`

Apparent Competition Between Native and Exotic Plants Mediated by a Native Insect Herbivore

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Scot Michael Waring

Lincoln University
2010

Abstract of a thesis submitted in partial fulfilment of the
requirements for the Degree of Doctor of Philosophy.

Apparent Competition Between Native and Exotic Plants Mediated by a Native Insect Herbivore

by

Scot Michael Waring

Invasive species can significantly impact native food webs through indirect effects. Examples of apparent competition typically involve a non-native consumer disproportionately affecting one host population in the presence of another. My research finds evidence for apparent competition between two herbs, one invasive and one endemic, and mediated by an endemic insect herbivore. The European pasture herb *Jacobaea vulgaris* (formerly *Senecio jacobaea*), is an invasive weed in several parts of the world, including New Zealand. New Zealand is also home to 19 native species of *Senecio* – thirteen of which are endemic – that support an endemic insect fauna. Some of these insects have since expanded their host range to include the invasive *J. vulgaris*. I examined the relationships between one of those herbivores, the New Zealand magpie moth (*Nyctemera annulata*, Lepidoptera: Arctiidae), *J. vulgaris* and one endemic (*S. wairauensis*) and two native host plants (*S. minimus* and *S. quadridentatus*). In my laboratory assays, magpie moth larvae found *J. vulgaris* as attractive as native host plants and larvae fed only *J. vulgaris* developed at comparable rates to those fed only native hosts. My landscape surveys revealed a strong association between *J. vulgaris* infestations, magpie moth abundance and increased levels of herbivore damage of the endemic *S. wairauensis*. Likewise, *S. wairauensis* was more likely to be present in transects where *J. vulgaris* was rare. There is convincing anecdotal evidence that the native magpie moth became far more abundant because of an invasive weed and my study suggests that this detrimentally affects native plants through population spillback.

Keywords: apparent competition, indirect effects, invasive, enemy release, *Jacobaea vulgaris, Senecio, minimus, quadridentatus, wairauensis, rufiglandulosus, dunedinensis, Nyctemera annulata*, magpie moth, New Zealand

`

Acknowledgements

While my name alone appears on this thesis, there were many others involved and without whom this project would not have been completed. First and foremost: my family. Thanks to my wife, Anna, who encouraged me to pursue a PhD and helped make it happen. She, along with my children, Sequoya, Anja, Ronin and Rigel, suffered with me through the tough times. I'm sorry and thank you. Many thanks to my parents, Lynn and Jayne, and brother, Shane, who helped support us in so many ways and during every step of this crazy adventure and who, along with my aunt and uncle, Russ & Sue, and Anna's family, Marty, Stan, Alison and Ron, helped in overcoming some difficult aspects of this journey. I sincerely appreciate their collective and individual sacrifices. I have an enormous amount of gratitude for my PhD advisor, Jon Sullivan. Unfortunately for many graduate students, they will never experience a mentor with a relentless sense of optimism, a wealth of skills and knowledge, and a love of life & science like I have. I consider myself lucky to have had the experience of working and learning with him. Thank you also to my co-advisors, Simon Fowler and Roddy Hale, for their support, particularly at vital points along the journey. Thanks also to the ecology graduate students (too many to list here) all of whom taught me something and most of whom made the complicated process of a doctoral program much more enjoyable. Without the many field assistants that helped with data collection in the final season I would not be writing this now: Ronny Groenteman, Raviv Carasuk, Sam Abercrombie, Tim Forrest, Leyla Cardenas, Gordon Gundlach, Katrina Wisniewski, Sequoya Waring, Mo Correll, John Mulhouse, Fannie Demarque, Virginie Laberge, Heather Rickard, Maren Poitras, Hamish Maule and Myles McKintosh. Much appreciation also to Corbin Jones and Judge Rebecca Knight. I received support from several people at Lincoln University and Landcare Research – particularly Simon Fowler (again), Hugh Gourlay, Lynley Hayes, Lindsay Smith, Stella Belliss and Brad Case. Thanks also to Rob Dunn, Andrea Lucky and the Dunn Lab at NCSU for their edits and support. Great thanks to Landcare Research for funding my PhD programme and for supplying research resources that were unavailable through the university. I appreciate the use of collection data from various national herbaria and the individual custodians of National Vegetation Survey data (listed in Appendix A) for letting me use their data in my analyses. Thank you to Sabrina Leucht, the Department of Conservation and the West Coast and Canterbury Conservancies for facilitating my access to Crown Lands for this research. Thank you also to the people of New Zealand for the experience of a lifetime, your support and hospitality and for such a comprehensive education (*sensu lato*) in your beautiful country.

`

Table of Contents

`

`

List of Tables

`

List of Figures

`

`

Chapter 1

Introduction

1.1 Species Invasions

In most geographic areas world-wide, the last several decades have seen the rate of successful establishment by non-natives accelerate, mainly through anthropogenic habitat disturbance and species introductions by humans (both intentional and unintentional) (Carlton, 1996; E. Grosholz, 2002; E. D. Grosholz, 2005; Keller & Lodge, 2007; J. M. Levine, Adler, & Yelenik, 2004; J. M. Levine, M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulus and S. Lavorel, 2003; J. L. Lockwood, Cassey, & Blackburn, 2009; McKinney & Lockwood, 1999; Pimentel, Zuniga, & Morrison, 2005; Pyšek et al., 2004, p.4; Vitousek, D'Antonio, Loope, & Westbrooks, 1996; Worm et al., 2006). While the vast majority of potential colonization events are unsuccessful, naturalised species are implicated in facilitating subsequent species invasions by changing habitat characteristics and ecosystem functioning (Adams, Pearl, & Bury, 2003; Altieri, van Wesenbeeck, Bertness, & Silliman, 2010; Bourgeois, Suehs, Vidal, & Médail, 2005; Bruno, Stachowicz, & Bertness, 2003; Dickie, Koide, & Steiner, 2002; Fridley et al., 2007; Carolyn M. Malmstrom, Shu, Linton, Newton, & Cook, 2007; Molina, Massicotte, & Trappe, 1992; Rowles & O'Dowd, 2009; Stachowicz & Byrnes, 2006; Van der Putten, 2009). While this increases the biodiversity of a habitat in the short-term, the native community can often see a long-term decline in species numbers as a result – sometimes dramatically so (Gurevitch & Padilla, 2004; O'Dowd, Green, & Lake, 2003; c.f. Dov F. Sax & Gaines, 2008; Simberloff & Von Holle, 1999).

Species invasions and their direct impacts on native habitats and biological communities are increasingly well documented (Allen, 2006; B. J. Brown, Mitchell, & Graham, 2002; Ehrenfeld, 2003; Juliano & Lounibos, 2005; Kenis et al., 2009; J. L. Lockwood, Hoopes, & Marchetti, 2007; Sher, Marshall, & Gilbert, 2000). Nevertheless, many of the mechanisms underlying the impacts of invasions and how invaded communities respond are still not well understood (Kenis, et al., 2009; Lau & Strauss, 2005; Martinez & Medel, 2002; Pages & Michalet, 2006; Pearson, D. E., McKelvey, & Ruggiero, 2000; D. E. Pearson & Callaway, 2003; Rand, Russell, & Louda, 2009; Schoener, 1993; E. M. White, Wilson, & Clarke, 2006). While progress is being made on understanding the direct effects of species invasions on native species, communities and food web interactions, indirect effects have been less frequently studied and are less well understood despite being important (J. M. Levine, M.

`

Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulus and S. Lavorel, 2003; Simberloff & Von Holle, 1999; E. M. White, et al., 2006; Wootton, 1994a).

Indirect effects between species occur when one species affects another by altering the abundance and/or behaviour of one or more intermediate species. Indirect effects can alter the trophic structure and ecosystem function of a community in sometimes inconspicuous ways. For example a predator can cause an increase the biomass of particular vegetation types by suppressing or changing the behaviour of herbivore populations (Ripple & Beschta, 2005 and references therein). It is increasingly believed that the occurrence of indirect effects has broad implications for all ecological disciplines including agriculture, evolution, biological control and conservation (Adams, et al., 2003; Giovanelli, Vieira, & Silva, 2003; Louda, Arnett, Rand, & Russell, 2003; C. M. Malmstrom, McCullough, Johnson, Newton, & Borer, 2005; Carolyn M. Malmstrom, et al., 2007; Martinez & Medel, 2002; Meisner, De Boer, Gera Hol, Krumins, & Van Der Putten, 2009; Miller & Travis, 1996; Ortega, Pearson, & McKelvey, 2004; Pearson, D. E., et al., 2000; D. E. Pearson & Callaway, 2003; Schoener, 1993; Styrsky & Eubanks, 2007; E. M. White, et al., 2006).

Direct ecological interactions between two species, like predation and interference competition, are relatively straightforward conceptually. For example, when non-native species establish in a habitat they can alter resource availability by out-competing native species for particular resources such as nutrients, habitat or mutualists. However, the underlying mechanisms of indirect effects are typically not as obvious because they are complex and can often be unpredictable. Despite this, indirect effects appear to exert strong pressures on native food webs. White et al. (2006) discussed several specific types of indirect effects of non-indigenous species invasions and how these impact (or potentially impact) native habitats and Simberloff and Von Holle (1999) detailed some of the strong influences species invasions have on ecosystems just through indirect effects. Both reviews argued that indirect effects appear to be common and highly influential in altering natural communities through restructuring food webs in invaded habitats and similarly concluded that there is a lack of comprehensive research on these phenomena.

In this chapter, the current state of knowledge of indirect effects is summarized. The summary is written with particular emphasis invasion facilitation, apparent competition and community-level impacts with examples for each. I conclude with a tie-in to the study system for my doctoral thesis and the important role indirect effects may play.

`

1.2 Invasion Facilitation

Increasingly, credence is being given to idea of interspecific facilitation as an important contributing factor to species invasions (J. L. Lockwood, et al., 2007; Ingrid M. Parker & Gilbert, 2007; Richardson, Allsopp, D'Antonio, Milton, & Rejmanek, 2000; Simberloff & Von Holle, 1999; E. M. White, et al., 2006). In these instances, invading species act unilaterally or in concert to facilitate and accelerate invasion success. In some cases invasions are facilitated through *direct mutualisms* where species interact with one another to affect their respective success (Aizen, Morales, & Morales, 2008; Christian, 2001; Jiu et al., 2007; Ness & Bronstein, 2004; M. A. Parker, 2001; Richardson, et al., 2000; Rudgers, Mattingly, & Koslow, 2005). The species engaged in direct mutualisms act on one another in a mutually positive manner and through direct interactions.

Co-facilitation differs from direct mutualism in that species may not interact with one another directly. Co-facilitation is affected through indirect mutualism or facilitative mutualism and can be complex and is usually context-driven (Schoener, 1993). Indirect mutualism can even occur between pairs of organisms that, historically and theoretically (and for all practical purposes), are antagonistic in their behaviour to one another (i.e. plant-herbivore, predator-prey, parasitoid-prey, disease-host), however in these instances they mutually assist one another in the presence of other species or novel food webs (J. L. Lockwood, et al., 2007; Simberloff & Von Holle, 1999; E. M. White, et al., 2006). So although these species they may have a +/- relationship (consumer-host), their net relationship in the new habitat is +/+ by contributing to each other's success relative to their respective competitors. Lockwood et al. (2007) found that potential invaders with a facilitator(s) are more likely to be successful than species without such counterparts. Richardson et al. (2000) concurs and found that many invaders have a higher probability of establishing with a facilitator species that is already present in the new habitat. Perhaps the most well-documented example of invasion facilitation is from the invasion of an ant and its impact community structure and function on Christmas Island (O'Dowd, et al., 2003).

Ants can have a disproportionately dramatic impact on the community that they invade because of a combination of factors that include eusociality, defence/aggression behaviours and numerical dominance (Holway, Lach, Suarez, Tsutsui, & Case, 2002; Holway & Suarez, 1999; Suarez, Holway, & Ward, 2005; Tsutsui & Suarez, 2003). In the early 20th Century, the yellow crazy ant (*Anoplolepis gracilipes*) was accidentally introduced to Christmas Island. Where it naturalized, the ants decimated populations of native red land crabs (*Gecarcoidea natalis*), an herbivore that is primarily responsible for preventing establishment of non-native

`

plants and snails in island forests, primarily through foraging. In areas where the crab populations were diminished in size or extirpated by the ants, several species of non-native plants and land snails were able to establish. As a further result of the ant’s proliferation, nine different species of exotic, honeydew-producing scale insect (Hemiptera: Coccoidea) were able to establish where they were tended and protected by the ant. The scales were ultimately found to be dependent on the yellow crazy ant since they fail to persist in locations where ants were experimentally removed (Abbott & Green, 2007). Presence of these scales mutually enhanced the fitness and fecundity of the ants by supplying them with an abundant supply of carbohydrates (honeydew) thereby further increasing the range and abundance of both taxa on the island. However, the trophic cascade on Christmas Island reached a crescendo when sooty mould (Fungi: Ascomycota), which thrives on the excess honeydew produced by the scales, began to blanket these areas. The overabundance of sooty mould more negatively affected indigenous vegetation and caused native canopy dieback, which in turn increased the amount of light that reached the forest floor. The dramatic increase in light to the ground favoured exotic flora over native vegetation. In combination with the demise of the red crabs, the increase in sunlight ultimately and dramatically changed the composition of the jungle to predominate with non-native trees and shrubs. In retrospect, the arrival of a single ant species effectively facilitated numerous invasions of the Christmas Island ecosystem by non-native plant and arthropod species, fundamentally altering the community composition of the island.

Another example of invasion facilitation was detailed by Power and Mitchell (2004) where a grassland plant and pathogen community was manipulated to better understand how the constituent species interacted. Plots that contained native and non-native grasses were manipulated to control for presence of the generalist pathogen, barley yellow dwarf virus (BYDV). From some of the plots, an exotic host plant, wild oats (*Avena fatua*), was also removed. An important characteristic of *A. fatua* is that it is able to tolerate higher loads of the pathogen than the native grasses and carries a much higher titre. From this, a picture emerged that showed there was strong virus spillover from *A. fatua* to all three of the other grass species monitored with significant, negative impacts on growth and production of the populations of two of those native species. By acting as a reservoir of BYDV, virus abundance remained consistently high in the landscape and served to suppress the less-tolerant native grasses making *A. fatua* the *de facto* dominant species in the community. Not unimportantly, BYDV and *A. fatua* have origins in the old world, where they presumably coevolved. Both species have since naturalized in North America, although it is likely that these naturalizations occurred at different times since BYDV can only be transmitted horizontally and only by infected aphids (Mitchell et al., 2006). In its native range *A. fatua*

`

and virus complex are considered to interact in an antagonistic relationship of host and pathogen: virus infects plant → plant's fitness reduced → natural selection for resistant/tolerant genes → ensuing arms race. In this system, however, evidence suggests that the dual introduction of the plant and the pathogen is a likely contributor to their individual success as invaders in grasslands where *A. fatua* competes with native grasses. In essence, the presence of this exotic pathogen facilitated the rise and dominance of its exotic host, resulting in a dramatic change in community structure.

In the both cases of facilitation described above, species act in concert to improve their success and relative fitness. Although they occur in novel food webs, in both of these cases (BYDV and *A. fatua*, yellow crazy ant and scale insects) the species directly interact. However there are also indirect effects on other species in the community (e.g. insects that obligately use native plants), which are negatively affected in both scenarios. Like other types of indirect effects, the facilitative mutualism mechanism that causes one species to affect another in the presence of a third is likely more common than previously recognized. This is certainly the case with one of the better known (but still often ignored) forms of indirect effect known as apparent competition.

1.3 Apparent Competition

Apparent competition occurs when two or more prey species, that may or may not utilize a common set of resources, share a common natural enemy and affect one another with impacts at the population level (Holt, 1977). In such instances one of the prey species will be preferred or can be fed upon more easily by the consumer (Blais & Maly, 1993; Bonsall & Hassell, 1998; Caccia, Chaneton, & Kitzberger, 2006; Chesson, 1983; Groner & Ayal, 2001; Hamback & Bjorkman, 2002; Langer & Hance, 2004; Libbrecht, Gwynn, & Fellowes, 2007; Morris & Lewis, 2002; Pastorok, 1981; Reitz, Funderburk, & Waring, 2006) and like direct competition, exclusion of the less apparently competitive species can result (Gause, 1934). Sometimes a dominant apparent competitor can also precipitate a significant increase in the population size of a shared consumer while still being more tolerant to predation pressure (like *A. fatua* in the example with BYDV above). A "population spillover" can result from this situation, where an inflation of a shared consumer's population on one host causes an alternative host to experience higher numbers of consumers. Spillover happens when these consumers move from areas of high density to low density or as they disperse through the landscape.

`

True competition can be contrasted with apparent competition by the mechanisms that cause the changes in population size. True competition is already acknowledged by ecologists as important in structuring natural communities, as well as a driving force behind natural selection and evolution (Badano, Cavieres, Molina-Montenegro, & Quiroz, 2005; Barrat-Segretain, 1996; Brose & Tielborger, 2005; Case, 1990; Corbin & D'Antonio, 2004; Finn & Gittings, 2003; Flores & Yeaton, 2000; Force, 1985; Forstmeier, Bourski, & Leisler, 2001; Kupferberg, 1997; McEvoy, Rudd, Cox, & Huso, 1993; Sher, et al., 2000; van Veen, Morris, & Godfray, 2006). But where pressures underlying interference and exploitation competition are typically straightforward to observe, those driving apparent competition are generally more complex, less conspicuous and may be inadvertently overlooked (Bonsall & Hassell, 1997; Chaneton & Bonsall, 2000; Connell, 1990; Denno, 1995; Holt, 1977; Holt & Lawton, 1993; Kelly, Paterson, Townsend, Poulin, & Tompkins, 2009; Morris & Lewis, 2002; Orrock & Witter, 2009; Power & Mitchell, 2004; Rand, 2003; Sessions & Kelly, 2002; Tompkins, Draycott, & Hudson, 2000; Turchin, 2003; van Veen, et al., 2006; E. M. White, et al., 2006). Regardless of its often-inconspicuous nature, apparent competition has been found to be integral in structuring and altering natural communities (Bonsall & Hassell, 1997, 1998; Dangremond, Pardini, & Knight, 2010; Hatcher, Dick, & Dunn, 2006; Holt, 1977; Kelly, et al., 2009; Lau & Strauss, 2005; Libbrecht, et al., 2007; Morris & Lewis, 2002; Morris, Lewis, & Godfray, 2004; Power & Mitchell, 2004; Rand, 2003; Reitz, et al., 2006; Rott & Godfray, 2000; Settle & Wilson, 1990; Valladares, Salvo, & Godfray, 2001; van Veen, et al., 2006). As suggested in most of these manuscripts, relatively little research on apparent competition's impact to communities has been carried out – particularly in proportion to its likely influence and their authors suggest that greater attention should be paid to this phenomenon.

Some of the best documented examples of apparent competition are incidental and come from studies of classical biological control. In this field, practitioners are charged with deliberately adding species to food webs to achieve a specific, anthropocentric goal. Although the overall investment in post-release monitoring is still paltry, review of specific examples of biological control reveal that that unintended indirect effects (under the umbrella definition of "non-target effects") can occur.

Perhaps the highest profile example of such inadvertent, indirect effects comes from an American biological control program for control of Eurasian thistles (particularly Musk thistle, *Carduus nutans* complex) that saw the importation and release of the flowerhead weevil, *Rhinocyllus conicus*, in 1969 (Louda, 2000). Although *R. conicus* was not anticipated to have any adverse effects on native thistles based on pre-release testing (H. Zwölfer &

`

Harris, 1984), Louda (2000) found abundant evidence of non-target plant use by *R. conicus.* She demonstrated that this feeding damage had a dramatic, negative impact the fitness of the individual native thistles that was likely to translate to population-level effects. Subsequent analyses showed that habitat use and direct competition with grasses had a greater negative influence on Musk thistle abundance and persistence than did the pressure generated by the weevil (Louda, et al., 2003; Louda et al., 2005; Rand, et al., 2009). Further examination of the system by Louda et al. (2005) lead to the conclusion that invasive thistles, which are still escaping significant control, are acting as reservoirs for the flowerhead weevil and that there is evidence of weevil spillover onto native thistle species at the local spatial scale. The final verdict is that the flowerhead weevil is responsible for mediating apparent competition in favour of the Musk thistle and to the detriment of natives.

In another example of an unanticipated, indirect effect resulting from a biological control effort, Carvalheiro et al. (2008) describes a situation in Australia where an introduced insect herbivore established and directly affected populations of the native parasitoid community. The Bitou bush seed fly, *Mesoclanis polana* (Diptera: Tephritidae), was introduced into the southern areas of Australia in 1996 to in an attempt to control the invasive costal herb, Bitou (*Chrysanthemoides monilifera* ssp. *rotundata*), by limiting its seed production (Edwards & Brown, 1997). Surveys carried out following its introduction found that *M. polana* had a negligible impact on limiting Bitou recruitment from seed (Adair & Bruzzese, 2000; Noble & Weiss, 1989). Collections and dissections of *M. polana* revealed that this introduced biocontrol agent was highly parasitized by at least three species of native parasitoid that also use native insects as hosts (A. J. Willis & Memmott, 2005). Carvalheiro et al. (2008) concluded that the presence of *M. polana* in the landscape, while failing to significantly limit the fitness of its target host, was causing an increase the populations of these shared parastoids. Furthermore, the spillover of these parasitoids from *M. polana* onto native seed-feeding insects was suppressing populations of the latter.

The examples of the flowerhead weevil and the Bitou bush seed fly both illustrate the effect of predator spillover and how proximity of the non-target host populations to target hosts can increase the vulnerability of the former to the spillover effects. The examples above also demonstrate how indirect effects can pose an important challenge for biological control programs. Indirect effects like these can alter entire natural communities by changing the way species interact, by fundamentally changing the type and level of existing connections, and by altering the overall community composition. Several of the following documented cases of

`

species invasions and introductions exemplify the way in which indirect effects can have strong, community-level impacts.

1.4 Community Impacts

Williams et al. (2002) examined several food webs and theorized how the *vast* majority of species in a community are impacted when perturbations, as a result of an invasion, flow through a community food web. These changes often disrupt the relative stability of the existing food web and can leave a natural community susceptible to further invasions (Chaneton & Bonsall, 2000; E. D. Grosholz, 2005; J. L. Lockwood, et al., 2009; J. L. Lockwood, et al., 2007; O'Gorman & Emmerson, 2009; D. E. Pearson & Callaway, 2003; Richardson, et al., 2000; Simberloff & Von Holle, 1999; van Veen, et al., 2006; Von Holle, 2005). An acute example of this is the yellow crazy ant invasion of Christmas Island, which was discussed above. This type of scenario was termed "invasional meltdown" by Simberloff and Von Holle (1999) and, although it is an extreme example, it illustrates how communities experience changes in the wake of species invasions and become destabilized as a result.

The establishment of the yellow crazy ant on Christmas Island also represents a "trophic cascade", which occurs from downward dominance by a predator on prey in the community thereby releasing organisms at the next lower trophic level. While a majority of the well-documented cases of trophic cascades are taken from marine and aquatic ecosystems (e.g. Lavrentyev, Gardner, & Yang, 2000; Rodriguez, Becares, Fernandez-alaez, & Fernandez-alaez, 2005; Simon, Townsend, Biggs, Bowden, & Frew, 2004; D.R. Strong, 1992) there are a growing number of terrestrial examples (e.g. Fortin et al., 2005; O'Dowd, et al., 2003; Simberloff & Von Holle, 1999; D. R. Strong, Whipple, Child, & Dennis, 1999). Like the examples above of apparent competition, much of the documented evidence of trophic cascades is from biological control attempts gone awry. As is often the case, the unintended consequences (non-target impacts) are felt beyond the one or two non-target species selected for study and can have a significant effect on the greater ecological community. Some of the previously mentioned examples of biological control can be further used to illustrate this.

In a comprehensive review on impacts to native thistle communities by *R. conicus,* which was introduced to control Musk thistle, Louda (2000) reported that there are at least five native insects recorded to feed on native wavyleaf thistle (*Cirsium undulatum*). These species only use this host and are unable or unwilling to use the abundant invasive, Musk thistle. This is similarly true for a native butterfly species, the swamp metalmark (*Calephelis muticum*) (Lepidoptera: Riodinidea), which relies solely on its host plant, swamp thistle (*Cirisum*

`

muticum), for food and reproduction (Louda et al., 1998). Louda (2000) also noted an inverse correlation between population size of a native tephridid fly (*Paracantha culta*) and the number of flowerhead weevils in a given area. Obviously the combination of the flowerhead weevil's host preference combined with the native insects' limited host range is likely to have far-reaching impacts to the survival of the wavyleaf thistle's fauna. It is a similar situation for both the Platte (*C. canescens*) and Pitcher's thistle (*C. pitcheri*) which both support unique, native insects as well. All of these native thistles are preferentially attacked by *R. conicus*, including *C. pitcheri* which is already considered a rare, federally protected species (Louda, 2000).

Researchers tracking the attempted control of spotted knapweed (*Centaurea maculosa*) found that the introduction of the gall fly (*Urophora affinis*, Diptera: Tephrididae) caused enormous impacts in the grassland community where it established. Native deer mice (*Peromyscus maniculatus*), which are considered mainly granivorous, switched to preferentially feeding on the introduced gall fly maggots. They changed their behaviour so much that they began switching microhabitats in winter to take advantage of the abundant novel food source (Pearson, D. E., et al., 2000). It was also normal for these deer mouse populations to experience a decline in the wintertime due to a seasonal decrease in food availability. However, Ortega et al. (2004) found that in habitats where introduced gall flies had naturalised there was double the number of deer mice, primarily from lower-than-expected winter population declines. The increase in mice generated dramatic changes to the trophic structure of the community through increased seed and arthropod predation by mice. Further examination found that increased mouse survival was correlated with a threefold-increase in the number of mice testing seropositive for the Sin Nombre virus (SNV) compared to previous years. SNV is the causal agent of hantavirus pulmonary syndrome (HPS) in humans and this increase in mouse infection rates was considered an indirect effect of the gall fly introduction by the authors.

Another notable point involving some of the cases of biological control outlined above is that, although many instances of indirect impacts and apparent competition involve organisms that have prior coevolutionary links, they also often involve species that have never encountered one another. Unlike the flowerhead weevil and BYDV, which still use their original host plants, Bach (1991) outlines a case in point of this type of interaction that ties together multiple invasive species with completely novel associations. This example is found in Hawai'i where serendipity and ecological fitting resulted in a multitrophic mutualism by three previously-allopatric species in a novel habitat. The mutualism is formed from an African ant (*Pheidole megacephala*), a South American scale insect (*Coccus viridus*) and an Asian plant

`

(*Pluchea indica*) that established on a Pacific island thousands of kilometres from any of those places. Like many other species of ants, *P. megacephala* tends a range of hemipteran insects, including scales. *Coccus viridus*, like other soft scales, produces honeydew that is consumed by the ants and in return for protection from potential predators and parasitoids. The presence of patrolling ants benefits the plant by significantly decreasing the amount of damage from other herbivores, while preventing the build-up of honeydew and build-up of sooty mould. For its part, *P. indica* is a widespread invader found in high densities which allow the polyphagous *C. viridus* and its tender ants to expand their geographic distribution into areas that are otherwise lacking in suitable hosts, like habitats characterised by salinity, marshes and high levels of disturbance where *P. indica* is common. In this case all three exotic species benefit from one another's presence, despite the fact that this community is formed from an amalgamation of immigrants that have no prior association.

1.5 Indirect Effects of Novel Plant-Herbivore Associations

As in the case of some of the organisms above, many herbivorous insects are able to make use of novel host plants which can potentially lead to indirect effects in a food web following an introduction or invasion of a plant or insect herbivore. The practice of using novel hosts is referred to in the literature as "host range expansion" (in cases where the original host is still occasionally used) and "host-switching" (where the original host is no longer used or is absent) (e.g. Agosta, 2006; S. M. Fraser & Lawton, 1994; Hanks, Millar, & Paine, 1995; Keane & Crawley, 2002; Velasco & Walter, 1993).

There may be several fitness-enhancing advantages to these strategies. For example, a number of parasitoids and predators use host plant volatiles to track herbivores (Allmann & Baldwin, 2010; Bjorkman, Larsson, & Bommarco, 1997; Bruinsma et al., 2009; de Boer, Hordijk, Posthumus, & Dicke, 2008; Grosman et al., 2005; Kappers, Verstappen, Luckerhoff, Bouwmeester, & Dicke, 2010; Puente, Magori, Kennedy, & Gould, 2008; Soler et al., 2007; Tentelier & Fauvergue, 2007; Unsicker, Kunert, & Gershenzon, 2009). By using an alternate host plant, the composition of volatiles emitted during feeding may fail to attract consumers, thereby providing herbivores with enemy-free space and a decrease in predation pressure (Fox & Eisenbach, 1992; Gratton & Welter, 1999; Grosman, et al., 2005; Oppenheim & Gould, 2002; Rossbach, Löhr, & Vidal, 2006b; Singer & Stireman, 2005; Stamp, 2001; Vet & Dicke, 1992). Obviously this may enhance fitness for herbivores enough to select for those that engage in host-switching, assuming there is little difference in nutritional quality (J. M. Brown, Abrahamson, Packer, & Way, 1995; Gratton & Welter, 1999; Grosman, et al., 2005; Holt & Lawton, 1993; Velasco & Walter, 1993; Zangerl, Huang, McGovern, & Berenbaum,

`

2002). Superior nutritional quality of an alternate host may also trigger host-switching behaviour (Bernays & Chapman, 1994; Brazner, Aberdeen, & Starmer, 1984; Chaneton & Bonsall, 2000), as may competition (Denno, 1995; Feder, Reynolds, Go, & Wang, 1995; Forbes, Fisher, & Feder, 2005; Fricke & Arnqvist, 2007; Messing & Wang, 2009), or the relative abundance of a particular plant (Graves & Shapiro, 2003; Horton, Capinera, & Chapman, 1988; D. R. Strong, Lawton, & Southwood, 1984). Most often it is likely to be a combination of factors (Gassmann, Levy, Tran, & Futuyma, 2006 and references therein).

One important prerequisite is the possession of traits that enable an herbivore to make use of a particular host plant, such as ovipositional cue detection, phytochemical/nutrient acquisition and use, and the ability to detoxify potentially harmful compounds. To describe this concept of preparedness, Janzen (1985) introduced the term “ecological fitting”, which encompasses all aspects of an organism’s ability to persist in novel environments. Particularly important in this endeavour is the ability to utilize novel resources and form novel associations. Agosta (2006) elaborated on this concept in reference to insect-host plant associations and discussed how species that may have no close co-evolutionary history can still form novel associations based on recognizable and/or compatible traits. This means that invaders that are ecologically fitted to interact with species in invaded communities are not only more likely to establish, but the associations that they form can cause significant perturbations of the food web in which they incorporate themselves.

There are several documented cases where exotic species have made use of novel hosts and trophic resources in their new range (Aizen, et al., 2008; B. J. Brown, et al., 2002; Crowl, Crist, Parmenter, Belovsky, & Lugo, 2008; Didham, Tylianakis, Hutchison, Ewers, & Gemmell, 2005; Kenis, et al., 2009; Koch, Venette, & Hutchison, 2006; Louda, et al., 2005; Ness & Bronstein, 2004; Sessions & Kelly, 2002; Styrsky & Eubanks, 2007; Verhoeven, Biere, Harvey, & van der Putten, 2009). In the same respect, many native insects have shown the ability to make use of exotic and invasive novel host plants (Agrawal, 2000; Auerbach & Simberloff, 1988; Gratton & Welter, 1999; Grosman, et al., 2005; Holmes, Dennill, & Moll, 1987; Keeler & Chew, 2009; Lau & Strauss, 2005; Louda, 2000; Louda, et al., 2005; Mitchell, et al., 2006; J. J. Sullivan, Winks, & Fowler, 2008). In both cases it is generally presumed that ecological fitting, host abundance and factors leading to greater or equal fitness (be it from higher nutritional value or the presence of fewer natural enemies) are the primary factors leading to the incorporation and use of novel hosts. This supports the possibility for a potential ecological scenario that was suggested by White et al. (2006), where native insect herbivores could make use of invading plants and create a population “reservoir”. The

`

resulting spillover of herbivores onto native species could facilitate apparent competition between the abundant weed and the herbivore’s native host plants. This, in turn, could have could have dramatic community-wide implications for individual native species that use those plants, as well as the intensity of biotic resistance produced by the community at-large.

One possible example of this scenario is found in the interactions between the native magpie moth of New Zealand (*Nyctemera annulata*, Lepidoptera: Arctiidae), the invasive weed, tansy ragwort (*Jacobaea vulgaris,* until recently *Senecio jacobaea*) and the magpie moth’s native

Table 1.1 - *Senecio* species in New Zealand, their biostatus and naturalisation period (for exotic species).

Species	**Biostatus**	**Naturalisation**
S. banksii Hook.f.	Endemic	–
S. carnosulus (Kirk) C.J.Webb (1988)	Endemic	–
S. dunedinensis Belcher	Endemic	–
S. glaucophyllus Cheeseman	Endemic	–
S. hauwai Sykes	Endemic	–
S. kermadecensis Belcher	Endemic	–
S. marotiri C.J.Webb (1988)	Endemic	–
S. radiolatus F.Muell.	Endemic	–
S. repangae de Lange & B.G.Murray (1998)	Endemic	–
S. rufiglandulosus Colenso (1895) [1896]	Endemic	–
S. scaberulus (Hook.f.) D.G.Drury	Endemic	–
S. sterquilinus Ornduff	Endemic	–
S. wairauensis Belcher	Endemic	–
S. biserratus Belcher	Native (non-endemic)	–
S. glomeratus Poir.	Native (non-endemic)	–
S. hispidulus A.Rich.	Native (non-endemic)	–
S. lautus G.Forst. ex Willd. (1803)	Native (non-endemic)	–
S. minimus Poir.	Native (Non-endemic)	–
S. quadridentatus Labill.	Native (Non-endemic)	–
S. angulatus L.f.	Exotic (Fully naturalised)	1940–1970
S. aquaticus Hill	Exotic (Fully naturalised)	1870–1900
S. bipinnatisectus Belcher	Exotic (Fully naturalised)	1900–1940
S. cineraria DC.	Exotic (Fully naturalised)	1940–1970
S. crassiflorus (Poir.) DC.	Exotic (Casual)	
S. diaschides D.G.Drury	Exotic (Fully naturalised)	1970–1990
S. elegans L.	Exotic (Fully naturalised)	1900–1940
S. esleri C.J.Webb (1989)	Exotic (Fully naturalised)	1990–2000
S. glastifolius L.f.	Exotic (Fully naturalised)	1940–1970
S. hypoleucus Benth.	Exotic (Casual)	–
J. vulgaris (= *S. jacobaea* L.)	Exotic (Fully naturalised)	1870–1900
S. linearifolius A.Rich.	Exotic (Fully naturalised)	1970–1990
S. macroglossus DC.	Exotic (Casual)	1990–2000
S. mikanioides Walp.	Exotic (Fully naturalised)	1840–1870
S. serpens G.D.Rowley	Exotic (Casual)	–
S. skirrhodon DC.	Exotic (Fully naturalised)	1900–1940
S. sylvaticus L.	Exotic (Fully naturalised)	1870–1900
S. vulgaris L.	Exotic (Fully naturalised)	1840–1870

`

host plants (*Senecio* spp.). The New Zealand flora includes 19 native species of *Senecio,* of which 13 species are endemic (Table 1.1). In the chapters that follow I investigate whether the invasion of New Zealand by *J. vulgaris* caused an increase in the abundance of the magpie moth which spilled back onto native *Senecio* species decreasing their fitness and depressing their populations as a result of apparent competition.

To confirm the occurrence of apparent competition a few criteria must be met. First, there must be at least two host species that share a common consumer. Second, the shared consumer must cause a greater negative impact to the fitness of one of the hosts in the presence of the other. Third, these impacts must be evident at the population level with populations of the weaker apparent competitor becoming scarcer over time or disappearing altogether.

1.6 Thesis Structure

The remainder of this doctoral thesis consists of four chapters assessing evidence for apparent competition mediated by the endemic magpie moth, *N. annulata* between the invasive *J. vulgaris* and three native New Zealand *Senecio* species (*S. minimus, S. quadridentatus* and *S. wairauensis*). These chapters are followed by a section devoted to my discussion and conclusions.

Chapter 2 provides anecdotal evidence from New Zealand's colonial period through to today and consists mainly of writings by New Zealand naturalists from this time period. It details the invasion of New Zealand by *J. vulgaris* and a correlated rise in *N. annulata* populations in invaded areas. Also documented is the decrease in these two species following the implementation of *J. vulgaris* control measures that began in 1901. My goal in writing this chapter is to give a historical foundation for the association between *J. vulgaris* and *N. annulata* and to convey how naturalists in the period before and after the invasion of the former were keenly aware how this led to an increased abundance of the latter.

In Chapter 3, I use herbarium and vegetation survey records collected over the last 140 years to perform a temporospatial analysis in order to find relationships between the locations of *J. vulgaris* records and those of native *Senecio* on the South Island. Using a variety of records establishing presence of *J. vulgaris* and native *Senecio* hosts at specific dates and locations, the analysis should show how encounters of these individual species shift in time and space. These results are intended to uncover evidence for population-level impacts to native *Senecio* species through time and in relation to *J. vulgaris* presence.

`

The purpose of the assays carried out and reported in Chapter 4 is to compare the preference of *N. annulata* for *J. vulgaris* and native *Senecio* host plants, as well as the suitability of the alternate hosts for larval development. Experiments consisted of standard choice and no-choice tests using newly-hatched larvae. In the choice tests, larvae were offered standardized amounts of plant tissue of *J. vulgaris* and three native host plants (*S. minimus, S. quadridentatus* and *S. wairauensis*) in order to find out which they preferred the most and how much of each they ate. In the no-choice tests, larvae were given access to just one of the species used in the choice tests and then followed in their development. These experiments were used to establish the trophic associations between *N. annulata* and its alternate hosts and to find out how each host plant affected the fitness of their shared consumer.

In Chapter 5, I report on field surveys from river valleys of the West Coast Region of New Zealand where *J. vulgaris* invasions have occurred most recently. Surveys for *J. vulgaris* and native *Senecio* were carried out at seven different sites and looked for the occurrence and abundance of these host plants at increasing distances from high-density *J. vulgaris* populations. Densities of each host species were recorded in disturbance corridors (stream beds, trails, landslips, etc.) at regular intervals along each valley. Numbers of *N. annulata* larvae and levels of larval feeding damage on each host species were also recorded in the same locations. The survey included three sites that were free of *J. vulgaris* infestations in order to uncover any differences in the pattern of native *Senecio* abundance and distribution between invaded and uninvaded sites. These surveys were carried out to determine if there are any discernable landscape-level impacts to native *Senecio* populations as a result of *J. vulgaris* presence and density.

The final chapter of this thesis summarizes the research findings and the conclusions I draw from those results. I also make suggestions for interested parties and end-users while offering ideas for future research in this area.

`

Chapter 2

Invasion of New Zealand by *Jacobaea vulgaris*

2.1 Introduction

New Zealand is home to 19 native species of herbaceous plants in the genus *Senecio* (Webb, Sykes, & Garnock, 1988). There are also several species of native herbivorous insect that feed and reproduce on these host plants, all of which contain toxic pyrrolizidine alkaloids (Benn, DeGrave, Gnanasunderam, & Hutchins, 1978; Langel, Ober, & Pelser, 2010; P. B. Pelser, Nordenstam, Kadereit, & Watson, 2007; E. P. White, 1969). In the mid- to late-17th Century, the European pasture weed, *Jacobaea vulgaris* (formerly *Senecio jacobaea* L.), was inadvertently introduced to New Zealand and rapidly spread across the colony (Gilruth 1904, Thompson 1922, Cameron 1935, Wardle et al. 1995). A few of the native insects that specialized on native *Senecio* began to successfully use this exotic host (J. J. Sullivan, et al., 2008). Between the eventual ubiquity and high density of *J. vulgaris* in New Zealand, the presence of this species in the landscape appears to have had significant impacts to the populations of the native insects that used it (Anonymous, 1929; Buller, 1881; Watt, 1914). Specifically, there is ample anecdotal evidence that one *Senecio*-specialist, *Nyctemera annulata* (Boisduval)[1] (the New Zealand magpie moth), experienced a population explosion following the invasion of *J. vulgaris* (see section 2.4 below). In this chapter, I review the natural history of *J. vulgaris*, present evidence for its novel association with *N. annulata*, and detail the effects that *J. vulgaris* invasion appears to have had on *N. annulata* populations. To conclude, I discuss the implications for native *Senecio* species, which likely experienced increased pressure in the form of herbivore spillback.

Jacobaea vulgaris is an herbaceous pasture weed native to Europe and eastern Asia that has been inadvertently introduced to many other geographic areas including North America, Australia and New Zealand. *Jacobaea vulgaris* is a facultatively annual, biennial or perennial herb in the daisy family (Asteraceae) with leaves that are lobed and glabrous and that are dark green on top, but paler to purple underneath (Radcliffe, 1969; Schmidl, 1972a). Wardle (1987) provides a comprehensive description of *J. vulgaris*, a summary of which follows.

On average, mature plants are about 50 cm in height and have long, stout stems and diffuse root systems, from which plants can readily regenerate. The morphology of the flowers

---

[1] This species was originally named *Leptosoma annulatum.*

`

reveals two concentric rings of florets; the outer ring of ray florets produces hairless seeds, while the inner ring of disc florets produces seeds with some pubescence. Seeds germinate in late autumn and from a rosette over winter. The upper part of the stem usually branches several times and can produce thousands of yellow florets which are insect pollinated. Rosettes generally bolt and flower during their second year of growth, although *J. vulgaris* is monocarpic and can persist until it sets seed. Flowering can be delayed by herbivory (E. van der Meijden & van der Waals-kooi, 1979) and if the plant is grazed on, or growth is otherwise interrupted, the plant can convert to a perennial with multiple crowns and a number of flowering stems (Wardle, 1987). Each plant produces 5,000 to 275,000 seeds (Radcliffe, 1969).

