of insects feed on more than three plant families, suggesting that specialism is an effective life history strategy for plant-feeding insects. Specialist adaptations, however, may also indicate the potential sensitivity of insects to altered foliage biochemistry, with herbivores showing reduced fitness when they feed on plants not from their natal origin (Pelini et al. 2010). In this situation, fitness may be manifested through larval performance, for example, the amount of leaf tissue consumed by chewing insects. Plant defence compounds can act as a deterrent or depress feeding of phytophagous insects (Levin 1976). Within plant species, local varieties can evolve which are nutritionally and chemically distinct across the species' geographic distribution (Siska et al. 2002; Santamaria et al. 2003),

and even small variations in plant chemical compounds may alter the feeding abilities of herbivores (Barbosa and Krischik 1987; Macel et al. 2005). These distinct intraspecific populations have been termed *ecotypes* by Turesson (1922) describing ecological units resulting from 'the genotypical response of an ecospecies to a particular habitat'. A geographic mosaic of local adaptation can exist which in a spatial context, describes the evolution of phenotypically distinct ecotypes (Thompson 2005). This term was a precursor to *deme* terminology (Turesson 1922). For example, Edmunds and Alstad (1978) found intraspecific variation in Ponderosa pine (*Pinus ponderosa*) defences induced differentiated demes of black pineleaf scale (*Nuculaspis californica*), and Karban (1989) found that the scale insect (*Apterothrips secticornis*) grew more on cuttings of their natal plant clone (of *Erigeron glaucus*) than on other clones. The root, *-deme* can then be applied to self-explanatory prefixes (Briggs and Block 1981) such genoecodeme (equivalent to Turessons ecotype) and topodemes (specified geographic area) which is what this study investigates. Species are able to adapt to localised habitats separated by distances as small as 10 km (Singer *et al.* 1995), and thus one would expect most efficient feeding (i.e. the ability to consume large quantities of leaf matter due to the ecotypic adaptation to plant defences) by herbivores on the natal host plants they are adapted to. This is however assuming that the co-evolutionary arms race between plant defences and a caterpillar's ability to overcome these defences is shifted in favour of the caterpillar. To our knowledge, there has been little research into how regional differences in plant biochemistry across a plants' range may, then, be detrimental to herbivores whose range is shifting into novel host-plant topodemes. The feeding ability, and therefore fitness, of herbivores may be compromised if they cannot adjust to the location-specific biochemistry of their food plant, potentially leading to a weakening of plant-herbivore interactions. This mismatch may be more pronounced at larger spatial scales

(Cogni and Futuyma 2009), with the degree of trophic weakening likely to increase with the distance an organism moves from its natal site.

Long term environmental changes such as climate change are likely to exert directional pressure on species, with populations at the geographic range peripheries likely to be most heavily impacted. Those at the polewards edge—where conditions are likely to become increasingly beneficial—are likely to be under less threat than populations at the trailing edge (Gibson et al. 2009). Species geographic ranges are expected to shift polewards (Parmesan *et al.* 1999; Thomas and Lennon 1999; Thomas 2010) and to higher elevations (Wilson *et al.* 2007; Colwell *et al.* 2008; Lenoir *et al.* 2008) through the expansion of polewards edge populations (Hellmann *et al.* 2008; Gibson *et al.* 2009) and the contraction of trailing edge populations (Hampe and Petit 2005; Franco *et al.* 2006; Parisod and Joost 2010).. Providing a model example of this, population extinctions of the Edith's Checkerspot butterfly (*Euphydryas editha*) on the Western coast of North America were four times higher at the trailing edge boundary in Baja Mexico than along the polewards edge boundary in Canada (Parmesan 1996). Climate-based projections of species distributional shifts usually assume that polewards edge peripheral populations are 'preadapted to warming' (Pelini et al. 2009) meaning they possess certain traits which promote expansion into novel areas. This preadaptation may be derived from genetic differences at margin ecotypes allowing adaption to change (Zakharov and Hellmann 2008) or historical selection to adjust to warmer climates (Hellmann *et al.* 2008) in polewards populations. Interspecific species interactions however also have a crucial influence over species responses to climate change, as documented by Suttle et al. (2007) who found that over time biotic interactions exert stronger influences on ecological responses than climate factors alone. In addition, Andrew and Hughes (2007)

carried out a transplant experiment to investigate potential colonisation of novel areas under a warmer climate, showing that host plant identity was more important than climate in determining the success of herbivore colonisation. The successful movement of herbivores will therefore not only rely upon suitable environmental conditions, but also on their ability to feed on host plants with potentially altered chemical concentrations that will be present in the novel locations.

Here, we investigated the ability of herbivores from a population at the polewards margin to feed on host plants from novel locations, highlighting how shifting populations of herbivores may alter the intensity of a plant-herbivore interaction under rapid range shifts. We firstly made the assumption that a herbivore's response to differences in plant defence compounds outweighed the response to differences in nutritional quality of topodemes. Secondly, we made the assumption that insect herbivores, being more mobile and having shorter generation times than plants, are likely to disperse faster than their host plants in response to climate changes. This leads to the expectation that insect populations are likely to shift polewards while populations of their host plants, which may exhibit regional differences in leaf biochemistry, remain relatively static. To mimic this process, we cultivated glasshouse populations of a single host plant species collected from across its geographic range, and experimentally translocated an insect herbivore, collected across the same geographic range, onto plants from their own and from novel regions. Our experiments do not directly replicate climate change *per se*, but do allow us to investigate differences in herbivory rates between topodemes, consequentially allowing us to infer how biotic interactions may alter in intensity with mismatched distributional shifts caused by environmental change. We had three specific hypotheses that we tested: (1) that herbivore's feeding performance is different on their natal compared with novel host plants; (2) that herbivores from the population at the poleward edge of a species distribution exhibit different feeding behaviours from those originating from the middle or equatorial edge of the host plant range; and (3) that herbivore-host interactions will change in intensity if herbivore distributions shift away from their historical natal host plants. Testing these hypotheses allowed us to predict whether the intensity of this species interaction will be weakened or intensified under future climate change.