Jacobaea vulgaris is perhaps best known for its toxicity and economic impact by reducing the grazing capacity of many pastures and as a causal agent of livestock mortality (Fuller & McClintock, 1986; Schmidl, 1972a, 1972b; Stables, 1983; Thompson, 1922; Wardle, 1987; Wardle, Nicholson, & Rahman, 1995). *Jacobaea vulgaris* produces a suite of hepatotoxic phytochemicals (pyrrolizidine alkaloids) and ingestion of sufficient quantities of plant tissue by livestock causes cirrhosis of the liver, especially in horses and cattle and notably less so in sheep (Adler, Karban, & Strauss, 2001; Cheeke, 1988, 1989; Gera Hol, Macel, van Veen, & van der Meijden, 2004; Hartmann & Toppel, 1987; Toppel, Witte, Riebesehl, Borstel, & Hartmann, 1987). *Jacobaea vulgaris* has been shown to cause more mortality in British livestock than all other toxic plants together (Forsyth, 1954).

Jacobaea vulgaris was first reported in New Zealand in 1869 near Dunedin (Fereday, 1872). Within a few decades it was established in other areas, including Invercargill, the West Coast Region, Bay of Plenty, the areas around Coromandel and Auckland, as well as Taranaki and became particularly abundant in farming areas (Anonymous, 1889a, 1891, 1899, 1902a, 1902b, 1902c, 1904; Gilruth, 1904; E. Howell, 1903; Meyrick, 1889; Thompson, 1922). In the 1880's *J. vulgaris* became associated with fatal Winton Disease in livestock – primarily horses (Cowan, 1889; Gilruth, 1904). It was declared a noxious weed in the Second Schedule of the Act of 1900, but was moved up to the First Schedule of the Act of 1908 (Poole & Cairns, 1940). More recently, in the Noxious Plant Act of 1986, it was again classified as a Class B noxious weed which required farmers to maintain a 20-metre wide *J. vulgaris*-free buffer around their pastures and made it illegal for them to allow *J. vulgaris* to flower on their property (Bird, 1977). Some New Zealand regional councils maintain similar provisions in current Regional Pest Management Strategies under the Biosecurity Act 1993 (MAF, 1993).

`

Since its introduction, all methods of control have been attempted including cultural control (e.g. prohibiting movement of plants and seed-infested soil), chemical control and biological control. Arguably, sheep were the first organisms used to control *J. vulgaris* in New Zealand and were often employed alone or alongside cattle in infested paddocks specifically for that purpose (Cameron, 1935; Hilgendorf, 1926; Mitich, 1995). Additionally, six insects have been imported and released as biological control agents, all but one of which established successfully (Table 2.1). Biological control has been largely successful in much of New Zealand, especially in drier areas typical of the eastern portion of the country. However, healthy *J. vulgaris* populations continue to persist in other areas of the country, particularly in the Westland Region (Harman and Syrett 1989, Gourlay et al. 2008). Perseverance of *J. vulgaris* populations is attributed to its high fecundity, its adaptation to disturbed habitats and its high tolerance to herbivory and disturbance (Crawley & Gillman, 1989; McEvoy, et al., 1993; E. van der Meijden & van der Waals-kooi, 1979; Wardle, 1987). This same research also indicates that *J. vulgaris* distribution and size is determined perhaps as much by competition and the availability of suitable disturbed habitat (microsites) as by pressure from natural enemies.

Over a century of research has been carried out on *J. vulgaris* in New Zealand, but many questions regarding its impacts to the native ecology are still unexamined. Since *J. vulgaris* is viewed mainly a pasture weed it has traditionally been considered as a farming issue. For example, the Department of Conservation (DOC) in Westland typically does not control *J. vulgaris* despite its abundance in grazed and recently retired lowland valleys since DOC is outside of the purview of the regional pest management strategy and does not regard *J. vulgaris* as an important environmental weed in these landscapes (Tom Belton, personal communication). Data collection in relation to this species has overwhelmingly focused on aspects of economic importance, such as impacts to agricultural livelihood, the costs/benefits/efficacy of different control methods and the effects of imported biological control agents on its control (e.g. Amor, Lane, & Jackson, 1983; Anonymous, 1904; Bird, 1977; Cameron, 1935; Harman & Syrett, 1989; McEvoy, et al., 1993; Mitich, 1995; Poole & Cairns, 1940; Radcliffe, 1969; Schmidl, 1972a; Stables, 1983; Wardle, 1987; Wardle, et al., 1995). Conversely there has been little research examining the ecological impacts of *J. vulgaris* on native plants and insects and the impacts of *J. vulgaris* biocontrols on native and endemic species. This is a potentially important omission for such an abundant invasive species.

`

Table 2.1 - Insects and the years they were introduced to New Zealand in an attempt to control the invasive pasture weed, *Jacobaea vulgaris*. An asterisk (*) indicates failure to establish.

Species	**Order: Family**	**Released**	**Geographic origin**	**Reference**
Tyria jacobaeae	Lepidoptera: Arctiidae	1929	England	(Cameron, 1935; Harman, Syrett, Hill, & Jessep, 1996)
Botanophila jacobaeae	Diptera: Tephrididae	1936	England	(Cameron, 1935; Harman, et al., 1996; Holloway, 1983)
*Botanophila seneciella**	Diptera: Tephrididae	1936	England	(Cameron, 1935; Harman, et al., 1996; Holloway, 1983)
Longitarsus jacobaeae	Coleoptera: Chrysomelidae	1983	Italy via Oregon (USA)	(Harman, et al., 1996; Syrett, Grindell, Hayes, & Winks, 1991; Syrett, Scheele, & Philip, 1983)
Cochylis atricapitana	Lepidoptera: Tortricidae	2008	Spain via Australia	(ERMA, 2005a, 2005b)
Platyptilia isodactyla	Lepidoptera: Pterophoridae	2008	Spain via Australia	(ERMA, 2005a, 2005b)

`

2.2 New Zealand *Senecio* Specialists

Many of the endemic and native insects that feed on *Senecio* species are specialists on this genus and some closely related Asteraceae. Prior to European colonization these *Senecio*-specialist insects were supported by a community of 13 endemic and 6 non-endemic native hosts (see Chapter 3, Table 3.1). Beginning with the arrival of European settlers, 13 non-native species of *Senecio* and *J. vulgaris* have naturalized in New Zealand, with casual introductions of five others (J. J. Sullivan, 2006; Webb, et al., 1988). Subsequent to these introductions, some of these genus-specific herbivores expanded their host range to use one or more of the non-native *Senecio* species and *J. vulgaris*. In a survey of host plant use, Sullivan et al. (2008) found that at least three endemic *Senecio* specialists regularly use both native and naturalized species as hosts. One of the species that Sullivan et al. (2008) followed, *Nyctemera annulata* (Lepidoptera: Arctiidae), was encountered nearly twice as often on the exotic *J. vulgaris* (23%) compared to the native species that was most used by the moth in their samples, *S. minimus* (14%). Another important part of the picture is that the authors found the exotic *Senecio* species to be far more common than the native hosts in both modified rural and urban habitats. One of the conclusions of the study was that the endemic *Senecio* specialists that have expanded their host range would likely be far less abundant and more restricted in their geographic distribution without the presence of the naturalized *Senecio* hosts and *J. vulgaris.* The pattern of host use by *N. annulata* combined with the abundance and distribution of the preferred, exotic host presents some interesting possibilities that call for further study. In particular, it is prudent to ask how the impact of *J. vulgaris* invasion and spread may have affected *N. annulata* populations.

2.3 Magpie Moth (*Nyctemera annulata*)

The New Zealand magpie moth *(Nyctemera annulata* Boisduval, Lepidoptera: Arctiidae), is a day-flying moth endemic to New Zealand. *Nyctemera annulata* is a bivoltine herbivore common throughout the country (Thomson, 1909; Watt, 1914). It is oligophagous and uses multiple hosts plants (Table 2.2). While it originally relied on native species of *Senecio* for development, it now feeds on most naturalized species from this genus as well (Benn, et al., 1978; Gaskin, 1966; Singh & Mabbett, 1976; Watt, 1914). It also uses plants in other closely-related genera such as rangiora (*Brachyglottis repanda*) (B. Patrick, 1994; Singh & Mabbett, 1976; Watt, 1914).

While *N. annulata* is parasitized by multiple species of native and naturalized hymenoptera (Table 2.3), the moths' bright aposematic coloration likely acts as a visual warning of their

Table 2.2 - Host plant species recorded for the endemic New Zealand magpie moths (*Nyctemera annulata*) and the reference for the association. Hosts are also annotated as to if they are endemic (§), non-endemic native (*) or exotic (†) species. Specious associations are also annotated (σ). Doubt as to host associations are collected from the sources cited or assumed by this author due to an absence of corroborating reports.

Host plant	**Family**	**Citation**
J. vulgaris †	Asteraceae	(Singh & Mabbett, 1976; Spiller & Wise, 1982; J. J. Sullivan, et al., 2008)
Senecio antipodus	Asteraceae	(B. Patrick, 1994)
S. bipinnatisectus †	Asteraceae	(Kay, 1980)
S. carnosulus §	Asteraceae	(Sullivan, unpub. data)
S. elegans †	Asteraceae	(S. Hartley pers. comm.)
S. esleri †	Asteraceae	(Martin, 2010)
S. glastifolius †	Asteraceae	(S. Hartley pers. comm.)
*S. glomeratus **	Asteraceae	(Spiller & Wise, 1982)
*S. hispidulus **	Asteraceae	(Martin, 2010)
*S. lautus **	Asteraceae	(Singh & Mabbett, 1976; Spiller & Wise, 1982)
S. mikanoides †	Asteraceae	(Spiller & Wise, 1982)
*S. minimus **	Asteraceae	(Singh & Mabbett, 1976; Spiller & Wise, 1982)
*S. quadridentatus **	Asteraceae	(J. J. Sullivan, et al., 2008; D. R. Woodward, 1984)
S. radiolatus §	Asteraceae	(Dugdale, 1971)
S. rufiglandulosus §	Asteraceae	(Martin, 2010; Watt, 1914)
S. scandens	Asteraceae	(Watt, 1914)
S. skirrhodon †	Asteraceae	(Martin, 2010)
S. spathulatus †	Asteraceae	(Benn, et al., 1978)
S. sylvaticus †	Asteraceae	(Spiller & Wise, 1982; Watt, 1914)
S. vulgaris †	Asteraceae	(Gaskin, 1966; Spiller & Wise, 1982; Watt, 1914)
S. wairauensis §	Asteraceae	Chapter 5
Erechtites arguta	Asteraceae	(Watt, 1914)
Brachyglottis repanda §	Asteraceae	(Dugdale, 1971; Watt, 1914)
B. bellidioides §	Asteraceae	(Watt, 1914)
B. hectori §	Asteraceae	(Watt, 1914)
B. turneri §	Asteraceae	(Watt, 1914)
Olearia sp. *§†σ*	Asteraceae	(Spiller & Wise, 1982)
Pelargonium sp. *†σ*	Geraniaceae	(Spiller & Wise, 1982)
Salvia sp. *†σ*	Lamiaceae	(Spiller & Wise, 1982)
Chrysanthemum sp. *†σ*	Asteraceae	(Spiller & Wise, 1982)
Lactuca sativa †σ	Asteraceae	(Gaskin, 1966; Spiller & Wise, 1982)
Leptinella plumose §σ	Asteraceae	(B. Patrick, 1994)
Pericallis xhybrida †	Asteraceae	(Gaskin, 1966)
Pleurophyllum criniferum §σ	Asteraceae	(B. Patrick, 1994)
Cineraria maritime †σ	Asteraceae	(Singh & Mabbett, 1976)
Cotula plumosa §σ	Asteraceae	(B. Patrick, 1994)
Hedera hibernica †σ	Araliaceae	(Buller, 1881)

`

Table 2.3 - Parasitoids of *Nyctemera annulata* (Bois.) and the lifestage they attack. Annotations indicate if species are endemic (§), native(*), non-native (†) and unknown (?).

Species	**Order: Family**	**Life stage attacked**	**Citation**
Pales nyctemeriana §	Diptera: Tachinidae	larva	(Thompson, 1922)
*Pales casta**	Diptera: Tachinidae	larva	(Cameron, 1935)
Diolcogaster perniciosus †	Braconidae: Microgastrinae	larva	(Saeed, Dangerfield, & Austin, 1999)
Echthromorpha intricatoria †	Hymenoptera: Ichnumonidae	pupa	(Cameron, 1935)
Microplitis sp.	Hymenoptera: Braconidae	larva	(Valentine, 1967)
Apantales sp.	Hymenoptera: Braconidae	larva	(Valentine, 1967)

`

toxicity and unpalatability to most potential bird predators, with the notable exception of the shining cuckoo (*Chrysococcyx lucidus,* Aves: Cuculidae) (Gill, 1980). The toxicity of this moth has been experimentally attributed to the sequestration of pyrrolizidine alkaloids from the host plant by the moth larvae (Benn, et al., 1978; Gaskin, 1966). All species regularly used by *N. annulata* are recorded to contain these compounds, including *J. vulgaris* and *S. minimus* (Benn, et al., 1978). These toxic alkaloids can be retained by the moth throughout its lifespan and gravid females can transfer this chemical protection to her ova (Benn, et al., 1978).

2.4 *Jacobaea vulgaris* invasion of New Zealand and the Response by *Nyctemera annulata*

The history of *J. vulgaris* in New Zealand has murky beginnings. The earliest account of "ragwort" in New Zealand was recorded by Fereday (1872) in his response to Bathgate (1870) and observations therein regarding *N. annulata*. Fereday (living in Christchurch) commented on Bathgate's observations from Otago – in particular the abundance of *N. annulata* and its association with "ragwort" (this presumably refers to *J. vulgaris,* as native *Senecio* species and the naturalised *S. vulgaris* are often referred to as "groundsel" in the written accounts from this era (e.g. Anonymous, 1889a; Anonymous, 1889b; Grapes, 1896)).

> *"The moth mentioned as having black wings with white spots, and the abdomen annulated with orange, is Leptosoma annulatum… It is very abundant here, and its larvae are common on a species of ragwort – I have never seen them on any other plant."(Fereday, 1872, p.218)*

However, Thompson (1922) is commonly considered the earliest reliable account of *J. vulgaris* invasion. In this retrospective he mentions first noticing *J. vulgaris* around Dunedin in 1874. Not unimportantly (and admittedly with the benefit of hindsight), he also suggests that proliferation of *J. vulgaris* was directly responsible for a dramatic increase in the abundance of the endemic New Zealand magpie moth, *N. annulata*.

> *"Since the vast increase in this weed, there has been a correspondingly enormous increase in numbers of New Zealand magpie moth – Nyctemera annulata – the larvae of which feeds mainly on this plant. In summer the moths are frequently to be seen almost in clouds in the infested districts… and coincidentally with [J. vulgaris]'s spread has been an enormous increase of Nyctemera annulata." (Thompson, 1922, p. 434)*

From the early stages of the invasion, naturalists have provided some evidence that *N. annulata* numbers were increasing. About a decade after Bathgate's (1870) initial observation, Buller (1881) noted the how the moth seemed to be increasingly common:

> *"This familiar moth occurs plentifully during the summer months in all parts of the colony… it appears to increase and multiply every year, while many of the other common moths are becoming extinct." (Buller, 1881, p. 238)*

`

A couple years later Smith (1893) published his own observations about *N. annulata* in which he declared that the apparent rise in moth numbers was a direct result of the invasion of exotic plants – the earliest such account I was able to locate. He went further and also made the claim that *N. annulata* larvae develop better on exotic *Senecio* species and that adult moths reared on exotic hosts reproduce at a higher rate compared to those reared on native hosts.

> *"When, however, alien plants of the same order have supplanted the native species, it is interesting to note how several species of insects have adopted the ailen plants as food, and continue to multiply more than when their larvae fed on native plants... The case of N. annulata, a large diurnal moth , may be cited as one of perfect adaptation to new food, by which the species continues to increase annually."* (Smith, 1893, p. 220)

Early in the *J. vulgaris* invasion, *N. annulata* was so closely associated with this exotic plant that many farmers initially suspected moth larvae as the cause of livestock mortality:

> *"I understand the danger lies in the grubs or worms which are to be found in every stalk of [J. vulgaris], presumably the young of the black moth so pleantiful whever the yellow weed is found." (Maclean, 1894, p. 11)*
>
> *"It was at one time thought that a disease which affects cattle grazing in districts overrun by Senecio jacobaea and its allies—the food plants of the larvae —had its origin in the animals inadvertently eating the larva along with its food plant. It is now known that the Senecio itself contains a poisonous substance."(Philpott, 1907, p. 213)*

Around the same time livestock deaths in New Zealand were on the rise from *J. vulgaris* poisoning, Meyrick (1889) reported how common *N. annulata* was is in some areas. He also gave some idea of the impact that larvae of the native moth could have on their host plants:

> *[regarding N. annulata:] "Common throughout the North and South Islands.... feeds on various species of Senecio, sometimes entirely stripping the plants. The imago has a curious habit of soaring in the early morning sunshine, soon after sunrise, in calm fine weather. I have seen them in numbers flying round the tops of trees at a height of over 100ft." (Meyrick, 1889, p. 218)*

Observations of high *N. annulata* population densities were affirmed by Hudson, who also commented on the ubiquity of the species:

> *"It is extremely common, especially during the latter end of the summer, when specimens may often be seen flying in all directions." (Hudson, 1898, p. 3)*

A bit further north in Taranaki, local newspapers of the time provide clues that Taranaki was in the early stages of invasion by *J. vulgaris*:

> *"Mr. G. Cliff brought to this office on Friday morning specimens of a weed found growing on his place near Upjohn's Bridge. The plant was identified by Mr F. P.Corkill as the ragwort, or golden cushag of the Isle of Man, where it grows freely and is not regarded as a pest. Some two years ago Mr. Corkill wrote to this paper warning settlers, however, against the plant, which he had seen on land near Inglewood. For although not objectionable in the Isle of Man, he foresaw that it would not be a desirable plant to get into this country." (Anonymous, 1899, p. 2)*

`

About a decade later, Taranaki was in the midst of a *N. annulata* population boom. Eventually locals began arriving at the realization that the increase in *J. vulgaris* in the landscape was the root cause of the increase in moth abundance:

> *"There has been a veritable plague of moths in Hawera during the past month… A well-known Ngaere settler is given as the Stratford Post's authority for stating that a species of black moth specially chooses ragwort plants as a depository for its eggs, and that when the caterpillars emerge therefrom they practically destroy the plant of this noxious weed, upon which they feed. These caterpillars are further said to be unusually numerous in the district this year." (Anonymous, 1910, p. 4)*

Just a couple years earlier, the naturalist James Drummond (1908) wrote a column entitled "Bird and Insect Notes" in the Wellington daily newspaper, *Evening Post.* In his column he made reference to this precise phenomenon:

> *"The magpie moth, whose scientific name is Nyctemera annulata, is a pretty diurnal moth. One of its most interesting features is the fact that it is a striking illustration of the manner in which some introduced plants help to bring about an increase in the numbers of some species of native insects. The accidental introduction of the ragwort (Senecio jacobaea) brought loss to farmers in Southland, but it also provided an additional and natural food for the larvae of the magpie moth, which has increased prodigiously every year. In Southland, where the ragwort grows in large masses over areas of country, the caterpillars may be seen in their tens of thousands feeding on the luxuriant plants. As a traveller walks through the forests of yellow flowers, the moths rise around him in great numbers, and pass from flower to flower." (Drummond, 1908, p. 13)*

Around the same time, the prolific entomologist Thompson (1909) made his earliest written acknowledgement that increasing *N. annulata* numbers seemed to be caused by *J. vulgaris* invasion and spread:

> *"Of late years there has been a very remarkable increase in the abundance of these insects, especially in the southern end of this island, and this is apparently due to the great abundance of ragwort (Senecio jacobaea) which has become such a serious pest in the south. Armies of the caterpillar are sometimes met with during the month of November, followed later by myriads of moths." (Thomson, 1909, p. 7)*

Bathgate (1922) also indicates that there were unusually high densities of *N. annulata* in areas of Southland where *J. vulgaris* was abundant.

> *"... if I may judge from what I saw in the neighbourhood of Lumsden a few years ago, where these moths were very abundant and the larvae were also numerous, feeding on the ragwort, which evidently afforded a suitable food supply and this resulted in these moths being present in far greater numbers than I had ever seen elsewhere."(Bathgate, 1922, p. 275)*

Thompson (1922) echoed this observation.

> *"The common magpie-moth (Nyctemera annulata) has certainly become extremely abundant wherever the introduced ragwort (Senecio jacobaea) has become a common pest… Wherever ragwort has spread and become an abundant weed the Nyctemera has also increased enormously, and may be seen rising in vast swarms from plants during the adult moth stage." (Thompson, 1922, p. 512)*

`

In his reminiscence on the previous 40 years, Thompson (1922) also included an account of a how invasion of the Waikato area of the North Island by *J. vulgaris* (almost 40 years after he watched it occur in Otago) coincided with a surge in *N. annulata* numbers:

> *"In June 1913 ragwort was reported as common on the Volcanic Plateau, an area of 5,000 acres lying to the south of Mangatautari and west of the Waikato River, and coincidently with its spread has been an enormous increase in Nyctemera annulata." (Thompson, 1922, p. 434)*

However, as Thompson (1922) noted some time later, the impact of magpie moth on *J. vulgaris* was not significant enough to curb its spread and abundance:

> *"The larva is hairy and distasteful to birds, and there is apparently nothing to check its increase, but it is quite unable to cope with the vast increase of the weed." (Thompson, 1922, p. 434)*

As is the case with population explosions, the dramatic increase in weed and moth populations was eventually followed by a similarly striking drop in these two species. Back in Otago – at about the same time Thompson (1922) recorded the weed and moth increase in the Waikato – Philpot (1916) recorded what he saw as a distinct drop in *N. annulata* abundance. He indicated that he believed the reason fewer moths were around was because of decreased *J. vulgaris* biomass in the landscape as a result of regional control measures:

> *"[N. annulata] is now less common than formerly, owing to the destruction of much of the food-plant (Senecio jacobaea) of the larva."(Philpot, 1916, p. 196)*

A few years later in a reflective paper, Bathgate (1922) recalled witnessing the same thing in the area of Dunedin, although he indicated that *J. vulgaris* was maintaining high population densities in other areas of the South Island:

> *"The moth with black wings spotted with white (Nyctemera annulata) was much more commonly to be seen in the neighbourhood of Dunedin than is the case at the present day, which is probably due to the extermination by cultivation of the food plant of the larvae. While this may be the case in this locality, it is very different in the situation where the introduced weed ragwort (Senecio jacobaea) abounds…"(Bathgate, 1922, p. 275)*

2.5 Discussion

After examining known collections of *N. annulata* and *J. vulgaris* it became apparent that there are not enough specimens with detailed records of host associations or abundances to quantitatively make these connections, although these two species are clearly associated in the minds of most naturalists in New Zealand based on many independent anecdotal observations. Similarly, after inquiring about survey data that document these patterns I was unable to find any which could be used to quantify these patterns. It was therefore necessary to rely on these anecdotal accounts.

`

Without exception, these early records that include both moth and host species suggest that the invasion of *J. vulgaris* in New Zealand greatly increased the abundance of magpie moth in *J. vulgaris*-infested areas. While the scale at which these observations are made is crude and lacks numbers with which to compare the state of things today, several of the authors make a link between the high densities of *J. vulgaris* and the explosion in magpie moth numbers. For instance, Drummond (1908) suggests that the *J. vulgaris* invasion is the reason for the population explosion of *N. annulata* and describes larvae in the "tens of thousands", presumably at one site. In comparison, I undertook a landscape survey in 2008 and 2009 of four *J. vulgaris*-infested valleys and a few dozen other road-side sites over several months and was unable to find anywhere near this many larvae altogether. In reference to the abundance of adult moths in *J. vulgaris*-infested locations, Drummond (1908) writes how they "rise… in great numbers", while Thompson (1922) describes them as "almost in clouds" and "vast swarms". All naturalists that I have spoken to concur, these observations indicate numbers unlike *N. annulata* abundances that are typically seen today.

Another theme in the later accounts of Bathgate (1922) and Philpot (1916) is that *N. annulata* populations experienced a decline following the implementation of *J. vulgaris* control measures. After the strict enforcement of laws that started in earnest in 1908 and aimed at curtailing *J. vulgaris,* it is likely that abundances of the weed began to decline. Given the association between the plant and moth and the generally low biomass of *Senecio* species in most agricultural landscapes, it is presumed that *N. annulata* populations also suffered a decline in the aftermath of aggressive weed eradication programmes. An informal survey of senior entomologists also reinforces the conclusion that *N. annulata* appears to be much less common than it was closer to the peak of *J. vulgaris* invasion.

Since 1970, there have been a few studies that have examined this relationship as it exists today (Benn, et al., 1978; Singh & Mabbett, 1976; J. J. Sullivan, et al., 2008; D. R. Woodward, 1984). In the most recent published survey, Sullivan et al. (2008) determined that *N. annulata* was found feeding on *J. vulgaris* significantly more often than on the other species they sampled, including native *Senecio* hosts. Observations from this study corroborate other accounts that larvae laid or reared on *J. vulgaris* that can still make use of native host plants (and vice versa) (Benn, et al., 1978; B. Patrick, 1994; Singh & Mabbett, 1976; D. R. Woodward, 1984). Previous and current research also indicates that feeding by larvae causes differential impacts on the alternate hosts (Helson 1974, Patrick 1994, Chapter 3). All of these factors suggest some interesting possible dynamics in the New Zealand *Senecio* food web.

`

The descriptions of the abundances of *N. annulata* during the peak of *J. vulgaris* infestation have some obvious implications for native *Senecio* populations adjacent to weed-infested areas. Based on my own observations, as well as those of Buller (1881) and Patrick (1994), *N. annulata* larvae have a propensity to move from areas of high larval density and disturbed or mostly-consumed plants in search of alternative food sources. Native *Senecio* near areas of high *N. annulata* density are more likely to experience the effects of spillover from migrating larvae and host-searching adults. If native species are more sensitive to *N. annulata* herbivory than is *J. vulgaris* (which is known for its high tolerance to herbivory) and/or are less fecund than the invader, the impacts to their fitness (particularly relative to *J. vulgaris*) would be significant. There is a strong likelihood in this scenario that the presence of *J. vulgaris* near native *Senecio* populations will have resulted in intensified negative pressure and possible population declines for native *Senecio* as a result of weed-induced increases of their shared insect herbivore.

The taxa affected by a significant increase in *N. annulata* abundance may also extend beyond native host plants to other native Lepidoptera. When *N. annulata* numbers increased abundance of its parasitoids probably did too. The buildup of this parasitoid guild may have very well resulted in a different spillover onto native species – this time onto native moths. Although a comprehensive list of native parasitoids shared between *N. annulata* and other native species is lacking, at least one native parasitoid (*Pales nyctemeriana*) is known to attack *N. annulata* and other native Lepidoptera (including *Tmetolophota purdii* and *Wiseana cervinata*) (Thompson, 1922). Two other parasitoids, one native (*Pales casta*) and one exotic (*Echthromorpha intricatoria*), likely use native moths as hosts and have been present in New Zealand since at least the early 20th century, when *J. vulgaris* and *N. annulata* were still in great abundance (Paynter et al., 2010). Although I do not have quantitative evidence for this trophic cascade in the New Zealand lepidopteran food web, it is certainly plausible.

The example of host-range expansion by *N. annulata* to include *J. vulgaris* and other non-native *Senecio* species can be viewed from the context of a "worst-case scenario" for a biological control programme. While *N. annulata* is native to New Zealand, the phenomenon of its rise in abundance following the invasion of *J. vulgaris* mirrors other examples where a biological control agent that was released proved to be less-than-effective but had demonstrably negative impacts on a native food web and species in it (e.g. Carvalheiro, et al., 2008; Clement, Smith, Prena, Kleene, & Johnson, 2009; Koch, 2003; Louda, et al., 2003; Messing & Wang, 2009; Ortega, et al., 2004; D. E. Pearson & Callaway, 2003; Simberloff & Stiling, 1996; Snyder, Clevenger, & Eigenbrode, 2004). In this respect, *N. annulata* was relatively ineffective at impacting *J. vulgaris* abundance which spread despite the fact that it was already abundant and established throughout the country. Although ineffective against the “target weed” (*J. vulgaris*), the invasiveness of this host precipitated a boon in *N. annulata* numbers that is likely to have had a suppression effect on native *Senecio* via spillover and on native Lepidoptera via shared parasitoid spillover. In real biological control programmes these events are analogous to unwanted non-target effects. In actuality, these events represent damage inflicted by unattended weed invasions. This is likely a much more common scenario than non-target effects of biological control given that the great majority of weeds are not biologically controlled and that modern biocontrol programmes undergo extensive pre-release host testing. This is despite weed-mediated indirect effects receiving little attention in scientific literature relative to vocal concerns about some biological control agents.

The impact of invasive plants on native insect herbivores and the resulting impacts on native plants by changes in native herbivore abundance and/or distribution should be considered in decisions regarding biological control of invasive weeds. Currently it is the direct impacts of invasive species, like competition with or predation on natives and modification of habitat, which are usually (sometimes only) considered as reasons for action on their control by introduced insects. The example involving *J. vulgaris*, native *Senecio* and *N. annulata* demonstrates that there should be other aspects of an invader’s presence that are considered. Even if an invasive and a native species do not occupy the same habitat type or use the same host (and therefore do not directly compete), the native may still be at risk from spillover of native or naturalised consumers that use both species. In terms of the present study system, this means that impact of increased numbers of *N. annulata* on native *Senecio* species (some of which have become locally rare or extirpated (de Lange et al., 2009), perhaps not coincidentally) should be considered in decisions to control *J. vulgaris*.

These raise some important research questions. For instance, what are the preferences of magpie moth for native *Senecio* species that co-occur with *J. vulgaris*? Also, what impacts do standardized levels of herbivory have on *J. vulgaris* and co-occurring native *Senecio* species (is *J. vulgaris* as unusually tolerant of damage as literature from its home range suggests)? Finally, is there any evidence for geographic changes in distribution for native species populations as a result of *J. vulgaris* invasion? In the chapters that follow seek to answer some of these questions.

`

Chapter 3

Spatial and Temporal Associations Between Native New Zealand *Senecio* and a Closely-Related Invasive Weed

3.1 Introduction

Jacobaea vulgaris[2] is a widespread weed and well researched from the standpoints of its natural history, its agricultural impacts and its biological control (Amor, et al., 1983; Anonymous, 1904; Bird, 1977; Cameron, 1935; Crawley & Gillman, 1989; Gourlay, Fowler, & Rattray, 2008; Harman & Syrett, 1989; Helson, 1974; Kunin, 1999; McEvoy, et al., 1993; Mitich, 1995; Poole & Cairns, 1940; Radcliffe, 1969; Schmidl, 1972a, 1972b; Stables, 1983; Sutherland, Betteridge, Fordham, Stafford, & Costall, 2000; Wardle, 1987; Wardle, et al., 1995). Despite this, surprisingly little is known about its impacts on native species through competition and shared food webs. In New Zealand, there is some anecdotal evidence that *J. vulgaris* invasion increased the abundance of endemic, genus-specialist native herbivores (J. J. Sullivan, et al., 2008 , Chapter 2 and references therein). The resulting change in food web interactions may have had a significant suppression effect on endemic *Senecio* species although this possibility has been unexplored until now. If native *Senecio* species have been suppressed near *J. vulgaris* populations, it is plausible that this will be detectable in New Zealand's herbarium and vegetation plot records for these species. In this chapter I report results from spatial analyses of *J. vulgaris* and native *Senecio* distributions using data from herbarium collections and vegetation survey records.

The genus *Senecio* is still one of the largest in the world and, despite a succession of genera-splitting events, contains about 1,500 species worldwide. Currently there are 36 species of *Senecio* recognized as native or naturalised in New Zealand (Webb, et al., 1988). Like other taxa in New Zealand, the genus *Senecio* exhibits a high level of species endemism with 13 of the 19 native species (roughly 2/3) being endemic (see Table 1.1 in Chapter 1). Since the arrival of European settlers around 1769, 17 species of exotic *Senecio* (including *J. vulgaris*) have naturalised. In New Zealand there are also native and endemic herbivorous insects that use both native and exotic species *Senecio* and *J. vulgaris* as host plants (J. J. Sullivan, et al., 2008 and Chapter 2).

---

[2] Formerly *Senecio jacobaea*.

`

For the most part, native New Zealand *Senecio* species are herbaceous and tend to be found in ruderal and disturbed habitats such as roadsides, pasture margins, walking tracks, riparian zones and landslips. These are also many of the same habitats where *J. vulgaris* is present. That being the case, and with the exception of grazed pastures where *J. vulgaris* is dominant (Chapter 5), there is clearly potential for some direct competition between *J. vulgaris* and the native *Senecio* species in such habitats. Likewise, indirect interactions between species are increasingly considered important in structuring communities and can strongly influence the abundances and distributions of species in them (Chapters 1 and 5 and references therein).

As detailed in Chapter 1, the influence of novel interactions between invaders and the species in native food webs can affect flow-on effects and food web stability (Bourgeois, et al., 2005; E. Grosholz, 2002; E. D. Grosholz, 2005; Janssen, Pallini, Venzon, & Sabelis, 1998; O'Gorman & Emmerson, 2009; Ortega, et al., 2004; D. E. Pearson & Callaway, 2003; Simberloff & Von Holle, 1999; Simon, et al., 2004; Styrsky & Eubanks, 2007; G. Woodward & Hildrew, 2001; Zedler & Kercher, 2004). Ecological fitting between previously-allopatric species plays a large role in how an invading species interacts with a food web’s members (Agosta, 2006; Daniel R. Brooks, León-Règagnon, McLennan, & Zelmer, 2006; Dostál & Palečková, 2010; Janzen, 1985; Morales & Traveset, 2009; Dov F. Sax et al., 2007; Zamora, 2000). Like the native New Zealand *Senecio* species, the tissues of *J. vulgaris* contain defensive compounds, predominantly pyrrolizidine alkaloids (henceforth referred to as PAs) (Benn, et al., 1978; Bicchi, Rubiolo, Frattini, Sandra, & David, 1991; Bohlmann et al., 1986; Mattocks, 1972; McLean, 1970; Pieter B. Pelser et al., 2005; P. B. Pelser, Nordenstam, B., Kadereit, J.W. & Watson, L.E. (2007) 56 (4): 1077–1104., 2007; Schoental, 1968). PAs have been shown to be toxic to other life forms, including animals, plants and microbial organisms (Ahmed & Wardle, 1994; Joosten, Mulder, Klinkhamer, & van Veen, 2009; Kowalchuk, Hol, & van Veen, 2006; Macel, Vrieling, & Klinkhamer, 2004; McLean, 1970; Schoental, 1968).

However, some groups have developed tolerance to PAs, as well as biological mechanisms to deal with them or adaptations to use them beneficially. This is true for some native New Zealand insect species that have coevolved with native *Senecio* to successfully deal with PAs and use these species as foodplants (e.g. Helson, 1974; J. J. Sullivan, et al., 2008). Interestingly, after the arrival of *J. vulgaris* in New Zealand, at least three native *Senecio*-specialist insects expanded their host range to effectively use *J. vulgaris* as a novel host, presumably due to the plasticity of the adaptations they possessed from feeding on native *Senecio* hosts. Sullivan et al. (2008) presented data on these species and their relationships

`

between exotic *Senecio*. The native insects *Patagonoides farnaria*, *Sphenella fascigera* (previously *Tephritis fascigera*) and *Nyctemera annulata* all use exotic species as hosts, including *J. vulgaris*.

Like Sullivan et al. (2008) found in Auckland, I found *N. annulata* to be the most common folivore on *J. vulgaris* and *Senecio* in the field sites I visited across the South Island and I also detected a trend of high *J. vulgaris* use by this endemic moth compared to other available host species (Chapter 5). There are several anecdotal accounts that describe the host preference for *N. annulata* and its performance on and preference for *J. vulgaris* and non-native *Senecio* species relative to natives (Chapters 2 and 4). However I have located only one quantitative study examining *N. annulata*-host interactions, although *J. vulgaris* was not included in the majority of the tests (D. R. Woodward, 1984). I am unaware of any other studies examining the impact of the flow-on effects of this large-scale, sustained herbivore outbreak on the New Zealand *Senecio* food web. As described in Chapter 2, the invasion of New Zealand by *J. vulgaris* was associated with a dramatic increase in populations of *N. annulata* that followed and herbivore spillover onto native *Senecio* are a distinct possibility.

The invasive *S. jacobaea* possesses a high tolerance of herbivory (Cameron, 1935; Islam & Crawley, 1983; Kunin, 1999; McEvoy, et al., 1993; Poole & Cairns, 1940; Schmidl, 1972a, 1972b; E. van der Meijden, De Boer, & van der Veen-van Wijk, 2000; E. van der Meijden & van der Waals-kooi, 1979; Wardle, 1987; Wardle, et al., 1995). Tolerance to herbivory by *J. vulgaris* appears greater than do tolerance levels by the native *Senecio* species I assayed (personal observation). So it is not unlikely that a combination of near-equitable use of available hosts by *N. annulata*, lower tolerance to herbivory by the native *Senecio* species relative to *J. vulgaris*, and a rise in herbivore numbers that is well above historic levels should have resulted in a negative impact on native *Senecio* species at multiple spatial scales.

As discussed in Chapter 1, one of the pieces of evidence sought in this thesis is of population-level changes to native species. In this chapter I examine herbarium and vegetation survey records for evidence of these impacts. By comparing the date and location of *J. vulgaris* records with those for native *Senecio* species, I expected to find a fine-scale spatial segregation between the two species that correlates with the spread of the former. One of the limitations of the resolution of the data I used in this approach is that it may be difficult to distinguish evidence for apparent competition from direct competition or the effect of habitat differences and changes. It may turn out that elucidation as to which of these factors are responsible could be accomplished with further analysis and incorporation of additional data – something which is now occurring, but was beyond the scope of this study. Nevertheless, if

`

any of these factors are at work they would likely appear as repulsion between *J. vulgaris* and native species at fine spatial scales (less than a few kms) while co-occurring at landscape scales (greater than a few kms).

The set of questions I attempt to answer in this section focus on the temporospatial relationships and changes in native *Senecio* records in relation to *J. vulgaris* presence and spread. In order to reveal historic patterns, I will perform this analysis using data from known and accessible herbarium records and plot data to answer six main questions:

1.) What is the extent to which *J. vulgaris* and native *Senecio* share the same habitats and what is the potential for direct competition and food web sharing?
2.) Are the records for endemic *Senecio wairauensis, S. dunedinensis* and *S. rufiglandulosus* collected farther away from records for *J. vulgaris* than would be expected by chance?
3.) Are the records for *S. minimus* and *S. quadridentatus,* non-endemic natives, collected farther away from records for *J. vulgaris* than would be expected by chance?
4.) Is there evidence of a decline in *S. wairauensis, S. dunedinensis* and *S. rufiglandulosus* collections in the most lowland areas (< 500 m)?
5.) Are the distributions of *S. wairauensis, S. dunedinensis* and *S. rufiglandulosus* along an elevational gradient affected by *J. vulgaris* presence?
6.) Are these records for *S. wairauensis, S. dunedinensis* and *S. rufiglandulosus* in the lowland areas disproportionately farther from records for *J. vulgaris* than would be expected by chance in just the lowland areas (< 500 m)?

The data used in this survey came from a variety of herbaria and vegetation surveys that included *J. vulgaris* and *Senecio* records. A complete list of sources and query criteria is provided in Appendix A.

3.2 Methods

Collection data for *J. vulgaris*, two non-endemic native (*S. minimus, S. quadridentatus*) and three endemic (*S. wairauensis, S. dunedinensis, S. rufiglandulosus*) congeners were assembled from various sources within New Zealand. Host records for the South Island were compiled from herbaria including the Allan Herbarium (CHR), the Lincoln University Herbarium (LINC), the Auckland Herbarium (AKL), the National Forestry Herbarium (NZFRI), the Dame Ella Campbell Herbarium (MPN), the Museum of New Zealand

`

Herbarium (WELT), The University of Waikato Herbarium (WAIK) and the British Museum in London (BM). Added to this are occurrence data from the Department of

`

Conservation’s BioWEB database, a New Zealand *Senecio* database maintained by Jon Sullivan (Lincoln University), as well as both public (NVS(p)) and special request records (NVS(s)) from the National Vegetation Survey database that were made available to us (Table 3.1).

Records for each species encounter were used only if they had both date and location data. Specimens with location data of poor resolution (e.g. location given as a map sheet with no coordinates) were also rejected. Analyses were carried out using New Zealand Map Grid (NZMG) projection coordinates given that most of the data supplied used were in this projection format. Location data in the herbarium or vegetation survey that were not supplied with NZMG coordinates were converted using the Land Information New Zealand Online Conversions webpage (LINZ, 2010). For points that were supplied without an elevation, elevation was determined using ArcGIS (Environmental Systems Research Institute, 2009) and a layer with New Zealand elevation data (Barringer, McNeill, & Pairman, 2002).

Some records were not supplied with specific dates. For vegetation surveys, which all were listed with the year(s) that the survey was carried out, the dates used in the analysis were recorded as January 1st of the latest year of the survey. For example, samples from plots in the survey labelled “AORANGI FOREST PARK FOREST 1983-1984” were labelled as January 1, 1984 for the analysis. For herbarium records without a date but with a known collector, a date was derived from the latest estimated time that the collector likely made collections (Table 3.2) (Gatehouse, 2008).