5.3. Methods

5.3.1. The study system

We selected an endemic New Zealand plant-herbivore system to investigate the potential impact of shifting ranges on herbivory rates, an important species interaction (Knight 2004). The host plant species, *Macropiper excelsum* (Piperales, Piperaceae), is endemic to New Zealand mixed-bush lowland forests (Smith 1975) and is relatively common within coastal forests down to a southern geographic range limit at 44˚ S latitude (Fig. 5.1). All *M. excelsum* subspecies contain a range of anti-insect bioactive compounds such as juvadecene, myristicine and novel ligans, which are thought to be toxic to many insects (Russell and Fenemore 1973). The species has one primary herbivore, larvae of the geometrid moth *Cleora scriptaria* (Lepidoptera, Geometridae), and this Lepidopteran species' primary host plant is also *M. excelsum* (Hudson 1928; Spiller and Wise 1982). There has been no investigation into regional variation in *M. excelsum* defence compounds, although morphological and anatomical variations are evident across the geographic range of *M. excelsum* (Gardner 1997). Given these differences it is likely that the concentration and composition of its chemical cocktail—which is enough to prevent the feeding of many

generalist species (Russell and Fenemore 1973)—is likely to vary among regional populations of *M. excelsum*. There has been no record of range expansions under climate change in these species. However, given the general polewards range shift trend across many taxa globally (Parmesan *et al.* 1999; Thomas and Lennon 1999; Chen *et al.* 2011) and in New Zealand (Whitehead *et al.* 1992; Leathwick *et al.* 1996; Mcglone and Penman 2001), we make the reasonable assumption that with environmental warming these species will tend to move southwards. In addition, as little is known about the distribution of *C. scriptaria*, we make the assumption that this species range extends to the limit of its primary host's range (42° S), and hence we refer to Banks Peninsula plant and caterpillars as the 'polewards edge' population.

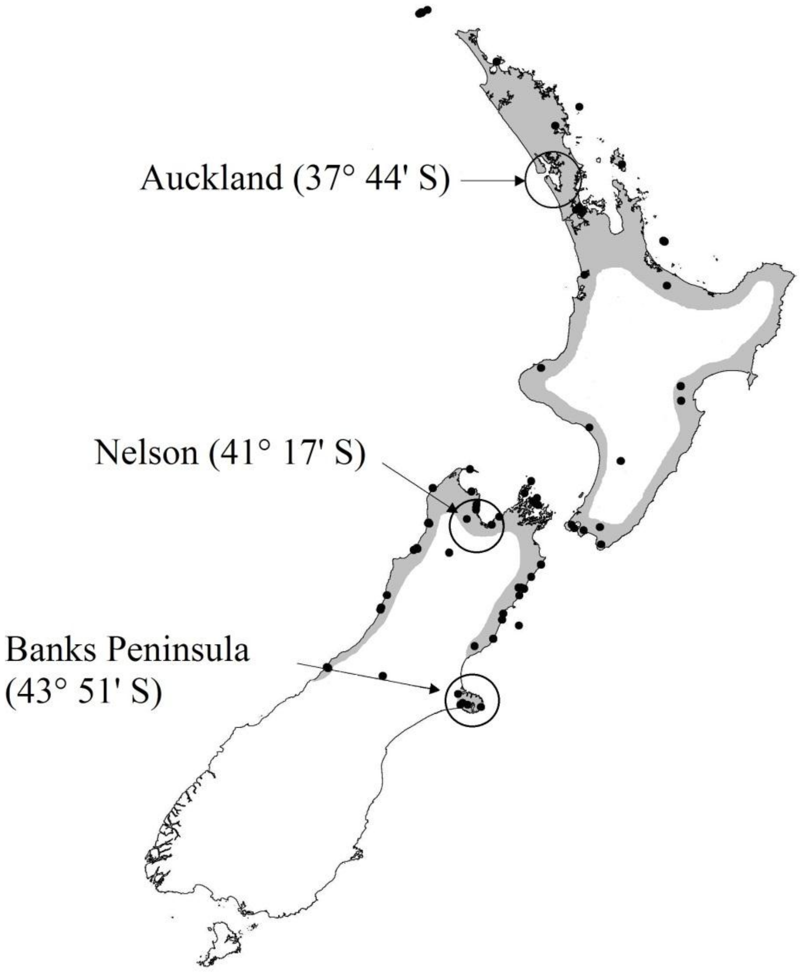


Figure 5.1. The distribution of *Macropiper excelsum* in New Zealand. Black dots represent locality records from museum specimens or direct field observations recorded by the authors, and grey areas show the extent of the species distribution (Gardner 1997). Experiments were conducted using *M. excelsum* seed and *C. scriptaria* caterpillars collected from each of the three labelled regions extending across a seven degree (790 km) latitudinal gradient.

5.3.2. Sample localities and specimen rearing

The geographic range of *M. excelsum* spans a temperature gradient of approximately 3.8 ˚C (NIWA 2009), but only a relatively narrow altitudinal range of 0–500 m (NZ Plant Conservation Network. 2011). We identified three sites within the current range of *M. excelsum* that span seven degrees of latitude (37° S, 41° S and 44° S), a total distance of 790 km (Fig. 5.1). The altitude of the sites varied from 74 to 136 m.a.s.l. The latitudinal gradient roughly corresponds to the temperature increases and latitudinal movement of plant species that are expected to arise from climate change in the next century. Temperatures in New Zealand have risen by 0.9 ˚C between 1909 and 2009 (NIWA Retrieved on 18/4/11), and are predicted to rise by a further 0.9 ˚C by 2040 and 2.1 ˚C by 2090 (Ministry for the Environment 2008). For every 1˚C rise in temperature, New Zealand plant species are expected to migrate approximately 2.22˚ of latitude south (approximately 250 km) to keep within their optimum physiological conditions (Whitehead et al. 1992). Although we cannot rule out the possibility that some of the individuals we collected have recently moved to their current locations, we make the assumption that all host-herbivore populations that we sampled are coevolved, allowing us to interpret variation in feeding intensities as reflecting the magnitude of potential feeding barriers given range shifts.

We obtained 30 *M. excelsum* plants from each of the three regions. Plants from Banks Peninsula (43° 51' S) and Nelson (41° 17' S) were collected as seeds in the 2008-09 austral summer. Plants from Auckland (37° 44' S) were one year older, the seeds being collected in August 2007. All 90 plants were grown under growth lamps in a glasshouse environment and then pruned to a height of approximately 500 mm in December 2009 so all plants were a similar size once they had grown back to an average height of 700 mm before the start of the experiment in February 2010. Caterpillars were collected in January and February 2010. Approximately 40 mixed instar larvae (average third instar at the start of the experiment) were collected from each of the three regions where the plants originated.

5.3.3. Feeding experiment and quantifying herbivory rates

One-third of the plants from each region received one-third of the caterpillars from each region in a fully-crossed factorial experimental design (Table 5.1; $N = 10$ plants per square). The number of leaves on each plant was counted before one caterpillar was placed on the plant, and then encapsulated with a muslin mesh (~1 mm weave) to prevent caterpillars from moving onto neighbouring plants. Caterpillars were left on plants, inside the glasshouse, for a five-month period until mid-June 2010 when herbivory levels were quantified.

At the end of the experimental period, we recorded the number of leaves on each plant, the number of abscised leaves, and all leaves that had evidence of herbivory were removed and digitally scanned. When feeding had occurred around the edge of the leaf, we manually reconstructed the digital leaf margin using graphical software. The resulting image was processed through the leaf area analysis program LAMINA (Leaf shApe deterMINAtion) which calculates blade dimensions and determines the total amount of cavity area, a proxy for herbivory (Bylesjo et al. 2008). These data provided three measures of herbivory that were used as response variables in our analyses: (1) total damaged area on all leaves, providing a measure of ‘*caterpillar feeding*’ i.e. a measure from the herbivores ‘perspective’; (2) the number of leaves attacked on each plant, giving a measure of the *‘feeding pattern’* of the caterpillars; and (3) the proportion of leaf area removed from leaves that were fed on (summed cavity area/summed leaf area), which estimates the level of *‘foliage damage’* i.e. a measure from the plants ‘perspective’. Temperature in the greenhouse was continuously recorded using iButton dataloggers (DS1923-F5), ensuring we were able to control for within-greenhouse variation in temperature that might confound caterpillar feeding patterns.

Table 5.1. Experimental crosses between plant origin and caterpillar origin. Hypothesis one tested the difference between natal (upper case letters) and novel (lower case) treatments, hypothesis two tested the difference between caterpillar populations at the polewards range margin (bottom row), mid-range (middle row) and equatorial range margin (top row), and hypothesis three tested how feeding patterns change when caterpillars are placed onto host plants originating from south (bold) or north (non-bold) of their natal region. The distance of the movement was either a single (corresponding to <500 km) or a double step (corresponding to 790 km), with the latter representing caterpillars moved from one extreme of the host plant distribution to the other.

		Plant Origin		
		Auckland	Nelson	Banks
Caterpillar Origin	Auckland	NATAL	***single south***	***double south***
	Nelson	*single north*	NATAL	***single south***
	Banks	*double north*	*single north*	NATAL

5.3.4. Data analysis

Each of the three response variables were analysed using a different statistical model appropriate to the nature of the data. Caterpillar feeding activity was continuous variable so linear models on $\log_e$-transformed data were appropriate. For feeding pattern, we used generalised linear models (GLM) with a quasi-Poission error distribution to account for over-dispersion in the data, and for foliage damage we used linear models on arcsine square-root transformed data. All analyses were conducted using the statistical environment R, version 2.11.1 (R Development Core Team 2010). Three plants exhibited no signs of herbivory which suggested that caterpillars either died immediately or escaped, so these records were omitted from all analyses. Inspection of temperature data from the dataloggers detected a temperature gradient within the glasshouse which had the potential to confound our results, so we added mean temperature as an offset to each model.

We tested three specific hypotheses using different combinations of the data (Table 5.1). First, we hypothesised *that herbivores feeding performance is different on their natal compared with novel host plants.* This was tested by comparing herbivory in 'natal' treatments (caterpillars from one region on plants from the same region) compared to 'novel' treatments (caterpillars from one region on plants from a different region). We used two-tailed tests analyse whether herbivory levels increased or decreased due to enhanced caterpillar feeding ability or enhanced plant defences. Second, we hypothesised that *herbivores from the population at the poleward margin of a species distribution exhibit different feeding behaviours from those originating from the middle or equatorial margin of the host plant range.* This required us to analyse the interaction between the natal-novel treatment and caterpillar origin. We used two-tailed statistical tests, analysing the difference in the natal-novel treatments as a measure of feeding generality, with no difference indicating general feeding and a large difference indicating feeding specificity. We then applied post hoc TukeyHSD tests to identify the source of the differences between treatment groups. Finally, we hypothesised that *herbivore-host interactions will change in intensity if herbivore distributions shift away from their historical natal host plants.* This hypothesis is designed to determine firstly whether the species interaction would strengthen or weaken when caterpillars from northerly regions grazed on plants from more southerly locations, and secondly whether an increase in the distance between host and herbivore locations would cause progressively larger changes to herbivory levels. We used two-tailed statistical tests, analysing the effect of direction (north or south) and distance (single or double 'step' movements corresponding to <500 or 790 km distances respectively), and their interaction (Table 5.1). Natal treatments were excluded from this analysis. We had no *a priori* expectation of the direction of this effect, so significance was assessed using two-tailed tests.

5.4. Results

In total, 3000 cavities were made on 618 (4 %) of the 14,455 leaves counted at the end of the experiment, from which 116,954 mm^2 (7 %) of lamina was removed in total over the five month period. Three plants had no evidence of herbivory indicating that the caterpillar had died early in the experiment, and a Grubbs test for outliers identified one additional plant that had much lower levels of herbivory than expected. These plants were excluded from all analyses. The average size of leaves after the experiment (including the area that was damaged) was 2692 mm^2 and there was no significant difference in leaf size among plants from the different regions (ANOVA, $F_{2,84} = 1.929$, $p = 0.152$). Across all plants, there were 3729 abscised leaves, but there was no evidence that the number of abscised leaves was related to any of the herbivory measures (caterpillar feeding, $F_{1,85} = 0.503$, $p = 0.480$; feeding pattern, $F_{1,85} = 0.129$, $p = 0.662$; foliage damage, $F_{1,85} = 3.769$, $p = 0.056$).

Table 5.2: Summary statistics showing mean (and standard error) rates of caterpillar feeding, feeding pattern and foliage damage for each of the treatment groups tested. Groups are rearranged according to the three separate hypotheses tested.

Treatment Group		Caterpillar Damage		Feeding Pattern		Foliage Damage	
		Mean	SE	Mean	SE	Mean	SE
Hypothesis 1:		*Herbivores feeding performance is different on their natal compared with novel host plants*					
	Novel	6.574	0.184	8.724	0.876	0.244	0.014
	Natal	6.760	0.287	11.414	1.639	0.264	0.022
Hypothesis 2:		*Herbivores from the population at the poleward margin of a species distribution exhibit different feeding behaviours from those originating from the middle or equatorial margin of the host plant range*					
Auckland	Novel	6.617	0.252	9.167	1.828	0.248	0.026
	Natal	6.229	0.507	6.600	1.893	0.259	0.043
Nelson	Novel	5.911	0.357	7.900	1.310	0.188	0.023
	Natal	6.685	0.572	10.000	2.179	0.238	0.033
Banks	Novel	7.200	0.270	9.150	1.489	0.295	0.020
	Natal	7.360	0.390	17.500	3.156	0.293	0.038
Hypothesis 3:		*Herbivore-host interactions will change in intensity if herbivore distributions shift away from their historical natal host plants.*					
	2N	6.744	0.440	8.400	2.093	0.257	0.026
	1N	6.515	0.382	7.550	1.360	0.256	0.027
	Ctrl	6.760	0.287	11.414	1.639	0.264	0.022
	1S	6.650	0.301	9.500	1.649	0.244	0.029
	2S	6.387	0.351	10.000	2.477	0.205	0.025

Contrary to our expectation in hypothesis one, we found no significant tendency for caterpillars to have different feeding levels on natal and novel plants (Fig. 5.2: Table 5.2). Caterpillar feeding ($F_{1,85}$ = 0.192, p = 0.662) and feeding pattern ($F_{1,85}$ = 0.343, p = 0.560) were slightly, but non-significantly, higher on natal than novel plants, and likewise there was no discernible difference in foliage damage ($F_{1,85}$ = 0.004, p = 0.950).