All analyses were performed in using R statistical software (R Development Core Team 2010). The first analysis was carried out using the statistical package “ads” for spatial point patters analysis (Pelissier & Goreaud, 2010). This package performs first- and second-order multi-scale analyses derived from Ripley's K-function, for univariate, multivariate and marked mapped data in rectangular, circular or irregular shaped sampling windows, with test of statistical significance based on Monte Carlo simulations. Ripley's K-function analyses a set of points by class (species) and determines if points of feature classes are clustered (closer together than would be expected at random) or dispersed (further away from one another than would be expected at random) and displays this relationship graphically. This relationship is compared at different distances from closest selected distance (starting point) outwards in discrete intervals (distance increment). The robustness of a Ripley’s-K analysis is determined by the number of points in each feature class (individual species records), as well as the repeated random sampling (permutations) of class points within the study area. The number

`

Table 3.1 - Counts of records used for the six species surveyed from listed herbarium and vegetation survey data sources. Source abbreviations: Allan Herbarium (CHR), the Auckland Herbarium (AKL), the National Forestry Herbarium (NZFRI), the Dame Ella Campbell Herbarium (MPN) and the Museum of New Zealand Herbarium (WELT). Added to this are occurrence data from the Department of Conservation's BioWEB database (BWEB), a New Zealand Senecio database maintained by Dr. Jon Sullivan (JJS), as well as both public and restricted access records from the National Vegetation Survey (NVS).

Source ***Species***	**AKL**	**BWEB**	**CHR**	**JJS**	**MPN**	**NVS**	**NZFRI**	**WELT**	***Total***
Jacobaea vulgaris	1	336	35	5	2	481	0	1	**861**
Senecio dunedinensis	3	83	26	0	0	24	0	2	**138**
S. minimus	9	0	13	3	0	269	2	2	**298**
S. quadridentatus	11	0	19	0	0	102	4	5	**141**
S. rufiglandulosus	3	1	7	0	0	0	1	3	**15**
S. wairauensis	40	0	34	10	0	432	3	5	**524**
TOTAL	**67**	**420**	**134**	**18**	**2**	**1308**	**10**	**18**	**1977**

`

Table 3.2 - Herbarium specimen collectors and the latest possible date of their collections, which are applied to attributed but undated specimens used in the spatial analysis in this chapter. Modified from Gatehouse (2008).

Collector	**Date used**
T. W. Kirk	January 1, 1935
T. F. Cheeseman	January 1, 1922
E. P. Turner	January 1, 1931
W. Townson	January 1, 1920
D. Petrie	January 1, 1920

`

of permutations loosely translates to the level of confidence (e.g. 9 for 90%, 99 for 99%, and 999 for 99.9%).

Boundary correction for the area analysed (South Island) was accomplished by using the Study Area Method to generate an absolute boundary (rectangular box encompassing all of the South Island) and exclusion of remaining non-terrestrial areas with individual, triangle-shaped bounding boxes – in order to prevent the underlying areas from being incorporated into the analysis. When the observed K value is larger than the expected K value for a particular distance, the distribution is more clustered than a random distribution at that distance (scale of analysis). The output of a Ripley's-K analysis provides an anticipated result (theoretical K) along with confidence bands or confidence intervals (CI), as well as the calculated result from the data provided (observed K). When the observed K value is smaller than the theoretical K, the distribution is more dispersed than a random distribution at a given distance from the starting point. When the observed K value is larger than the upper CI value, points are more clustered than would be expected at random. When the observed K value is smaller than the lower CI value, points are more dispersed than would be expected at random.

The second set of analyses compared the distributions of *J. vulgaris* and native *Senecio* species through 1985 with those after this year. This year was selected as it was the average of the median year of the samples for all native species analysed (*S. minimus* = 1985, *S. wairauensis* = 1986, *S. quadridentatus* = 1986, *S. dunedinensis* = 1985 and *S. rufiglandulosus* = 1983). The analysis was repeated for each time interval to determine if there are any changes in the distributions of these species and if there are any observable correlations in these changes between *J. vulgaris* and the natives. I used *t*-tests to compare altitudinal distributions of each species earlier and later than the median year all sample dates. While a superior analysis would have compared records in multiple time periods (as opposed to just before and after 1985), there was insufficient replication for some species and in some time periods that prevented subdividing samples sets.

Another potential tool in assessing the distribution of *J. vulgaris* specifically is the use of remote sensing and satellite image analysis. Prior to undertaking this herbarium analysis, some progress was made with the help of Stella Belliss at Landcare Research with the use of images from the Quickbird satellite. These images captured *J. vulgaris* patches in flower and were able to determine their distribution within a 5 x 5 km window and estimate the amount of land they occupied. While this approach has potential and this type of analysis would be helpful in estimating the current distribution of *J. vulgaris* and tracking its spread or contraction and over time, it was not feasible in terms of finances or time for this thesis (while

`

I demonstrated the feasibility of this work in principle, ground-truthing is still needed especially in in landscapes with other, widespread, yellow-flowering species – most notably gorse (*Ulex europaeus*) and Scotch broom (*Cytisus scoparius*).

3.3 Results

A random labelling of *J. vulgaris* and *S. wairauensis* points in the analysis found that the two species are significantly segregated along the entire range of spatial scales (Fig. 3.1a). From 0 to 10 km the two species were clustered at levels below random chance indicating that these two species, despite both using habitats characterised by disturbance, were not found disproportionately near one another in the landscape. The same was true for *J. vulgaris* and *S. minimus* (Fig. 3.1c).

However, this was not the case for *J. vulgaris* and *S. rufiglandulosus* (Fig. 3.1b), which are segregated at smaller spatial scales but not at scales larger than about 4.3 km. However, if the sampling window is reduced to the smallest size rectangle possible that still incorporates the area where *S. rufiglandulosus* is located, then a segregation trend becomes stronger at larger scales too.

In terms of elevation, the collections for each species oscillated through time (Figure 3.2) with some measurable trends. The invasive *J. vulgaris* was the species that was the most well-represented at lower elevations (Figure 3.3). With the exception of the range between 0 to 50 m, *J. vulgaris* records were collected more often than all other species in the analysis and had more records in each 50 m increment of elevation between 0 and 500 meters than all other species combined in the analysis. Only *S. minimus* had more records from the 0 to 50 m range than *J. vulgaris*. Both *J. vulgaris* and *S. minimus* had the highest number of records at low elevations with records decreasing with increasing elevation. Records of the native *S. quadridentatus* exhibited bimodal distribution with a large number of specimens collected at 0 to 50m and then another spike in records between 350 and 400 m. The endemic *S. rufiglandulosus* had a few records that were distributed more-or-less evenly below 1200 m. *Senecio rufiglandulosus* was the least encountered species of all and exhibited an irregular distribution on the South Island. One other endemic, *S. dunedinensis,* demonstrated a normal, unimodal distribution with the number of records that peaked between and 850 to 900 m. The last species and endemic, *S. wairauensis,* peaked between 700 to 750 m, although it did have a smaller peak in the number of records collected between 0 and 50 m.

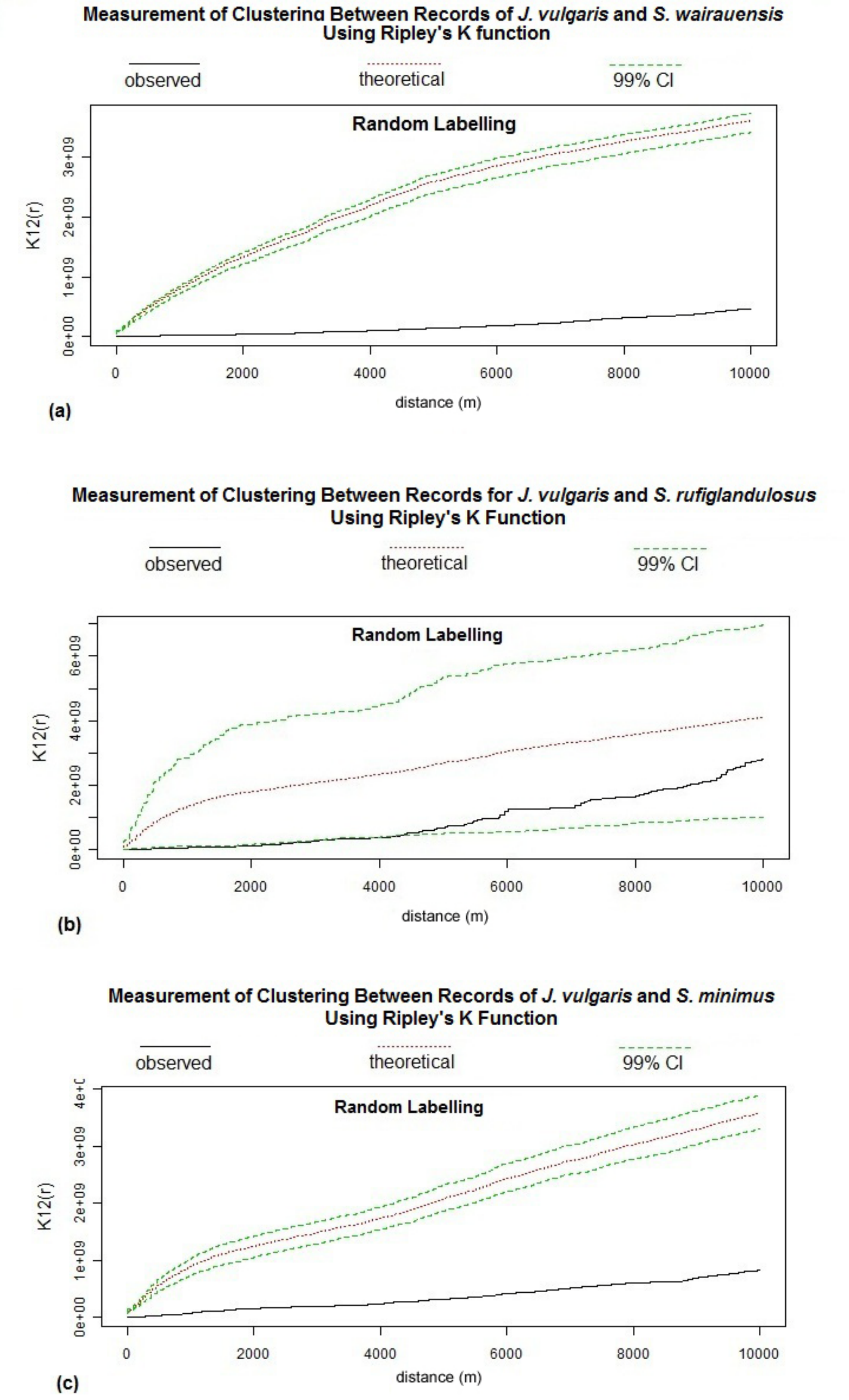

Figure 3.1 - The level of herbarium and vegetation survey clustering between *Jacobaea vulgaris* and three native *Senecio* species (*S. wairauensis, S. rufiglandulosus* and *S. minimus*) at differing spatial scales from 0 to 10,000 meters using Ripley's K Function. The solid black line indicates the observed level of clustering, the red dashed line indicates the theoretical level of clustering by chance and the green dashed lines indicate the 99% confidence intervals.

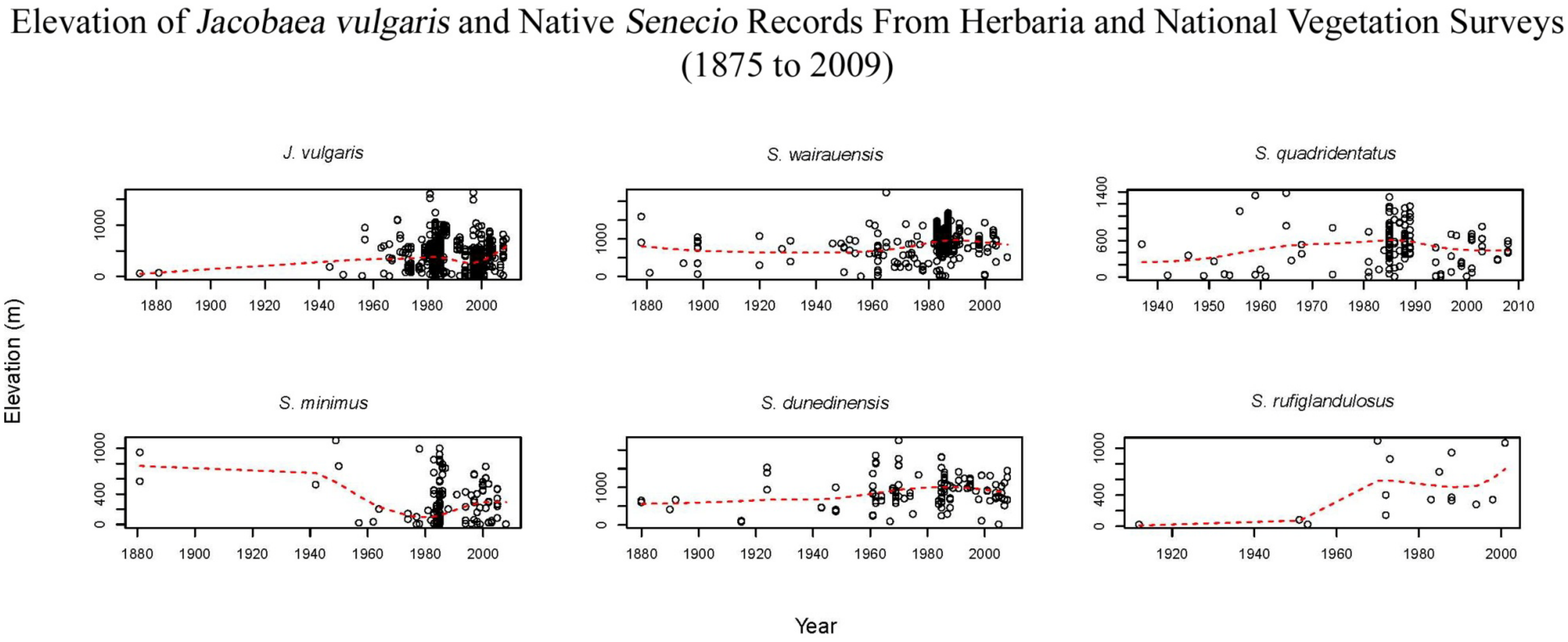

Figure 3.2 - Collections of an invasive weed (*Jacobaea vulgaris*) and two native herbs (*Senecio minimus* and *S. quadridentatus*) and three endemic herbs (*S. dunedinensis, S. rufiglandulosus* and *S. wairauensis*) in New Zealand. The horizontal axis indicates the year collected and the vertical axis is the elevation (m) of the samples recorded. The dashed red line indicates a running mean of elevation through time.

`

Elevational Distributions of Herbarium and Vegetation Survey Records For *Senecio jacobaea* and Five Species of Native New Zealand *Senecio*

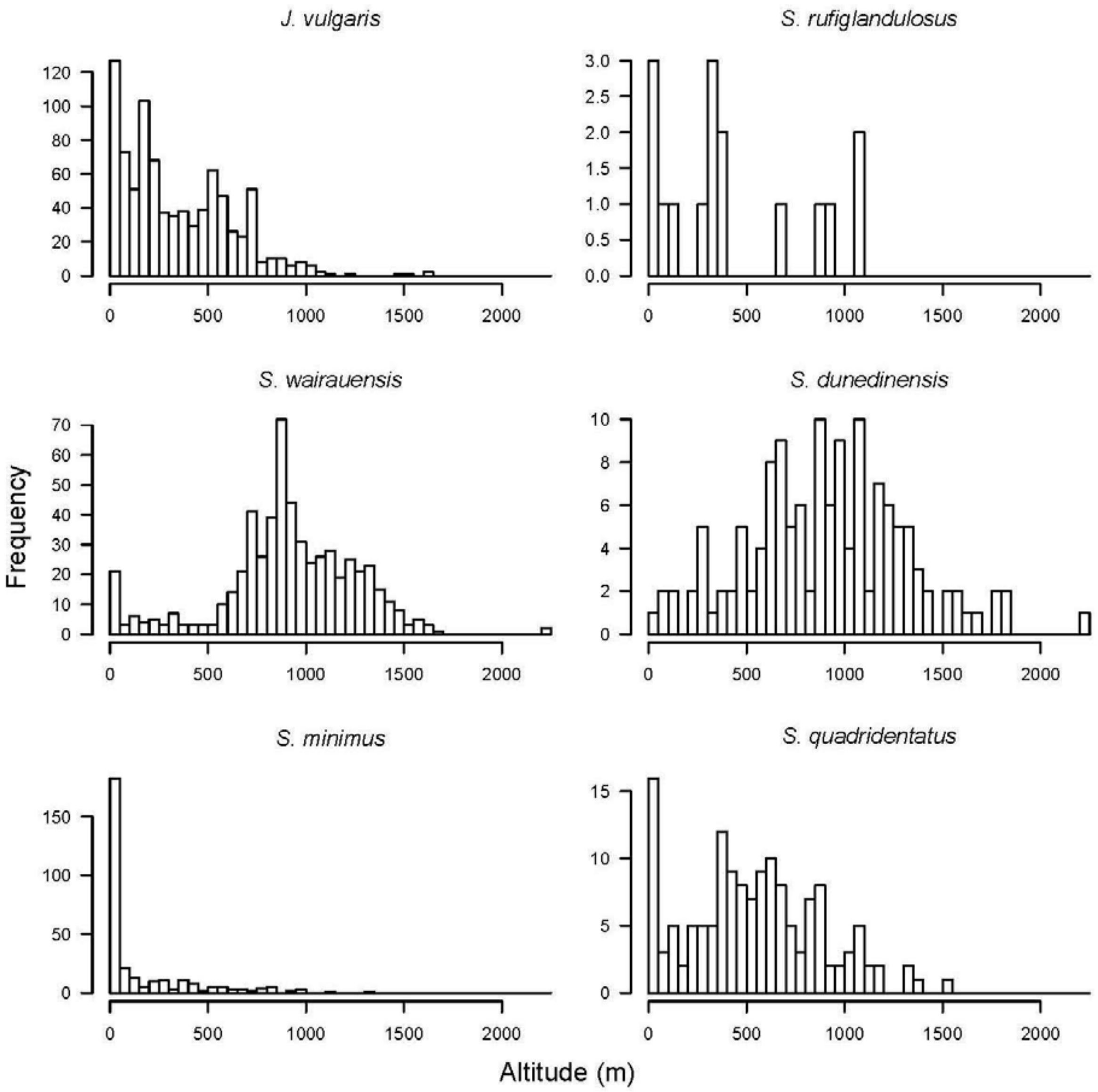

Figure 3.3 - Distributions by elevation of herbarium and vegetation survey records for *Jacobaea vulgaris* and five native *Senecio* species in New Zealand collected between 1874 and 2009. The horizontal axis indicates elevation in 50 m intervals and the vertical axis is the number of samples recorded.

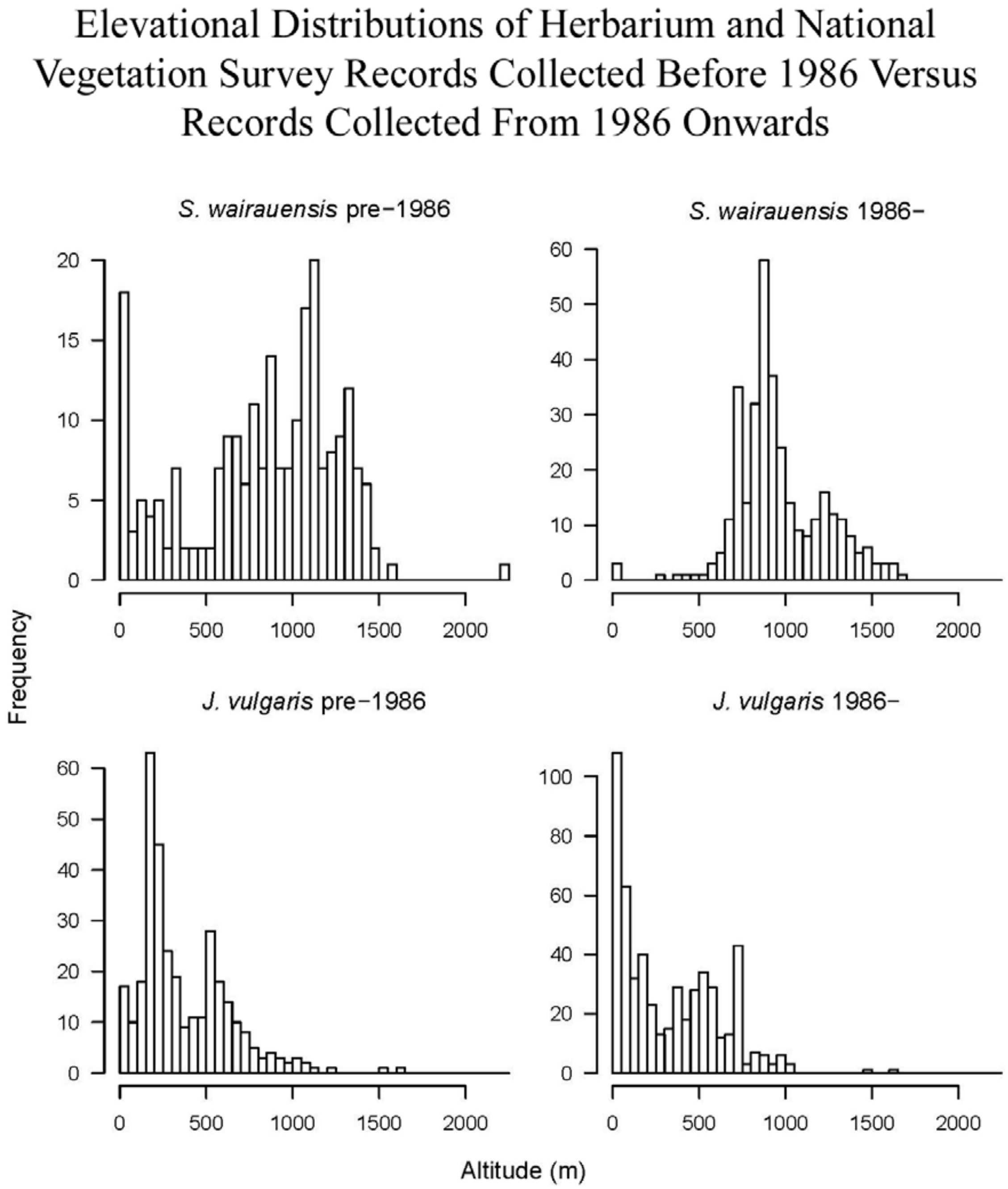

Figure 3.4 - Distributions by elevation of herbarium and vegetation survey records for an invasive weed (*Jacobaea vulgaris*) and the endemic herb (*S. wairauensis*) in New Zealand. Comparison is of records collected up to 1986 versus records collected from 1986 onwards. The horizontal axis indicates elevation in 50 m intervals and the vertical axis is the total number of collections from that period.

`

There was an interesting trend noted when comparing the records for *J. vulgaris* and *S. wairauensis* collected before 1986 with records collected from 1986 onwards. This year is significant in that it is the median collection year. In general, it appears that the relative altitude for the years preceding 1986 increased for both species. However, the lack of uniform collecting methods and standards makes it difficult to draw any conclusions as to why.

At this point it must be noted that the earliest collections of all native New Zealand *Senecio* species are from around the same time or since *J. vulgaris* was first conclusively recorded in New Zealand (1874). This means that much of any change that likely resulted from apparent competition occurred prior to the collection of the vast majority of these records (Figure 3.5). For instance, only 33 (less than 2%) of the 1,977 *Senecio* records used for this analysis were collected before 1940. On the other hand and while this is a small sample on which to base generalizations, of these 33 records the majority of them (19) are records for *S. wairauensis* and 7 of which (36.8%) are below 500 m. Comparatively, of the other 491 encounters for *S. wairauensis* that were recorded from 1940 on, only 50 (10%) were recorded below 500 m.

3.4 Discussion

Despite the fact that *Senecio* species all use disturbed, ruderal habitats, the records from herbaria and vegetation surveys for the invasive *J. vulgaris* did not demonstrate any level of clustering with the endemic *S. wairauensis* or the native *S. minimus*. Even at distances up to 10 km, the two native species were rarely encountered near the invasive *J. vulgaris*. However, I have also observed this and the other native and endemic *Senecio* species growing in close proximity or intermixed with *J. vulgaris* at several Westland locations (Chapter 5) suggesting that the lack of overlap at fine spatial scales in my analysis may be an artefact of collection bias. The pattern of clustered between *J. vulgaris* and *S. rufiglandulosus* at local scales, but not at distances of more than about 4 km, may be indicative of the few locations on the South Island at which this endemic is found. In fact, I have only been able to locate three populations of this species on the South Island – all of them on roadsides where *J. vulgaris* is present. Sullivan et al. (2008) notes that this species has become more rare over time on the North Island lending more support to the idea that the geographic range of this species is contracting.

Whether these patterns are correlative, causal or an artefact of collection bias is unclear. These results are consistent with apparent competition between these species, although they could likewise be driven by other factors such as direct competition with other plants and land use changes. For instance, *J. vulgaris* is associated with livestock grazing

`

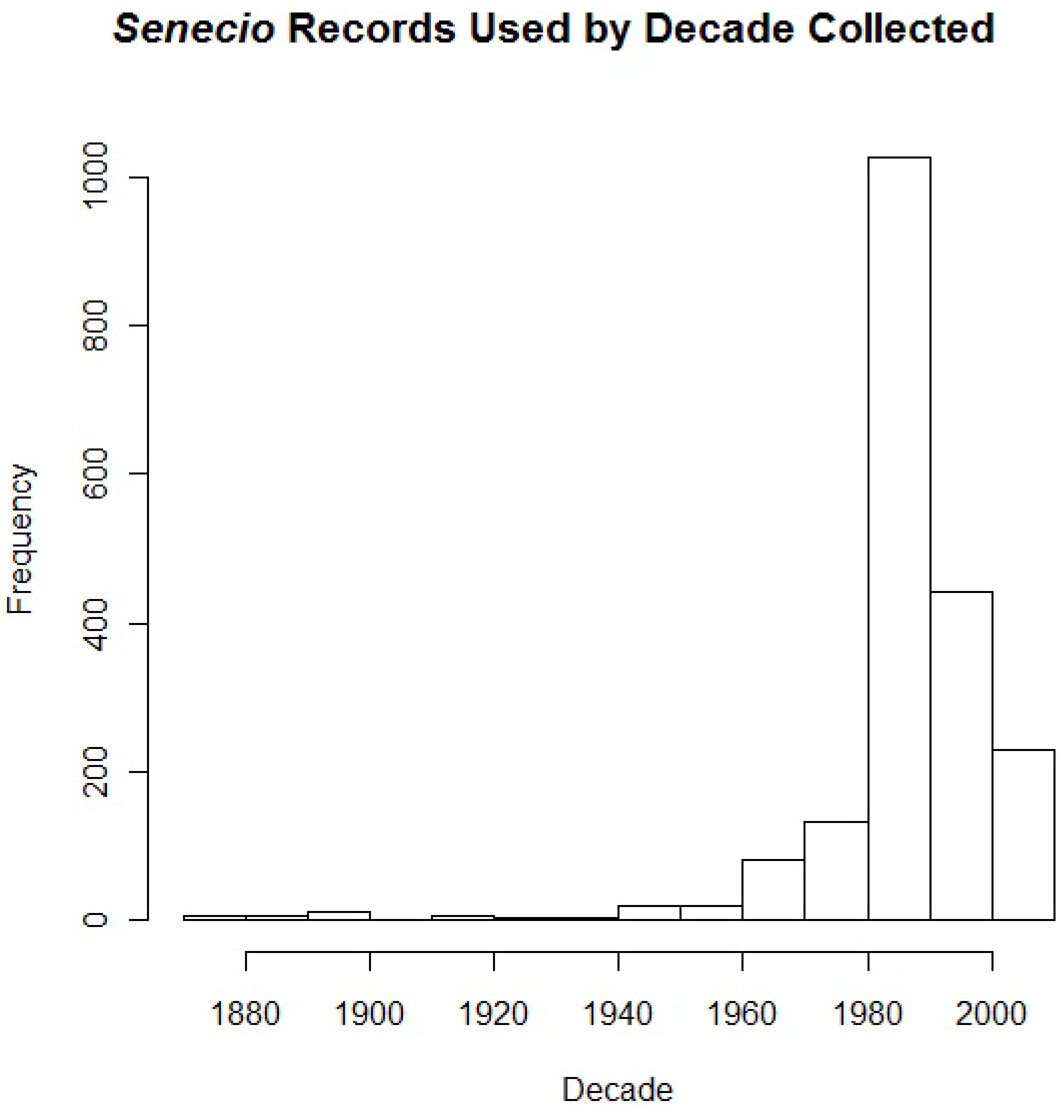

Figure 3.5 - Number of all herbarium and vegetation survey records used in the accompanying analysis collected by decade, including an invasive weed (*Jacobaea vulgaris*), two native herbs (*Senecio minimus* and *S. quadridentatus*) and three endemic herbs (*S. dunedinensis, S. rufiglandulosus* and *S. wairauensis*) in New Zealand. The horizontal axis indicates decade collected and the vertical axis is the number of records used.

(Hanley, Fenner, & Edwards, 1995; Kunin, 1999; Lozon, 1997; McEvoy, et al., 1993; Myers & Post, 1981; Poole & Cairns, 1940; Schmidl, 1972a; Sutherland, et al., 2000; Wardle, 1987), while native *Senecio* species may be readily eaten by stock. If this is the case, the clustering of *J. vulgaris* with native *Senecio* would be low at small spatial scales in these areas.

Another issue is that the overall sampling method for these data is not systematic and the data resolution is poor. For example, half of the records used were collected below the median elevation of 480 m with most of these collected from between 0 and 50 m (Figure 3.5). Likewise half of the records were collected in the last 24 years (since 1986) (Figure 3.6). Each data source also appears to have its own distinct geographic distribution patterns and some areas are well represented and while others are not (Figure 3.7). If these data sets are broken up into native status, the distribution of the groups indicates that endemics are generally found away from population centres, native *Senecio* are found in highly-visited yet protected areas, and invasive *J. vulgaris* is found everywhere else (Figure 3.8).

The individual species included in this analysis have distribution patterns that fit into my own field observations; however the collections within a species geographic range are not as uniform as I would have hoped. For instance, *S. minimus* is both widely-distributed and common across the South Island (personal observation, Jon Sullivan personal communication), but the map of collection points for this species would indicate that it is less commonly encountered than *S. wairauensis* and is largely found along the West Coast Highway near Haast (Figure 3.9).

Perhaps a good way to increase resolution is by incorporating absence data into the analysis. The National Vegetation Survey (NVS) database system records both presence and absence data within their plots. However, for the present set of data there were issues with regards to accurately identifying absence data – since different surveys were undertaken to varying taxonomic details (Hazel Broadbent, personal communication). Subsequent work on these analyses should focus on the NVS data which would ensure that there is a certain level of systematic sampling and more evenness in sampling effort. Additionally use of NVS data would allow incorporation of absence data which would further increase the resolution and robustness of observed trends.

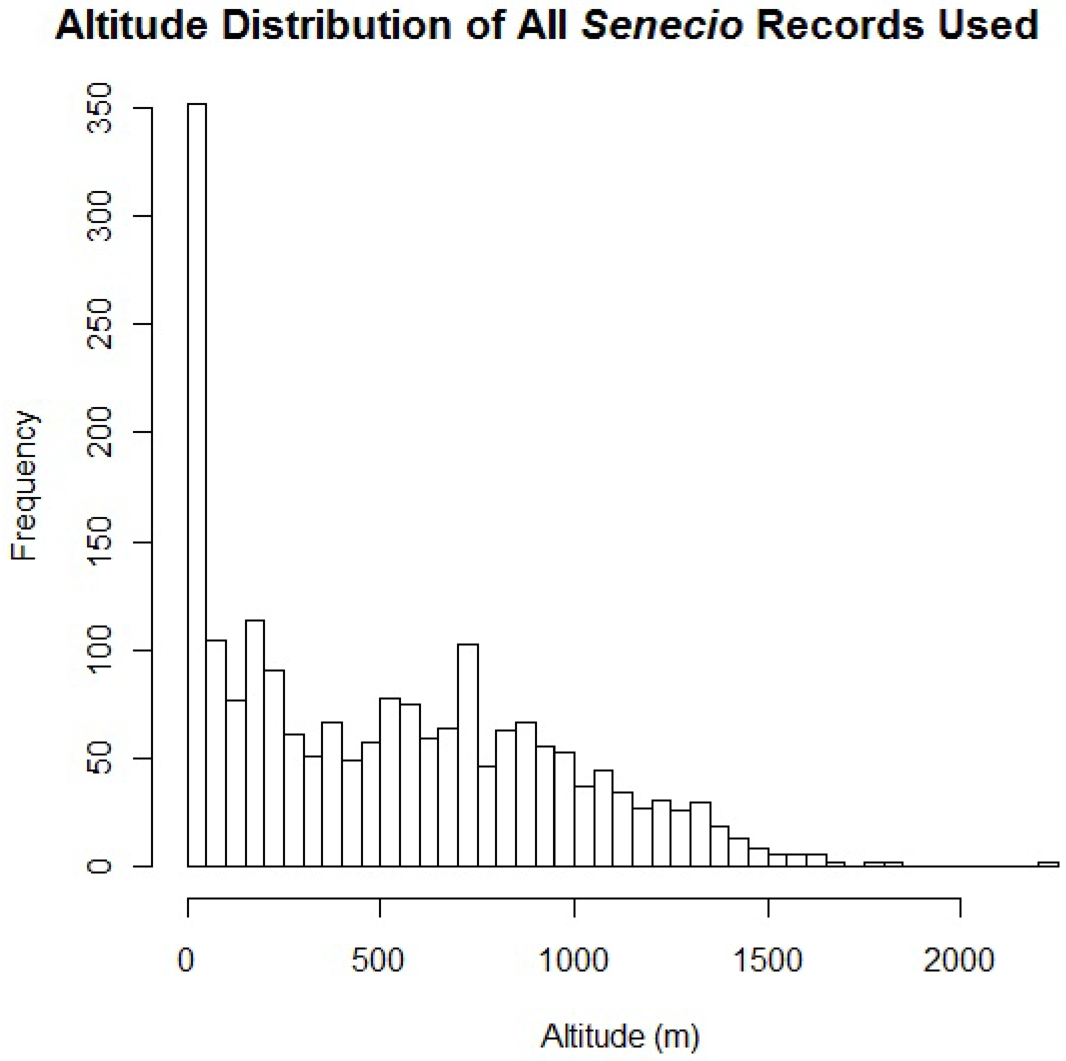

Figure 3.6 – Distribution by elevation of all *Senecio* records used for this survey, including an invasive weed (*Jacobaea vulgaris*), two native herbs (*Senecio minimus* and *S. quadridentatus*) and three endemic herbs (*S. dunedinensis, S. rufiglandulosus* and *S. wairauensis*) in New Zealand. The horizontal axis indicates elevation in 50 m intervals and the vertical axis is the number of records used.

`

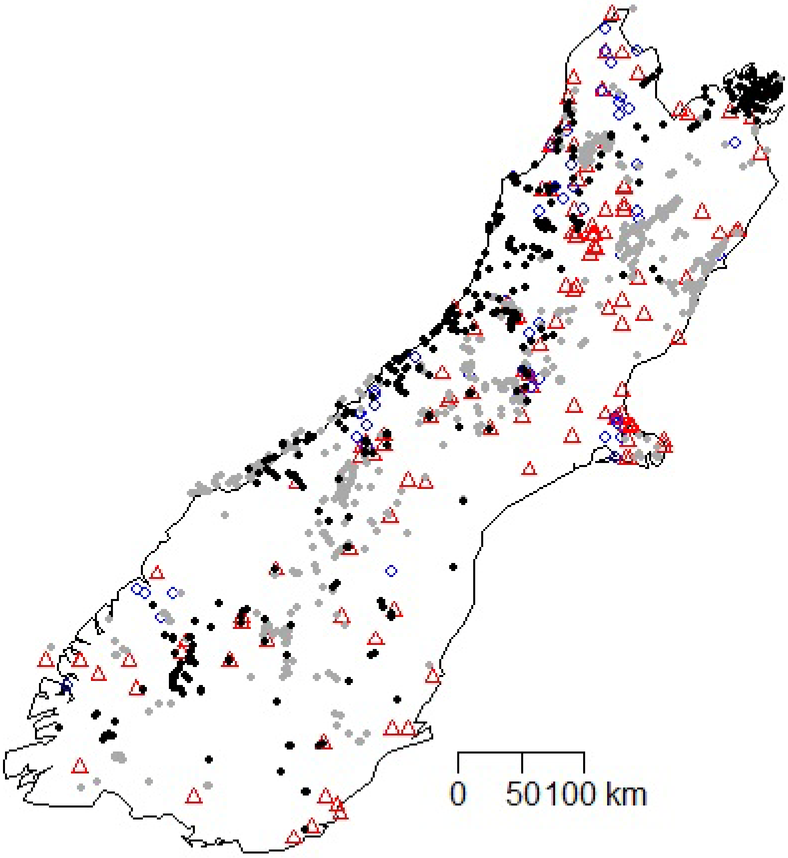

Figure 3.7 – Geographic distribution of six *Nyctemera annulata* host plant species records used for this analysis (*Jacobaea vulgaris, Senecio minimus, S. quadridentatus, S. dunedinensis, S. rufiglandulosus* and *S. wairauensis*) on the South Island of New Zealand and labelled by record source. The black dots are records from the Department of Conservation BioWEB database (BWEB), the grey dots are National Vegetation Survey (NVS) data, the blue open circles are records from the University of Auckland Herbarium (AK) and the red triangles are records from the Allen Herbarium (CHR).

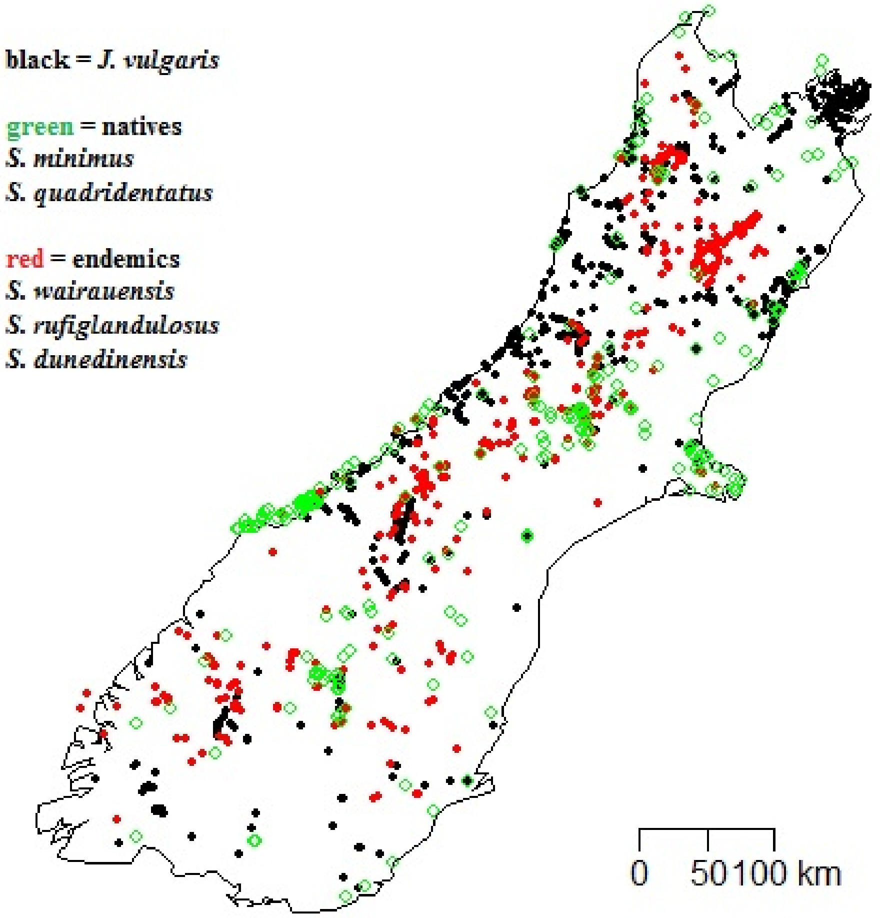

Figure 3.8 – Geographic distribution of six *Nyctemera annulata* host plant species records used for this analysis: the invasive (*Jacobaea vulgaris* (black circles)), the non-endemic natives (*Senecio minimus* and *S. quadridentatus* (green circles)), and the endemic host plants (*S. dunedinensis, S. rufiglandulosus* and *S. wairauensis* (red circles)) on the South Island of New Zealand and labelled by record source. The black dots are records from the Department of Conservation BioWEB database (BWEB), the grey dots are National Vegetation Survey (NVS) data, the blue open circles are records from the University of Auckland Herbarium (AK) and the red triangles are records from the Allen Herbarium (CHR).

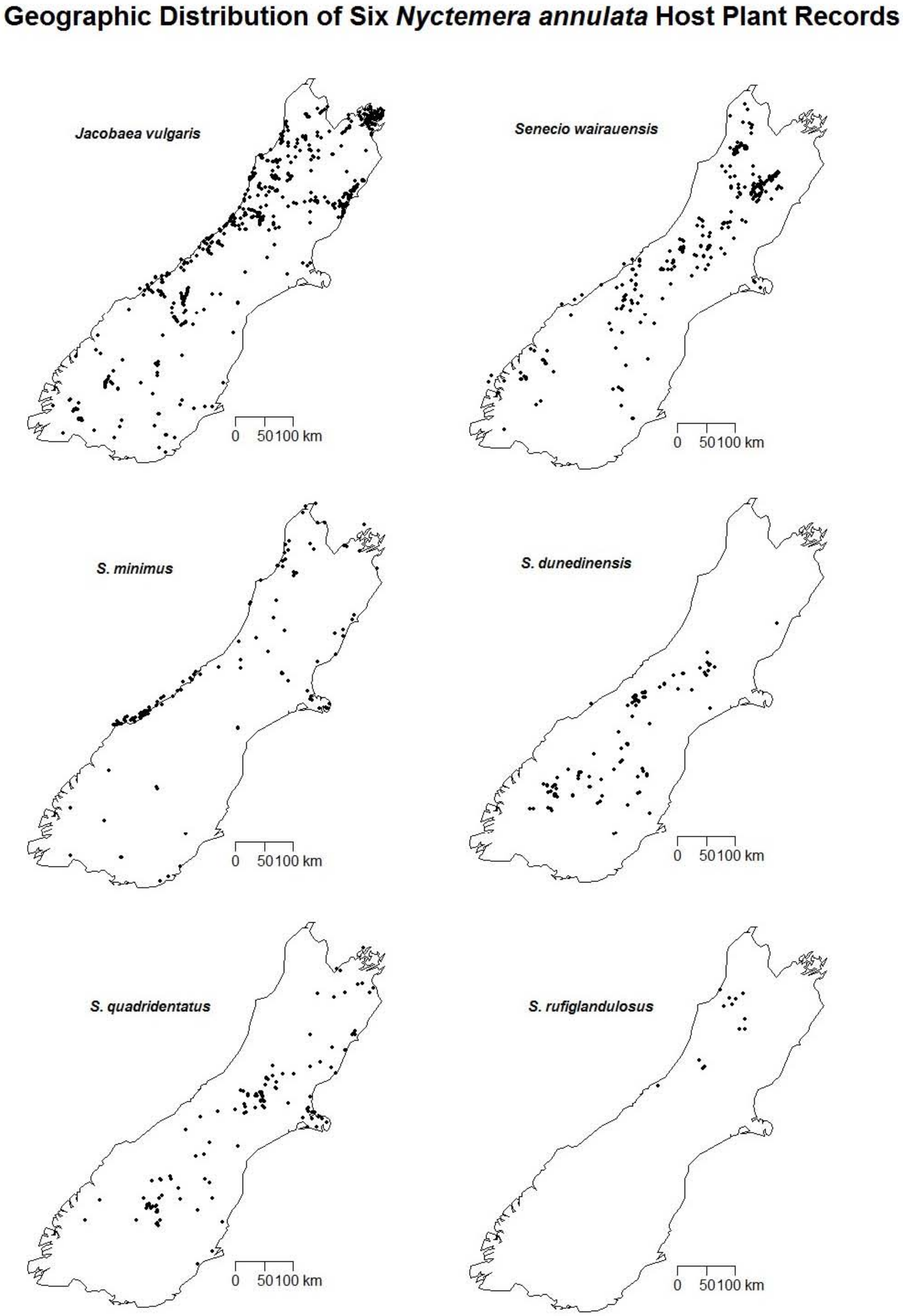

Figure 3.9 – Geographic distribution of records for six *Nyctemera annulata* host plant species used for this analysis (*Jacobaea vulgaris, Senecio minimus, S. quadridentatus, S. dunedinensis, S. rufiglandulosus* and *S. wairauensis*) on the South Island of New Zealand. Data sources listed in Table 3.1.

`

Another useful way to verify population level impacts on native *Senecio* from *J. vulgaris* presence in the native food web would have been to repeat this analysis using a control group. Performing the same analysis with a functionally-analogous set of endemic herb species with no invasive congeners would supply a model with which to compare native *Senecio*. This control species would, theoretically, demonstrate impacts from the same pressures of direct competition and habitat modification, but not from the impact of shared, specialist insect herbivores. If repulsion was detected from *J. vulgaris* on endemic *Senecios* – but not detected for the co-occurring control species – this would be a stronger indicator of apparent competition. Another way to help address the motivating factors for the trends seen in these analyses is to carry out a systematic field survey in areas where these species exist today. By surveying areas where *Senecio* species are present and absent and by comparing their distribution patterns, stronger conclusions could be drawn as a result. So to address the weaknesses outlined above, I ultimately carried out a landscape survey of *Senecio* and co-occuring *N. annulata* to determine whether apparent competition is occurring (Chapter 5).

In examining the altitudinal trends of all species through all years, it is apparent that, in addition to being encountered more overall, *J. vulgaris* is proportionally recorded much more often at low elevations (< 500 m) than are the endemic *Senecio* species. At the same time, endemics like *S. wairauensis* and *S. dunedinensis* are notably rare at these same elevations – especially in recent decades. Only *S. minimus* has been regularly and commonly collected from areas below 500 m, although the number of overall encounters is fewer compared to those for *J. vulgaris* and *S. wairauensis*. The other interesting trend in these distributions is that as *J. vulgaris* encounters begin to drop off at 500 to 600 m, encounters of *S. wairauensis* and *S. dunedinensis* begin their greatest increase in collection numbers. Taken together, this pattern suggests that the presence of *J. vulgaris* at low elevations correlates with a dip in populations of *S. wairauensis* and *S. dunedinensis*. While my analyses did not explicitly examine the distance between records for these same endemic species in the lowest elevations and their relative distance from *J. vulgaris* records, my own field surveys suggests that at least one endemic (*S. wairauensis*) can be common in low elevation areas where *J. vulgaris* is absent (Chapter 5).

The significant changes in altitudinal distribution of three species, in particular, demonstrate that there is dynamism in this system. While the invasive *J. vulgaris* shows shifts through expansion along the altitudinal gradient, the endemics *S. wairauensis* and *S. dunedinensis* demonstrate contraction, especially from the lower elevation areas of New Zealand. Ongoing

`

analysis of this and associated data is likely to lead to more insights into the association of *J. vulgaris* with these changes.

`

Chapter 4
Host Expansion in the New Zealand Magpie Moth, *Nyctemera annulata*

4.1 Introduction

The general consensus is that insect herbivores (particularly specialists) prefer their original host plants over novel potential hosts in their naturalised range (Bernays & Chapman, 1994; Fowler, Syrett, & Hill, 2000; Joshi & Vrieling, 2005; Liu & Stiling, 2006; McEvoy, 1996; Via, 1990; Eve M. White, Sims, & Clarke, 2008, c.f. Keane and Crawley 2002; H Zwölfer & Harris, 1971). The general assumption had long been that oliophagous and monophagous insect consumers have evolved physiological requirements for specific phytochemicals which they need for growth and development and that can only be found in a narrow range of plants (e.g. Bernays & Chapman, 1994). Additionally, many plants have evolved complex chemical compounds that make them unpalatable and toxic to insect herbivores not adapted for overcoming these defenses. These requirements, in turn, inform which plants they find palatable. Fidelity in host selection and feeding is one of the underpinning principles behind the classical biological control of plant invaders: insects selected for release are tested to ensure that they prefer their original host plant (target) over other plant species available to them (non-targets).

An example of narrow host specificity in an insect is the alligator weed flea beetle (*Agasicles hygrophila* (Coleoptera: Chrysomelidae)) which was introduced for control of the aquatic weed *Alternanthera philoxeroides* in North America and elsewhere (reviewed in Buckingham, 1996). *Alternanthera philoxeroides* is native to South America, but invaded waterways in Florida beginning in the early 20th Century. It soon became a problem in that it hindered navigation, blocked drains and water intake valves, severely reduced sunlight penetration in the water column and outcompeted native aquatic and shoreline plants. Alligator weed flea beetles were collected from Argentina and introduced beginning in the mid-1960s into parts of the U.S. where *A. philoxeroides* had spread, which included the Gulf Coast states, the Carolinas and California. In Florida, alligator weed flea beetle was not established until 1977-78 and after re-importation of new genetic stock, however it rapidly set to work decimated *A. philoxeroides* across the region. To date there are few reports of impacts on non-target plants in the U.S. by the alligator weed flea beetle and a manuscript that includes a summary of pre- and post-release testing published this year reports that this species does not

`

develop well on other species in the U.S., aside from *A. philoxeroides* (Lu et al., 2010). So it appears that the alligator weed flea beetle needs to feed on *A. philoxeroides* in order to complete its lifecycle and that it finds few other hosts palatable. Like other specialist insect herbivores, the alligator weed flea beetle is highly restricted in its diet making it ideally suited for the purposes of biological control.

The literature also contains many examples of host expansions and shifts. There are numerous recorded instances where native consumers have successfully fed and reproduced on exotic hosts that invade an area (Agosta, 2006; Alleyne & Wiedenmann, 2002; Cuda, Parker, Coon, Vasquez, & Harrison, 2002; Grosman, et al., 2005; Keeler & Chew, 2009; Newman, Borman, & Castro, 1997; Strauss, Lau, & Carroll, 2006; J. J. Sullivan, et al., 2008; Thomas et al., 1987; Tscheulin, Petanidou, & Settele, 2009), as well as a history of host-range expansion by invasive insects that make use of the plant species in a new geographical range (Agosta, 2006; Gassmann, et al., 2006; Korenchenko, 1980; C. M. Malmstrom, et al., 2005; Marchetti, 1962; Settle & Wilson, 1990; Thomas, et al., 1987; Ueno, Fujiyama, Yao, Sato, & Katakura, 2003; Verhoeven, et al., 2009). Host-range expansion and host shifts rely on the ecological fitting between an insect herbivore and a novel host plant (Agosta, 2006; Agrawal, 2000; Becerra & Venable, 1999; M. Deane Bowers, Stamp, & Collinge, 1992; S. M. Fraser & Lawton, 1994; Gassmann, et al., 2006; Peccoud et al., 2008). Instances of host-range expansion in monophagous and oligophagous insect herbivores occurs most frequently with closely related host plants (reviewed in Futuyma & Mitter, 1997).

Brooks and McLennan (2002) cited three key concepts regarding ecological fitting and how they function to mediate plant-insect associations. In brief, these concepts are that adaptations can be used to perform novel functions, insect herbivores track host resources (e.g. phytochemistry, phenology, architecture, etc.) and that these traits in hosts are evolutionarily conserved (although occasionally convergent) in alternate hosts. In other words, associations between insect herbivores and host plants that they use are determined by the available genetic variation in the insect herbivore and the genetic composition of the host(s). The likelihood in occurrence of host shifts and host-range expansions decreases the longer an insect maintains an association with a particular host(s) (discussed in Futuyma & Mitter, 1997). For example, melaphidine aphids discussed in Moran (1989) have complex life cycles and have used sumac (*Rhus* spp.) and mosses as hosts for millions of years. Examination of the modern day host faithfulness of this group of aphids endemic to different continents that have roughly 40 million years of biogeographic separation (North America and Asia) reveals that the ancient association has severely limited the ability of the aphids to use other plants hosts. Obviously the inability to expand host range or shift hosts ties the insect herbivore's fate to that of the host plant(s).

Host shifts, like host-range expansions, require ecological fitting between insect and host plant. Facilitation of a host shift also requires a fitness-enhancing component, such as enemy-free space (J. M. Brown, et al., 1995; Gratton & Welter, 1999; Zangerl, et al., 2002) or a greater abundance of hosts (Agrawal, Lau, & Hamback, 2006; Menken, Boomsma, & Van Nieukerken, 2010; Shannon & Feeny, 2006), and results in greater use of the novel host (Weis, 1992). Expanding a host range to incorporate a more widely-distributed and abundant host is a particularly successful strategy for insect herbivores that are able to do so. Such as host-range expansion occurred with the Colorado potato beetle (*Leptinotarsa decimlineata*). This insect is native to southwestern North America and is presumed to have fed on native solanaceous plants in that area. The history of this *L. decimlineata* is reviewed in Jacques (1988) and states that this beetle was first discovered in 1811 by Thomas Nuttal who collected it from buffalo-bur (*Solanum rostratum*) in the southern range of the Rocky Mountains. It wasn't until 1859 – well after the potato (*S. tuberosum*) was first cultivated in Europe in the late 16th Century and introduced to North America in the early 17th Century – that the beetle became one of the most widespread and destructive potato pests. By expanding its host range to a crop widely cultivated on four continents, it eventually expanded its geographic range to become widespread throughout much of the world. The strategy used by *L. decimlineata* of using existing traits to exploit abundant and widespread, alternate hosts to become abundant and widespread itself is a successful one. As a genus-specific monophage it was able to colonize a new species with which it had no prior evolutionary history, but which it was genetically suited to exploit. Even within a given area, like New Zealand, if an insect herbivore is able to make good use of an abundant host (wither a cultivated crop or an invasive weed) in areas where its original host plant(s) are rare or absent, the implications for increased fitness of the insect are obvious.

New Zealand is home to 19 native species of *Senecio*, 13 of which are endemic. These plants support a community of native, specialist insect fauna that feed exclusively on *Senecio* and close relatives. *Jacobaea vulgaris* (formerly *Senecio jacobaea*) is an herbaceous pasture weed that is native to Europe and has spread to several other places around the world. It established in New Zealand around 1870 and has since been present in the landscape, particularly in disturbed landscapes characterized by livestock grazing. Previous research supports the assertion that *J. vulgaris* has a relatively high tolerance for herbivory and that its abundance and distribution appears more limited by the availability of suitable, disturbed

`

habitat than by herbivores – even in its native range (McEvoy et al. 1993, Wardle 1987, Stables 1983, Radcliffe 1969, Poole and Cairns 1940).

As reviewed in Chapter 2, the New Zealand magpie moth (*Nyctemera annulata*, Lepidoptera: Arctiidae) is a day-flying moth that generally uses only plants in the genus *Senecio* (and closely-related taxa, including *J. vulgaris*) as hosts. Numerous lab and field observations confirm that it has successfully expanded its host range to feed and develop on *J. vulgaris*. Indeed, despite having an evolutionary history with the native *Senecio* species, it has arguably become more closely associated with *J. vulgaris* in people's minds and quite possibly numerically in some modern New Zealand landscapes. However, the quantitative aspects of the relationships between moth and the plants have yet to be examined.

This research is designed to compare a few dimensions of the relationship between *N. annulata* and four New Zealand host species: *J. vulgaris* (exotic), *S. minimus* (native), *S. quadridentatus* (native) and *S. wairauensis* (endemic). I used choice tests to establish host plant preference by larvae and no-choice tests to determine moth performance on monophagous diets of the four different species. A field experiment was also conducted using the same species to further examine preference and performance, as well as the impact of magpie moth herbivory on whole plants. My expectations were that *N. annulata* larvae would prefer feeding on native *Senecio* species with which they have a closer evolutionary relationship over the invader, *J. vulgaris*. For the same reason, I expect larvae that feed on native *Senecio* will grow more and develop faster than larvae fed *J. vulgaris*, as is often the case with a host range expansion. Given a lower expected preference for *J. vulgaris*, as well as its reputation to greater tolerance to herbivory (discussed in Chapter 2), I expected *J. vulgaris* to incur less negative impact as a result of *N. annulata* herbivory than the native *Senecio* species.

4.2 Methods

4.2.1 Magpie Moth

All magpie moth larvae (*Nyctemera annulata*) used in these assays were selected at random from freshly hatched eggs produced by a lab colony maintained at Landcare Research in Lincoln, New Zealand. The colony was started from larvae found on *S. quadridentatus* plants growing along the Summit Road on the Port Hills above Christchurch and adult moths found in-flight and larvae that I came across on potted *Senecio* plants of 3 additional species in the greenhouse were subsequently added to the colony in order to increase numbers and potentially the genetic diversity. The larvae were placed in mesh cages (60 cm^3) and kept in a

`

rearing room at Landcare Research in Lincoln under a 16L:8D photoperiod and with temperatures of 24°C during the light phase and 15°C during the dark phase.

All four of the *Senecio* (or formerly *Senecio*) species being assayed (the non-native *J. vulgaris* and the natives, *S. minimus, S. wairauensis* and *S. quadridentatus*) were offered as larval food to the magpie moth colony in an effort to prevent a larval performance or choice bias. Larval feeding on all of these species was noted each time plants were removed and added throughout the lifetime of the colony. In total, 12 plants (3 of each species) were placed in a cage and larvae were allowed to move about freely within a cage and feed on any of the host plants provided. Larvae were reared through to adulthood on this mixed diet, at which time they were placed in a new cage and allowed to mate and (in the case of the females) oviposit. Another measure taken in order to avoid host preference bias is that all larvae used in the assays came from ova that were freshly laid on the interior surface of the cage (as opposed to those laid on plants). These ova were scraped off the cage and placed in a Petri dish that was lined with moist filter paper (in order to maintain humidity). When hatching events took place, larvae less than 24 h in age were selected at random from the dish(es) to be used in the assays. Any unused larvae were returned to the colony.

4.2.2 Host Plants

All of the plants used in the assays were grown from seed taken from wild plants in Canterbury and Westland Regions (see below for site details). Four of the 37 species of *Senecio* established in New Zealand were selected for this experiment because they are known to co-occur in several areas of Te Wai Pounamou/South Island and because they all host magpie moth. This selection also incorporates species that are endemic, non-endemic native and exotic to New Zealand.

Seeds of *J. vulgaris* were taken from an area on Department of Conservation land known as Calf Paddock (about 2 km east of Springs Junction on Highway 7 (lat/long: -42.350045°,172.226143°) in May 2007 and promptly potted in the Lincoln University Greenhouse Facility. Seeds of *S. minimus* and *S. wairauensis* were collected from an overlook along HWY 6 in the Buller Gorge (lat/long: -41.784783°, 172.034163°) also in May 2007. Seeds of *S. quadridentatus* were collected along the Summit Road, Port Hills (lat/long: -43.590528°, 172.695131°) in December 2007. All seeds were germinated in the Lincoln University greenhouses using “3-4 month potting mix” which has fertilizing agents that are active for 3 to 4 months (contains per 1m3: 800 litres composted bark, 200 litres pumice 1-

`

4mm, Osmocote exact 16 - 3.9 - 10 (N,P,K) 3-4 month 1000g, Agricultural lime 500g, Hydraflo 500g (Wetting agent)).

Once plants were approximately 10 cm in height the host plant seedlings were transferred into 3 litre pots with fresh potting mix and placed back into a greenhouse where they were watered from above daily and allowed to drain freely. Between the first round of choice and no-choice assays and the second round, the plants became infested with aphids (*Macrosiphium euphorbiae*) and were sprayed with Key Pyrethrum™ (5 mL/L) using a hand sprayer. Plants were not used in second round of assays until at least 14 days after the most recent insecticidal treatment and were selected at random. Plants used in the first round of assays were transferred to a Landcare Research (Lincoln, Canterbury, New Zealand) rearing room where the tests were carried out. The second round of assays was carried out on the Lincoln University campus.

4.2.3 Laboratory and Field Cage Assays

Each assay was conducted in an arenas constructed of a plastic Petri dish 85 mm in diameter and 15mm in height (Fig. 4.1). For the initial no-choice assays, each arena was assigned one host species and an excess of leaf tissue was offered in a single mass (an unmeasured amount that was greater than could be consumed by the larva). The subsequent choice and no-choice assays were carried out in the same type dish, but quadrats were created and larvae were offered a uniform measurement of leaf tissue by leaf area in each quadrant.

4.2.3.1 Initial No-Choice Assays

A series of no-choice tests were carried out to determine if development rates of magpie moth caterpillars differ significantly on different food plants. A preliminary assay was conducted where the four species of host plant were offered in no-choice arenas. A single leaf from one of the host species was placed in the arena and a newly-hatched larva was placed on the leaf. Ten replicates were assembled for each of the four species tested. The arenas were placed together on a bench top in a rearing room at in the Landcare Research Insect Quarantine Building in the same room and with the same environmental conditions in which the *N. annulata* colony was maintained. Every other day Petri dishes were opened to add fresh leaves and remove the accumulated frass, but otherwise the caterpillars were not removed except for a brief cleaning (once a fortnight, the interior of the arena was wiped clean with a single-use, moistened paper towel). For all arenas, an excess of plant material was added to ensure a surplus of food and adequate humidity for the developing larvae and pupae.

`

Figure 4.1 - Petri dish arena used for *Nyctemera annulata* preference and performance assays and measuring 85mm in diameter by 15mm in height (shown with one leaf disc within each quadrant and positioned on top of moist filter paper).

`

Each time the arenas were cleaned and refreshed with new plant material, a visual scan for exuvae or pupal cases was conducted and the corresponding event was recorded for that specimen. The temperature, percent humidity and time of day were also recorded. After new plant material was added to an arena with a caterpillar, the larva was placed directly on top of it using a paintbrush. At each feeding one individual plant was divided among all of the Petri dishes of that food plant species to keep food plant quality the same between subject arenas. The experiment began with *N. annulata* hatching on 20 Jan 2008 and ran through to the last pupation event of the cohort on 26 March 2008.

4.2.3.2 Choice and Second No-Choice Assays

A second round of experiments to determine host preference by larvae and the impact of host plant diet on larval development were carried out using arenas similar to those used for the no-choice assays. However, all Petri dishes used were labelled with four quadrats using an indelible marker on the outside of the dish. In the arenas that were to be used for the choice tests, each quadrat of the dish was designated and labelled for one of the four host species (Fig. 4.2a). In the no-choice tests, the same species was placed in each of the four arenas within a dish (Fig. 4.2b).

Leaf discs measuring 15 mm in diameter were cut out of individual leaves of each species using an insect collection vial in a “cookie cutter” fashion. Each vial used was used for only one species in order to prevent cross contamination. Leaf discs were cut while avoiding the mid vein in order to standardize the amount of biomass being collected. Once cut, the discs were transferred to their respective quadrants in the dish and a single larvae was placed in the middle of the arena. Since *S. quadridentatus* has long, thin leaves, sometimes it was necessary to use more than one leaf to cut out a comparable amount of biomass.

Each day, prior to opening the lid, the location of the larvae was recorded and new leaf discs were made and placed in the arenas. Upon being removed, the leaf discs were collected in paper bags and placed in a drying oven for 15 days at 75°C. These samples were then weighed and the amount of post-consumption biomass remaining from each disc was recorded. The discs were collected and replaced every 1–2 days over a period of 8 days. A group of control arenas was also established with the same composition as the test arenas, but had no larva added. With the exception of being weighed 4 weeks later, the discs from these arenas were collected and processed in the same manner as those from the experimental arenas. The masses of the experimental and control arena leaf discs were compared and the difference was attributed to consumption by larvae. Larval masses were recorded on days 1, 4

`

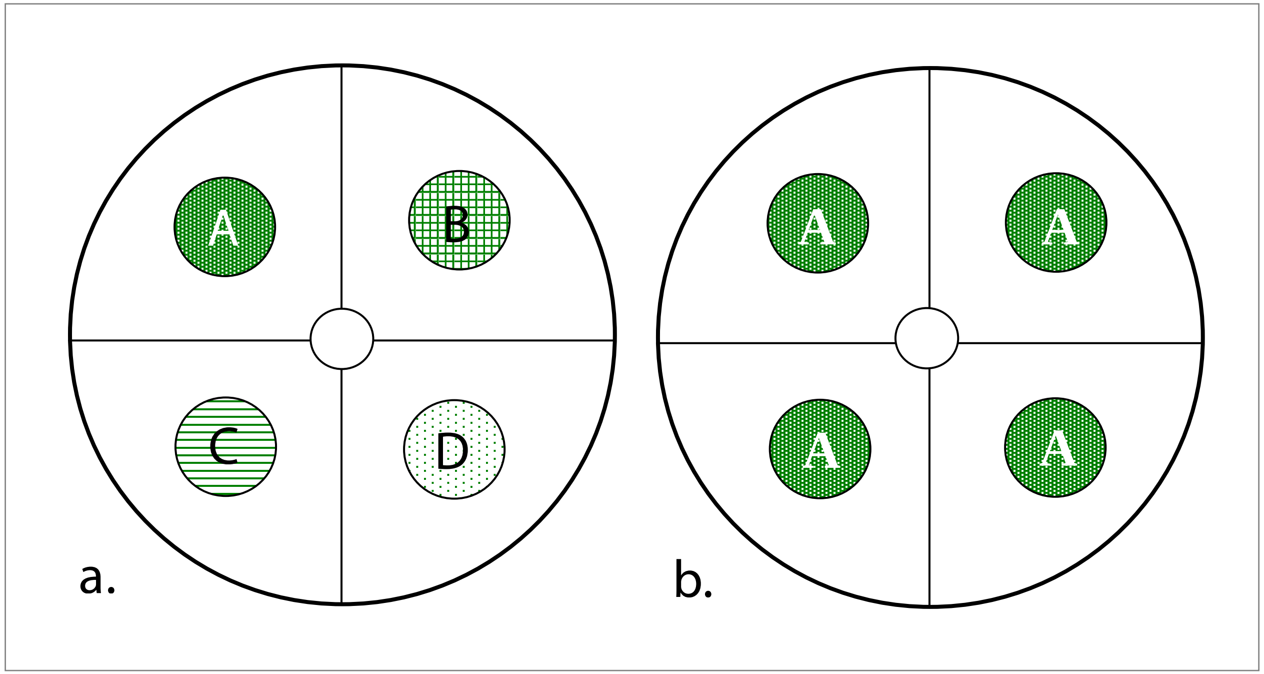

Figure 4.2 - A diagram of experimental arenas used for *Nyctemera annulata* choice (a) and no-choice (b) assays. Petri dish arenas were divided into quadrants. The choice test arenas consisted of four leaf discs from the four *Senecio* host species assayed. No-choice arenas also featured four leaf discs, but all from the same *Senecio* species. Each time the leaf discs were changed out the single *N. annulata* larva was placed in the centre of the arena. Control arenas were identical in their layout, but lacked larvae.

`

and 8. Similarly, daily visual estimates of percent herbivory were recorded for each disc removed.

4.2.3.3 Whole Plant Trials

A series of whole plant experiments was conducted in a field on the Landcare Research campus in Lincoln using polyester mesh cages measuring 8 m^3. The cages had steel pole frames that were securely pushed into the ground and then tied to an existing vineyard-type wire structure. The mesh cage was then draped over the frame and the bottom of the cage was secured to the ground with tent stakes and the bottom edge buried. A total of 24 cages were erected in the field, each of which was assigned a homogeneous or heterogeneous host composition. Heterogeneous host compositions consisted with one of the other (native) species being paired with *J. vulgaris* (see below for details).

Styrofoam "mushroom boxes" were used to hold the potted plants within each cage. Water levels in the mushroom boxes were maintained at about 5 cm in order to prevent caterpillars from moving off of the plants, as well as to keep the plants from drying out. Two mushroom boxes were placed in each cage and four potted plants were placed in each box. Single-species cages had four plants of the same species in each box, while boxes in mixed-species cages had two plants each from *J. vulgaris* and another host species. Pots in all boxes were placed in the mushroom boxes a zigzag configuration in order to fit, with heterogeneous boxes arranged so conspecifics are not directly touching one another (Fig 4.3). One of the mushroom boxes in each cage was selected as the experimental group. On this group, twelve newly-emerged, randomly selected larvae from the *N. annulata* colony were placed – three per plant. During the experiment the cages were only reopened in order to put water in the mushroom boxes.

After nine weeks, the cages were sampled by manually and visually, surveying the plants and the cage interior for *N. annulata.* Their location in the cage and lifestage were recorded for each individual, as well as the gender for adults. After searching for any final *N. annulata,* a 25 x 45 cm paper bag was placed over the plant before the above ground portion of the plant was lopped off at ground level. This was then placed completely inside the bag, which was subsequently folded closed at the top. All plant samples collected were placed in the drying ovens at 75ºC for 8 days before being weighed.

All data was analysed using R statistical analysis software (Version 2.10.0) (R Development Core Team, 2010). To determine any difference in growth rates and pupation times between the species treatments, I used GLMs constructed from the data with the ANOVA function.

`

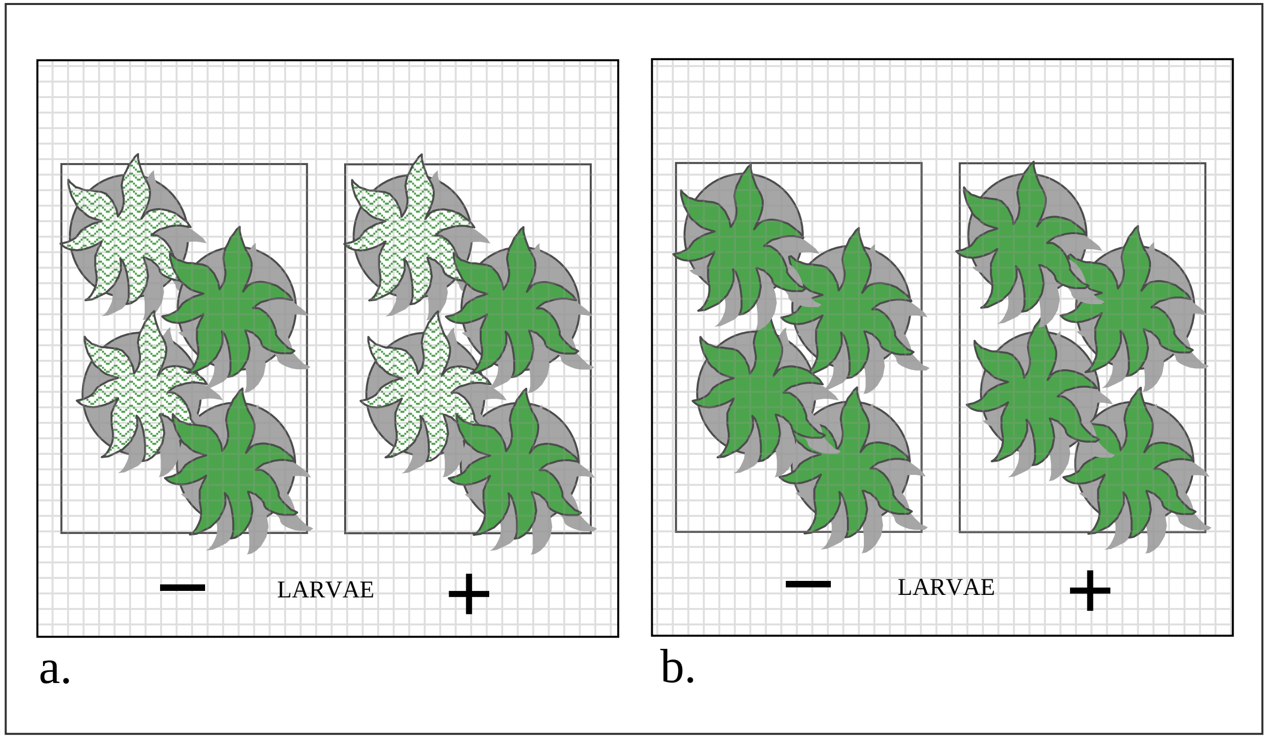

Figure 4.3 - Diagrams of cages used in field experiments to test whole-plant preference and performance by *Nyctemera annulata* larvae. Each cage has two identical replicates, each composed of a Styrofoam mushroom box containing four potted host plants. Some cages contained (a) mixtures of two host species, with some others were (b) composed of one individual species. Three newly-hatched *N. annualata* larvae were added to each plant in one of the boxes in each cage. Five cm of water in the mushroom boxes were maintained for the purposes of hydrating the plants, as well as preventing the larvae from leaving the plants in the box.

`

Chi-square tests were used to find any differential rates of larval mortality in the no-choice tests, as well as to confirm differences in host species preference.

4.3 Results

4.3.1 No-Choice Assays

4.3.1.1 Initial No-Choice Assay

In the initial no-choice assay, larval development time on *J. vulgaris* was the same or higher than on two of the native hosts tested (Fig. 4.4). Overall, I found a significant difference in the impact of diet on the number of days required to reach adulthood ($F_{3, 26} = 14.56$, $P < 0.0001$). When compared to caterpillars fed *J. vulgaris* (53.0 ± 1.6 d), larvae fed S. wairauensis developed at about the same rate (54.5 ± 2.4 d) while those that ate *S. minimus* took significantly longer to develop (57.7 ± 3.3 d). The caterpillars fed *S. quadridentatus* were the only group to develop faster (47.3 ± 0.7 d). When compared to those larvae fed *J. vulgaris*, there were no detectable differences among species on larval mortality ($\chi^2_{3, N = 36} = 4.40$, $P = 0.265$) nor on the number of days larvae spent in pupation ($F_{3, 22} = 2.43$, $P = 0.093$).

Post-pupation, there were no significant differences in adult mass between the different treatments ($F_3 = 2.61$, $P = 0.077$). As expected, female moths were larger and more massive than males ($F_1 = 47.10$, $P < 0.0001$), but even after accounting for sex no significant difference between adult masses emerged from the different treatments. However, the general trend (for both sexes) was for those fed J. *vulgaris* and *S. wairauensis* to be heavier as adults, while moths fed *S. minimus* were slightly smaller (Table 4.1).

There was also a trend for more ova to be produced by females that consumed *J. vulgaris* and *S. wairauensis* than the other species. However, this result was not significant ($F_{3, 9} = 0.231$, $P = 0.087$) and was likely due to the very low number of females in some treatments (Table 4.2).

4.3.1.2 Subsequent No-Choice Assay

In the second series of tests using leaf discs in no-choice assays, all of the larvae feeding on *S. quadridentatus* died and this treatment was excluded from the final analysis. Results indicate that the plant species on which larvae fed had a significant impact on larval mass after 13 days ($F_2 = 9.88$, $P = 0.0021$). Larvae reared on *J. vulgaris* were the heaviest, and significantly more so than larvae that ate *S. minimus* and *S. wairauensis* (Figure 4.5). The *S. minimus* and *S. wairauensis* treatments did not differ significantly from one another. As in the initial no-

`

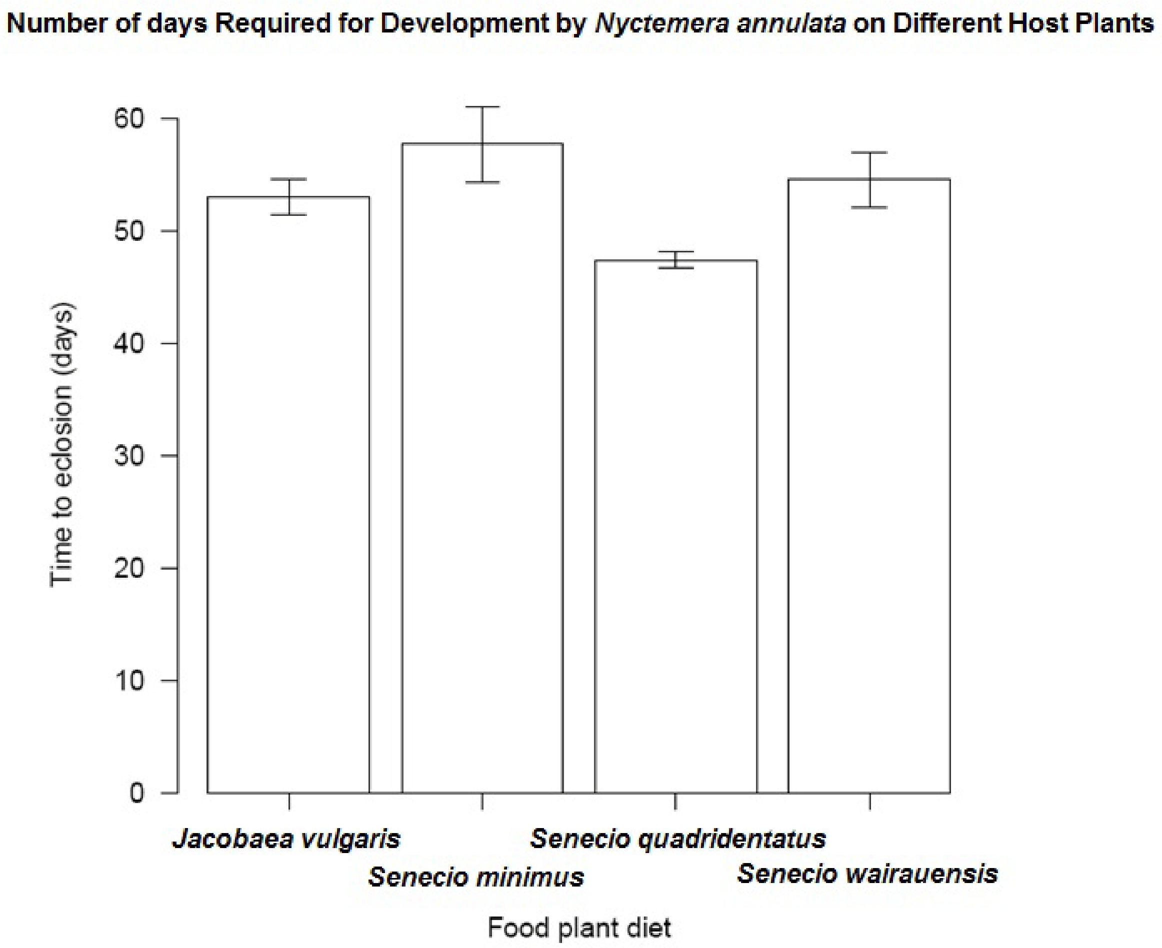

Figure 4.4 - The mean number of days required for *Nyctemera annulata* to develop on exotic *Jacobaea vulgaris*, versus the natives *Senecio minimus* and *S. quadridentaus* and the endemic *S. wairauensis*. Bars are one standard error of the mean.

Table 4.1 - Final mean mass of adult magpie moths (*Nyctemera annulata*) fed different host plants in a no-choice assay. Standard errors are reported in parentheses (n=1 for males fed *S. minimus*).

	J. vulgaris	***S. minimus***	***S. quadridentatus***	***S. wairauensis***
females	0.118 (*0.001*)	0.106 (*0.003*)	0.113 (*0.005*)	0.118 (*0.012*)
males	0.077 (*0.001*)	0.047 (*0*)	0.060 (*0.007*)	0.083 (*0.011*)

Table 4.2 - Mean numbers of ova produced by gravid female *Nyctemera annulata* reared on one of four species of host plant with number of specimens sampled. Numbers in parentheses indicate the standard error.

Species diet	***J. vulgaris***	***S. minimus***	***S. quadridentatus***	***S. wairauensis***
Mean number of ova produced	91.5 (*6.3*)	75.5 (*22.2*)	75 (*23.1*)	92 (*25.2*)
n	4	4	2	3

`

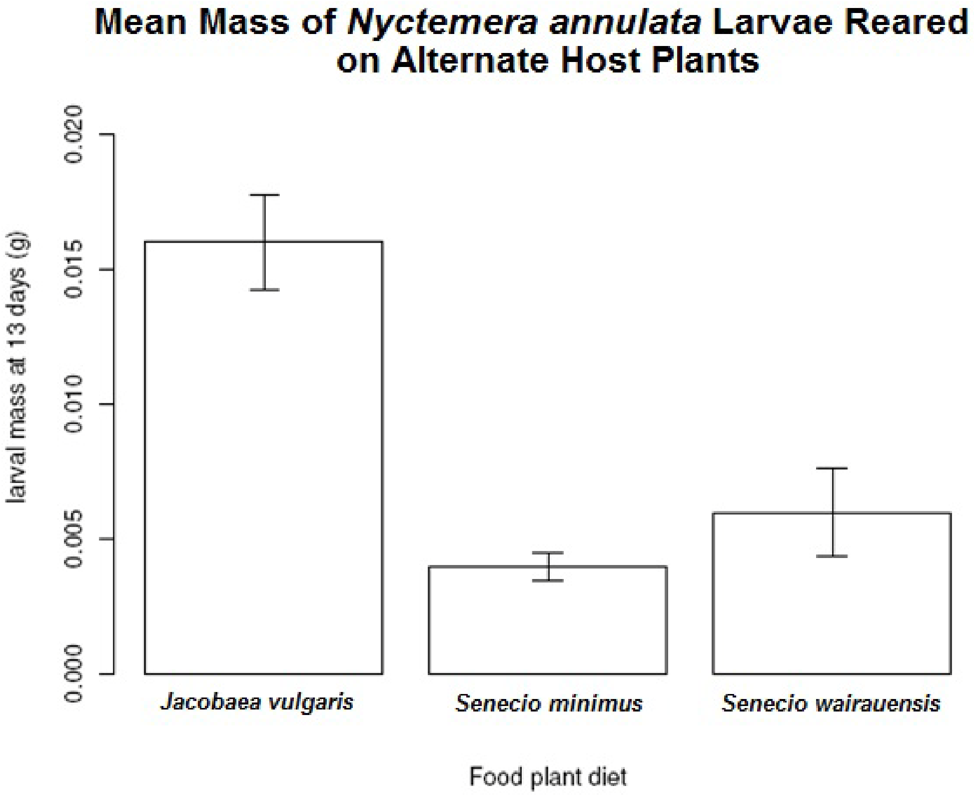

Figure 4.5 - Mean masses after 13 d of larval *Nyctemera annulata* fed different host species in no-choice assays. Of the four species assayed, larvae fed *J. vulgaris* were significantly heavier than larvae fed other species, including *S. minimus* and *S. wairauensis*. All larvae fed *S. quadridentatus* died prior to weighing.

`

choice assay, there were no differences in larval mortality between the three species treatments ($\chi^2_{2,\, N = 22}$ = 1.31, P = 0.520). Similarly larval mass was unaffected by the particular plant species eaten in relation to the amount of biomass consumed (F_2 = 0.213, P = 0.811).

4.3.2 Choice Assay

Daily visual observations of the location of larvae in the choice arenas revealed that they were found on *J. vulgaris* discs disproportionately often, with larvae being observed on them 53% of the time – significantly more often than they were found on *S. wairauensis* (25%), *S. quadridentatus* (13%) and *S. minimus* (9%) combined ($\chi^2_{3,\, N = 113}$ = 22.1, P < 0.0001). When I analyzed the visual observations to determine if any species discs incurred any feeding at all during the 13-day period I found a significant preference for the exotic *J. vulgaris* (t = 2.900, d.f. = 453, *P* = 0.00374) over the *S. quadridentatus* (t = -5.525, d.f. = 452, *P* < 0.0001) and *S. minimus* discs (t = -6.658, d.f. = 452, *P* < 0.0001).