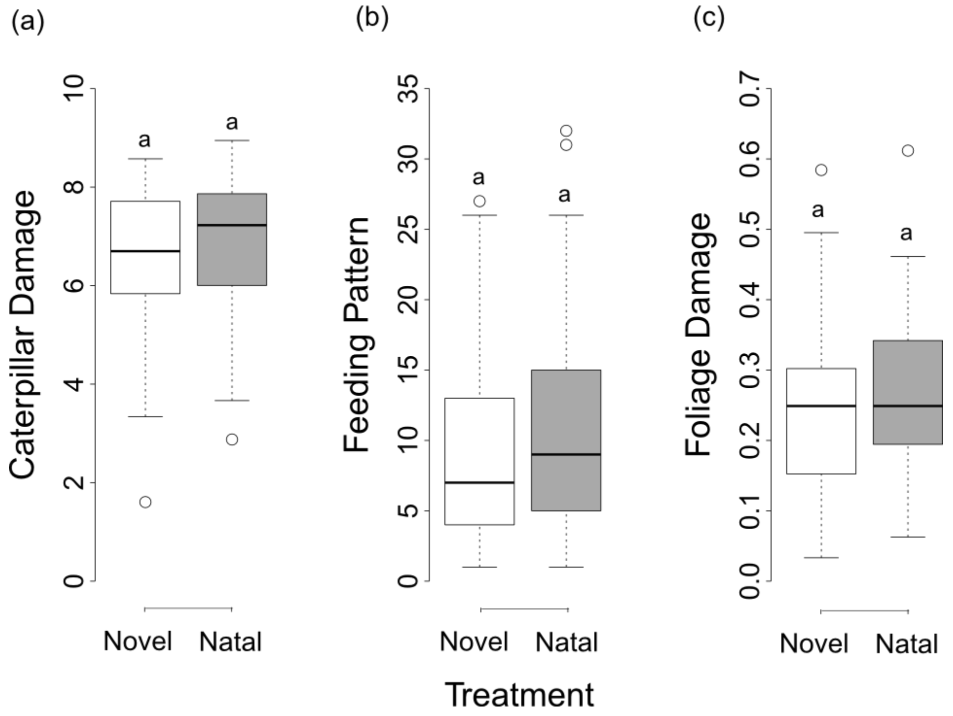


Figure 5.2. Herbivory on host plants from a natal and novel origin. Herbivory levels by caterpillars originating from the same region as their host plant ('natal' treatments, coloured grey) or from host plants from a different region ('novel' treatments, coloured white). Herbivory was quantified by three variables representing: (a) caterpillar feeding (total area damaged per plant, mm2, loge transformed); (b) feeding pattern (total number leaves attacked per plant); and (c) foliage damage (proportion of leaf area removed from leaves fed on, respectively). Thick lines represent the median, boxes the interquartile range and whiskers the range of data points. Mean values are represented by solid circles and outliers by hollow circles and treatments are labelled alphabetically to denote significance, same letters represent $p > 0.05$.

Herbivory difference on natal and novel plants was, however, dependent on the region (hypothesis 2). In all three measures of herbivory there was a significant interaction between the natal-novel treatment and caterpillar origin: caterpillar feeding ($F_{2,81} = 15.694$, $p < 0.001$), feeding pattern ($F_{2,81} = 13.305$, $p < 0.001$) and foliage damage ($F_{2,81} = 42.095$, $p < 0.001$). In line with our hypothesis, all three response variables showed trends that indicated caterpillars originating from poleward margin population fed differently from those from the central and equatorial populations. Overall, feeding by caterpillars from the poleward population was significantly greater than that from central population (Fig. 5.3a) and the plant damage exerted on novel host plants by caterpillars from the poleward population was significantly greater than by caterpillars from the central population (Fig. 5.3c). Significant differences in caterpillar feeding and plant damage were found between natal and novel feeding in both marginal (Auckland and Banks) populations (Fig. 5.3a,c), with caterpillars from the marginal population feeding equally as well (Fig. 5.3b) or significantly more (Fig. 5.3c) on novel host plants. Caterpillars from the central population (Nelson) appeared to feed more effectivelyover a greater area and did more damage on natal than novel plants, however these differences were non-significant (Fig. 5.3; Table 5.2).

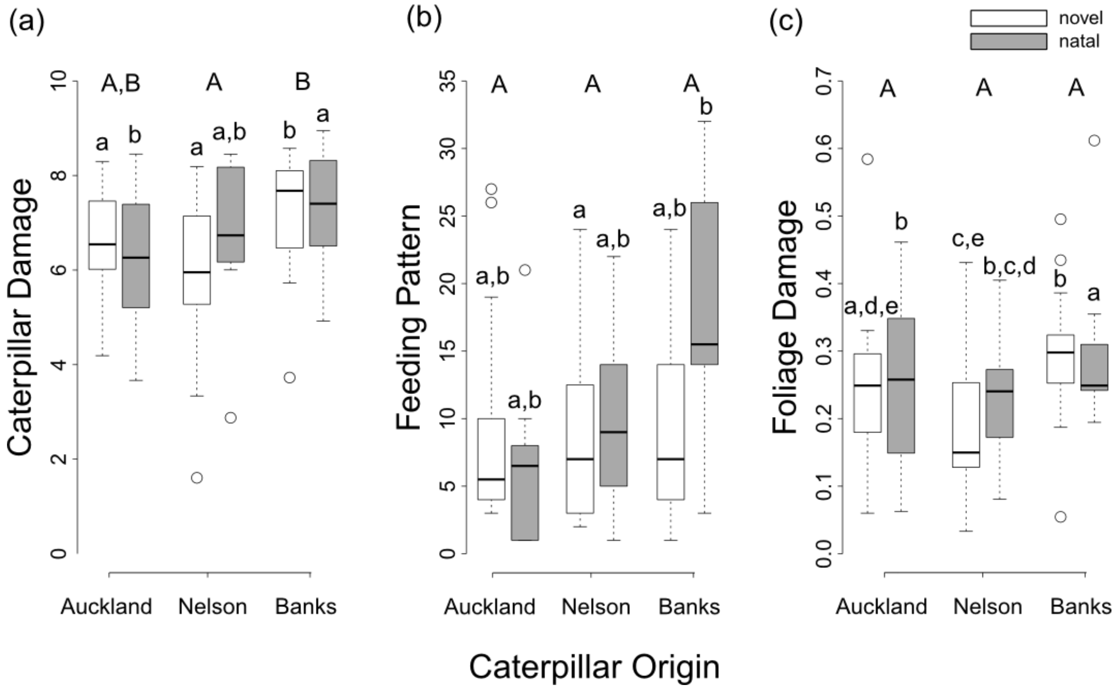


Figure 5.3. Effect on the location of population within the caterpillar range on the preference for natal or novel host plants. Herbivory levels of caterpillars originating from the same region as their host plant (‘natal’ treatments, coloured grey) or from host plants from a different region (‘novel’ treatments, coloured white). The gradient from Auckland to Nelson to Banks Peninsula represents a north to south latitudinal gradient. Herbivory was quantified by three variables representing: ((a) caterpillar feeding (total area damaged per plant, mm^2, $\log_e$ transformed); (b) feeding pattern (total number leaves attacked per plant); and (c) foliage damage (proportion of leaf area removed from leaves fed on)) respectively. Thick lines represent the median value, boxes represent the interquartile range and whiskers represent the range of values. Outliers are represented by hollow circles and treatments are labelled alphabetically to denote significance, same letters represent $p > 0.05$.

Caterpillars placed on plants originating from locations south of their natal origin exhibited a decrease in the amount of herbivory in all three response variables (hypothesis three; Fig. 5.4a,b,c; Table 5.2). Significant interactions were detected between direction (north *vs*. south) and distance (single <510 km *vs*. double 780 km) for all three herbivory variables: caterpillar feeding ($F_{1,54} = 10.533$, $p = 0.002$), pattern ($F_{1,54} = 7.471$, $p = 0.008$), and foliage damage ($F_{1,54} = 17.690$, $p < 0.001$). In all cases, herbivory on southerly plants (i.e. the most likely direction that caterpillars will move) was reduced relative to natal treatments, and the magnitude of that reduction increased with distance of movement for two of the three response variables (Fig. 5.4a,b) although this difference was non-significant.

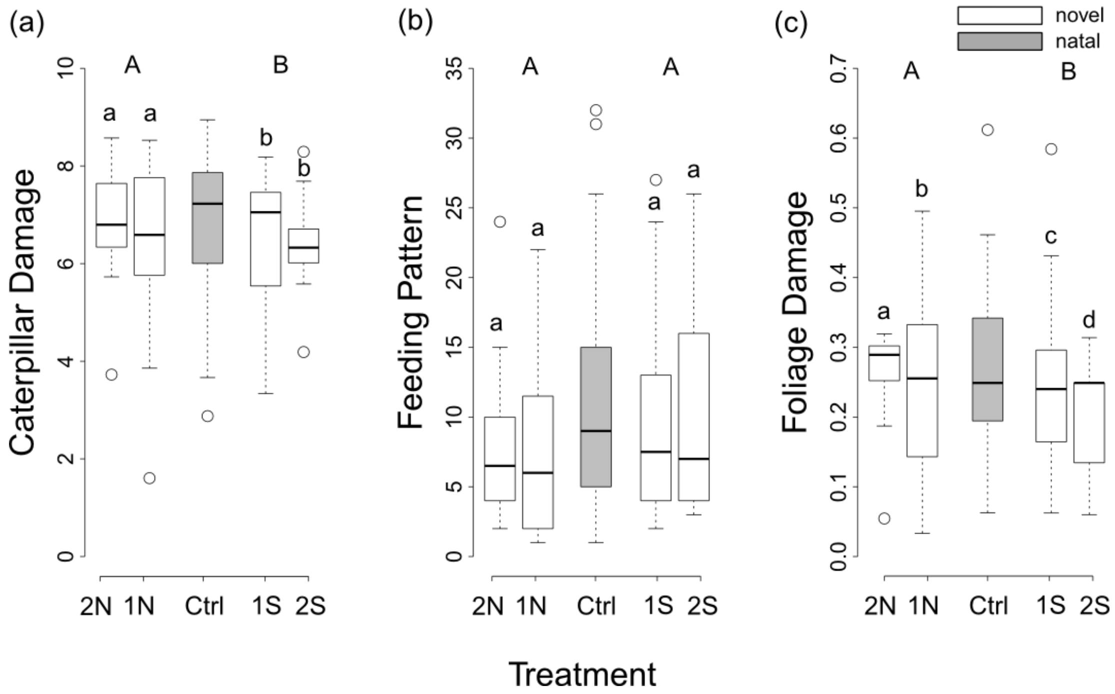


Figure 5.4. Herbivory levels by caterpillars placed on host plants from novel regions across their range. Grey plots represent the natal treatments (caterpillars and host plants originating from the same region) and white plots are novel associations (caterpillar and host plant originate from different regions). Caterpillars were either placed onto plants originating south (S), north (N) or from the natal region (Ctrl) of the caterpillar origin, and movements were either on the order of <500 (1) or ~800 km (2). Herbivory was quantified by three variables representing: (a) caterpillar feeding; (b) feeding pattern; and (c) foliage damage respectively. Thick lines represent the median value, boxes represent the interquartile range and whiskers represent the range of values. Outliers are represented by hollow circles and treatments are labelled alphabetically to denote significance, same letters represent $p > 0.05$.

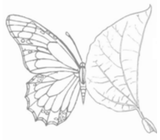
5.5. Discussion

Recent decades have seen a proliferation of empirical and modelling research into the impact of shifting climate envelopes on species movements, yielding insights into the impact of climate change on geographic ranges (Parmesan et al. 1999; Warren et al. 2001; Walther et al. 2002). In this study, we used an *ex-situ* experiment to test the potential limitations to species range shifts that might arise from geographic variation in herbivore-host plant interactions. Our findings shed light on three pertinent issues. Firstly, we found that when all populations were considered together, there was no evidence that caterpillars fed differently on natal ecotypic host plants than novel ones. However, this general pattern obscured regional differences between poleward edge and ‘other’ (central and equatorial edge) populations, with the latter populations exhibiting a tendency to feed more (although non-significantly) on their natal host plants. Therefore our second important finding was that individuals from the poleward edge population did not increase feeding on local host plant topodemes whereas other populations showed signs of enhanced natal feeding. Thirdly, there was evidence that the plant-herbivore interaction reduced in strength as caterpillars were placed onto plants further south of their origin. In combination, our findings indicate that polewards range shifts that may be brought about by climate change may result in a weakening of the plant-herbivore trophic interaction across much of the species range, but that this negative effect may be ameliorated by the ability of poleward edge populations to expand onto novel host topodeme. An expansion of the species range therefore may not be hindered by geographic variation in plant biochemistry.

In the New Zealand plant-herbivore system we studied, we initially found little evidence for differences in feeding of the herbivorous caterpillar, *C. scriptaria*, between their host plant *M. excelsum* in their natal regions compared to novel regions (hypothesis one). Local adaptation is a scale-dependent process, and the spatial scale of a study can influence the results (Levin 1992; Lajeunesse and Forbes 2002). For example, Cogni & Futuyma (2009) found significant differences between populations of the arctiid moth *Utetheisa ornatrix* among continents (Brazil *vs.* Florida), but they found no significant difference in local adaptations among three Brazilian populations separated by 150 km. Our study sites were separated by a minimum of 275 km, so perhaps it was not surprising that we found only weak patterns of local adaptation.