Feeding incidence on *S. wairauensis* discs were not significantly different from those of *J. vulgaris* (t = -1.601, d.f. = 452, *P* = 0.10945), despite larvae being present on *J. vulgaris* discs more often (Table 4.3). For the percentage of each leaf disc eaten each day, for just those leaf disks that were eaten, larvae ate significantly more of the *J. vulgaris* discs than of *S. minimus* (t = -1.88, d.f. = 14, *P* = 0.004) (Fig. 4.6). Eaten *S. quadridentatus* discs tended to have less area removed than ragwort but this was not significant (t = -1.24, d.f. = 14, *P* = 0.12). Eaten discs of *J. vulgaris* and *S. wairauensis* showed very similar amounts of feeding (t = 0.44, d.f. = 14, *P* = 0.99).

4.3.3 Field Cage Assay

The field cage experiment failed to function as intended, mainly due to my failure to anticipate the speed at which the grass in the cages grew. This resulted in the grass providing a “bridge” for the caterpillars to walk across from the infested tray to the control tray. Similarly, there were multiple storms with high winds that upset most of the cages and allowed the caterpillars to escape, be preyed upon or parasitized. Of the 384 larvae that were placed on plants in the cages, only 55 (14.3%) were recovered.

Although there was no significant difference in the mean amount of biomass eaten in the control treatments versus the herbivore-added treatments, significantly more larvae were recovered from plants in mixed-species groups containing *J. vulgaris* than from plants in single species groups (z = -2.023, d.f. = 75, P = 0.042) (Fig 4.7). In cages with this species,

`

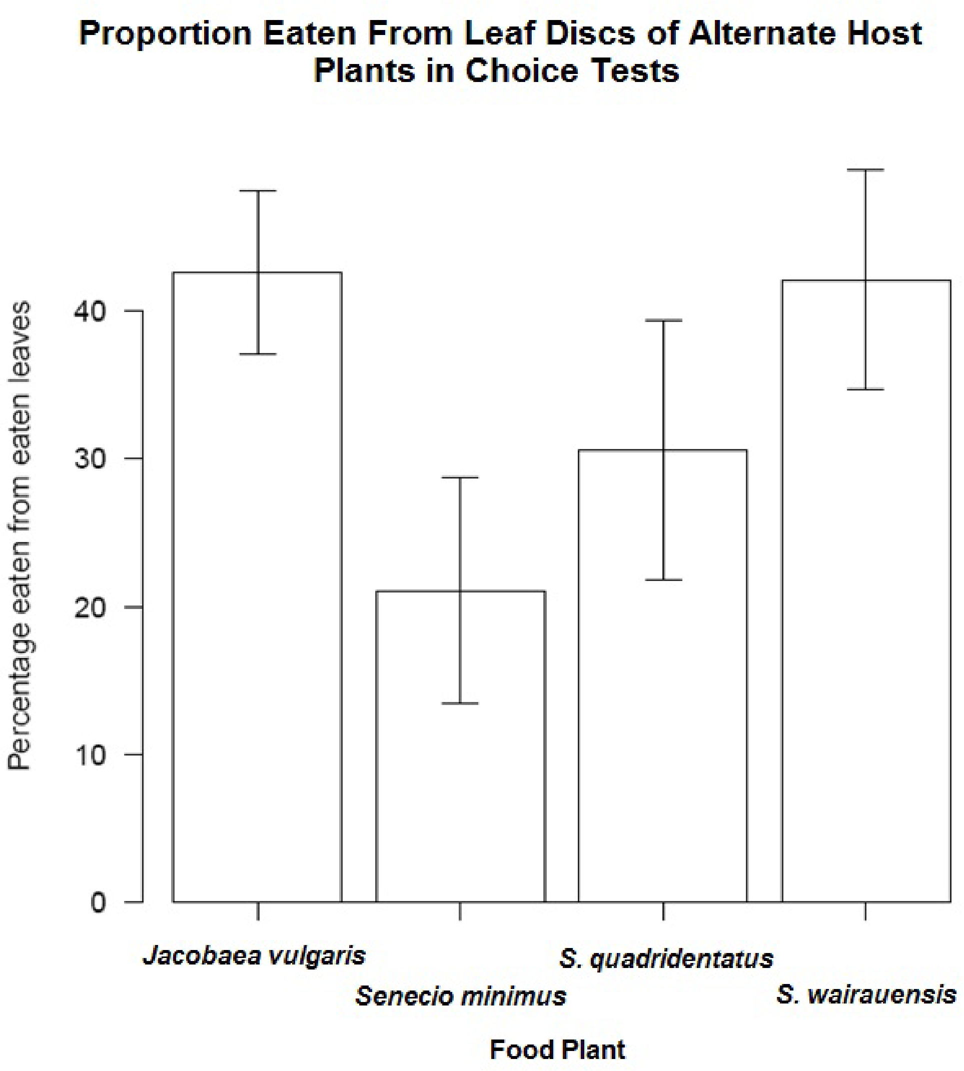

Figure 4.6 - Mean visual estimates of the amount of leaf discs eaten (%) by *Nyctemera annulata* larvae in choice tests where the invasive *Jacobaea vulgaris* and three native species of *Senecio* were offered (*S. minimus, S. quadridentatus* and *S. wairauensis*).

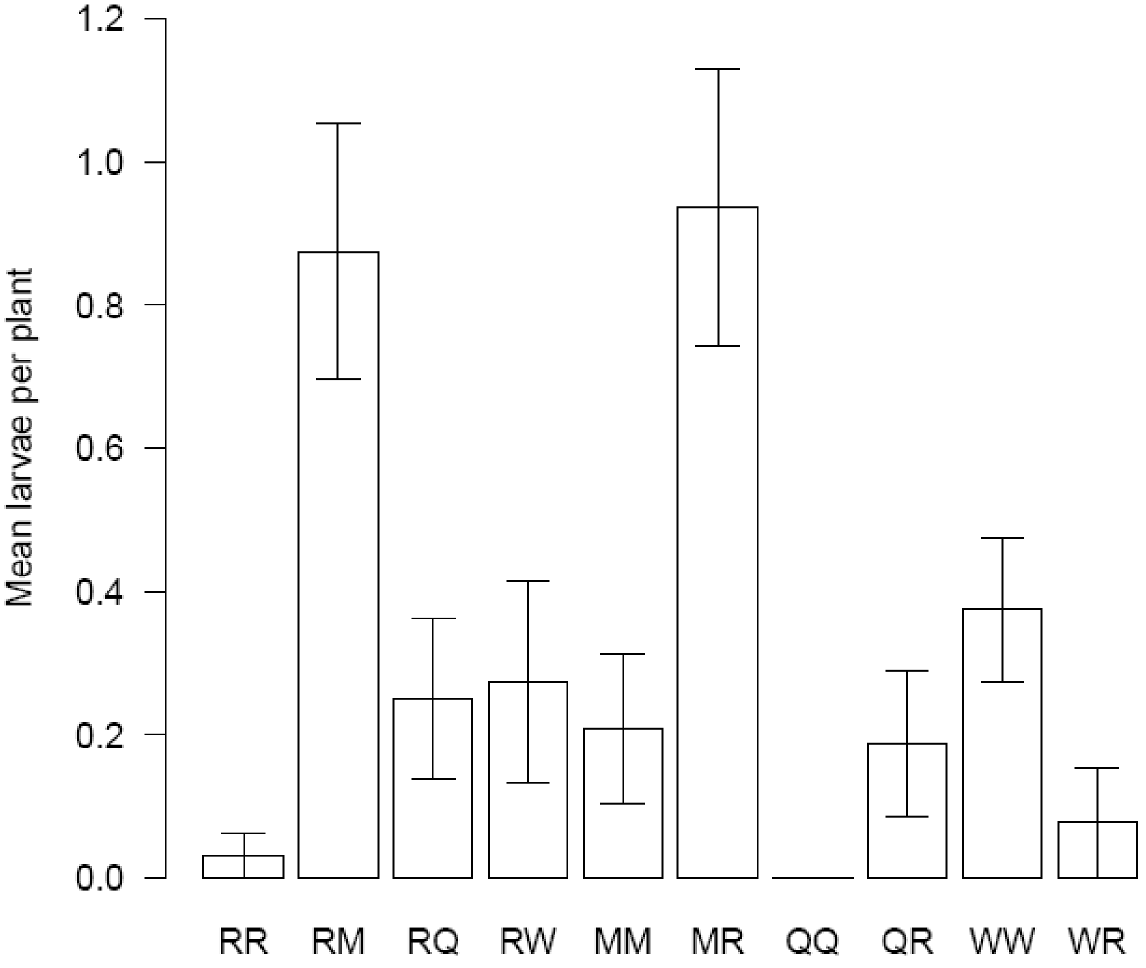

Figure 4.7 - Mean number of larvae recovered from whole plants in an experiment where four species of host plant were tested. Each host species was paired with *Jacobaea vulgaris* (R) or itself. The other species included in the testing are *Senecio minimus* (M), *S. quadridentaus* (Q) and *S. wairauensis* (W). The first letter in the category labels along the x-axis is the species from which larvae were recovered and the second letter is the species with which it was paired.

`

Table 4.3 - Proportion of leaf discs fed on from four species in a choice assay: *Jacobaea vulgaris* (exotic), *Senecio minimus* (native), *S. quadridentus* (native) and *S. wairauensis* (endemic).

	J. vulgaris	***S. minimus***	***S. quadridentatus***	***S. wairauensis***
Proportion of discs eaten	0.673 (*0.021*)	0.319 (*0.020*)	0.239 (*0.017*)	0.575 (*0.023*)
n	113	113	113	113

significantly more larvae were recovered from the conspecific pairings than from *S. wairauensis* with *J. vulgaris* (Fig. 4.8). There was also a detectible difference in the amount of estimated biomass eaten when comparing plants paired with *J. vulgaris* versus those paired with conspecifics (Fig. 4.9). More biomass was removed from *J. vulgaris* in cages where it was by itself (3.50 ± 0.56 g) compared to when it was in cages with *S. minimus* (0.33 ± 0.16 g), *S. quadridentatus* (2.61 ± 0.53 g) or *S. wairauensis* (1.81 ± 0.25 g). Similarly, more *S. minimus* (8.74 ± 3.01 g) and *S. quadridentatus* (3.20 ± 0.34 g) were eaten when they were alone compared to when they were paired with *J. vulgaris* (1.79 ± 0.48 g and 0.59 ± 0.17 g, respectively). However, *S. wairauensis* lost more biomass to *N. annulata* herbivory when it by itself (7.49 ± 1.85 g) than when it was paired with *J. vulgaris* (19.08 ± 7.74 g). The net results from these assays are summarized in Table 4.4.

4.4 Discussion

It is traditionally assumed that genus-specific monophagous insects prefer their original host plant(s) and host-shifts to heterogeneric hosts are rare. However, my current results for *N. annulata* show that this species has clearly incorporated *J. vulgaris* into its host range. Moreover, the invasive *J. vulgaris* was found to be and more attractive, more palatable than native hosts offered, was associated with faster larval development, produced larger adult moths than a diet of the native host plant *S. minimus*. This result has several implications.

Results of choice tests show that *N. annulata* abundance is higher on *J. vulgaris* than on native *Senecio* species. In a similar study by White et al. (2008) involving species congeneric to those in this study, the authors concluded that preferential host use of a native *Senecio* species over an invasive by a native Australian *Nyctemera* species was evidence for the enemy release hypothesis (ERH). However, several studies of invasive plants indicate that enemy release fails to broadly explain invasiveness and that biological resistance is often more influential when invaders are congenerics of native species (Agrawal et al., 2005; M. Deane Bowers, et al., 1992; Connor, Faeth, Simberloff, & Opler, 1980; National Research Council, 2002; Keane & Crawley, 2002; Liu, Stiling, & Pemberton, 2007; Maron & Vilà, 2001; J. D. Parker & Hay, 2005).

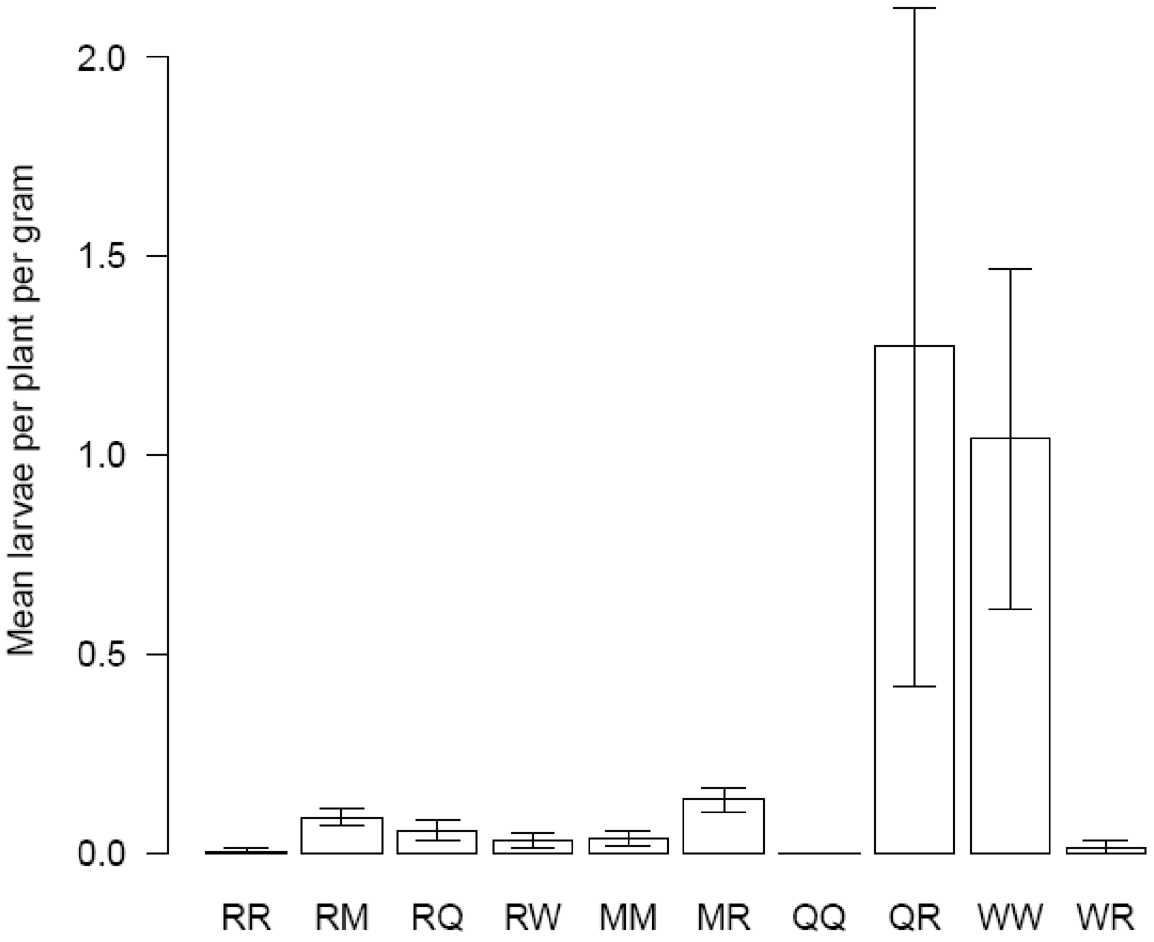

Figure 4.8 - The mean number of *Nyctemera annulata* larvae per gram of plant biomass collected from four host species in same-species and mixed-species cage assays. The first letter of the species pair along the x-axis is the species from which the larvae were collected and the second letter is the species with which it was paired in the enclosure. The four host plant species are *Jacobaea vulgaris* (R), *Senecio minimus* (M), *S. quadridentatus* (Q) and *S. wairauensis* (W).

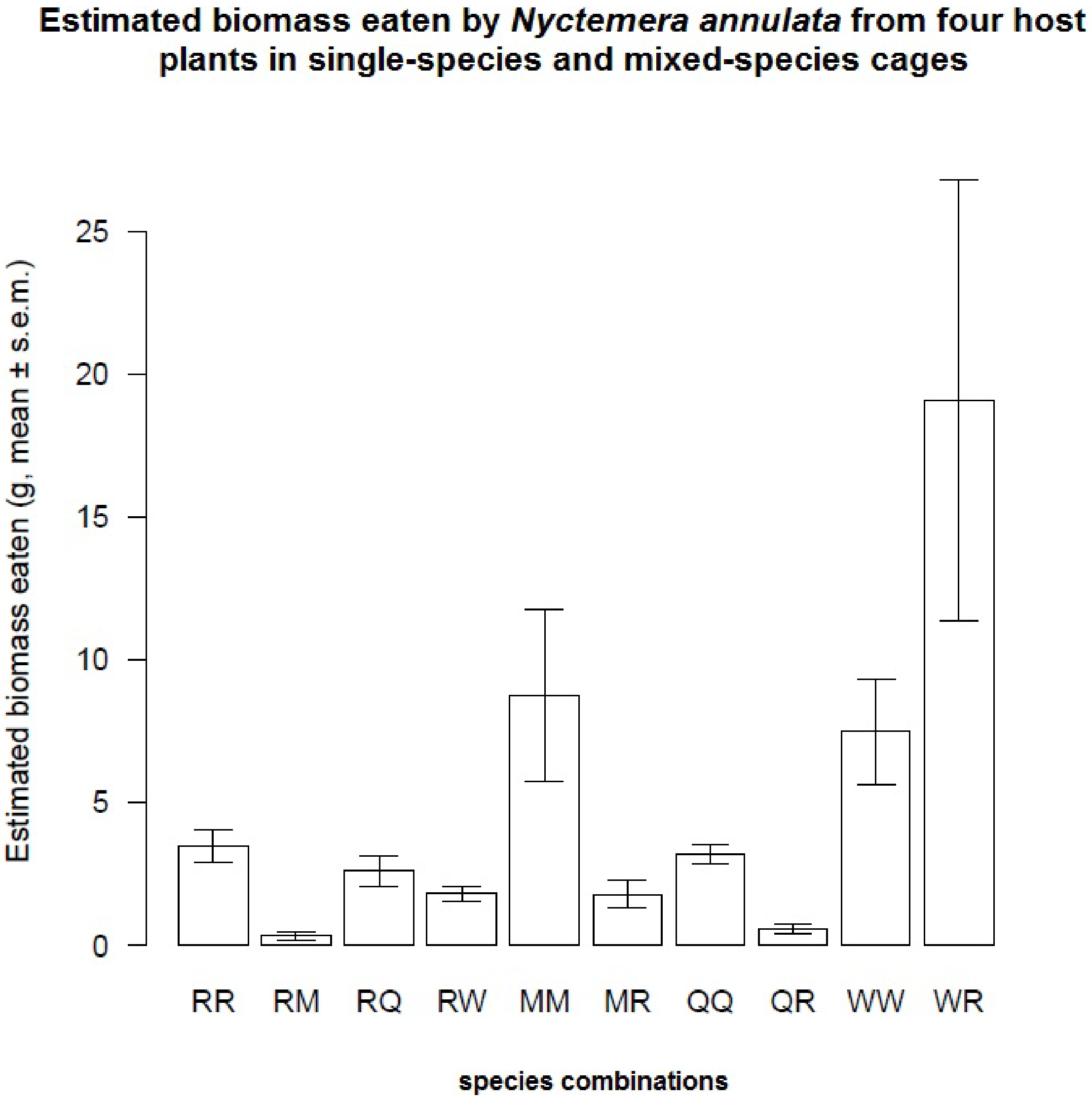

Figure 4.9 - Estimated biomass eaten by *Nyctemera annulata* from four species of host plant in cages with four plants of a single-species or four plants from two species per cage. Mixed-species treatments consisted of one native *Senecio* host plant mixed with the invasive weed, *Jacobaea vulgaris*. In addition to *J. vulgaris* (R), the other species offered were *S. minimus* (M), *S. quadridentatus* (Q) and *S. wairauensis* (W). Estimated biomass eaten was derived from the final dry biomass of the plants adjusted by the proportion of herbivore damage observed.

`

Table 4.4 - A summary of the choice and no-choice assay results for the performance of *Nyctemera annulata* on ragwort (*Jacobaea vulgaris*) versus the two non-endemic native hosts (*Senecio minimus* and *S. quadridentatus*) and one endemic host (*S. wairauensis*). “>” indicates a significantly better performance on *J. vulgaris* (P < 0.05), “~>” indicates a trend for better performance on *J. vulgaris* (P < 0.10), “=” indicates no detectable difference in performance (P > 0.10), “NA” indicates that measures were not addressed due to high mortality in one of the treatments. By only one measure did *N. annulata* perform significantly better on a native than on *J. vulgaris* (larvae feeding on *S. quadridentatus* eclosed on average 7 days earlier than those fed *J. vulgaris*). Notations of the different comparisons measured indicate if they were collected in the (a) initial choice (4.3.1.1), (b) subsequent no-choice (4.3.1.2), or (c) choice (4.3.2) assay.

Species comparison	**larval mass**[a,b]	**feeding choice**[c]	**feeding amount**[a,b,c]	**time to eclosion**[a]	**mortality**[a,b]	**adult mass**[a]	**ova per ♀**[a]
J. vulgaris vs. *S. minimus*	>	>	>	>	=	~>	~>
J. vulgaris vs. *S. quadridentatus*	*NA*	>	>	<	=	~>	~>
J. vulgaris vs. *S. wairauensis*	>	=	=	=	=	=	=

My results contradict the conclusions of White et al. (2008) and show that the invasiveness of *J. vulgaris* in New Zealand is not explained by a lack of herbivore pressure.

Indeed, *J. vulgaris* arrived in New Zealand facing a considerable level of biotic resistance from natural enemies, at least from *N. annulata*. Despite this, *J. vulgaris* still rapidly spread and established across much of the landscape. Even with the introduction and establishment of five natural enemies from its home range it continues to be invasive in parts of New Zealand with high amounts of rainfall (although its geographic distribution has retracted noticeable from drier areas following the release of biological control agents) (Simon Fowler and Hugh Gourlay, unpublished data). Considering this, the escape from top-down pressure of consumers seems to be an inadequate explanation for the invasive success of *J. vulgaris*. Anecdotal observations from whole *J. vulgaris* plant used in the field cage trials and for feeding *N. annulata* colonies both align with the reputation of this species as having a high level of tolerance to herbivory. Unfortunately I was unable to quantify the differences in herbivore tolerance between *J. vulgaris* and the other species assayed due to the shortcomings of the field cage trials. However, the difference in biomass in an individual *J. vulgaris* and a *S. wairauensis* of the same age are striking with the latter being a significantly smaller plant and produces significantly less seed.

Anecdotal observations of both of these species being used to feed colonies also support the assertion that *J. vulgaris* in more tolerant of herbivory. After individuals of both species had been completely defoliated by *N. annulata* in the colony cages, only *J. vulgaris* was able to generate regrowth. While in itself, plant tolerance to herbivory is not a reliable predictor of invasiveness (Hayes & Barry, 2008; Maschinski & Whitham, 1989), it is clearly important in herbivore-dense environments (Ashton & Lerdau, 2008; Augustine & McNaughton, 1998; Jogesh, Carpenter, & Cappuccino, 2008; Rogers & Siemann, 2005; J. P. Rosenthal & Kotanen, 1994; Strauss & Agrawal, 1999; Strauss & Murch, 2004; P. S. White & Allison, 1998; Wise & Abrahamson, 2005; Zou, Rogers, & Siemann, 2008). Therefore given the significant levels of biotic resistance that was likely incurred in the form of herbivory by *N. annulata*, as well as the limited success of the introduced natural enemies in suppressing *J. vulgaris*, this characteristic was likely important in the establishment of *J. vulgaris* in New Zealand.

An intriguing result from these assays is that *N. annulata* performance was as good (or better) on *J. vulgaris* compared to native host species. Most notably, by many measures, *N. annulata*

`

performed better on *J. vulgaris* than on the natives *S. minimus* and *S. quadridentatus*. There are a few possible hypotheses for this. The first is that *J. vulgaris* is chemically more poorly defended against *N. annulata* herbivory than these natives. The “red queen” hypothesis is based on the idea that prey and their consumers constantly counter one another’s new adaptations with novel adaptations of their own (Clay & Kover, 1996; Marrow, Law, & Cannings, 1992; Van Valen, 1974). Locked in this evolutionary arms race, plant hosts evolve defences selected by the consumer threats it encounters. I do know that these *Senecio* species differ in their tissue phytochemistry and, although the components responsible for making *S. minimus* less palatable to *N. annulata* are still unidentified, the native species differ in their pyrrolizidine alkaloid composition (Benn, et al., 1978), which may serve as an attractant to some *Senecio* specialists.

Another possible explanation could be the impact of more recent selection pressures on *N. annulata* following invasion by *J. vulgaris* that endowed moths that used it with higher fitness. Several reasons have been suggested for observations of disproportionately high performance on novel hosts in other systems. These include the benefits of enemy-free space (J. M. Brown, et al., 1995; Gratton & Welter, 1999; Holt & Lawton, 1993; Zangerl, et al., 2002), lower levels of competition (Abrahamson, Eubanks, Blair, & Whipple, 2001; Feder, et al., 1995; Messing & Wang, 2009) and a greater abundance of an alternate host (Munday, van Herwerden, & Dudgeon, 2004; Rossbach, Löhr, & Vidal, 2006a; Shirai & Morimoto, 1999). Any of these could fit the situation with *J. vulgaris* in New Zealand. If these strategies result in higher fitness for the magpie moth populations that employ them, increased performance on these hosts will likely be selected for over time (Agosta, 2006; Agrawal, 2000; Mayhew, 1997; Nosil, Crespi, & Sandoval, 2002; Schoonhoven, van Loon, & Dicke, 2006).

Of all species tested in the choice assays one of the non-endemic natives, *S. minimus*, was consistently the least palatable overall. In the initial no-choice assay *S. quadridentatus* showed a high level of palatability, which is not as surprising given the fact that the initial founders of the colony population were taken from *S. quadridentatus* plants. However, in the second round of tests, larvae were less attracted to *S. quadridentatus* and ate far less of it. Of note is the fact that all test subjects fed *S. quadridentatus* in the second round of no-choice assays died before the end of the trial period. One possible explanation for this outcome is that the plants used in the second no-choice assay were considerably older than those used in the initial no-choice assay and that the newly hatched larvae has difficultly accessing the plant tissues as a result of greater indumentum. *Senecio quadridentatus* has a much greater length and density of pubescence on its leaves than the other species assayed and this trait is enhanced on leaves of older plants. Lower levels of feeding on *S. quadridentatus* is echoed in the choice test results that showed larvae feeding on *S. quadridentatus* less than on the other species offered. This was also a reason given for poor *N. annulata* larval feeding on *S. quadridentatus* in similar research by Woodward (1984). Another possible explanation for complete larval mortality in the *S. quadridentatus* treatment is that the knock-down herbicide used to treat the greenhouse aphid infestation persisted longer on *S. quadridentatus* than on the other species. Steps were taken to make sure that plant leaves used in the assays were collected and used beyond the maximum persistence time for the pyrethroid and that all plants were watered daily from above. With the exception of *S. quadridentatus*, the results from both sets of assays were consistent with one another and the same level of mortality was not experienced by larvae feeding on any other species; however death of all six larvae fed *S. quadridentatus* is the one obvious difference. Again, *S. quadridentatus* differs from the other species in the dense pubescence of its leaves, which in this case may have prevented the degradation or washing off of insecticidal residue.

Results from the whole plant trials show that *N. annulata* feeds on a mixed-species diet when available. In terms of biomass removed through herbivory, more *J. vulgaris* was eaten when it was by itself and with *S. quadridentatus* than when it was paired with *S. minimus* or *S. wairauensis*. The two non-endemic native species, *Senecio minimus* and *S. quadridentatus*, were both eaten more when they were alone compared to when they were paired with *J. vulgaris*. The endemic, *Senecio wairauensis,* was heavily consumed in both treatments, but significantly more so when it was paired with *J. vulgaris*. Fewer larvae were collected per plant from *J. vulgaris* alone compared to when it was paired with another species despite this species retaining its vigour throughout the trial. Although *N. annulata* developed well on *J. vulgaris* in the no-choice assay and preferred it to other hosts, larvae in the cage assays did not settle for a diet of pure *J. vulgaris* when other hosts were available. When two of the native hosts (*S. minimus* and *S. quadridentatus*) were paired with *J. vulgaris* more larvae were collected from them than when they were offered alone. Fewer larvae were collected from *S. wairauensis* when it was paired with *J. vulgaris* than by itself, but this result may have more to do with the low quality of the heavily-eaten *S. wairauensis* plants at the end of the assay than with its overall attractiveness. Combined with the other two choice assays, data from the cage trials indicate that larvae will readily move between host plants and feed on more than one species. This trend was also reported by Woodward (1984). They clearly like to eat *J. vulgaris* but will move onto other host species that are nearby and eat them. Specifically, the results for *S. wairauensis* indicate that *N. annulata* finds this species highly palatable but that the small and delicate nature of this endemic make it vulnerable to levels of herbivory that

`

larger and more robust species, like *J. vulgaris* and *S. minimus*, can tolerate. When *J. vulgaris* is near this species it likely allows *N. annulata* larvae to move back and forth between these two resources; feeding on *S. wairauensis* when available, then moving back onto *J. vulgaris* once *S. wairauensis* is decimated.

In light of the results presented here, many new questions arise. The success of *J. vulgaris* cannot be interpreted as enemy release in New Zealand as *J. vulgaris* was likely subject to substantial biotic resistance through *N. annulata* and perhaps others of the native *Senecio*-feeding herbivores (J. J. Sullivan, et al., 2008). Similarly, if *N. annulata* populations readily feed on *J. vulgaris* and develop well on it, what impact does this have on nearby populations of native *Senecio* species that appear to have a lower tolerance to herbivory? Many examples have been reported where susceptible populations near other infested populations experience consumer spillover (e.g. Cronin & Reeve, 2005; Hamback & Bjorkman, 2002; Power & Mitchell, 2004; Rand & Louda, 2006; Rand, Russell, & Louda, 2004; Tscharntke, Rand, & Bianchi, 2005; J. A. White & Whitham, 2000). Is there any evidence for a population spillover by these herbivores from *J. vulgaris* infestations on to nearby patches of native *Senecio* species? I address this question in Chapter 5.

`

Chapter 5

Field Surveys of *Nyctemers annulata* Abundance and Distributions on Alternate Hosts in Relation to *Jacobaea vulgaris* Presence and Abundance

5.1 Introduction

Species invasions are occurring at their highest rate in history (Arim, Abades, Neill, Lima, & Marquet, 2006; Drake et al., 1989; Fridley, et al., 2007; Julie L. Lockwood, Cassey, & Blackburn, 2005; J. L. Lockwood, et al., 2007; Richard N. Mack & Lonsdale, 2001; Dov F. Sax, Gaines, & Brown, 2002; Vitousek, D'antonio, Loope, Rejmanek, & Westbrooks, 1997; Williams, et al., 2002), although the vast majority of species introductions fail to result in invasions (Colautti, Grigorovich, & MacIsaac, 2006; Drake, et al., 1989; Hopper & Roush, 1993; Lodge, 1993; Moyle & Light; D. F. Sax & Brown, 2000; M. Williamson, 1999; Mark Williamson & Fitter, 1996). While potential weed invaders are likely to experience biotic resistance from competitors, consumers and pathogens that are already established – particularly if they are related to species in the invaded habitat (Agrawal & Kotanen, 2003; Agrawal, et al., 2005; Becerra & Venable, 1999; Cadotte, Cardinale, & Oakley, 2008; Darwin, 1859; G. S. Gilbert & Webb, 2007; J. M. Levine, et al., 2004; R. N. Mack, 1996; Novotný et al., 2006; J. D. Parker & Hay, 2005; M. Rejmanek, 1996; Marcel Rejmanek & Richardson, 1996; Strauss, 2006), a growing body of research shows that many potential weed invaders actually experience a net benefit from the presence of natural enemies (novel and original) in invaded ranges via apparent competition (Dangremond, et al., 2010; Juliano, 1998; Kenis, et al., 2009; Carolyn M. Malmstrom, et al., 2007; C. M. Malmstrom, Stoner, Brandenburg, & Newton, 2006; Mitchell, et al., 2006; Orrock, Witter, & Reichman, 2008; Power & Mitchell, 2004; Reynolds, 1988; Roemer, Coonan, Garcelon, Bascompte, & Laughrin, 2001; Rushton, Lurz, Gurnell, & Fuller, 2000; Sabelis, Janssen, & Kant, 2001; Sessions & Kelly, 2002; Tompkins, White, & Boots, 2003). In these situations, the shared natural enemies disproportionately affect established competitors. In the current research I examine such a situation in New Zealand where the invasive weed *Jacobaea vulgaris* formed a novel association with a native insect herbivore (*Nyctemera annulata*, Lepidoptera: Arctiidae) that also uses native *Senecio* host plants – several of which have contracted in their geographic distributions since the arrival and spread of *J. vulgaris*.

`

The addition of exotic species to native communities sometimes results in negative impacts to the species present and can cause important changes in native ecosystem function (Beggs, 2001; Jaenike, 1990; Juliano & Lounibos, 2005; C. M. Malmstrom, et al., 2005; Rand, et al., 2009; Rodriguez, et al., 2005; Ruiz, Carlton, Grosholz, & Hines, 1997; Simberloff & Von Holle, 1999; Simmonds & Bennett, 1966; G. Woodward & Hildrew, 2001). To prevent loss of native biodiversity and function it is important to know why some exotic species become naturalized and why some habitats are more prone to invasions than others. The foci of some of these studies are on various aspects of ecosystem ecology, such as the physical and biological characteristics of the habitats that have been invaded (Byers, 2002; Simberloff, 1995; Zalba, Sonaglioni, Compagnoni, & Belenguer, 2000), climate similarities between the invaded and home range of a species (Bradford & Lauenroth, 2006; Lennon, Smith, & Williams, 2001; S. G. Willis & Hulme, 2002) and the influence of anthropogenic disturbance (Didham, et al., 2005; Gibb & Hochuli, 2003; Larson, Anderson, & Newton, 2001). Other studies have looked at the physiological and behavioural traits of a species that correlate with successful invasion, including reproductive strategies (Aron, 2001; Barrett, Colautti, & Eckert, 2008; Gross, 1984; Sakai et al., 2001), modes of dispersal (Benvenuti, 2007; Herron, Martine, Latimer, & Leicht-Young, 2007; Kot, Lewis, & van den Driessche, 1996), lifecycle characteristics (Castro, Figueroa, Muñoz-Schick, & Jaksic, 2005; Devin & Beisel, 2007; Sakai, et al., 2001) and competition strategies (Barrat-Segretain, 1996; B. J. Brown, et al., 2002; Fogarty & Facelli, 1999). A fair amount of investigation has also probed the pressure exerted on invaders from natural enemies (or a lack thereof) and how this may influence invasion success, which is the basis for the enemy release hypothesis (ERH).

The ERH assumes that natural enemies apply significant pressure to an organism's populations and that removing this pressure allows the organism to become disproportionately abundant. Competitors, consumers and pathogens are considered primarily responsible for controlling species' populations. Darwin (1859) had this in mind when he predicted that the taxonomic relatedness of potential invaders to one or more species in a native community can have an impact on invasion success. Darwin also suggested that the effects of relatedness to a native species can, like a double-edged sword, cut both ways by potentially encumbering or facilitating an exotic species in the process of naturalization.

Recent research examining the phenomenon of biotic resistance by native ecosystems has shown a greater probability of invasion success by phylogenetically-novel species (Cahill Jr, Kembel, Lamb, & Keddy, 2008; Hill & Kotanen, 2009; C. M. Malmstrom, et al., 2005; Strauss, 2006). This is rooted in the idea that plants are more apt to compete with other plants with which they are related (Cahill Jr, et al., 2008; Juliano & Lounibos, 2005; Lambdon & Hulme, 2006; Procheş, Wilson, Richardson, & Rejmánek, 2008; Strauss, 2006; Thuiller et al., 2010; Valiente-Banuet & Verdú, 2008) and native consumers are more likely to suppress potential invaders that are closely related to their original hosts (Dawson, Burslem, & Hulme, 2009; Jogesh, et al., 2008; Lau & Strauss, 2005; R. N. Mack, 1996; I. M. Parker & Gilbert, 2004; Prowse & Goodridge, 2003). In terms of species invasions, this means that immigrant species are more likely to encounter biotic resistance in the novel habitat the more genotypically and phenotypically similar they are to species that are already present and support enemies. An example of this comes from Knevel et al. (2004) who found that the introduced exotic grass *Ammophila arenaria* experienced negative effects on growth and vigour from a soil-borne pathogen associated with a grass species already present in the community, *Sporobolus virginicus*. The authors concluded that biotic resistance to potential plant invaders comes from interspecific competition, but also from the presence of soil pathogens that negatively affect the invader and use already established species as hosts.

Conversely, similar analyses have found the role of taxonomy in regards to biotic resistance oversimplified and the role of species relatedness in invasions more complex. Researchers found that a potential invader's relatedness to a native counterpart can also prove beneficial to its success (Dawson, et al., 2009; Diez et al., 2009; Dostál & Palečková, 2010; Lambdon & Hulme, 2006; Morales & Traveset, 2009; Procheş, et al., 2008). Relatedness to natives contributes to success in cases where an invasive species makes use of a close relative's specific nutritional resources (such as host plants, prey or trophobionts) or mutualists (such as pollinators, rhizobia and trophobiont tenders). Several studies have shown that plants (Dickie, et al., 2002; Freiberg et al., 1997; Richardson, et al., 2000; van Rhijn & Vanderleyden, 1995), pathogens (Chandramohan & Charudattan, 2001; G. S. Gilbert & Webb, 2007; L. Gilbert, Norman, Laurenson, Reid, & Hudson, 2001; I. M. Parker & Gilbert, 2004; Power & Mitchell, 2004; Tompkins, et al., 2003) and parasites (Bonsall & Hassell, 1998; Caro, Combes, & Euzet, 1997; Greenman & Hudson, 2000; Jones, Hassell, & Godfray, 1997; MacNeil et al., 2003; Poulin & Mouillot, 2003; Rott & Godfray, 2000) are more likely to be able to utilize fitness-enhancing biotic resources the more taxonomically similar they or their hosts are to extant species in that habitat. The benefits that invading species gain from expanding their geographic range into areas with taxa related to taxa in their habitat of origin are not always direct as in the case with parasites and related hosts. Often indirect relationships that are formed within the invaded food can equally contribute to the success or suppression of the invader. One class of ecological interactions formed from indirect

`

relationships that are based on relatedness and that can affect the relative success of invaders is the phenomenon of apparent competition.

First described by Holt (1977), apparent competition occurs when a common consumer creates a differential suppression effect on prey populations in the presence of one another compared to a situation where they are presented independently. While shared prey in cases of apparent competition are not always closely related species (e.g. Roemer, et al., 2001), they often are in the case of generalist consumers and almost always are in case of specialist and oligophagous consumers. For example, Reitz et al. (2006) documented a situation where two thrips species, one invasive (*Frankliniella occidentalis*) and one native (*F. bispinosa*), shared a common generalist consumer (*Orius insidiousus*) in a common agroecosystem. The predators are active, skilled hunters and were found to prey on both thrips species equally well when the individual species were presented monospecifically. However *O. insidiosus* preferentially fed on *F. occidentalis* when the two thrips species were presented together. It was determined that individual predators were able to take a limited number of thrips per day before reaching satiation. Behavioural differences between the prey species left the exotic thrips more vulnerable to capture. These factors translated to a situation in the field where *F. bispinosa* populations persisted longer in into the autumn than those of *F. occidentalis*. In this case apparent competition between thrips functioned to suppress the exotic species while allowing the native thrips to prolong their time in the landscape.

A converse example – where invasion by an exotic species was facilitated via apparent competition – is typified by the invasive purple loosestrife (*Lythrum salicaria*). Upon its arrival in North America purple loosestrife was able to make use of native pollinators associated with a native congener (*L. alatum*) based on their taxonomic relatedness. Brown et al. (2002) documented how the native pollinators exhibited a stronger attraction to purple loosestrife than *L. alatum* and that, although pollinators moved between both *Lythrum* species, the presence of the exotic decreased overall pollinator visits and seed set size in the native. The authors concluded that the reduction of pollen quantity and quality has an overwhelming negative effect on the native *L. alatum*. In this case, relatedness of the invader to one of the species in this native food web undermined the relationship established between pollinators and a native plant and caused significant population impacts to the latter. But how common is apparent competition in facilitating species invasions of natural communities?

White et al. (2008) examined a native *Senecio* food web in Australia that was invaded by an exotic congener (*S. madagascariensis*). Experiments and field surveys were carried out to determine if the native *Senecio*-specialist moth (*Nyctemera amica*) demonstrated any

`

differential consumption and use of the invasive and a native host plant (*S. pinnatifolius*) and if the results conformed to the enemy release hypothesis (ERH). The authors found that, although the *N. amica* used both host plants, it preferred its native host over the invasive. The authors concluded that this result conformed to the ERH.

I searched for evidence of apparent competition and support of the ERH in a similar *Senecio* food web on the South Island of New Zealand that includes hosts plants and a consumer congeneric to those studied by White et al. (2008). The specialist consumer, *Nyctemera annulata* (Lepidoptera: Arctiidae), a close relative of *N. amica* from White et al. (2008), successfully uses several native and naturalised species of taxonomically-related host plants for oviposition material and food in the landscape (Benn, et al., 1978; Singh & Mabbett, 1976; J. J. Sullivan, et al., 2008, listed in Chapter 2; Watt, 1914; D. R. Woodward, 1984). Results from the assays performed in Chapter 3 indicate that there are differing levels of preference by *N. annulata* for the alternative host species which include the abundant exotic, *J. vulgaris.* Whole plant assays also indicate different levels of tolerance by the various host plant species in response to equal levels of *N. annulata* feeding damage. I performed a landscape survey to determine if there are any herbivore-influenced, population-level trends influencing *Senecio* distributions on the South Island.