This general result, however, obscured a strong latitudinal gradient in local adaptation (hypothesis two). While caterpillars from the poleward edge population showed no sign of local adaptation, other populations from the centre and northern edge of the species distribution did. For these latter two populations, herbivory was higher on natal than novel plants, perhaps indicating that natal plants pertained lower defences to locally adapted *C. scriptaria* across the majority of their range. There is a substantial amount of empirical evidence suggesting that many species exhibit locally adapted phenotypes (McNeilly and Antonovic 1968; Santamaria et al. 2003; Kawecki and Ebert 2004; Riihimaki et al. 2005; Atkins and Travis 2010), often in response to geographic variation in nutritional quality and the defensive compounds of host plants (Salgado and Pennings 2005). Regionally distinct topodemes can be nutritionally, chemically and genetically distinct across the geographic range of a species (Santamaria *et al.* 2003), leading to local adaptations in the herbivores feeding on those plants.

Some ecological theory suggests that biotic interactions are more intense at lower latitudes (Dobzhansky 1950; MacArthur 1972; Pennings and Silliman 2005), but our findings do not support this: the intensity of interactions was not strongest at equatorial margins as shown by the fact that the northern caterpillars are not eating northern plants more than southern caterpillars are eating southern plants. Our results, in contrast, found that caterpillar feeding was significantly higher on the southern plants of Banks Peninsula (Fig. 5.3a). A review of empirical research on latitudinal gradients of feeding intensity similarly does not support this long held theory, with just 37 % of 38 studies finding more intense herbivory in equatorial regions, and of these, average effect sizes were not significantly different from zero (Moles et al. (2011). The theory also suggests that plants at equatorial range margins will have enhanced defences relative to those at poleward margins as a consequence of feeding intensity gradients. Moles et al. (2011) however found no latitudinal variation in the physical defences of plants. Our results also run counter to the latitudinal plant defence theory. We found no evidence for plant defence to be strongest at the equatorial (Auckland) region, i.e. southern caterpillars did not struggle to eat northern (novel) plants more than northern caterpillars struggled to eat southern plants. Novel feeding was in fact higher in both of these groups and the difference in damage inflicted to novel plants was greater by caterpillars originating from the southern, poleward, population (Fig. 5.3c). We therefore suggest that there is another mechanism generating an interactive effect between latitude and natal/novel host plant feeding. At higher latitudes there was no preference for natal feeding, and conversely feeding was significantly greater on novel plants (Fig. 5.3a,c). We suggest that this poleward population may be able to feed more effectively on novel plant topodemes. If we assume that caterpillars from Banks Peninsula are at the margin of this species range and that evolutionary adaptations occur in expanding populations (Hill *et al.* 2011), then we propose that these populations may be predisposed to efficiently feed upon novel plants.



Further investigation into poleward populations is, however, required to more definitively support this interpretation.

We found significant reductions in herbivory levels when caterpillars fed on host plants from increasingly distant southerly regions (hypothesis three). Most literature on trophic mismatch caused by climate change focuses on the altered phenology of bud burst, reproductive cycles and migration causing restricted nutrient flow to higher trophic levels (Winder and Schindler 2004; Post and Forchhammer 2008; Thomson et al. 2010). However, the disruption of efficient feeding can also be caused by bottom-up effects of reduced quality or absent food sources, with declines in host quality having the potential to disrupt larval survivorship and hence the population size of herbivorous insects (Hellmann 2002). The weakening of such plant-herbivore interactions could potentially counteract any positive population growth or movement caused by warming. As equatorial edge populations typically experience high levels of emigration or extinction, the prevention of poleward edge range expansion could lead to population declines. A decline in host plant quality may also precipitate a switch to alternative host plants, as shown for the butterfly *Euphydryas editha bayensis* in the USA (Hellmann 2002). Although *C. scriptaria* feeds predominantly on *M. excelsum*, it is known to occasionally feed on other species such as *Lophomyrtus bullata*, *Pseudowintera* spp, *Aristotelia* spp, *Coriaria arborea*, *Pennantia corymbosa*, and *Sophora microphylla* (Spiller and Wise 1982), all except for the former are distributed south of *M. excelsum's* limit at 43 °S (GBIF 2012). These species may potentially become more important as host plants for *C. scriptaria* as the climate changes over the coming century.

5.6. Conclusion

Herbivores fed slightly better on host plant topodemes from their natal origins across most of the plants range however, poleward margin populations appeared to feed equally well on novel host topodemes. This suggests that herbivory constraints may not limit this species from expanding at its range margin and that understanding how biotic interactions impact species distributions may improve predictions of range shifts under environmental change.

5.7. Acknowledgements

We acknowledge the support of the Grantham Institute for Climate Change and the Gilchrist Educational Trust for providing funding for this research and the University of Canterbury, New Zealand for hosting this experiment. We thank Auckland, Nelson and Canterbury regional councils for access to forest reserves and Mark and Sonia Armstrong for access to their private land. For the provision of seedlings we are grateful to Rebecca Bell and Naturally Native plant suppliers. Finally we would like to thank Graham Banton, Mike Lewis, Chris and Judith Lakeman Fraser for their assistance with this research.

6

Discussion: Key research findings and conservation recommendations

6 Discussion

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."

(Darwin 1859)

6.1. Exploration of the research question

Darwin's renowned statement magnificently encapsulates the complexities of ecological interactions and the influence of external forces acting on these biotic linkages. A wealth of research has been carried out in the century and a half since and what we can add to this equation is an examination of the complexities of the nature of the environmental drivers acting on these linkages. Within this thesis I sought to untangle interactions, both between causal drivers of change and between the biotic trophic levels on which these drivers act. This was investigated under the overarching aim to research the *simultaneous impact of climate change and land use modification on a tri-trophic species interaction.* To gain an insight into this question, I used five different approaches involving: a review of the ecological literature on land use modification in New Zealand (Chapter 2); utilisation of field observation techniques to investigate what might happen to biotic interactions in a fragmented landscape given temperature rises (Chapter 3); employment of field experiments (Chapter 4) and finally

glasshouse experiments (Chapter 5) to understand how range shifts under climate change have the potential to affect biotic relationships.

6.2. Summary of chapters

This research focused on understanding the direct (Chapter 3) and indirect (Chapter 4 & 5) influence of drivers of global environmental change on forest ecology. I monitored this change using three biotic measures: organism abundance (Chapter 3)and species interactions (Chapter 3). Biotic interactions are not only influenced by these drivers but themselves drive changes in the persistence of biota under conditions of change (Chapter 4 & 5).

Land use modification has drastically altered the New Zealand landscape and in Chapter 2, I found a wealth of empirical and theoretical research reporting widespread ecological impacts. In Chapter 3, I found that multiple drivers of change exert a non-additive impact on biota. The nature and magnitude of that impact was dependent on trophic level and the biotic measure recorded. Biotic interactions were not only influenced by GEC drivers, but combined with these drivers to modify species distribution and abundance. This was exemplified in Chapter 4 which found that the growth of host plants was correlated with herbivore attack rates; the lower the attack rate the greater the growth, suggesting that colonisation may be enhanced in novel areas by a temporary release from herbivory. The two-way nature of this interactive relationship was realised in Chapter 5 which found significant effects of bottom-up control on feeding efficiency. Here, shifting ranges, brought about by climate change for example, are likely to cause an attrition of host-herbivore feeding rates due to suppression in attack rates on novel plant topodemes (distinct regional ecological varieties of organisms).

6.3. Key findings

6.3.1. Interactive effects of multiple drivers

Three main points emerge from this investigation of multiple GEC drivers. Firstly, although main effects exhibit a mixture of positive and negative effects on abundance & distribution when they interact, the net effects are all negative; abundance is reduced, interactions are weakened and distribution restricted. Secondly, climate and habitat fragmentation combine in a non-additive fashion across biotic measures and trophic levels. Thirdly, of these non-additive interactions, both antagonistic and synergistic responses are recorded depending on the trophic level and biotic measure investigated. Plant densities are impacted by the former impact whereas insect densities, the latter. Moreover, interacting drivers exacerbate effects on abundance and ameliorate the effect on the frequency of interactions at higher trophic levels (Chapter 3).

6.3.2. Importance of studying species interactions

Every chapter has demonstrated the importance of studying interactions between species; either from the perspective of the varied influence that pressures exert on trophic levels

(Chapters 2) or from the direct influence that interactions can exert on the abundance and distribution (Chapters 4 & 5).

6.3.2.1. Trophic levels respond differently

Clear patterns have emerged from observational and predictive investigations suggesting that the abundance (Chapter 3) of bottom trophic levels show an inverse response to GEC pressures in comparison to upper trophic levels. It is however clear that the two GEC drivers exhibit antagonistic effects on the abundance of the bottom trophic level, in that one driver ameliorates the impact of the other; whereas the upper levels appear to be affected synergistically. In a review of 171 studies in marine systems, Mullan Crain et al. (2008) found a similar trend in that autotrophs exhibited antagonistic interaction effects and heterotrophs synergistic.

6.3.2.2. Influence of interactions on species persistence & distribution

Field experiments found that levels of herbivory directly correlate with plant growth, indicating a strong effect of top-down control. Plant growth was significantly greater outside the natural range of *M. excelsum* than inside, suggesting a release from suppressive effects of Lepidopteran feeding which benefitted the plant (Chapter 4). Bottom- up control is also evident in this system. Controlled glasshouse experiments found that herbivores are highly sensitive to their food plants. Small differences in plant matter from different regions had an effect on the intensity of feeding even when feeding on the same species (Chapter 5). Given the fundamental empirical influence that species interactions exert on abundance, it appears important to include species interactions in predictions of future population dynamics.

6.3.3. Generalisations *vs*. exceptions: the value of predictions

Ecological investigations can provide fundamental insights for land managers and conservation planners as well as informing political decisions. This often requires broad scale generalisations to be applied to phenomena which are complex in nature. Making generalisations from metaa-nalyses such as the predominant polewards movement of species distributions in climate envelope theories or the negative influence of habitat loss on biota derived from the SAR have been applied to reserve management, corridor creation to name a few. The literature is however rife with exceptions to these general rules. In this thesis although I have identified major trends in this research, there are of course, exceptions in my data. For example, significant interactions were not found for all trophic levels e.g. three way interactions were found for the top trophic levels but not for the bottom (Chapter 3) Even within the same functional unit differences frequently emerge. For example, Schmitz and Suttle (2001) found within the same guild, predatory spiders can have differing impacts on trophic levels.

Working on a small section of a trophic assemblage i.e. one producer, one herbivore and two parasitoids required an awareness that these patterns are unable to accommodate broad scale trends. In fact, it is unlikely that any study will ever have the ability to account for all possible trends. The nature of investigating these broad scale phenomena in a relatively short

time frame of a PhD required the use of limited numbers of species to act as bio-indicators. With more time and resources it would be fascinating to expand study into the broader ecological network linked to this kawakawa tri-trophic interaction, including below ground predators (as yet none are known), pollinators (e.g. kereru and skinks) and hyperparaitoids (e.g. *Mesochorus* sp.). The specific nature of this research however did allow the investigation of global change issues across a national scale, in a variety of experimental approaches and in a relatively short time frame and has provided the basis on which other studies can investigate ecological dynamics in a changing world.

Generalisations were made regarding the investigation of global change drivers. Given climatic changes occur over decades, centuries and millennia, detecting the effects of these changes can be challenging over shorter time frames. One method to do this is by using a surrogate for the aspect of climate change which is under investigation. In this research, I studied a latitudinal gradient to investigate how differences in average temperature and rainfall may impact forest biota. The aim of which was to predict, for a certain increase in temperature for instance, how abundance and biotic interactions may respond. There are of course a number of assumptions about other potential variables that may influence results that need to be made in order to interpret results. With this research being conducted in the field and study sites being up to 800 km apart variations in topography, community assemblage, disturbance regimes etc., will vary between plots. Sites were chosen by remote sensing to limit this variation, however it is important to consider that controls cannot eliminate all external influences in field conditions. In addition, the number of study sites along that latitudinal gradient will determine how possible it is to have confidence in the findings. For example two of the data chapters (3&4) investigated trends across three sites whereas one (Chapter 5) investigated trends across only three sites. The larger the sample size, the better; and given time and resources for further work more study locations would be studied along this latitudinal gradient. However given the challenges associated with climate change research this collection of studies provides novel insights which can be investigated further.

6.4. Conservation recommendations

Maximising conservation gains are a fundamental goal for much ecological research. New Zealand boasts one of the highest proportions of protected land of any nation (Ministry for the Environment 1997), hosts a government department committed to conservation (Department of Conservation 2007), has pioneered several largely successful species recovery programmes (Merton 1992; Clout and Craig 1995; O'Donnell and Sedgeley 2007), and maintains widespread public support for environmental preservation (Craig et al. 1995; Ministry for the Environment 1997). Yet despite all this, the loss of species is ongoing (Craig *et al.* 2000; Department of Conservation 2000; Norton 2000; Walker, Price, *et al.* 2006; Ewers *et al.* 2006) and significant ecological reactions to climatic changes which are a ‘strong possibility’ in the next 100 years (Mcglone and Penman 2001). Advice issued to the New Zealand Government by Landcare Research, Lincoln in 2001 suggested that the most serious threats to biota will largely be experienced through ‘exacerbating pre-existing ecological and biodiversity problems’ and that conservation steps already being taken to reduce the impact of these main factors would help mitigate these issues. Below I assimilate the conservation recommendations that emerge from my own and other empirical investigations into one of the ‘pre-exisiting problems’ in New Zealand: habitat modification. A discussion of how this can be integrated into a multiple stressor approach then ensues.