Jacobaea vulgaris is particularly abundant in disturbed areas of the West Coast Region and where it co-occurs at a landscape scale with several native congeners, including *S. minimus* and *S. wairauensis* assayed in Chapter 3. *Nyctemera annulata* is a common *Senecio* specialist herbivore that is widespread across New Zealand, including the West Coast of the South Island. The West Coast of the South Island was therefore chosen as a suitable location to look for evidence of apparent competition in this food web. Specifically I looked for the presence of *N. annulata* larvae and feeding damage to test the hypothesis that *N. annulata* densities will be highest where *J. vulgaris* is present (and abundant) versus areas where it is absent or in lower densities. Given the results from Chapter 3, my prediction is that *N. annulata* will show a similar preference for *J. vulgaris* compared to the available native host plants. Given its tolerance to herbivory, I also expect that *J. vulgaris* will demonstrate a greater ability to compensate for *N. annulata* herbivory leading to a positive correlation between high-density *J. vulgaris* patches and herbivory on native *Senecio* hosts. I presume that the lower tolerance to herbivore damage by the native hosts will result in a reduction in their distribution near where *J. vulgaris* is present as this differential impact to their fitness will impede re-establishment by these species.

`

5.2 Methods

5.2.1 Site Selection

Prior to the initial survey, I collated records of known plant populations. Most of this information came from Allan Herbarium records (herbarium code: CHR), as well as from earlier visits to the West Coast. After narrowing the survey down to a general region where four *N. annulata* host plants co-occur (*J. vulgaris, S. wairauensis, S. rufiglandulosis* and *S. minimus*), I made visits to these areas and recorded *Senecio* occurrences. Based on this preliminary survey and data, I selected seven candidate valleys for more in-depth data collection (Fig. 5.1 and Table 5.1).

5.2.2 Field Survey

The abbreviations used for the sites where I carried out field surveys and where *J. vulgaris* was present are STYX (Styx River Valley), DECEPT (Deception River Valley), TARAMAK (Taramakau River Valley), WANG (Wanganui River Valley), and the abbreviations for the sites where the invader were absent are MING (Mingha River Valley), WAIHO (Waiho River Valley), WAIMAK (Waimakariri River Valley). After a valley was selected (referred to as a "site"), my field assistants and I travelled up river and sampled at disturbance corridors (i.e. stream, walking track, landslip) with no less than 1 km between each disturbance corridor sampled (each disturbance corridor referred to as a "transect"). After I selected a disturbance corridor, other data collectors and I walked along the middle of the transect heading in both directions perpendicularly, away from the trail, for a total distance of at least 150 m in each direction. In some areas where disturbance corridors were less defined (e.g. open flat areas like pastures and grassy saddles) transects sampled exceeded 150 m in order to better capture the overall composition of that area, which may have been missed with a smaller sampling window. For all transects, I recorded the number of plants of each *Senecio* species present within 1 m of each side of the transect midline for every 15 m along a transect. Each 2 x 15 m sample area was termed a "quadrat" and each transect was made up of at least 20 of them (10 on each side of the trail where this feature was defined). During the early portion of the season transects and quadrats were measured out in paces instead of meters thereby deviating slightly from 15 m in length. However, the points between each quadrat sampled was recorded using GPS and this inconsistency was accounted for in the model created using that data (described in the Data Analysis section below).

`

Figure 5.1 - Location of the river valley transects sampled on the South Island, including three sites that were free of significant *Jacobaea vulgaris* populations (*open stars*: Waiho, Upper Waimakariri, and Mingha) and four sites with dense *J. vulgaris* populations (*black stars*: Deception, Taramakau, Styx, and Whanganui).

Table 5.1 - The number of plants of each species sampled in seven sites over the 2008-2009 field season. All samples were also sampled for presence of *N. annulata* larvae and herbivory. In none of the sites was *S. rufiglandulosus* present. All three populations of this plant that I encountered in the South Island occur in small clusters on roadside embankments.

Location (coordinates)	**plants sampled**					**number sampled**		**elevation range**
	J. vulgaris	*S. minimus*	*S. wairauensis*	*S. rufiglandulosus*	***Total***	transects	quadrats	
Styx River Valley *42.88S 171.17E*	144	138	162	- 0 -	**444**	11	424	100-775 m
Deception Valley *42.78S 171.60E*	180	63	85	- 0 -	**328**	11	250	300-1075 m
Taramakau River Valley *42.76S 171.64E*	56	9	5	- 0 -	**70**	5	68	210-430 m
Wanganui River Valley *43.18S 170.63E*	54	12	27	- 0 -	**93**	7	110	110-240 m
Mingha River Valley *42.98S 171.60E*	- 0 -	- 0 -	38	- 0 -	**38**	5	66	650-1170 m
Waiho River Valley *43.42S 170.17E*	- 0 -	- 0 -	15	- 0 -	**15**	2	37	150-250 m
Upper Waimakariri *43.01S 171.57E*	- 0 -	4	44	- 0 -	**48**	4	117	600-750m
Total	**434**	**226**	**376**	**0**	**1036**	**45**	**1072**	**-**

`

After plant counts were completed for a quadrat, one plant from each species that was determined to be the closest to the end point of that quadrat (referred to as an "interquadrat point") was sampled for presence of arthropods and herbivore damage. If no plants of a given species were located within 5 m of the interquadrat point, no sample data were recorded for that particular species at that location. Percent canopy cover, habitat type and GPS data were also recorded at each interquadrat point. Canopy cover was estimated using visual estimations of the percentage of sky blocked by canopy while standing at the sampled plant. Habitat types were subjective and derived from geographic features (e.g. SS (stream side), SC (stream center), LS (landslip), RE (river edge)), habitat use characteristics (e.g. GP (grazed paddock), TR (trailside)), community type (e.g. SB (scrub habitat), UP (tussock/ungrazed grassland)) and canopy characteristics (e.g. FF (full forest cover), FE (forest edge), FG (forest gap)). Each sample was assigned two habitat types if applicable. All adult magpie moths seen in-flight were recorded for the quadrat that it passed through or closest to.

Of the seven sites I surveyed, the Styx and the Deception Valleys were the most comprehensively sampled and were compared in greater depth. The length of both of these sites is approximately the same (~ 13 km), but their elevation ranges differ with the Styx Valley site ranging from about 100 m to about 775 m above sea level and the Deception Valley elevation gradient runs between 300 m and 1075 m above sea level. Comparing the distribution of *Senecio* species in these two otherwise-similar valleys is important in understanding the factors affecting distribution apart from elevation.

5.2.3 Data Analysis

Of the seven river valleys I surveyed using the transect-sampling method described above, four of the valleys had *J. vulgaris* infestations. Using the species distribution, abundance, and site characteristic data that I collected from just these sites, I created GLM models using the statistical program R. Models were constructed by testing the significance of individual coefficients. As each coefficient was individually added to and removed from an overall working model, the relative explanatory power of each factor was determined by following the Akaike's information criterion (AIC) value. For each iteration, the model(s) with the lowest AIC value(s) was/were considered to have greater explanatory power. For models with similar AIC values (< 10 points difference), the more complex model(s) (greater number of covariates) was/were favoured over less complex models. Determining the significance of potential interaction effects between covariates was carried out in the same way. Once the importance of all possible covariates was tested at each phase of model construction, the model was considered complete.

The specific covariates selected for the full models of each species were: site, transect, the interaction effect of site and transect, elevation, quadrat length and habitat type (forest edge, full forest, forest gap, grazed pasture, land slip, river edge, scrub, stream side (along the edge of a stream), trail edge or ungrazed pasture (perhaps maintained by wild deer)). Once the optimal models were selected for *S. wairauensis* and *S. minimus*, *J. vulgaris* presence was incorporated into their presence-absence model, while *J. vulgaris* abundance was incorporated into the abundance models for the native species. Effects of *J. vulgaris* presence and abundance were tested for significance at different response variables of transect and quadrat. Abundance of *J. vulgaris* per transect was calculated from the sum of plants counted in all quadrats of that transect.

To determine the impact of *J. vulgaris* density on herbivore populations and herbivore damage to native species, larval counts and damage levels on individual plants were compared with both presence and density of *J. vulgaris* at the response variables of site, transect and quadrat. Full models for the presence of larvae on the native species were mixed-effect models with nesting of plants within quadrats within transects within sites and incorporated elevation, and presence-absence of *J. vulgaris*. Full models for percent herbivory on the native species were mixed-effect models with nesting of plants within quadrats within transects within sites and incorporated transect, abundances of each host species, presence of *J. vulgaris*, and quadrat length.

5.3 Results

5.3.1 *Nyctemera annulata* and Herbivory

Nyctemera annulata larvae were significantly more likely to be found on individual *S. wairauensis* plants in quadrats with *J. vulgaris* present ($\chi^2_{1, N=375} = 12.14$, $P = 0.0005$) (Table 5.2a), with larvae collected from 35 % (11 out of 31 plants) of the endemic plants in quadrats with *J. vulgaris* present versus collections from 1% (3 out of 209 plants) of plants in quadrats without the invader (Table 5.3). Overall, elevation did not appear to be a significant factor in this relationship ($\chi^2_{1, N=375} = -0.001$, $P = 0.599$). For the most part, the same was true of *S. minimus* ($\chi^2_{1, N=225} = 6.50$, $P = 0.0108$) (Table 5.2b) with larvae collected from 25% (18 out of 73 plants) of the native plants in quadrats with *J. vulgaris* versus 7% of plants (5 out of 71 plants) in transects without the invasive. However, the analysis revealed that this relationship was significantly and inversely correlated with elevation ($\chi^2_{1, N=225} = 15.27$, $P < 0.0001$), with more larvae collected in the lower end of the valleys. The effect of *J. vulgaris* density on the number of *N. annulata* larvae collected from sympatric *S. wairauensis* was not significant,

`

Table 5.2 - Generalised linear models of different landscape patterns listing the importance of different response variables used in the final models. The model code used in R analyses are in the shaded boxes. Habitat types include forest edge (FE), full forest (FF), forest gap (FG), grazed pasture (GP), land slip (LS), river edge (RE), scrub (SB), stream side (SS), trail side (TR) and ungrazed pasture (UP). Other terms refer to "*Jv*" for *J. vulgaris*, "*Sm*" for *Senecio minimus*, and "*Sw*" for *S. wairauensis.* From the terms used in the models: "ragwort.valley" indicates a site with dense *J. vulgaris* populations present, "ja" indicates *J. vulgaris* presence in a quadrat, "ja.transect" refers to the presence of *J. vulgaris* in a transect, "altitude" refers to elevation above sea level, "transect" refers to the transect sampled (and correlates with distance from the *J. vulgaris* population center), "ja.1m" is the density of *J. vulgaris* in a given quadrat, "mi.1m" is the density of *S. minimus* in a given quadrat, and "wa.1m" is the density of *S. wairauensis* in a given quadrat.

a.) Presence of *N. annulata* larvae on *S. wairauensis* in quadrats

Model: glm (larvae.wa.presence_absence ~ ragwort_valley + ja + altitude + (1|site_num), family = binomial)

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**LRT**	**Pr(Chi)**	**AIC**
intercept		-3.929	1.534	100.58			108.58
ragwort.valley	1	-0.108	1.265	100.59	0.007	0.932	
ja	1	2.362	0.819	112.72	**12.141**	**0.0005**	
altitude	1	-0.001	0.002	100.86	0.277	0.599	

b.) Presence of *N. annulata* larvae on *S. minimus* in quadrats

Model: glm (larvae.mi.presence_absence ~ ragwort_valley + ja + altitude + (1|site_num), family = binomial)

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**LRT**	**Pr(Chi)**	**AIC**
(Intercept)		-10.96	120	128.9			136.85
ragwort.valley	1	9.631	120	128.9	0.008	0.930	
ja	1	1.266	0.535	135.4	6.504	**0.011**	
altitude	1	-824.1	0.003	144.1	15.272	**<0.0001**	

c.) Presence of *N. annulata* larvae on *J. vulgaris* in quadrats

Model: glm (larvae.ja.presence_absence ~ altitude + transect + ja.1m + (1|site_num), family = binomial)

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**LRT**	**Pr(Chi)**	**AIC**
intercept		-2.537	0.364	329.4			337.3544
altitude	1	0.002	0.001	333.5	4.11	**0.043**	
transect	1	-0.007	0.041	329.4	0.03	0.865	
ja.1m	1	0.001	0.002	329.5	0.12	0.730	

d.) Herbivory on *J. vulgaris* in those quadrats with *J. vulgaris*.

Model: glm (percent.herbivory.jacobeaea ~ site + ja.1m + mi.1m + wa.1m + quadrat_length, family = "quasipoisson")

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**F value**	**Pr(F)**
intercept		2.05	0.605	8193.4		
ja.1m	1	0.00	0.001	8285.8	4.07	**0.044**
mi.1m	1	0.00	0.008	8193.5	0.00	0.966
wa.1m	1	-0.11	0.064	8341.9	6.54	**0.011**
quadrat length	1	0.06	0.039	8243.1	2.19	0.140
site	3			8539.7	5.08	**0.002**

e.) Herbivory on *S. wairauensis* in those quadrats with *J. vulgaris*.

Model: glm (percent.herbivory.wairauensis ~ site + ja.1m + mi.1m + wa.1m + ja.transect + transect + site:transect + quadrat_length, , family = "quasipoisson")

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**F value**	**Pr(F)**
intercept		2.10	0.950	1646.7		
ja.1m	1	0.00	0.011	1646.7	0.0001	0.99
mi.1m	1	-0.09	0.120	1662.2	1.97	0.162
wa.1m	1	0.01	0.014	1649.8	0.39	0.534
ja.transect	1	0.00	0.001	1685.9	4.98	**0.027**
quadrat_length	0	*na*	*na*	1646.7		
site:transect	4			1869	7.05	**<0.0001**

f.) *J. vulgaris* presence in quadrats in those valleys with any *J. vulgaris*.

***Model*:** glm (ja ~ transect*site + altitude + habitat_FE + habitat_FF + habitat_FG + habitat_GP + habitat_LS + habitat_RE + habitat_SB + habitat_SS + habitat_TR + habitat_UP + quadrat_length, family = "binomial")

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**LRT**	**Pr(Chi)**	**AIC**
intercept		4.202	1.693	405.4			445.4498
altitude	1	-0.037	0.007	449.9	44.4	**<0.0001**	
habitat_FE	1	0.591	0.502	406.9	1.4	0.230	
habitat_FF	1	-0.982	0.600	408.2	2.8	0.096	
habitat_FG	1	0.852	0.743	406.8	1.4	0.245	
habitat_GP	1	2.131	0.610	419.4	13.9	**<0.0001**	
habitat_LS	1	-0.195	0.582	405.6	0.1	0.738	
habitat_RE	1	0.209	0.658	405.6	0.1	0.751	
habitat_SB	1	1.782	0.953	408.7	3.2	0.072	
habitat_SS	1	-0.038	0.518	405.5	0.0	0.941	
habitat_TR	1	0.697	0.356	409.3	3.9	**0.049**	
habitat_UP	1	-1.323	1.296	406.6	1.2	0.277	
quadrat_length	1	0.0002	0.095	405.4	0.0	0.998	
transect:site	3			431.0	25.6	**<0.0001**	

g.) *J. vulgaris* abundance in quadrats of transects containing *J. vulgaris*.

***Model*:** glm (ja.1m ~ transect*site + altitude + habitat_FE + habitat_FF + habitat_FG + habitat_GP + habitat_LS + habitat_RE + habitat_SB + habitat_SS + habitat_TR + habitat_UP + quadrat_length, family = "quasipoisson")

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**F value**	**Pr(F)**
intercept		3.348	1.040	13502.29		
altitude	1	-0.007	0.004	13656.54	4.06	**0.045**
habitat_FE	1	0.298	0.237	13572.59	1.85	0.175
habitat_FF	1	0.243	0.918	13505.47	0.08	0.773
habitat_FG	1	-0.140	0.539	13505.51	0.08	0.771
habitat_GP	1	1.650	0.578	13988.01	12.77	**<0.0001**
habitat_LS	1	-1.372	0.262	15153.70	43.42	**<0.0001**
habitat_RE	1	-0.993	1.358	13530.15	0.73	0.393
habitat_SB	1	-0.190	3.158	13502.47	0.00	0.946
habitat_SS	1	-0.091	0.820	13502.87	0.02	0.902
habitat_TR	1	0.783	0.328	13768.44	7.00	**0.009**
habitat_UP	1	-3.020	6.831	13532.54	0.80	0.373
quadrat_length	1	-0.092	0.043	13718.44	5.68	**0.018**
transect:site	3			16626.75	27.38	**<0.0001**

h.) *S. wairauensis* abundance in quadrats of transects containing *S. wairauensis*.

Model: glm (log(density_wa) ~ ragwort_valley + ja.transect + transect_altitude + (1|site_num), family = gaussian)

Coefficient	**Df**	**Estimate**	**s.e.**	**Deviance**	**F value**	**Pr(F)**
intercept		-2.598	0.565	70.66		
ragwort.valley	1	-0.458	0.418	72.37	1.21	0.278
ja.transect	1	-0.008	0.0003	86.83	**11.44**	**0.001**
transect_altitude	1	0.001	0.0007	74.34	2.60	0.113

`

Table 5.3 - The number of each host plant species sampled, the total number of larvae collected on them, the percentage of each species with larvae, the average number of larvae per plant, their overall levels of herbivory, and the number of egg masses recovered on the total numbers of plants from each species and overall. Standard error in italics. These statistics are from all seven sites combined.

Host	***n***	**Total larvae**	**Plants with larvae (%)**	**Larvae per plant** mean, (*s.e.*)	**% herbivory** mean, (*s.e.*)	**Egg masses,** (number of plants)
Jacobaea vulgaris	434	102	56 (12.9)	0.24 (*0.0009*)	16.5, (*20.0*)	44. (10)
Senecio minimus	226	37	23 (10.2)	0.16 (*0.002*)	9.8, (*13.2*)	4, (2)
Senecio wairauensis	376	19	14 (3.7)	0.05 (*0.0008*)	5.6, (*12.5*)	12, (3)
TOTAL	**1036**	**158**	**93**	**0.15 (*0.004*)**	**11.1, (*15.8*)**	**60, (15)**

`

although there was a trend in this direction ($\chi^2_{1, N=375} = 2.57$, $P = 0.109$). The same was true for *S. minimus* ($\chi^2_{1, N=225} = 3.55$, $P = 0.0595$).

Within transects, the level of herbivory on *S. wairauensis* in quadrats where *J. vulgaris* was present was also significant and positively correlated with the density of *J. vulgaris* in the same quadrat ($F_{1,214}= 4.98$, $P = 0.027$) (Table 5.2e). Herbivory recorded on *S. wairauensis* was 2.13 times greater on plants near grazed pastures (the habitat type most closely associated with *J. vulgaris* (Table 5.2f)) ($P < 0.0001$). This relationship also decreased by 0.05% with every 100 m rise in elevation ($P < 0.0001$).

Overall, 158 *N. annulata* larvae were found in the survey on 93 of the 1036 individual plants sampled from all species (Table 5.3). Across all plants surveyed, *N. annulata* larvae demonstrated the strongest association with *J. vulgaris* with 12.9% of the plants surveyed hosting at least one larva. In comparison, larvae were collected from 10.2% of all *S. minimus* and 3.7% of the *S. wairauensis* surveyed. The invasive *J. vulgaris* also had the greatest densities of larvae with 0.24 (± 0.0009) caterpillars per plant surveyed, while the native *S. minimus* and endemic *S. wairauensis* were found supporting 0.16 (± 0.002) and 0.05 (± 0.0008) larvae per plant, respectively. Although *N. annulata* larval abundance appeared to be lower than during the previous field season when site selection was carried out, significantly more larvae were collected from *S. wairauensis* plants in areas where *J. vulgaris* was present (Table 5.4). The naturalized host also displayed the highest levels of *N. annulata* herbivory with 246 individuals (56.6%) exhibiting feeding damage with 16.5% of leaves showing >5% folivory. *Senecio minimus* and *S. wairauensis* surveyed were slightly less injured with 106 (35%) and 79 (21%) plants herbivore damaged, respectively. Overall, *S. minimus* had >5% damage on 9.8% of leaves while *S. wairauensis* had 5.6% of leaves damaged in the same way.

No populations of the endemic *S. rufiglandulosus* were found in any of the sites sampled. However at the three isolated populations of this species encountered during the early site selection surveys, I found at least 20 *N. annulata* larvae feeding on this species at one site (unpublished data). Larvae that managed to get into the glasshouse at Lincoln where I was growing *S. rufiglandulosus* also readily fed on this species, which indicates that it is a suitable and palatable plant for its growth and development. A third endemic, *S. dunedinensis*, was not located in any of the field sites nor were any populations encountered in initial site surveys. This species appears to have a current geographic distribution in the southern part of the South Island and outside the area I surveyed (see Chapter 3, Figure 3.8).

`

Table 5.4 - Percentage of *Senecio wairauensis* plants from which *Nyctemera annulata* larvae were collected in areas with the invasive *Jacobaea vulgaris* present versus in areas where it was absent.

	***J. vulgaris* present**	***J. vulgaris* absent**
% with larvae	35.5	1.1
N	93	283

`

5.3.2 Host Plants

When the presence of *S. wairauensis* was compared between sites with *J. vulgaris* versus uninvaded sites, there were significantly more endemic hosts in the valleys where the invader was absent ($\chi^2_{1, N=66} = 4.27$, $P = 0.039$) (Fig. 5.2). The density of *S. wairauensis* in valleys where *J. vulgaris* was present was 1.75 (± 0.23) per 30m^2 quadrat, while the number of this endemic host plant in sites free of *J. vulgaris* was 3.56 (± 0.52) per quadrat. *Senecio wairauensis* was also more likely to occur in transects of sites without invasions than in invaded sites ($\chi^2_{1, N=66} = 5.94$, $P = 0.015$) (Fig. 5.3). The endemic *S. wairauensis* was present in 37.3% of the quadrats of sites without *J. vulgaris* infestations in them, but only in 18.5% of quadrats at sites with infestations. *Senecio jacobaea* dominated the low elevation portion of the sites that it infested while *S. wairauensis* was present across all elevations in uninfested sites (Fig 5.4). Furthermore, sites that were free of *J. vulgaris* also, for the most part, appeared to lack the native *S. minimus*. While a very few individuals were present in the *J. vulgaris*-free Mingha River Valley, they were close to the car park and not in the areas sampled in the systematic survey.

Tests of alternative models revealed a significant interaction effect between the covariates of site and the distance from the area with the highest density (in terms of increasing transect number) on *J. vulgaris* presence ($\chi^2_{2, N=851} = 76.12$, $P < 0.0001$) and abundance ($F_{3, 374} = 27.76$, $P < 0.0001$). After taking this interaction, as well as habitat type and elevation into account, *J. vulgaris* was still found to be present significantly more often in grazed pastures ($\chi^2_{1, N=851} = 39.10$, $P < 0.0001$), forest gaps ($\chi^2_{1, N=851} = 4.02$, $P = 0.0450$) and along landslips ($\chi2_{1, N=851} = 4.15$, $P = 0.041$) than in other habitats. Furthermore, grazed pasture ($F_{1, 374} = 13.39$, $P = 0.0003$), landslip ($F_{1, 374} = 39.45$, $P < 0.0001$) and trailside terrain ($F_{1, 374} = 5.59$, $P = 0.0186$) all had a positive effect on the abundance of *J. vulgaris*.

The distribution and abundances of *S. wairauensis* populations also demonstrated a significant effect of habitat as it was more often found in forest gaps ($\chi^2_{1, N=228} = 77.23$, $P < 0.0001$), on trailsides ($\chi^2_{1, N=222} = 75.03$, $P < 0.0001$), in ungrazed pastures ($\chi^2_{1, N=221} = 29.24$, $P < 0.0001$), as well as along forest edges (($\chi^2_{1, N=230} = 13.20$, $P < 0.0001$), landslips ($\chi^2_{1, N=226} = 10.31$, $P < 0.0001$) and river margins ($\chi^2_{1, N=225} = 8.09$, $P = 0.0044$). The endemic was significantly less common in grazed pastures ($\chi^2_{1, N=227} = 22.60$, $P < 0.0001$) and scrub habitat ($\chi^2_{1, N=224} = 4.66$, $P = 0.0301$). The abundance models created from collection data for *S. minimus* and *S. wairauensis* were compared with the distribution and abundance data for *J. vulgaris*. Models of distribution for the native *Senecio* species were also compared to abundance and presence-

`

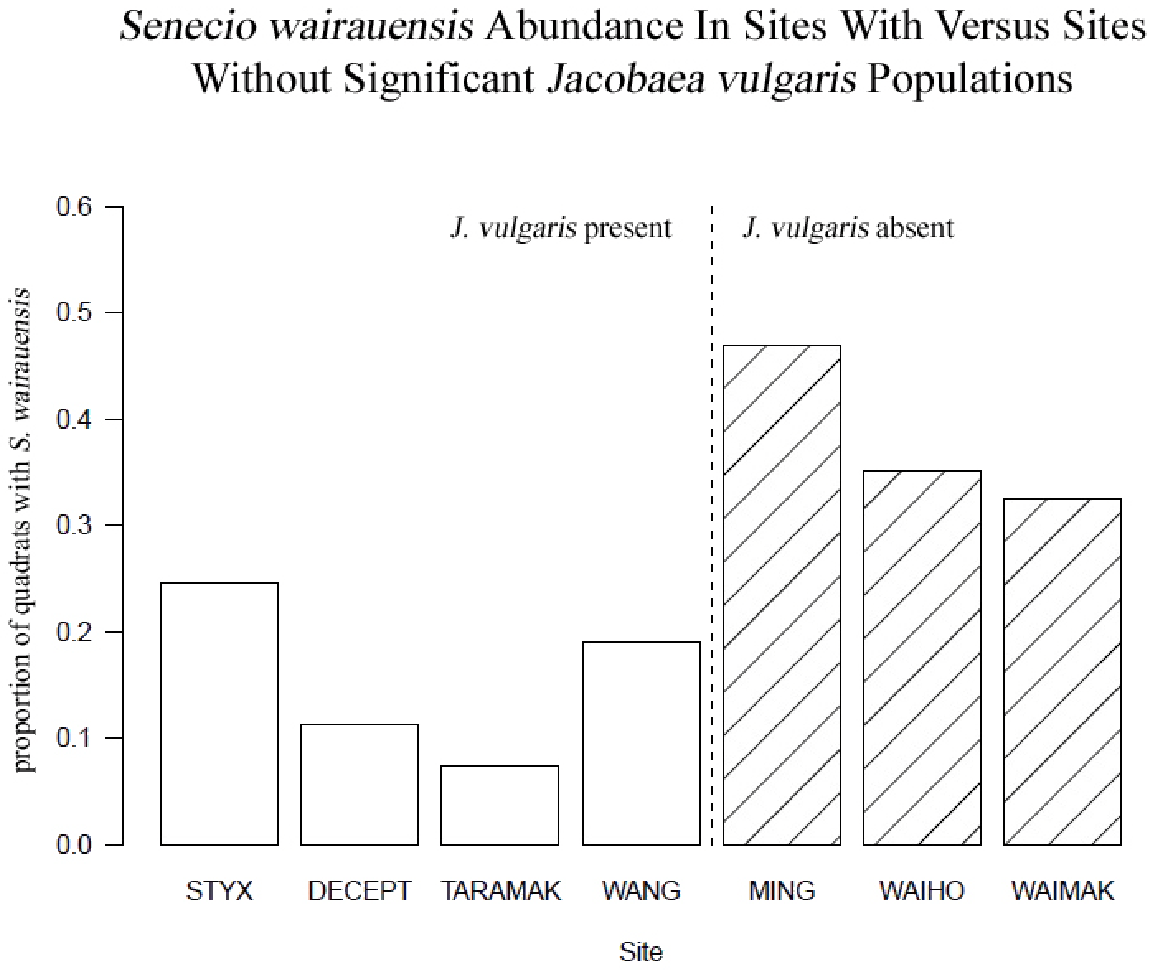

Figure 5.2 - The proportion of quadrats containing *Senecio wairauensis* in sites with *Jacobaea vulgaris* present versus sites without the invader present. See Methods for site abbreviations.

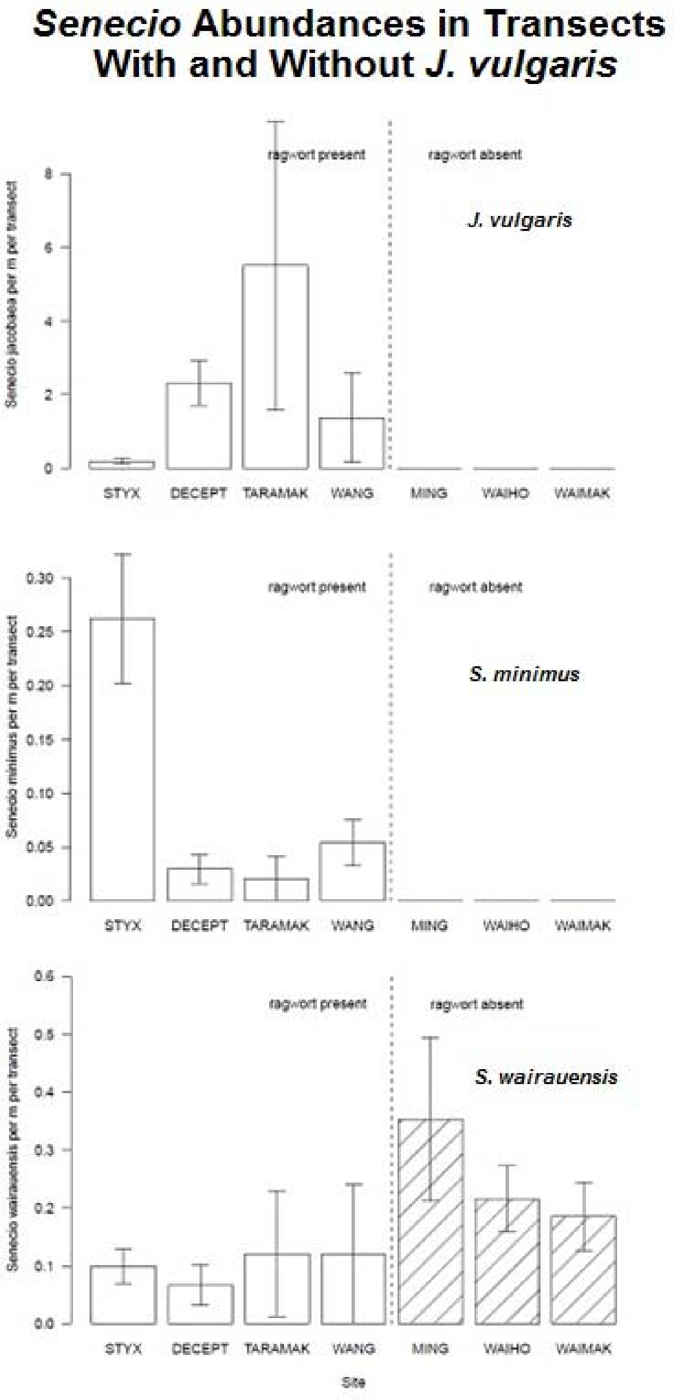

Figure 5.3 - Mean numbers of plants of three *Nyctemera annulata* host plant species (*Jacobaea vulgaris*, *Senecio minimus* and *S. wairauensis*) sampled per meter in transects for all seven river valley sites surveyed. Valleys with *J. vulgaris* infestations are on the right of the dashed line, while valleys without *J. vulgaris* populations are on the right.

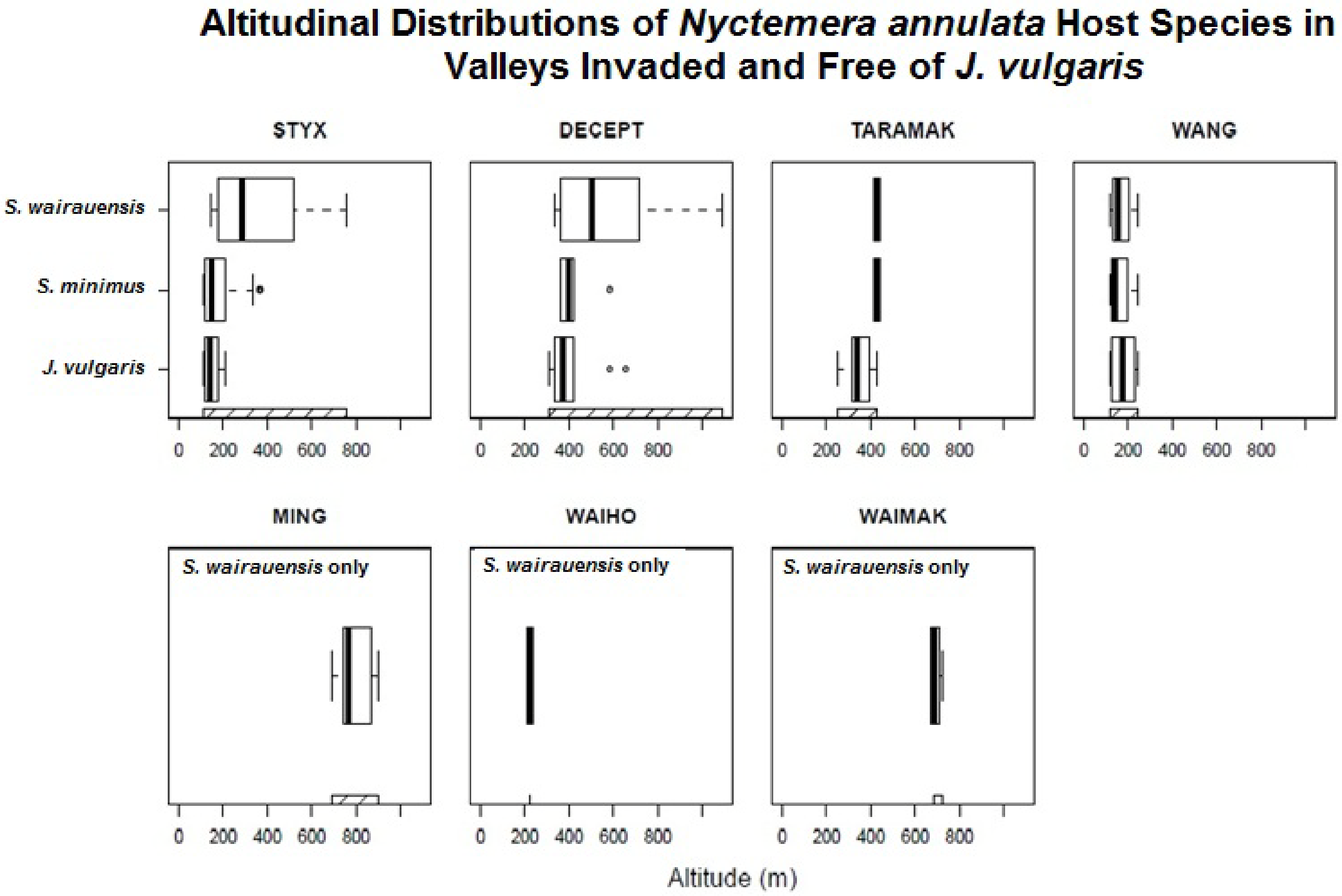

Figure 5.4 - Elevational distributions of *Senecio wairauensis* (endemic), *S. minimus* (non-endemic native) and *Jacobaea vulgaris* (invasive) in seven survey sites with and without *J. vulgaris* invasions. Note that *Senecio wairauensis* typically occurs at higher elevations than *J. vulgaris* regardless of the overall elevation of the site, suggesting that factors within each landscape are affecting on *S. wairauensis*. Black lines indicate median values, boxes indicate the interquartile range (IQR) and bars indicate the IQR x the range, and dots indicate outliers. Hashed boxes at the bottom of each site plot indicate the full elevation range surveyed.

`

absence data for *J. vulgaris*. The two native species were found to inversely correlate with *J. vulgaris* occurrence in quadrats, however this relationship is confounded with habitat. Specifically, in grazed pasture sites *J. vulgaris* is at its most abundant while *S. minimus* and *S. wairauensis* are sparse and absent, respectively. Outside of grazed pasture habitats, there is an inverse relationship in abundance between the endemic *S. wairauensis* and the invasive *J. vulgaris* in the transects where they co-occur (Fig.5.5).

5.4 Discussion

Most models of species invasions assume that invaders influence native species through direct mechanisms like (resource) competition (Callaway & Walker, 1997; Case, 1990; Corbin & D'Antonio, 2004; Kupferberg, 1997; Procheş, et al., 2008; Stachowicz & Byrnes, 2006; Tilman, 2004) and predation (Carlsson, Brönmark, & Hansson, 2004; Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; D. F. Fraser & Gilliam, 1992; Kenis, et al., 2009; J. M. Levine, et al., 2004; Snyder, et al., 2004; Taniguchi, Fausch, & Nakano, 2002; G. Woodward & Hildrew, 2001) or by altering an ecosystem's nutrient cycling (Allison & Vitousek, 2004; Bohlen et al., 2004; Ehrenfeld, 2003; Hawkes, Wren, Herman, & Firestone, 2005; Hobbie, 1992; Stadler, Müller, & Orwig, 2006), fire regime (M. L. Brooks et al., 2004; D'Antonio & Vitousek, 1992; Keeley, 2001; Simberloff & Von Holle, 1999; Zedler & Kercher, 2004) or hydrology (Bunn, Davies, Kellaway, & Prosser, 1998; Calder & Dye, 2001; Caraco et al., 1997; Crowl, et al., 2008; Décamps, Planty-Tabacchi, & Tabacchi, 1995; Ford & Vose, 2007; Maerz, Brown, Chapin, & Blossey, 2005; Stromberg et al., 2007; Tickner, Angold, Gurnell, & Mountford, 2001). My results suggest a more complex effect from the introduced plant invader, *J. vulgaris*. They are consistent with apparent competition is occurring between *J. vulgaris* and the endemic *S. wairauensis* through their shared, endemic consumer, *N. annulata*. Where it is present, *J. vulgaris* leads to increases in native herbivore abundance which, in-turn, leads to increased herbivory on the endemic host plant. Evidence for this includes higher levels of *N. annulata* herbivory on *S. wairauensis* samples that are positively correlated with their proximity to *J. vulgaris* infestations. Likewise, the majority of larval *N. annulata* larvae captured in the survey on both native species were also positively correlated with their proximity to *J. vulgaris* infestations. Association of high *N. annulata* densities with *J. vulgaris* incidence matches historic accounts linking population eruptions of these two species (Chapter 2).

Perhaps as a consequence of apparent competition, I found a paucity or absence of *S. wairauensis* populations near dense *J. vulgaris* infestations. The data show that *S.*

`

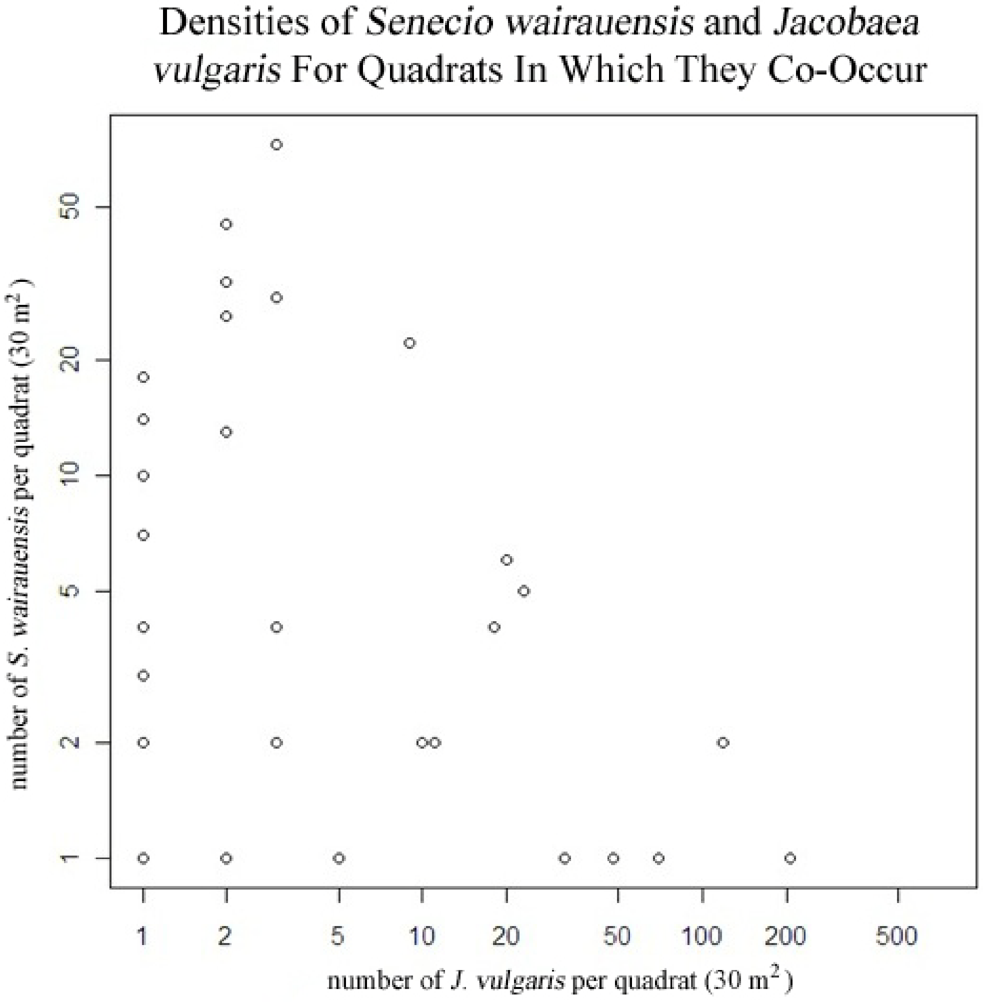

Figure 5.5 - The logrithm of *Senecio wairauensis* (endemic) density plotted against the logrithm of *Jacobaea vulgaris* (invasive) density for just the quadrats in which they co-occur at seven survey sites on the South Island of New Zealand.

wairauensis abundance was significantly lower in valleys with *J. vulgaris* infestations when compared to those without the invader. Segregation of the host species along the length of *J. vulgaris*-infested valleys also supports the assertion that apparent competition is affecting native species at the population level. In infested valleys *J. vulgaris* occupies areas that correlate with high disturbance while *S. wairauensis* inhabits those parts of the valleys where the exotic is absent. While high levels of disturbance alone could be seen as an explanation as to why *J. vulgaris* persists in these areas, the influence of *J. vulgaris* in the models for *S. wairauensis* was still present after taking into account covariates relevant to habitat type. Likewise, analyses of the survey data show that in valleys where *J. vulgaris* is absent or rare, the highly-disturbed, low-elevation areas occupied by this species in invaded sites are used by *S. wairauensis. Senecio wairauensis* also exhibits far less *N. annulata* herbivory in sites and transects without *J. vulgaris* present.

It is important to point out that the segregation phenomenon between these two species is not due to the effects of elevation. Of the seven sites surveyed, four were invaded by *J. vulgaris* and shared the same pattern of spatial separation between the invader and *S. wairauensis*. However the point along the altitudinal gradient at which these species switch over in dominance occurs at different elevations for each valley. Furthermore, *S. wairauensis* occupies the entire range of elevations in the valleys where *J. vulgaris* is absent, including locations far below the lowest elevation it occupies in infested valleys (i.e. Deception Valley compared to Waiho Valley).

In light of evidence for apparent competition between an invasive species and a rare, endemic congener, there are clear and important implications for invasion ecology and conservation. First, it is widely accepted that invasive species, including *J. vulgaris*, damage native ecosystems by outcompeting native or economically important species for finite resources (B. J. Brown, et al., 2002; Gherardi & Daniels, 2004; Human & Gordon, 1996; Kenis, et al., 2009; J. M. Levine, et al., 2004; Morrison, 2000; Sher, et al., 2000). However, these data show that the presence of *J. vulgaris* in the landscape is also causing an increase in the numbers of an endemic, insect herbivore that uses native host plants. One indirect effect of this increase is the application of elevated herbivore stress on populations of at least one rare, endemic herb (as mentioned above, two other endemics, *S. dunedinensis* and *S. rufiglandulosus* were not present in any of my field sites so likely impacts to their populations are not covered here). In contrast to direct competition, which is experienced in close proximity to an invader, pressure exerted on *S. wairauensis* in this instance is transferred along greater distances. One recommendation is for stronger control measures of *J. vulgaris*

`

near populations of *S. wairauensis* and other endemic *Senecio* species that are now rare and are declining in their abundance (e.g. *S. rufiglandulosus*, *S. scaberulus* and *S. dunedinensis*). While *N. annulata* adults (and larvae to a lesser extent) can move some distance between high-density *J. vulgaris* patches and areas with native *Senecio* hosts, curtailing *J. vulgaris* densities and presence is likely to reduce the pressure felt by nearby native *Senecio* host populations. Recognizing *J. vulgaris* infestation as a conservation issue (not just as a farming issue) would likely have an effect of promoting further efforts aimed at its control. The recent release of two biological control agents on the West Coast presents a unique opportunity to examine the response of endemic *Senecio* species (particularly *S. wairauensis* and *S. rufiglandulosus*) during and following the expected retractions in the distribution and abundance of *J. vulgaris*. If *J. vulgaris* is having an effect and then is successfully controlled, the endemics are likely to respond by extending their distributions and altitudinal ranges

Of particular consideration to the field of invasion ecology is the likelihood that similar cases exist of native herbivore spillback onto native species following exotic plant invasions, with these phenomena occur primarily along taxonomic lines. In selecting organisms for release and control of invasive species, biological control practitioners perform host range testing to gain a clear picture of what impact candidate biological control agents (BCAs) may have on native and agricultural species (non-target species). Most non-target organisms tested are selected because they are taxonomically related to the target weed or pest and are therefore the most likely species to be attacked by BCAs. As discussed in the introduction, however, the consequences of relatedness in species interactions are multifarious and complex. My research suggests that the effects of relatedness between target and non-target species may be detrimental to the latter even *before* BCAs are released. In a review by White et *al.* (2006), the authors theorized that apparent competition between native and invasive plants and mediated by native insect herbivores was probably occurring, however they were unable to find a single instance of it in the literature.

In the current example of the invasion of New Zealand by *J. vulgaris*, evidence presented in Chapter 2 suggests that the population explosion of the native *N. annulata* and the top-down pressure this exerted on *S. wairauensis* from it was far more intense prior to the importation and release of BCAs for *J. vulgaris*. Reviews on the efficacy of *J. vulgaris* biological control efforts conclude that the impacts of *Tyria jacobaeae* and *Longitarsus jacobaeae* have significantly decreased the density and geographic distribution of this invader in New Zealand (e.g. Fowler, et al., 2000; Syrett, 1983; Syrett, Briese, & Hoffmann, 2002). Compared to observations recorded prior to 1901 when *J. vulgaris* control measures were first

`

implemented, abundances of *N. annulata* have likely declined substantially (although there may be multiple explanations as to why). Regardless, the effects from *N. annulata* herbivory detected in this field survey must have been much stronger over 100 years ago and reduction of *J. vulgaris* populations is a likely reason why this has changed. For all intents and purposes, instances of native consumer-mediated apparent competition between target and non-target organisms and their impact on non-target species should be recognized and weighed in decisions involving control invasive species.

There are also clear implications for species conservation, as the impact of invasive species may go deeper than previously acknowledged. A case-in-point is the current Department of Conservation (DOC) policy on management of *J. vulgaris*. Currently, DOC is not required to control *J. vulgaris* on any of its holdings under the various Regional Pest Management Strategies including the West Coast's. Regardless, DOC generally does apply chemical controls in *J. vulgaris*-invaded areas when legitimate claims are laid for agricultural reasons. Likewise, DOC has lent their support to the idea and application of biological control as the strategy with the best long-term chance of controlling *J. vulgaris*. Given that there are several species of endemic New Zealand *Senecio* with populations that have dramatically declined in abundance and significantly retracted in terms of their geographic distribution, the results presented here may be cause for a revision in DOC's status of *J. vulgaris* as a weed. Currently this species is not considered of importance to conservation (Tom Skelton, personal communication), although my research findings are evidence that this is not necessarily true and that *J. vulgaris* had and is still having an impact on at least one of the 13 species of *Senecio* endemic to New Zealand. DOC policies regarding exotic weed control and consideration for more aggressive strategies at some locations.

The other native host included in the survey, *Senecio minimus*, exhibited a distribution pattern which contrasts with that of *S. wairauensis* and was often found interspersed with patches of *J. vulgaris* outside of grazed paddocks. This hearty native, also native to Australia, had few larvae on it in the landscape surveys and exhibited less sensitivity to *N. annulata* herbivory in caged field trials when compared to *S. wairauensis*. Low preference for *S. minimus* by the moth larvae aligns with the results of the host preference analysis in Chapter 4 which showed this host to be the least palatable of the species included in the landscape survey. One possible explanation for this is that *S. minimus*, while still suitable as food plant to *N. annulata* larvae, is protected from greater levels of herbivory by a phytochemistry that deters consumers and reduces fitness of moths that feed on it relative to those that feed on *J. vulgaris* and *S. wairauensis*.

`

The results of this landscape survey, as well as those from the host preference and performance analyses in Chapter 4, do not show a clear difference between the naturalized *J. vulgaris* versus native hosts. Clearly *J. vulgaris* is an acceptable host for *N. annulata* and its use provides some advantages for this native consumer, most notably its abundance relative to native hosts and its ability to use highly disturbed habitats (specifically livestock-grazed paddocks). Furthermore *N. annulata* began exploiting *J. vulgaris* immediately following its establishment in New Zealand and has become intimately associated with its novel host plant both in its ecology and in the minds of early European settlers and modern day New Zealanders. These results contradict the generalization that endemic, specialist herbivores prefer their native host plants as was suggested by White et *al.* (2008). The authors of that study concluded that demonstrated preference by a *Nyctemera* congener for a native *Senecio* species over an exotic invader was further support for the ERH.

Interspecific competition is another ecological influence that is generally thought of as being stronger between closely related species. For the most part, this appears to be the case for *J. vulgaris* and the native *Senecio* species in most of the habitats surveyed. *Jacobaea vulgaris, S. minimus* and *S. wairauensis* were similarly likely to be sampled at landslips, stream sides, along trail margins and at forest edges. However, *J. vulgaris* and *S. wairauensis* were rarely encountered in the same quadrat . Out of 584 quadrats in which at least one of these species was present, they were found together in only 31 of them (of the other 553 quadrats, *J. vulgaris* was absent from 209 of them and *S. wairauensis* was absent from the other 344). The most obvious exception to this trend is cattle-grazed paddocks, with which *J. vulgaris* is strongly associated. In fact, *J. vulgaris* is practically unchallenged by native *Senecio* in grazed pastures, mainly due to the fact that the native *Senecio* species are readily eaten by cattle. The data collected indicates that in grazed quadrats, the invasive *J. vulgaris* was at its highest levels of abundance, while the native *S. minimus* is rare and the endemic *S. wairauensis* is completely absent. Facilitation of *J. vulgaris* infestations by cattle grazing is supported by previous studies (Hanley, et al., 1995; Kunin, 1999; Lozon, 1997; McEvoy, et al., 1993; Myers & Post, 1981; Poole & Cairns, 1940; Schmidl, 1972a; Sutherland, et al., 2000; Wardle, 1987) and appears to be a very important component in its presence and abundance in the current survey.

`

Chapter 6

Conclusion

6.1 Evidence for Apparent Competition

In my current study of the New Zealand *Senecio* food web, I found evidence consistent with apparent competition between *Jacobaea vulgaris* and *S. wairauensis* mediated by a shared herbivore, *Nyctemera annulata*. As outlined in the Introduction, three important criteria characterize apparent competition. First, there must be at least two host species that share a common consumer. Second, the shared consumer must cause a greater negative impact on the fitness on one or more species of host(s) in the presence of another. Third, these impacts must be evident at the population level, with the weaker apparent competitor declining in occupancy and abundance. Results from my research found evidence for all three of these phenomena in the study system, which I expand on below.

Nyctemera annulata fills the role of a shared herbivore by feeding on native *Senecio* species and the invasive weed, *J. vulgaris*. Historic anecdotal evidence since the arrival of *J. vulgaris* in New Zealand (presented in Chapter 2) indicates that multiple naturalists linked the exotic plant’s invasion and spread with a distinct increase in the local abundance of *N. annulata* larvae and imagos. Host preference and performance analyses (presented in Chapter 4 show) that *J. vulgaris* is at least as suitable a host for gravid female *N. annulata* as the three native *Senecio* hosts assayed and that larvae develop at least as well on the invasive host. *Nyctemera annulata* larvae readily moved between alternate hosts in the field cage trials and fed on all species in choice assays. My field surveys found that larvae were using both *J. vulgaris* and native *Senecio* hosts in the landscape. In addition to my tests and surveys, previous research and observations also confirm that *N. annulata* uses multiple hosts, including the species assayed.

The impact of *N. annulata* on the endemic *S. wairauensis* is disproportionately greater in the presence of *J. vulgaris*. In choice assays *S. wairauensis* was attractive to larvae and in field cage experiments *N. annulata* larvae fed heaviest on *S. wairauensis*. In the field cage experiment feeding on *S. wairauensis* was even greater when this species was paired with the invasive *J. vulgaris*. In field surveys, more larvae were collected from both *S. wairauensis* and *S. minimus* that were in close proximity to *J. vulgaris* than on plants farther away from the invasive species. Likewise more herbivore damage on these two native species was recorded when they were near *J. vulgaris*. While my cage assays failed and, as a result, I was

`

unable to effectively quantify the impact of *N. annulata* larvae on the *S. wairauensis*, there are reasonable indications that this host species is more delicate and sensitive to similar levels of herbivory than the invasive species (e.g. it is smaller, produces far less seed than *J. vulgaris*). Altogether, these results suggest that there are differing levels of impact on these two host species and that damage to *S. wairauensis* by *N. annulata* is more intense in the presence of *J. vulgaris*.

There is also evidence for these impacts at the population level for *S. wairauensis* in that this species is generally less abundant in areas with *J. vulgaris* populations. My analysis of herbarium records in Chapter 3 suggests that, despite using similar types of habitat, there is little evidence for clustering between *J. vulgaris* and native *Senecio* species. Similarly, this analysis suggests that there has been an upward shift in the elevational distribution of *J. vulgaris* since its arrival along with a corresponding shift in the elevational ranges of native and endemic *Senecio* species. In my field surveys I found a similar trend where the endemic *S. wairauensis* was less common (or absent) at all scales (sites, quadrats and transects) when *J. vulgaris* was present. In sites without *J. vulgaris* the endemic was consistently well-represented across all scales and independent of the elevation of the site surveyed.

6.2 Possible Alternative Explainations

While the results above suggest that apparent competition is occurring in the New Zealand *Senecio* food web, there are other factors that could explain the patterns that I observed. Given that species distributions are be influenced by many factors, several possible alternative explanations for the patterns in the data should be considered. In the following paragraphs I discuss some of these.

Patterns detected in the distribution analyses could be more strongly influenced by other factors such as direct competition, specific habitat types, and/or historic land changes. For instance, presence data used in the spatial analysis in Chapter 3 have a relatively weak resolution (e.g. no accompanying habitat data, no absence data, collection times and locations are patchy) which makes it difficult to be certain of the reasons for the patterns observed. As mentioned in Chapter 3, incorporating the use of GIS data layers into an analysis would help to clarify the effect of other habitat and site characteristics. Adding land characteristic data (such as soil type, disturbance regimes, aspect, etc.) over the *Senecio* records would help determine if any such features are influential in predicting host distribution. Incorporation of absence data in addition to presence data (particularly for the systematically-sampled NVS plots), would also add more context to the distribution of these species and generate a more

`

robust analysis in comparing and contrasting species distributions. The current analysis fails to distinguish between plots from which a species is absent and plots that were simply not surveyed for the focal species (or at all).

The distribution patterns observed in the field survey show an undeniable segregation between *J. vulgaris* and *S. wairauensis*. However, there are other possible explanations as to why this is the case aside from apparent competition. One alternative explanation is direct competition. Non-natives account for more than half of the vascular flora species in the New Zealand landscape (C. Howell & Sawyer, 2006; NZPCN), many of these invaders are adapted to the same disturbed habitats that native *Senecio* species favour (e.g. Pyšek & Richardson, 2006; J. J. Sullivan, Williams, Timmins, & Smale, 2009). In my field surveys, I regularly found that other invasive plant taxa (e.g. grasses) were competing with *J. vulgaris* and native *Senecio* species in the same patch. The outdoor cage assays in Lincoln were meant to remove direct competition as a factor and look at just the impact of *N. annulata* herbivory; however the experiment did not proceed as planned and failed to produce much useful data in this regard.

The densest populations of *J. vulgaris* encountered in my field surveys were in cattle-grazed pastures. At the same time, native *Senecio* species were in significantly low abundance or absent in the same places. So it stands to reason that the distribution of *Senecio* could be an artefact of grazing behaviour. *Jacobaea vulgaris* has a much longer window of exposure to livestock grazing given its Eurasian ancestry (Caño, Escarré, Vrieling, & Sans, 2009; del-Val & Crawley, 2004; McEvoy, et al., 1993). As a result, it is highly tolerant to the damage and disturbance associated with the dairy cattle paddocks of the West Coast. Likewise, *J. vulgaris* produces a particularly potent blend of toxins that dissuades roaming cattle from eating large, luxurious plants growing there. During the field surveys I rarely found *S. minimus* or *S. wairauensis* in grazed paddocks, but it was occasionally on the field periphery. Several *S. wairauensis* plants that I became familiar with over two field seasons appeared to have been eaten or fed on by deer. So it seems possible that grazing in general and cattle grazing specifically could influence the patterns seen in the data. Despite this, fenced forest areas were frequently adjacent to cattle pastures containing ragwort and *Senecio wairauensis* was both less common in these forests than further from ragwort and also experienced greater folivory. It remains plausible that past grazing in these adjacent forested habitats has left an imprint on current distributions.

As indicated above (and from over a century of observation in New Zealand), *J. vulgaris* dominates habitats in and around the grazed pastures of the lowlands. My conclusion that *N.*

`

annulata larval densities are highest in areas because *J. vulgaris* biomass is the greatest here assumes a causal relationship. However, both of these results could be correlated with the habitat itself. As some authors in Chapter 2 indicate, the behaviour of *N. annulata* adults is unusual for moths in that they tend to casually fly around in open spaces (like paddocks). So it's important to consider that the reason so many larvae are found in and around the disturbed, open areas of the lowlands is for some of the same reasons that *J. vulgaris* is so common in these same areas: preferred habitat. The same grazed paddocks that afford *J. vulgaris* abundant sunlight and fewer competitors provide *N. annulata* with the sunny, open spaces that it seems to prefer. As such, there's the slight possibility that abundances of *N. annulata* larvae associated with *J. vulgaris* patches in lowlands (and not with native *Senecio*) is an artefact of habitat characteristics and not one of association between the moth and its novel host plant. Despite this, some of my sites, especially in valleys without ragwort, had large open spaces free of ragwort and also had less *Nyctemera*.

While the alternative explanations above are important to take into consideration, they still fail to explain away some other key factors in reaching the conclusions of this thesis. There are a number of valid concerns regarding the herbarium record analysis in Chapter 3. The methodology used should be re-assessed and the data reanalysed, but at the same time there are clear trends to suggest that populations of *J. vulgaris* and native *Senecio* species are less likely to be found near one another and that the natives are less prevalent at the lower elevations than formerly and that *J. vulgaris* is more common in these same areas. In order to determine the actual influence of *J. vulgaris* on native *Senecio* it would be prudent to perform tandem analyses with at least one other native-invasive species pair and/or a native lowland plant without an invasive relative in New Zealand. These analyse would indicate how much of the pattern shift in native *Senecio* species is attributable to changes in land use and habitat modification and how much the changes are as a result of apparent competition.

Determining the influence of cattle grazing on native hosts would also be a simple (yet effort-intensive) undertaking. Making cages more livestock-proof and setting up an experiment to try and isolate the effects of *J. vulgaris* proximity on native *Senecio* through shared herbivores would help determine how much of the impact on native hosts is due to *N. annulata* feeding and how much is from other factors. So while all of the possible alternative explanations are feasible, they tend to fall short of explaining away the experimental results.

`

6.3 Conservation Implications

Together, these results raise significant conservation issues surrounding an invasive plant that has traditionally been viewed and handled as a strictly agricultural issue, not one of conservation. All of the *J. vulgaris*-infested sites chosen for the survey were on Department of Conservation (DOC) lands and selected for their high densities of the weed, which is in large part due to the lack of regular control measures at those sites. DOC is exempt from controlling *J. vulgaris* under all regional pest management strategies and does not consider this invasive species as a serious environmental weed (Tom Belton, personal communication). With a limited budget for control of weeds in general, DOC does not apply chemical controls unless it is warranted (e.g. in high priority conservation areas, or when a complaint from an adjacent landowner is laid). DOC instead considered biological control of *J. vulgaris* as the only current cost-effective solution and DOC has been a participating member of the West Coast Ragwort Control Trust since its inception, which petitioned the Environmental Risk Management Authority (ERMA) to release two additional biological control agents (*Platyptilia isodactylus* and *Cochylis atricapitana*) in the West Coast Region in 2008. As yet, this has done little to tamp down high *J. vulgaris* numbers on the DOC holdings that I surveyed.

The response of the native host plant, *S. minimus*, differs in that it appears to be less preferred than *J. vulgaris* or *S. wairauensis* and is more tolerant of herbivory than *S. wairauensis*. It not surprising then that, in the landscape, it appears to overlap more closely with *J. vulgaris*. In my field observations it was not uncommon to find them both in the same location. In fact, when comparing the seven valleys in this survey, looking just at those with *J. vulgaris* versus those without-, no *S. minimus* was recorded from any transects in valleys without the invasive but it was present in all valleys with *J. vulgaris*. The reasons for this are uncertain.

6.4 Apparent Competition Past

While my surveys were able to detect higher levels of *N. annulata* herbivory on native species near infestations of *J. vulgaris*, the evidence in Chapter 2 indicates overall densities of *N. annulata* were historically much higher. If the densities of adult and larval moths were once enormous there was undoubtedly more spillover of *N. annulata* onto native *Senecio* populations. While there is no evidence for the level of damage done to native *Senecio* populations during this time, I can extrapolate from the evidence in this thesis and surmise that it must have been significant for small, delicate and less fecund species like *S. wairauensis* and *S. dunedinensis*, especially during a period of rapid modification and loss

(Brooking, 2004). Presumably this pressure has decreased with an implied decrease in *N. annulata* abundance since the early 20th Century.

There are two leading theories as to the reason for the suggested decline in *N. annulata*. One theory is that the abundance of host plants has dropped significantly thereby limiting the amount of larvae from the bottom-up. There is both scientific data and anecdotal evidence that seems to support this idea for *J. vulgaris* and some native *Senecio* in many areas of their respective ranges (Fowler, personal communication; Helson, 1974; Poole & Cairns, 1940; Radcliffe, 1969; Syrett, 1983; Wardle, 1987). Although competition from other exotic species may play a role, decreases in *J. vulgaris* abundance have been recorded across much of New Zealand. This decrease in distribution and density of *J. vulgaris* is often attributed to the impact of introduced biological control organisms, particularly *Longitarsus jacobaea* and *Tyria jacobaea* (e.g. Fowler, et al., 2000), as well as improved cultural and chemical control strategies (e.g. Wardle, 1987). However, attributing this drop in *N. annulata* solely to a decrease in food plant still seems unsatisfactory in that even in the densest infestations of *J. vulgaris* of the modern day, they typically exhibit nothing approaching the “clouds of *N. annulata*” or “vast swarms” described in Thompson (1922).

Nyctemera annulata populations may be regulated as much (or more) from the top-down by parasitoids (Benn, et al., 1978; Cameron, 1935; Gaskin, 1966; Paynter, et al., 2010). Increased pressure by parasitoids is another theory for why there are fewer adult *N. annulata* observed today. There is some evidence for this, although the exact reasons why are a point of conjecture (Smith 1893, Watt 1914, McLaughlin 1967, Singh and Mabbett 1976, Benn et al. 1978, Woodward 1984b). One likely explanation is that, since the invasion of *J. vulgaris*, there have been new records for non-native parasitoids that use *N. annulata* as a host (listed in Chapter 2). Additional consumers would have a greater suppression effect on *N. annulata*. Additionally, under these same conditions a vast increase in *N. annulata* biomass would create selection pressure for parasitoids to use and optimize use of this food supply.

Perhaps as importantly, many of the parasitoids of *N. annulata* also use other Lepidoptera, including exotic (e.g. *Tyria jacobaeae, Plutella xylostella*) and native species (e.g. *Danaus plexippus, Vanessa gonerilla*). Alternate hosts and parasitoid sharing can influence parasitoid abundance and result in parasitoid spillover and spillback onto alternate host populations (Bonsall, Bull, Pickup, & Hassell, 2005; Bonsall & Hassell, 1999; Frere, Fabry, & Hance, 2007; Harrison & Thomas, 1991; Langer & Hance, 2004; Messing & Wang, 2009; Muller & Godfray, 1997; Settle & Wilson, 1990; van Veen, et al., 2006). Buller (1881) remarked to the fact that as *N. annulata* numbers seemed to increase, the number of other moths seemed to

`

decrease. While the observation is probably due mostly to habitat loss and dwindling host plant populations, it is conceivable that a dramatic increase in *N. annulata* numbers may also have contributed additional pressure on native Lepidoptera populations through shared parasitoid spillover.

Looking forward, if biological control of *J. vulgaris* were successful in further suppressing its abundance and restricting its distribution, this should further reduce *N. annulata* numbers and weaken the impact of *N. annulata*-mediated apparent competition with endemic *Senecio*. As a result endemic *Senecio* should expand their presence in the lowlands and, to a greater extent, into areas where high density populations of *J. vulgaris* are present.

6.5 Recommended Research

Further research into the impact of *J. vulgaris* and *N. annulata* on native *Senecio* species should be carried out. As mentioned above as perhaps the most useful data that could be collected is a field experiment quantifying the strength of apparent competition along a gradient extending away from an area with a high density of *J. vulgaris*. Again, this was attempted in the last part of my final field season, but the experiment failed due a combination of factors. Data from the successful implementation of such an experiment would help to clarify precisely how much pressure is exerted on transplanted native species by *N. annulata* in relation to *J. vulgaris* proximity while limiting the influence of habitat and competition.

Apparent competition with *J. vulgaris* may also be impacting other endemic species that have shown a contraction in their geographic ranges and altitudinal distributions. The impact of *J. vulgaris* and *N. annulata* on *S. rufiglandulosus, S. dunedinensis* and other endemic *Senecio* species should be investigated further. In my Ph.D. research I was unable to examine the effect of *J. vulgaris* proximity on populations of *S. rufiglandulosus* as there were only three small populations on the South Island that I was able to locate. Cage trials using transplanted *S. rufiglandulosus* were unsuccessful after the cages were trampled by livestock and washed away in a flood. No populations of *S. dunedinensis* were encountered in my survey area. The analysis of the herbarium records indicate that *S. dunedinensis* is no longer found in most of the areas and elevations that it once was. While the analysis was less clear as to the effects on *S. rufiglandulosus,* the distribution of this species is thought to have retracted from many areas of New Zealand (e.g. J. J. Sullivan, et al., 2008). Future research should include these species and the effects of *J. vulgaris*-enhanced populations on them.

In addition to examining if observed levels of *N. annulata* herbivory are sufficient to limit populations of endemic *Senecio* species, future research should investigate the impact of other native, genus-specific insect herbivores that use *J. vulgaris* and native *Senecio* species (J. J. Sullivan, et al., 2008). Suggested research includes finding out if these herbivores function in mediating apparent competition between *J. vulgaris* and native host species. One example, the native blue stem borer (*Patagoniodes farnaria,* Lepidoptera: Pyralidae), is commonly found feeding in the stems of *J. vulgaris*. While *P. farnaria* does not appear to use *S. wairauensis*, it does use the native species *S. minimus* and *S. hispidulus* (J. J. Sullivan, et al., 2008) and endemic *S. rufiglandulosus* (personal observation). Incidentally, the use of *S. rufiglandulosus* by *P. farnaria* may be one reason why this host is now so much rarer than *S. wairauensis*.

Another research goal could be determination of *S. minimus* traits that make it less attractive to *N. annulata* and allow it to persist in the landscape near *J. vulgaris*. Chemical defense may be one such trait. *S. minimus* is also found in Australasia where it co-occurs with other *Nyctemera* species. Existence in the New Zealand landscape as a non-endemic native may give *S. minimus* an advantage over endemic *Senecio* species in the form of greater evolutionary "experience" in chemically defending itself against other *Senecio* herbivores (including congeneric moth species) and in developing a greater tolerance to feeding. While *S. minimus* was evolving these adaptations in other parts of its geographic range, *N. annulata* was evolving under different conditions with endemic New Zealand *Senecio*. When expanding into new geographic ranges, species like *S. minimus* bring along with them adaptations acquired through their prior history of ecological interactions (Agrawal, 2007; Agrawal & Fishbein, 2006; Agrawal, et al., 2006; M. D. Bowers, 1992; Mauricio & Rausher, 1997; J. Rosenthal & Dirzo, 1997; Strauss & Agrawal, 1999). Some of these adaptations and traits may be responsible for low palatability to *N. annulata* and may have given this host species the ability to persist in areas where *J. vulgaris* is present.

Identification of the shared parasitoids (discussed above) is another area where more research is needed. Determining the relationships between parasitoids that use *N. annulata* and their other moth hosts has been accomplished to a small extent, but there is plenty of work to be done on this area (discussed in Chapter 2). Finding out how parasitoid sharing translates in the landscape - in terms of preference and performance in different hosts - and how this affects *N. annulata* populations would be a valuable next step. It would also be helpful in determining what effects that a *N. annulata* population explosion might have had on native Lepidoptera, several of which are considered rare and/or endangered (B. H. Patrick & Dugdale, 2000).

`

Another recommendation of this research is to once again survey *Nyctemera* populations across New Zealand (and to a greater degree, the North Island) to determine the distribution of the Australian congener, *N. amica*. Preference for the various species of *Senecio* available in New Zealand by *N. amica* is still unknown. Given that *N. amica* is not native to New Zealand it may have a preference for different *Senecio* species that contrasts somewhat with that of *N. annulata*. The resulting dominance of *N. amica* in particular areas may change the *Senecio* community composition in the long term – although it is still unclear how much *Nyctemera* herbivory (at densities that are not elevated by *J. vulgaris*) would actually limit *Senecio* populations. Of similar concern is the extent to which *N. amica* is interbreeding with *N. annulata* (Kay, 1980). This should be considered a conservation issue and one of cultural importance to Māori. Geographic range expansion by *N. amica* and widespread interbreeding may effectively exclude *N. annulata* from large areas or even cause this iconic, endemic moth to go extinct altogether while being replaced by an Australian species. Finally, this phenomenon of apparent competition between *J. vulgaris* and native and endemic *Senecio* and mediated by shared herbivores should be examined at other locations in New Zealand.

6.6 Concluding Remarks

In their review of indirect effects, White et al. (2006) noted that one theoretical outcome from a species invasion is that the invader will interact with native herbivores in a way that causes increased pressure on native hosts. They hypothesized that an invasive weed could provide an insect herbivore with additional food biomass in the landscape and increase the insect's population. The resulting swell in herbivore abundance would almost certainly increase the intensity of the negative impacts to native host species in the presence of the alien plant; however they were unable to find any record of apparent competition between an alien and a native plant species and mediated by a native herbivore. My research shows that apparent competition between an exotic and a native and mediated by a native insect herbivore has occurred as a result of *J. vulgaris* invasion. As White et al. (2006) noted, it is not uncommon for native insect herbivores to expand their host range to use invasive plants and there are numerous documented examples (Agrawal, 2000; Auerbach & Simberloff, 1988; Gratton & Welter, 1999; Grosman, et al., 2005; Holmes, et al., 1987; Keeler & Chew, 2009; Lau & Strauss, 2005; Louda, 2000; Louda, et al., 2005; Mitchell, et al., 2006; J. J. Sullivan, et al., 2008). That being the case, it is likely that indirect, herbivore-mediated effects of invasive weeds on native plants are mistaken for competition and are actually more common than realized. Therefore this issue urgently requires more attention and study.

`

The concern that indirect effects on native plants via native insect herbivores may be influenced by weed invasion is also pertinent to the field of biological control. In the study system that I used for my research, *N. annulata* may be viewed as a “worst case scenario” for biological control. While it readily uses *J. vulgaris* and inflicts measurable damage on this host, it was still unable to control this species’ establishment and spread. As a result of the *J. vulgaris* invasion, *N. annulata* reached high abundances, which appears to have had consequences for native plants and moths. The host range for *N. annulata* includes several native plant species and it shares parasitoids with several moth species – including natives and introduced biological control agents. These outcomes are examples of the risks of biological control that are of primary concern to researchers and the public

In reality, however, *N. annulata* is not a biological control agent, but rather an endemic moth. The impacts described above were not related to its introduction, but rather influenced by weed invasion. One could therefore argue that the end results here, in terms of impacts to native food webs from weed invasions, are not that different from a “worst case scenario” biological control introduction. If indirect effects of weed invasions on native food webs are as common as my research suggests), it is incongruous that researchers and the public should place so much attention on the risks of biological control but give comparatively little attention to the impacts of invasive weeds on native food webs. The implications for biological control risk assessment are that the all of the impacts from invasive weed in the landscape need to be considered in the calculation of whether to undertake importation and release of biological control agents. This decision should include assessing influence on resident species and native food webs by the invader through indirect effects and acknowledging the damage caused in the absence of control measures.

`

References

Abbott, K. L., & Green, P. T. (2007). Collapse of an ant-scale mutualism in a rainforest on Christmas Island. *Okios, 116*, 1238-1246.

Abrahamson, W. G., Eubanks, M. D., Blair, C. P., & Whipple, A. V. (2001). Gall Flies, Inquilines, and Goldenrods: A Model for Host-race Formation and Sympatric Speciation. *Amer. Zool., 41*(4), 928-938. doi: 10.1093/icb/41.4.928

Adair, R. J., & Bruzzese, A. (2000). Evaluation and host specificity of two seed flies Mesoclanis polana and M. magnipalpis (Diptera: Tephritidae): biological control agents for Chrysanthemoides monilifera (Asteraceae) in Australia. *Bulletin of Entomological Research, 90*(06), 467-474. doi: doi:10.1017/S0007485300000596

Adams, M. J., Pearl, C. J., & Bury, R. B. (2003). Indirect facilitation of an anuran invasion by non-native fishes. *Ecology Letters, 6*, 343-351.

Adler, L. S., Karban, R., & Strauss, S. Y. (2001). Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. *Ecology, 82*(7), 2032-2044.

Agosta, S. J. (2006). On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. *Oikos, 114*(3), 556-565.

Agrawal, A. A. (2000). Host-range evolution: adaptation and trade-offs in fitness of mites on alternative hosts. *Ecology, 81*(2), 500-508.

Agrawal, A. A. (2007). Macroevolution of plant defense strategies. *Trends in Ecology & Evolution, 22*(2), 103-109. doi: DOI: 10.1016/j.tree.2006.10.012

Agrawal, A. A., & Fishbein, M. (2006). Plant defense syndromes. *Ecology, 87*(sp7), 132-149. doi: doi:10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2

Agrawal, A. A., & Kotanen, P. M. (2003). Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters, 6*(8), 712-715. doi: 10.1046/j.1461-0248.2003.00498.x

Agrawal, A. A., Kotanen, P. M., Mitchell, C. E., Alison, G. P., Godsoe, W., & Klironomos, J. (2005). Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology, 86*(11), 2979-2989.

Agrawal, A. A., Lau, J. A., & Hamback, P. A. (2006). Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review Of Biology, 81*(4), 349-376. doi: citeulike-article-id:7847483

Ahmed, M., & Wardle, D. (1994). Allelopathic potential of vegetative and flowering ragwort (Senecio jacobaea L.) plants against associated pasture species. *Plant and Soil, 164*(1), 61-68.

Aizen, M. A., Morales, C. L., & Morales, J. M. (2008). Invasive Mutualists Erode Native Pollination Webs. *PLoS Biol, 6*(2), e31.

Allen, R. B., and W. G. Lee (eds.). (2006). *Biological Invasions in New Zealand*. Heidelberg, Germany: Springer.

Alleyne, M., & Wiedenmann, R. N. (2002). Effect of time in culture on the suitability of two novel-association pyralid hosts for Cotesia sesamiae (Hymenoptera: Braconidae) development. *Biological Control, 25*(2), 116-122.

Allison, S. D., & Vitousek, P. M. (2004). Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia, 141*(4), 612-619. doi: 10.1007/s00442-004-1679-z

Allmann, S., & Baldwin, I. T. (2010). Insects Betray Themselves in Nature to Predators by Rapid Isomerization of Green Leaf Volatiles. *Science, 329*(5995), 1075-1078. doi: 10.1126/science.1191634

Altieri, A. H., van Wesenbeeck, B. K., Bertness, M. D., & Silliman, B. R. (2010). Facilitation cascade drives positive relationship between native biodiversity and invasion success. *Ecology, 91*(5), 1269-1275.

Amor, R. L., Lane, D. W., & Jackson, K. W. (1983). Observations on the influence of grazing by sheep or cattle on the density and cover of ragwort. *Australian Weeds, 2*, 94-95.

Anonymous. (1889a, April 16). untitled, *Timaru Herald*.

Anonymous. (1889b, March 1). The Winton Stock Disease, *Southland Times,* p. 2.

Anonymous. (1891, January 17). untitled, *Otago Daily Times,* p. 2.

Anonymous. (1899, February 4). untitled, *Taranaki Herald,* p. 2.

Anonymous. (1902a, March 12). By Telegraph, *Evening Post,* p. 6.

Anonymous. (1902b, March 8). untitled, *Evening Post,* p. 4.

Anonymous. (1902c, March 7). untitled, *Wanganui Herald,* p. 2.

Anonymous. (1904, April 3). Disasterous effects of ragwort, *Bay of Plenty Times,* p. 2.

Anonymous. (1910, March 11). Local and General, *Hawera & Normandy Star,* p. 4.

Anonymous. (1929, August 1). Ragwort Control, *Evening Post,* p. 19.

Arim, M. a., Abades, S. n. R., Neill, P. E., Lima, M., & Marquet, P. A. (2006). Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences of the United States of America, 103*(2), 374-378. doi: 10.1073/pnas.0504272102

Aron, S. (2001). Reproductive strategy: an essential component in the success of incipient colonies of the invasive Argentine ant. *Insectes Sociaux, 48*(1), 25-27. doi: 10.1007/pl00001740

Ashton, I. W., & Lerdau, M. T. (2008). Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American

`

temperate vines. *Diversity and Distributions, 14*(2), 169-178. doi: 10.1111/j.1472-4642.2007.00425.x

Auerbach, M., & Simberloff, D. (1988). Rapid leaf-miner colonization of introduced trees and shifts in sources of herbivore mortality. *Oikos, 52*, 41-50.

Augustine, D. J., & McNaughton, S. J. (1998). Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. *The Journal of Wildlife Management, 62*(4), 1165-1183.

Bach, C. E. (1991). Direct and indirect interactions between ants (Pheidole megacephala), scales (Coccus viridis) and plants (Pluchea indica). *Oecologia, 87*(2), 233-239.

Badano, E. I., Cavieres, L. A., Molina-Montenegro, M. A., & Quiroz, C. L. (2005). Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile. *Journal of Arid Environments, 62*(1), 93-108.

Barrat-Segretain, M. H. (1996). Strategies of reproduction, dispersion, and competition in river plants: A review. *Plant Ecology, 123*(1), 13-37. doi: 10.1007/bf00044885

Barrett, S. C. H., Colautti, R. I., & Eckert, C. G. (2008). Plant reproductive systems and evolution during biological invasion. *Molecular Ecology, 17*(1), 373-383. doi: 10.1111/j.1365-294X.2007.03503.x

Barringer, J. R. F., McNeill, S., & Pairman, D. (2002). *Progress on assessing the accuracy of a high resolution digital elevation model for New Zealand.* Paper presented at the The 5th International Symposium on Spatial Accuracy Assessment in Natural Resources and Environmental Data, Melbourne.

Bathgate, A. (1870). On the Lepidoptera of Otago. *Transactions of the Royal Society of New Zealand, 3*, 137-141.

Bathgate, A. (1922). Some changes in the fauna and flora of Otago in the last sixty years. *New Zealand Journal of Science and Technology, 4*, 273-283.

Becerra, J. X., & Venable, D. L. (1999). Macroevolution of insect–plant associations: The relevance of host biogeography to host affiliation. *Proceedings of the National Academy of Sciences of the United States of America, 96*(22), 12626-12631.

Beggs, J. (2001). The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biological Conservation, 99*(1), 17-28.

Benn, M., DeGrave, J., Gnanasunderam, C., & Hutchins, R. (1978). Host-plant pyrrolizidine alkaloids in *Nyctemera annulata* Boisduval: Their persistence through the life-cycle and transfer to a parasite. *Experientia, 35*(6), 731-732.

Benvenuti, S. (2007). Weed seed movement and dispersal strategies in the agricultural environment. *Weed Biology and Management, 7*(3), 141-157. doi: 10.1111/j.1445-6664.2007.00249.x

Bernays, E. A., & Chapman, R. F. (1994). *Host Plant Selection by Phytophagous Insects*. New York: Chapman & Hall.

Bicchi, C., Rubiolo, P., Frattini, C., Sandra, P., & David, F. (1991). Off-line Supercritical Fluid Extraction and Capillary Gas Chromatography of Pyrrolizidine Alkaloids in Senecio Species. *Journal of Natural Products, 54*(4), 941-945. doi: 10.1021/np50076a003

Bird, M. (1977). Ragwort control, Biological approach. *New Zealand Journal of Agriculture, 135*(21).

Bjorkman, C., Larsson, s., & Bommarco, R. (1997). Oviposition preference in pine sawflies: a tade-off between larval growth and defence against natural enemies. *Oikos, 79*, 45-52.

Blais, J. M., & Maly, E. J. (1993). Differential predation by Chaoborus americanus on males and females of two species of diaptomus. *Canadian Journal of Fisheries and Aquatic Sciences, 50,* 410-415.

Bohlen, P. J., Groffman, P. M., Fahey, T. J., Fisk, M. C., Suarez, E., Pelletier, D. M., et al. (2004). Ecosystem Consequences of Exotic Earthworm Invasion of North Temperate Forests. *Ecosystems, 7*(1), 1-12. doi: 10.1007/s10021-003-0126-z

Bohlmann, F., Zdero, C., Jakupovic, J., Grenz, M., Castro, V., Kino, R. M., et al. (1986). Further pyrrolizidine alkaloids and furoeremophilanes from Senecio species. *Phytochemistry, 25*(5), 1151-1159. doi: 10.1016/s0031-9422(00)81571-x

Bonsall, M. B., Bull, J. C., Pickup, N. J., & Hassell, M. P. (2005). Indirect effects and spatial scaling affect the persistence of multispecies metapopulations. *Proceedings of the Royal Society of London Series B, Biological Sciences, 272*(1571), 1465-1471.