6.4.1. Recommendations based on the fragmentation literature

6.4.1.1. Maintain the ecological integrity of remaining habitat

The protection of indigenous habitats is fundamental to the persistence of native biodiversity. One approach now being employed to maintain the integrity of ecosystems is the ‘Mainland Islands’ initiative. There are currently five mainland islands in New Zealand’s unique ecosystems, many of which are demarcated with predator-proof fences separating a forest fragment from intensively managed non-conservation land (Department of Conservation 2012). This mainland scheme is built on a “multi-species, multi-threat” approach (Saunders and Norton 2001), which emphasises the interaction between diverse drivers of biodiversity loss alongside the effective management of habitats (Rutledge et al. 2004).

This approach aims to support the persistence of whole communities across entire catchments, and ultimately the restoration of forest ecosystem processes. For example, the Rotoiti Island statement epitomises this approach: describing it as the ‘restoration of a beech forest community with emphasis on the honeydew cycle’ (Butler 1998).

6.4.1.2. *Manage native habitats on private land*

Seventy percent of New Zealand’s landscape is in private ownership (DOC 2000). This land constitutes a range of distinctive New Zealand habitats such as lowland and coastal forest, shrublands, wetlands and tussock-land, many of which have been reduced and fragmented by human activity and are under-represented in the protected area network (Awimbo et al. 1996). Inevitably, these areas host a large portion of native flora and fauna, with 20 % of New Zealand’s threatened vascular plants being confined to private land (Norton 2000). Successful conservation management requires the active assistance of willing landowners (DOC 2000). Governmental initiatives such as The Resource Management Act of 1991 (Walker et al. 2008) and the Forest Amendment Act 1993 have long recognised the value of integrating public and private lands for the conservation of native biodiversity (Norton 2000). The majority of natural habitats on private land still exist due to landowner effort (DOC 2000), and binding conservation agreements on private lands have been formalised since 1977 with the creation of open space covenants under the New Zealand Queen Elizabeth Trust (QEII Trust). The Trust scheme now protects almost 110 000 hectares of private land (QEII National Trust. 2010b). The Trust not only provides legal protection but it offers funding, advice and monitoring services to fence, maintain and eradicate pests from native forest and wetlands. This ensures small isolated fragments of forest persist and brings the landowner added benefits that can raise property values (Halloy 1995; Wratten 2003; QEII National Trust. 2010a). The QEII Trust promotes the regeneration of native species by using seed obtained from local sources, suggests buffering habitat fragments from the surrounding matrix by planting fast-growing extreme-weather resistant species along habitat boundaries (such as *Aristotelia serrata*), and implements schemes to reconnect isolated forest fragments (Porteous 1993).

6.4.1.3. Conservation priorities

As discussed in greater detail in Chapter 2, there are three priorities that arise from literature on habitat fragmentation in New Zealand: optimising the shape of habitat fragments; connecting fragments with corridors and maintaining habitat area above landscape thresholds. In conjunction, these three management suggestions could enhance the amount of core habitat (most similar in quality to historical indigenous forest), connect disjunct sections of this habitat between patches, create passages through which organisms can freely disperse (which may be fundamental if species are tracking their optimum climate envelope) and protect the integrity of remaining fragments by maintaining at a certain level of native habitat cover (for example, 30 % for birds and mammals (Andrén 1994)) in landscapes to aid connectivity.

6.4.2. A multiple stressor approach

Adopting further strategies to protect entire ecological communities through simultaneous targeting of multiple threats may be an effective use of resources. For instance, efforts to improve habitat quality through connecting and increasing fragment size could be combined with appropriate actions to create conservation corridors for shifting species distributions under climate change or to minimise the harmful impacts of pests in New Zealand’s forests.

Fencing of habitat fragments to prevent stock grazing (Smale et al. 2005; Smale et al. 2008), combined with mammalian pest exclusion (Porteous 1993; Didham et al. 2009), would help safeguard native understory shrubs, improving the integrity of floral communities and consequentially improving the integrity of the habitat for faunal communities. Predator proof fences have been promoted as an effective means to preserve forested areas from stoats and other pests (Clapperton and Day 2001), although Scofield et al. (2011) suggested that the 'rate of growth of predator proof fence building is out of proportion to its benefits'. In some cases, however, introduced species can enhance conservation gains and help to restore natural ecological systems. For example, populations of certain non-native birds (Williams and Karl 1996) and possums (Dungan et al. 2002) could provide additional pollination services for native plants. In a similar vein, the non-native gorse (*Ulex europaeus*) can promote rapid habitat restoration through serving as a nursery plant sheltering newly emerging native seedlings (Wilson 1994).

I report with cautious optimism that the majority of interactions in this system are of an antagonistic nature. This is positive from a conservation perspective as the detrimental impacts of antagonistic GEC drivers are likely to be less damaging to biodiversity than synergistic impacts (Didham *et al.* 2007; Brook et al.</i> 2008). However, in attempting to manage these effects, antagonistic stressors are thought to produce management challenges as all stressors involved would simultaneously need to be eliminated in order to see a noticeable recovery (Mullan Crain *et al.* 2008). The authors of this review however suggest that the exception would be when an antagonism is driven by a dominant stressor (as with Folt et al. (1999)). In this situation, as different drivers appear to be dominant in different situations i.e.

depending upon the biotic measure studied and the species (/trophic level) analysed, the former circumstance is more likely the case.

6.5. Concluding remarks

The combined influence of habitat fragmentation and climate change is likely to stimulate ecological surprises globally and in New Zealand. The national–scale of this research has provided insights into how one endemic terrestrial study system has responded non-linearly to multiple environmental change drivers. The synergistic effect of these drivers on densities of species at higher trophic levels combined with the antagonistic responses of ecosystem processes and dispersal patterns, parallels with findings in other studies investigating simultaneous drivers. As such, the species investigated in this thesis may exhibit responses indicative of general trends occurring across trophic levels and biotic measures. This study highlights the fundamental importance of considering that biotic interactions both influence the abundance and distribution of organisms but also are influenced themselves by multiple drivers. Interactions, whether they be within or between abiota and biota have been shown in this thesis to be fundamental research themes in the developing study of global change ecology.

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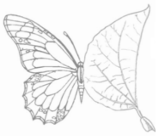

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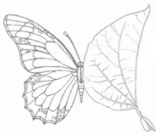

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Exploring Field Sites

West Coast Road to Arthurs Pass

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