Bonsall, M. B., & Hassell, M. P. (1997). Apparent competition structures ecological assemblages. *Nature London, 388*(6640), 371-373.

Bonsall, M. B., & Hassell, M. P. (1998). Population dynamics of apparent competition in a host-parasitoid assemblage. *Journal of Animal Ecology, 67*(6), 918-929.

Bonsall, M. B., & Hassell, M. P. (1999). Parasitoid-mediated effects: apparent competition and the persistence of host-parasitoid assemblages. *Researches on Population Ecology, 41*(1), 59-68.

Bourgeois, K., Suehs, C. M., Vidal, E., & Médail, F. (2005). Invasional meltdown potential: facilitation between introduced plants and mammals on French Mediterranean islands. *Ecoscience, 12*(2), 248-256.

`

Bowers, M. D. (1992). The evolution of unpalatability and the coast of checmical defense in insects. In B. D. Roitberg & M. B. Isman (Eds.), *Insect chemical ecology: an evolutionary approach* (pp. 216-243): Springer.

Bowers, M. D., Stamp, N. E., & Collinge, S. K. (1992). Early stage of host range expansion by a specialist herbivore, *Euphydryas phaeton* (Nymphalidae). *Ecology, 72*(3), 526-536.

Bradford, J. B., & Lauenroth, W. K. (2006). Controls over invasion of Bromus tectorum: The importance of climate, soil, disturbance and seed availability. *Journal of Vegetation Science, 17*(6), 693-704. doi: 10.1111/j.1654-1103.2006.tb02493.x

Brazner, J., Aberdeen, V., & Starmer, W. T. (1984). Host-plant shifts and adult survival in the cactus breeding Drosophila mojavensis. *Ecological Entomology, 9*(4), 375-381.

Brooking, T. (2004). *The History of New Zealand*: Greenwood Press.

Brooks, D. R., León-Règagnon, V., McLennan, D. A., & Zelmer, D. (2006). Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology, 87*(sp7), 76-85. doi: doi:10.1890/0012-9658(2006)87[76:EFAADO]2.0.CO;2

Brooks, D. R., & McLennan, D. A. (2002). *The nature of diversity: an evolutionary voyage of discovery*: University of Chicago Press.

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., et al. (2004). Effects of Invasive Alien Plants on Fire Regimes. *BioScience, 54*(7), 677-688. doi: doi:10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Brose, U., & Tielborger, K. (2005). Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. *Plant Ecology, 178*(1), 51-59.

Brown, B. J., Mitchell, R. J., & Graham, S. A. (2002). Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology, 83*(8), 2328-2336. doi: doi:10.1890/0012-9658(2002)083[2328:CFPBAI]2.0.CO;2

Brown, J. M., Abrahamson, W. G., Packer, R. A., & Way, P. A. (1995). The role of natural-enemy escape in a gallmaker host-plant shift. *Oecologia, 104*(1), 52-60.

Bruinsma, M., Posthumus, M. A., Mumm, R., Mueller, M. J., van Loon, J. J. A., & Dicke, M. (2009). Jasmonic acid-induced volatiles of *Brassica oleracea* attract parasitoids: effects of time and dose, and comparison with induction by herbivores. *Journal of Experimental Botany, 60*(9), 2575-2587. doi: 10.1093/jxb/erp101

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution, 18*(3), 119-125.

`

Buckingham, G. R. (1996). Biological Control of Alligatorweed, Alternanthera philoxeroides, the World's First Aquatic Weed Success Story. *Castanea, 61*(3), 232-243.

Buller, P. (1881). Notes on some species of diurnal moths. In J. Hector (Ed.), *Transactions of the New Zealand Institute 1880.* (pp. 237-239). Wellington.

Bunn, S. E., Davies, P. M., Kellaway, D. M., & Prosser, I. P. (1998). Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology, 39*(1), 171-178. doi: 10.1046/j.1365-2427.1998.00264.x

Byers, J. (2002). Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia, 130*(1), 146-156. doi: 10.1007/s004420100777

Caccia, F. D., Chaneton, E. J., & Kitzberger, T. (2006). Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos, 113*(3), 469-480.

Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences, 105*(17012-17017).

Cahill Jr, J. F., Kembel, S. W., Lamb, E. G., & Keddy, P. A. (2008). Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics, 10*(1), 41-50. doi: 10.1016/j.ppees.2007.10.001

Calder, I., & Dye, P. (2001). Hydrological impacts of invasive alien plants. *Land Use and Water Resources Research, 1*(7), 1-8.

Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology, 78*(7), 1958-1965. doi: doi:10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Cameron, E. (1935). A study of the natural control of ragwort (*Senecio jacobaea* L.). *Journal of Ecology, 23*(2), 265-322.

Caño, L., Escarré, J., Vrieling, K., & Sans, F. (2009). Palatability to a generalist herbivore, defence and growth of invasive and native <i>Senecio</i> species: testing the evolution of increased competitive ability hypothesis. *Oecologia, 159*(1), 95-106. doi: 10.1007/s00442-008-1182-z

Caraco, N. F., Cole, J. J., Raymond, P. A., Strayer, D. L., Pace, M. L., Findlay, S. E. G., et al. (1997). Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology, 78*(2), 588-602. doi: doi:10.1890/0012-9658(1997)078[0588:ZMIIAL]2.0.CO;2

Carlsson, N. O. L., Brönmark, C., & Hansson, L.-A. (2004). Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology, 85*(6), 1575-1580. doi: doi:10.1890/03-3146

Carlton, J. T. (1996). Pattern, process, and prediction in marine invasion ecology. *Biological Conservation, 78*(1-2), 97-106. doi: Doi: 10.1016/0006-3207(96)00020-1

Caro, A., Combes, C., & Euzet, L. (1997). What makes a fish a suitable host for Monogenea in the Mediterranean? *Journal of Helminthology, 71*, 203-210.

Carvalheiro, L. G., Buckley, Y. M., Ventim, R., Fowler, S. V., & Memmott, J. (2008). Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecology Letters, 11*(7), 690-700. doi: 10.1111/j.1461-0248.2008.01184.x

Case, T. J. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the United States of America, 87*(24), 9610-9614.

Castro, S. A., Figueroa, J. A., Muñoz-Schick, M., & Jaksic, F. M. (2005). Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. *Diversity and Distributions, 11*(3), 183-191. doi: 10.1111/j.1366-9516.2005.00145.x

Chandramohan, S., & Charudattan, R. (2001). Control of Seven Grasses with a Mixture of Three Fungal Pathogens with Restricted Host Ranges. *Biological Control, 22*(3), 246-255. doi: DOI: 10.1006/bcon.2001.0974

Chaneton, E. J., & Bonsall, M. B. (2000). Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos, 88*(2), 380-394.

Cheeke, P. R. (1988). Toxicity and metabolism of pyrrolizidine alkaloids. *Journal of Animal Science, 66*, 2343-2350.

Cheeke, P. R. (1989). Pyrrolizidine alkaloid toxicity and metabolism in laboratory animals and livestock. In P. R. Cheeke (Ed.), *Toxicants of Plant Origin* (Vol. 1, pp. 1-22). Boca Raton, Florida: CRC Press.

Chesson, J. (1983). Estimation and analysis of preference and its relationship to foraging models. *Ecology, 64*(5), 1297-1304.

Christian, C. E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature, 413*, 635-639.

Clay, K., & Kover, P. X. (1996). The Red Queen Hypothesis and plant/pathogen interactions. *Annual Review of Phytopathology, 34*(1), 29-50.

`

Clement, S. L., Smith, L. J., Prena, J., Kleene, M. D., & Johnson, R. C. (2009). Non-target plant use by a weed biocontrol agent in idaho: host expansion or opportunistic behavior? *Biocontrol Science and Technology, 19*, 455-461.

Colautti, R., Grigorovich, I., & MacIsaac, H. (2006). Propagule Pressure: A Null Model for Biological Invasions. *Biological Invasions, 8*(5), 1023-1037. doi: 10.1007/s10530-005-3735-y

Connell, J. H. (1990). Apparent versus "real" competition in plants. *Perspectives on plant competition*.

Connor, E. F., Faeth, S. H., Simberloff, D., & Opler, P. A. (1980). Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology, 5*(205-211).

Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology, 85*(5), 1273-1283. doi: doi:10.1890/02-0744

Council, N. R. (2002). *Predicting invasions of nonindigenous plants and pests*. Washington, D.C.: National Academy Press.

Cowan, C. (1889, 7 March 1889). The Winton Stock Disease, *Otago Witness*.

Crawley, M. J., & Gillman, M. P. (1989). Population dynamics of cinnabar moth and ragwort in grassland. *Journal of Animal Ecology, 58*, 1035-1050.

Cronin, J. T., & Reeve, J. D. (2005). Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences, 272*(1578), 2225-2235. doi: 10.1098/rspb.2005.3286

Crowl, T. A., Crist, T. O., Parmenter, R. R., Belovsky, G., & Lugo, A. E. (2008). The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment, 6*(5), 238-246. doi: doi:10.1890/070151

Cuda, J. P., Parker, P. E., Coon, B. R., Vasquez, F. E., & Harrison, J. M. (2002). Evaluation of exotic Solanum spp. (Solnanales: Solanaceae) in Florida as host plants for the leaf beetles Leptinotarsa defecta and L. texana (Coleoptera: Chrysomelidae). *Florida Entomologist, 85*, 599-610.

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics, 23*, 63-87.

Dangremond, E. M., Pardini, E. A., & Knight, T. M. (2010). Apparent competition with an invasive plant hastens the extinction of an endangered lupine. *Ecology, 91*(8), 2261-2271. doi: doi:10.1890/09-0418.1

`

Darwin, C. E. (1859). *On the Origin of Species*: Oxford University Press.

Dawson, W., Burslem, D. F. R. P., & Hulme, P. E. (2009). Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions, 15*(1), 141-147. doi: 10.1111/j.1472-4642.2008.00527.x

de Boer, J., Hordijk, C., Posthumus, M., & Dicke, M. (2008). Prey and Non-prey Arthropods Sharing a Host Plant: Effects on Induced Volatile Emission and Predator Attraction. *Journal of Chemical Ecology, 34*(3), 281-290. doi: 10.1007/s10886-007-9405-z

de Lange, P. J., Norton, D. A., Courtney, S. P., Heenan, P. B., Barkla, J. W., Cameron, E. K., et al. (2009). Threatened and uncommon plants of New Zealand (2008 revision). *New Zealand Journal of Botany, 47,* 61-96.

Décamps, H., Planty-Tabacchi, A. M., & Tabacchi, E. (1995). Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. *Regulated Rivers: Research & Management, 11*(1), 23-33. doi: 10.1002/rrr.3450110104

del-Val, E., & Crawley, M. J. (2004). Importance of tolerance to herbivory for plant survival in a British grassland. *Journal of Vegetation Science, 15*(3), 357-364. doi: 10.1111/j.1654-1103.2004.tb02272.x

Denno, R. F., M. S. McClure and J. R. Ott. (1995). Interspecific interactions in phytophagous insects: competition rexamined and resurrected. *Annual Review of Entomology, 40,* 297-331.

Devin, S., & Beisel, J.-N. (2007). Biological and ecological characteristics of invasive species: a gammarid study. *Biological Invasions, 9*(1), 13-24. doi: 10.1007/s10530-006-9001-0

Dickie, I. A., Koide, R. T., & Steiner, K. C. (2002). Influences of established trees on mycorrhizas, nutrition, and growth of Quercus rubra seedlings. *Ecological Monographs, 72*(4), 505-521.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution, 22*(9), 489-496. doi: DOI: 10.1016/j.tree.2007.07.001

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution, 20*(9), 470-474. doi: DOI: 10.1016/j.tree.2005.07.006

Diez, J. M., Williams, P. A., Randall, R. P., Sullivan, J. J., Hulme, P. E., & Duncan, R. P. (2009). Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters, 12*(11), 1174-1183. doi: 10.1111/j.1461-0248.2009.01376.x

Dostál, P., & Palečková, M. (2010). Does relatedness of natives used for soil conditioning influence plant-soil feedback of exotics? *Biological Invasions*, 1-10. doi: 10.1007/s10530-010-9824-6

Drake, J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M., et al. (Eds.). (1989). *Biological Invasions: A Global Perspective*. New York: John Wiley & Sons.

Drummond, J. (1908, August 1, 1908). Bird and Insect Notes, *Evening Post*, p. 13.

Dugdale, J. S. (1971). Entomology of the Aucklands and other islands south of New Zealand: Lepidoptera, excluding non-crambine Pyralidae. *Pacific Insects Monograph, 27*, 55-172.

Edwards, P. B., & Brown, E. M. (1997). *Mesoclanis* seed flies (Diptera: Tephritidae) on *Chrysanthemoides* (Asteraceae) in South Africa: distribution, attack strategy and impact on seed production. *Bulletin of Entomological Research, 87*(02), 127-135. doi: doi:10.1017/S0007485300027267

Ehrenfeld, J. G. (2003). Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems, 6*(6), 503-523. doi: 10.1007/s10021-002-0151-3

ERMA. (2005a). *APPLICATION: Importation and release of two moths, Cochylis atricapitana and Platyptilia isodactyla, for the biological control of the pasture weed ragwort.* Wellington: Retrieved from http://www.epa.govt.nz/Documents/NOR05002-application.pdf.

ERMA. (2005b). *DECISION: Importation and release of two moths, Cochylis atricapitana and Platyptilia isodactyla, for the biological control of the pasture weed ragwort.* (NOR05002). Wellington: Retrieved from http://www.epa.govt.nz/Documents/NOR05002-decision.pdf.

Feder, J. L., Reynolds, K., Go, W., & Wang, E. C. (1995). Intra- and interspecific competition and host race formation in the apple maggot fly, Rhagoletis pomonella (Diptera: Tephritidae). *Oecologia, 101*(4), 416-425.

Fereday, R. W. (1872). Observations on a paper read by Mr. A. Bathgate before the Otago Institute, 11th January 1870, "On the Lepidoptera of Otago". *Transactions of the New Zealand Institute, 4*, 214-218.

Finn, J. A., & Gittings, T. (2003). A review of competition in north temperate dung beetle communities. *Ecological Entomology, 28*(1), 1-13.

Flores, J. L., & Yeaton, R. I. (2000). La impotancia de la competencia en la organizacion de las comunidades vegetales en el altiplano Mexicano.; The role of competition in plant community organization in the Mexican highlands. *Interciencia, 25*(8), 365-371.

Fogarty, G., & Facelli, J. (1999). Growth and competition of Cytisus scoparius, an invasive shrub, and Australian native shrubs. *Plant Ecology, 144*(1), 27-35. doi: 10.1023/a:1009808116068

Forbes, A. A., Fisher, J., & Feder, J. L. (2005). Habitat avoidance: overlooking an important aspect of host-specific mating and sympatric speciation? *Evolution, 59*(7), 1552-1559.

Force, D. C. (1985). Competition among parasitoids of endophytic hosts. *American Naturalist, 126*(3), 440-444.

Ford, C. R., & Vose, J. M. (2007). *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in Southern Appalachian forest ecosystems. *Ecological Applications, 17*(4), 1156-1167. doi: doi:10.1890/06-0027

Forstmeier, W., Bourski, O. V., & Leisler, B. (2001). Habitat choice in Phylloscopus warblers: the role of morphology, phylogeny and competition. *Oecologia, 128*(4), 566-576.

Forsyth, A. A. (1954). British Poisonous Plants.: Ministry of Agriculture and Fisheries.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology, 86*(5), 1320-1330. doi: doi:10.1890/04-0953

Fowler, S. V. (2009).

Fowler, S. V., Syrett, P., & Hill, R. L. (2000). Success and saftey in the biological control of environmental weeds. *Austral Ecology, 25*, 553-562.

Fox, L. R., & Eisenbach, J. (1992). Contrary choices: possible exploitation of enemy-free space by herbivorous insects in cultivated vs. wild crucifers. *Oecologia, 89*(4), 574-579. doi: 10.1007/bf00317166

Fraser, D. F., & Gilliam, J. F. (1992). Nonleathal impacts of predator invasion: facultative suppression of growth and resproduction. *Ecology, 73*(3), 959-970.

Fraser, S. M., & Lawton, J. H. (1994). Host range expansion by British moths onto introduced conifers. *Ecological Entomology, 19*(2), 127-137. doi: 10.1111/j.1365-2311.1994.tb00402.x

Freiberg, C., Fellay, R., Bairoch, A., Broughton, W. J., Rosenthal, A., & Perret, X. (1997). Molecular basis of symbiosis between Rhizobium and legumes. [10.1038/387394a0]. *Nature, 387*(6631), 394-401.

Frere, I., Fabry, J., & Hance, T. (2007). Apparent competition or apparent mutualism? An analysis of the influence of rose bush strip management on aphid population in wheat field. *Journal of Applied Entomology, 131*(4), 275-283.

Fricke, C., & Arnqvist, G. (2007). Rapid adaptation to a novel host in a seed beetle (*Callosobruchus maculatus*): the role of sexual selection. *Evolution, 61*(2), 440-454.

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., et al. (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology, 88*, 3-17.

Fuller, T. C., & McClintock, E. (1986). *Poisonous plants of California*. Berkeley, CA (USA): University of California Press.

Futuyma, D. J., & Mitter, C. (1997). Insect-plant interactions: the evolution of component communities. In J. Silvertown, M. Franco & J. L. Harper (Eds.), *Plant life histories - ecology, phylogeny and evolution* (pp. 253-264). Cambridge, UK: Cambridge University Press.

Gaskin, D. E. (1966). *The Butterflies and Common Moths of New Zealand.* Auckland: Whitcombe & Tombs Ltd.

Gassmann, A. J., Levy, A., Tran, T., & Futuyma, D. J. (2006). Adaptations of an insect to a novel host plant: a phylogenetic approach. *Functional Ecology, 20*(3), 478-485.

Gatehouse, H. A. W. (2008). *Ecology of the naturalisation and geographic distribution of the non-indigenous seed plant species of New Zealand.* Ph.D., Lincoln University, Lincoln, New Zealand.

Gause, G. F. (1934). *The Struggle for Existence*. Baltimore: Williams & Wilkins.

Gera Hol, W. H., Macel, M., van Veen, J. A., & van der Meijden, E. (2004). Root damage and aboveground herbivory change concentration and composition of pyrrolizidine alkaloids of Senecio jacobaea. *Basic and Applied Ecology, 5*(3), 253-260. doi: DOI: 10.1016/j.baae.2003.12.002

Gherardi, F., & Daniels, W. H. (2004). Agonism and shelter competition between invasive and indigenous crayfish species. *Cananadian Journal of Zoology, 82*(12), 1923-1932.

Gibb, H., & Hochuli, D. F. (2003). Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. *Oikos, 103*(3), 469-478. doi: 10.1034/j.1600-0706.2003.12652.x

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences, 104*(12), 4979-4983. doi: 10.1073/pnas.0607968104

Gilbert, L., Norman, R., Laurenson, K. M., Reid, H. W., & Hudson, P. J. (2001). Disease persistence and apparent competition in a three-host community: an empirical and analytical study of large-scale, wild populations. *Journal of Animal Ecology, 70*(6), 1053-1061.

Gill, B. J. (1980). Foods of the shining cuckoo (Chrysococcyx lucidus, Aves: Cuculidae) in New Zealand. *New Zealand Journal of Ecology, 3*(138-140).

Gilruth, J. A. (1904, 27 January 1904). The toxic effects of ragwort, *Star,* p. 4.

Giovanelli, A., Vieira, M. V., & Silva, C. L. P. A. C. d. (2003). Apparent competition through facilitation between Melanoides tuberculata and Biomphalaria glabrata and the control of schistosomiasis. *Memorias do Instituto Oswaldo Cruz, 98*(3), 429-431.

Gourlay, A. H., Fowler, S. V., & Rattray, G. (2008). Abundance of Ragwort Flea Beetle (*Longitarsus jacobaeae*) at Five Sites on the West Coast, South Island, New Zealand. Lincoln, NZ: Landcare Research.

Grapes, G. T. (1896). New Zealand magpie moth - *Nyctemera annulata*. *New Zealand Farmer, 16*, 160.

Gratton, C., & Welter, S. C. (1999). Does "enemy-free space" exist? Experimental host shifts of an herbivorous fly. *Ecology, 80*(3), 773-785.

Graves, S. D., & Shapiro, A. M. (2003). Exotics as host plants of the California butterfly fauna. *Biological Conservation, 110*, 413-433.

Greenman, J. V., & Hudson, P. J. (2000). Parasite-mediated and direct competition in a two-host shared macroparasite system. *Theoretical Population Biology, 57*(1), 13-34.

Groner, E., & Ayal, Y. (2001). The interaction between bird predation and plant cover in determining habitat occupancy of darkling beetles. *Oikos, 93*(1), 22-31.

Grosholz, E. (2002). Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology & Evolution, 17*(1), 22-27. doi: Doi: 10.1016/s0169-5347(01)02358-8

Grosholz, E. D. (2005). Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the United States of America, 102*(4), 1088-1091. doi: 10.1073/pnas.0308547102

Grosman, A. H., Breemen, M. v., Holtz, A., Pallini, A., Rugama, A. M., Pengel, H., et al. (2005). Searching behaviour of an omnivorous predator for novel and native host plants of its herbivores: a study on arthropod colonization of eucalyptus in Brazil. *Entomologia Experimentalis et Applicata, 116*(2), 135-142.

Gross, M. R. (1984). Sunfish, Salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In R. Wootton & G. Potts (Eds.), *Fish reporduction: Strategies and Tactics* (pp. 55-75). London: Academic Press.

Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution, 19*(9), 470-474. doi: DOI: 10.1016/j.tree.2004.07.005

Hamback, P. A., & Bjorkman, C. (2002). Estimating the consequences of apparent competition: a method for host-parasitoid interactions. *Ecology, 83*(6), 1591-1596.

Hanks, L. M., Millar, J. G., & Paine, T. D. (1995). Biological Constraints on Host-Range Expansion by the Wood-Boring Beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America, 88,* 183-188.

Hanley, M. E., Fenner, M., & Edwards, P. J. (1995). An Experimental Field Study of the Effects of Mollusc Grazing on Seedling Recruitment and Survival in Grassland. *Journal of Ecology, 83*(4), 621-627.

Harman, H. M., & Syrett, P. (1989). Establishment and seasonality of two ragwort feeding insects at Hanmer, New Zealand. *Proceedings of the 42nd New Zealand Weed Pest Control Conference*, 48-51.

Harman, H. M., Syrett, P., Hill, R. L., & Jessep, C. T. (1996). Arthropod introductions for biological control of weeds in New Zealand, 1929 - 1995 *New Zealand Entomologist, 19*, 71-80.

Harrison, S., & Thomas, C. D. (1991). Patchiness and Spatial Pattern in the Insect Community on Ragwort *Senecio jacobaea*. *Oikos, 62*(1), 5-12.

Hartmann, T., & Toppel, G. (1987). Senecionine n-oxide, the primary product of pyrrolizidine alkaloid biosynthesis in root cultures of Senecio vulgaris. *Phytochemistry, 26*(6), 1639-1643. doi: Doi: 10.1016/s0031-9422(00)82261-x

Hatcher, M. J., Dick, J. T. A., & Dunn, A. M. (2006). How parasites affect interactions between competitors and predators. *Ecology Letters, 9*(11), 1253-1271.

Hawkes, C. V., Wren, I. F., Herman, D. J., & Firestone, M. K. (2005). Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters, 8*(9), 976-985. doi: 10.1111/j.1461-0248.2005.00802.x

Hayes, K., & Barry, S. (2008). Are there any consistent predictors of invasion success? *Biological Invasions, 10*(4), 483-506. doi: 10.1007/s10530-007-9146-5

Helson, G. A. H. (1974). Beneficial insects. Cinnabar moth and ragwort seed fly. *New Zealand Journal of Agriculture, 128,* 56-59.

Herron, P. M., Martine, C. T., Latimer, A. M., & Leicht-Young, S. A. (2007). Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Diversity and Distributions, 13*(5), 633-644. doi: 10.1111/j.1472-4642.2007.00381.x

`

Hilgendorf, F. W. (1926). *Weeds of New Zealand and how to eradicate them.* Christchurch: Whitcombe & Tombs.

Hill, S., & Kotanen, P. (2009). Evidence that phylogenetically novel non-indigenous plants experience less herbivory. *Oecologia, 161*(3), 581-590.

Hobbie, S. E. (1992). Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution, 7*(10), 336-339. doi: Doi: 10.1016/0169-5347(92)90126-v

Holloway, B. A. (1983). Species of ragwort seedflies imported into New Zealand (Diptera: Anthomyiidae). *New Zealand Journal of Agricultural Research, 26*, 245-249.

Holmes, P. M., Dennill, G. B., & Moll, E. J. (1987). Effects of feeding by native alydid insects on the seed viability of an alien invasive weed, Acacia cyclops. *South African Journal of Science, 83*(10), 580-581.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. [Journal Article]. *Theoretical Population Biology, 12*, 197-229.

Holt, R. D., & Lawton, J. H. (1993). Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist, 142*(4), 623-645.

Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., & Case, T. J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology & Systematics, 33*, 181-233.

Holway, D. A., & Suarez, A. V. (1999). Animal behavior: an essential component of invasion biology. *Trends in Ecology and Evolution, 14*, 328-330. doi: 10.1016/s0169-5347(99)01636-5

Hopper, K. R., & Roush, R. T. (1993). Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology, 18*(4), 321-331. doi: 10.1111/j.1365-2311.1993.tb01108.x

Horton, D. R., Capinera, J. L., & Chapman, P. L. (1988). Local Differences in Host Use by Two Populations of the Colorado Potato Beetle. *Ecology, 69*(3), 823-831.

Howell, C., & Sawyer, J. W. D. (2006). New Zealand Naturalised vascular plant checklist (pp. 60). Wellington: New Zealand Plant Conservation Network.

Howell, E. (1903, 20 April 1903). That ragwort, *Bay of Plenty Times*, p. 2.

Hudson, G. V. (1898). *New Zealand Moths and Butterflies (Macrolepidoptera).* London: West, Newman & Co .

Human, K. G., & Gordon, D. M. (1996). Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia, 105*(3), 405-412. doi: 10.1007/bf00328744

Institute, E. S. R. (2009). ArcGIS. Redlands, California.

`

Islam, Z., & Crawley, M. J. (1983). Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by cinnabar moth (*Tyria jacobaeae*). *Journal of Ecology, 71*, 829-843.

Jacques, R. (1988). *The potato beetles: the genus Leptinotarsa in North America (Coleoptera, Chrysomelidae)*: E.J. Brill.

Jaenike, J. (1990). Host specialization in phytophagous insects. *Annual Review of Ecological Systematics, 21*, 243-273.

Janssen, A., Pallini, A., Venzon, M., & Sabelis, M. W. (1998). Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. *Experimental and Applied Acarology, 22*(9), 497-521.

Janzen, D. H. (1985). On ecological fitting. *Oikos, 45*, 308-310.

Jiu, M., Zhou, X.-P., Tong, L., Xu, J., Yang, X., Wan, F.-H., et al. (2007). Vector-Virus Mutualism Accelerates Population Increase of an Invasive Whitefly. *PLoS ONE, 2*(1), e182.

Jogesh, T., Carpenter, D., & Cappuccino, N. (2008). Herbivory on invasive exotic plants and their non-invasive relatives. *Biological Invasions, 10*(6), 797-804.

Jones, T. H., Hassell, M. P., & Godfray, H. C. J. (1997). Host-multiparasitoid interactions. *Multitrophic interactions in terrestrial systems: the 36th symposium of the British Ecological Society, Royal Holloway College, University of London, 1995*.

Joosten, L., Mulder, P. P. J., Klinkhamer, P. G. L., & van Veen, J. A. (2009). Soil-borne microorganisms and soil-type affect pyrrolizidine alkaloids in *Jacobaea vulgaris*. *Plant Soil, 325*, 133-143.

Joshi, J., & Vrieling, K. (2005). The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters, 8*(7), 704-714. doi: 10.1111/j.1461-0248.2005.00769.x

Juliano, S. A. (1998). Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology, 79*(1), 255-268.

Juliano, S. A., & Lounibos, L. P. (2005). Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecology Letters, 8*(5), 558-574.

Kappers, I., Verstappen, F., Luckerhoff, L., Bouwmeester, H., & Dicke, M. (2010). Genetic Variation in Jasmonic Acid- and Spider Mite-Induced Plant Volatile Emission of Cucumber Accessions and Attraction of the Predator *Phytoseiulus persimilis*. *Journal of Chemical Ecology, 36*(5), 500-512. doi: 10.1007/s10886-010-9782-6

Kay, M. (1980). *Nyctemera amica* x *N. annulata* colony at Woodhill (Lepidoptera: Arctiidae). *New Zealand Entomologist, 7*(2), 154-158.

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution, 17*(4), 164-170.

Keeler, M. S., & Chew, F. S. (2009). Escaping an evolutionary trap: preference and performance on a native insect on an exotic invasive host. *Oecologia, 156*, 559-568.

Keeley, J. E. (2001). *Fire and invasive species in Mediterranean-climate ecosystems of California.* Paper presented at the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species., Tall Timbers Research Station, Tallahassee, FL.

Keller, R. P., & Lodge, D. M. (2007). Species Invasions from Commerce in Live Aquatic Organisms: Problems and Possible Solutions. *BioScience, 57*(5), 428-436. doi: doi:10.1641/B570509

Kelly, D. W., Paterson, R. A., Townsend, C. R., Poulin, R., & Tompkins, D. M. (2009). Parasite spillback: A neglected concept in invasion ecology? *Ecology, 90*(8), 2047-2056. doi: doi:10.1890/08-1085.1

Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Péré, C., Cock, M. J. W., et al. (2009). Ecological effects of invasive alien insects. In D. W. Langor & J. Sweeney (Eds.), *Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems* (pp. 21-45): Springer Netherlands.

Knevel, I. C., Lans, T., Menting, F. B. J., Hertling, U. M., & Putten, W. H. v. d. (2004). Release from Native Root Herbivores and Biotic Resistance by Soil Pathogens in a New Habitat Both Affect the Alien Ammophila arenaria in South Africa. *Oecologia, 141*(3), 502-510.

Koch, R. L. (2003). The multicolored Asian ladybird beetle, Harmonia axyridis: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science, 3*(32).

Koch, R. L., Venette, R. C., & Hutchison, W. D. (2006). Invasions by Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) in the Western Hemisphere: implications for South America. *Neotropical Entomology, 35*(4), 421-434.

Korenchenko, E. A. (1980). New species of nematodes from the family Aphelenchoididae, parasites of trunk pests of Larix dahurica. *Zoologicheskii Zhurnal, 59*(12), 1768-1780.

Kot, M., Lewis, M. A., & van den Driessche, P. (1996). Dispersal Data and the Spread of Invading Organisms. *Ecology, 77*(7), 2027-2042. doi: doi:10.2307/2265698

Kowalchuk, G. A., Hol, W. G. H., & van Veen, J. A. (2006). Rhizosphere fungal communities are influenced by *Senecio jacobaea* pyrrolizidine alkaloid content and compostition. *Soil Biology & Biochemistry, 38*, 2852-2859.

Kunin, W. E. (1999). Patterns of Herbivore Incidence on Experimental Arrays and Field Populations of Ragwort, Senecio jacobaea. *Oikos, 84*(3), 515-525.

Kupferberg, S. J. (1997). Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology, 78*(6), 1736-1751. doi: doi:10.1890/0012-9658(1997)078[1736:BRCIOA]2.0.CO;2

Lambdon, P. W., & Hulme, P. E. (2006). How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. *Journal of Biogeography, 33*(6), 1116-1125. doi: 10.1111/j.1365-2699.2006.01486.x

Langel, D., Ober, D., & Pelser, P. B. (2010). The evolution of pyrrolizidine alkaloid biosynthesis and diversity in the Senecioneae. *Phytochemistry Reviews, in press*.

Langer, A., & Hance, T. (2004). Enhancing parasitism of wheat aphids through apparent competition: a tool for biological control. *Agriculture, Ecosystems and Environment, 102*(2), 205-212.

Larson, D. L., Anderson, P. J., & Newton, W. (2001). Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications, 11*(1), 128-141. doi: doi:10.1890/1051-0761(2001)011[0128:APIIMG]2.0.CO;2

Lau, J. A., & Strauss, S. Y. (2005). Insect herbivores drive important indirect effects of exotic plants on native communities. [Journal Article]. *Ecology, 86*(11), 2990-2997.

Lavrentyev, P. J., Gardner, W. S., & Yang, L. (2000). Effects of the zebra mussel on nitrogen dynamics and the microbial community at the sediment-water interface. *Aquatic Microbial Ecology, 21*, 187-194.

Lennon, J. T., Smith, V. H., & Williams, K. (2001). Influence of Temperature on Exotic Daphnia lumholtzi and Implications for Invasion Success. *Journal of Plankton Research, 23*(4), 425-433. doi: 10.1093/plankt/23.4.425

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters, 7*(10), 975-989. doi: 10.1111/j.1461-0248.2004.00657.x

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulus and S. Lavorel. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B, Biological Sciences, 270*, 775-781.

Libbrecht, R., Gwynn, D. M., & Fellowes, M. D. E. (2007). Aphidius ervi preferentially attacks the green morph of the pea aphid, Acyrthosiphon pisum. *Journal of Insect Behavior, 20*(1), 25-32.

LINZ. (2010). Online Conversions, 2010, from http://www.linz.govt.nz/geodetic/conversion-coordinates/online-conversion-service/index.aspx

Liu, H., & Stiling, P. (2006). Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions, 8*(7), 1535-1545. doi: 10.1007/s10530-005-5845-y

Liu, H., Stiling, P., & Pemberton, R. (2007). Does enemy release matter for invasive plants? evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. *Biological Invasions, 9*(7), 773-781. doi: 10.1007/s10530-006-9074-9

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution, 20*(5), 223-228. doi: DOI: 10.1016/j.tree.2005.02.004

Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2009). The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions, 15*(5), 904-910. doi: 10.1111/j.1472-4642.2009.00594.x

Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2007). *Invasion Ecology*. Malden, MA: Blackwell.

Lodge, D. M. (1993). Biological invasions: Lessons for ecology. *Trends in Ecology & Evolution, 8*(4), 133-137. doi: Doi: 10.1016/0169-5347(93)90025-k

Louda, S. M. (2000). Negative ecological effects of the Musk thistle biological control agent, Rhinocyllus conicus. In P. A. Follett & J. J. Duan (Eds.), *Nontarget Effects of Biological Control* (pp. 215-243). Norwell, MA (USA): Kluwer Academic Publishers.

Louda, S. M., Arnett, A. E., Rand, T. A., & Russell, F. L. (2003). Invasiveness of some biological control insects and adequacy of their ecological risk assessment and regulation. *Conservation Biology, 17*(1), 73-82.

Louda, S. M., Rand, T. A., Arnett, A. E., McClay, A. S., Shea, K., & McEachern, A. K. (2005). Evalution of ecological risk to populations of a threatened plant from an invasive biocontrol insect. *Ecological Applications, 15*(1), 234-249.

Louda, S. M., Simberloff, D., Boettner, G., Connor, J., Kendall, D., & Arnett, A. E. (1998). Insights from data on the non-target effects of the flowerhead weevil. *Biocontrol News and Information, 19*, 70N-71N.

Lozon, J. D. (1997). Biological invasions: are they dependent on disturbance? *Environmental Reviews, 5*(2), 131.

Lu, J., Zhao, L., Ma, R., Zhang, P., Fan, R., & Zhang, J. (2010). Performance of the biological control agent flea beetle Agasicles hygrophila (Coleoptera: Chrysomelidae), on two plant species Alternanthera philoxeroides (alligatorweed) and A. sessilis (joyweed). *Biological Control, 54*(1), 9-13. doi: DOI: 10.1016/j.biocontrol.2010.02.012

Macel, M., Vrieling, K., & Klinkhamer, P. G. L. (2004). Variation in pyrrolizidine alkaloid patterns of *Senecio jacobaea*. *Phytochemistry, 65*(7), 865-873. doi: 10.1016/j.phytochem.2004.02.009

Mack, R. N. (1996). *Biotic barriers to plant naturalization.* Paper presented at the Proceedings of the IX International Symposium on Biological Control of Weeds, University of Cape Town, Cape Town.

Mack, R. N., & Lonsdale, W. M. (2001). Humans as Global Plant Dispersers: Getting More Than We Bargained For. *BioScience, 51*(2), 95-102. doi: doi:10.1641/0006-3568(2001)051[0095:HAGPDG]2.0.CO;2

Maclean, T. (1894, 29 March 1894). The Spead [sic] of Tansy, *Otago Witness*.

MacNeil, C., Dick, J. T. A., Hatcher, M. J., Terry, R. S., Smith, J. E., & Dunn, A. M. (2003). Parasite-mediated predation between native and invasive amphipods. *Proceedings of the Royal Society of London Series B, Biological Sciences, 270*(1521), 1309-1314.

Maerz, J. C., Brown, C. J., Chapin, C. T., & Blossey, B. (2005). Can secondary compounds of an invasive plant affect larval amphibians? *Functional Ecology, 19*(6), 970-975. doi: 10.1111/j.1365-2435.2005.01054.x

Biosecurity Act of 1993 (1993).

Malmstrom, C. M., McCullough, A. J., Johnson, H. A., Newton, L. A., & Borer, E. T. (2005). Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. *Oecologia, 145*(1), 153-164.

Malmstrom, C. M., Shu, R., Linton, E. W., Newton, L. A., & Cook, M. A. (2007). Barley yellow dwarf viruses (BYDVs) preserved in herbarium specimens illuminate historical disease ecology of invasive and native grasses. *Journal of Ecology, 95*(6), 1153-1166. doi: 10.1111/j.1365-2745.2007.01307.x

Malmstrom, C. M., Stoner, C. J., Brandenburg, S., & Newton, L. A. (2006). Virus infection and grazing exert counteracting influences on survivorship of native bunchgrass seedlings competing with invasive exotics. *Journal of Ecology Oxford, 94*(2), 264-275.

Marchetti, M. A. (1962). Infection of Quercus macrocarpa by white and gray isolates of Ceratocystis fagacearum. *Proc Iowa Acad Sci*, 122-127.

Maron, J. L., & Vilà, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos, 95*(3), 361-373. doi: 10.1034/j.1600-0706.2001.950301.x

Marrow, P., Law, R., & Cannings, C. (1992). The Coevolution of Predator--Prey Interactions: ESSS and Red Queen Dynamics. *Proceedings: Biological Sciences, 250*, 133-141.

Martin, N. A. (2010). Plant SyNZ Database. Retrieved November 3, 2010, from New Zealand Institute for Plant & Food Research, Ltd. http://www.crop.cri.nz/home/plant-synz

Martinez, G., & Medel, R. (2002). Indirect interactions in a microcosm-assembled cladoceran community: implications for apparent competition. *Oikos, 97*(1), 111-115.

Maschinski, J., & Whitham, T. G. (1989). The Continuum of Plant Responses to Herbivory: The Influence of Plant Association, Nutrient Availability, and Timing. *The American Naturalist, 134*(1), 1-19.

Mattocks, A. R. (1972). Toxicity and metabolism of Senecio alkaloids. In J. B. Harborne (Ed.), *Phytochemical Ecology* (pp. 179-200). London: Academic Press.

Mauricio, R., & Rausher, M. D. (1997). Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant disease. *Evolution; international journal of organic evolution, 51*(5), 1435-1444.

Mayhew, P. J. (1997). Adaptive Patterns of Host-Plant Selection by Phytophagous Insects. *Oikos, 79*(3), 417-428.

McEvoy, P. B. (1996). Host Specificity and Biological Pest Control. *BioScience, 46*(6), 401-405.

McEvoy, P. B., Rudd, N. T., Cox, C. S., & Huso, M. (1993). Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. *Ecological Monographs, 63*(1), 55-75.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution, 14*(11), 450-453. doi: Doi: 10.1016/s0169-5347(99)01679-1

McLean, E. K. (1970). The toxic actions of pyrrolizidine (*Senecio*) alkaloids. *Pharmaceutical Reviews, 22*(4), 429.

Meisner, A., De Boer, W., Gera Hol, W. H., Krumins, J. A., & Van Der Putten, W. H. (2009). No Paradox for Invasive Plants. *Science, 325*(5942), 814-. doi: 10.1126/science.325_814

Menken, S. B. J., Boomsma, J. J., & Van Nieukerken, E. J. (2010). Large-scale evolutionary patterns of host plant associations in the Lepidoptera. *Evolution, 64*(4), 1098-1119. doi: 10.1111/j.1558-5646.2009.00889.x

Messing, R. H., & Wang, X.-G. (2009). Competitor-free space mediates non-target impact of an introduced biological control agent. *Ecological Entomology, 34*(1), 107-113.

`

Meyrick, E. (1889, November 7, 1889). *Descriptions of New Zealand Leipdoptera.* Paper presented at the Transactions of the New Zealand Institute, Canterbury.

Miller, T. E., & Travis, J. (1996). The evolutionary role of indirect effects in communities. *Ecology, 77*(5), 1329-1335.

Mitchell, C. E., Agrawal, A. A., Bever, J. D., Gilbert, G. S., Hufbauer, R. A., Klironomos, J. N., et al. (2006). Biotic interactions and plant invasions. *Ecology Letters, 9*(6), 726-740.

Mitich, L. W. (1995). Tansy Ragwort. *Weed Technology, 9*(2), 402-404.

Molina, R., Massicotte, H., & Trappe, J. M. (1992). Specificity phenomena in mycorrhizal symbiosis: Community-ecological consequences and practical implications. In M. F. Allen (Ed.), *Mycorrhizal functioning: an integrative plant-fungal process* (pp. 357-423): Springer.

Morales, C. L., & Traveset, A. (2009). A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters, 12*(7), 716-728. doi: 10.1111/j.1461-0248.2009.01319.x

Moran, N. A. (1989). A 48-million-year-old aphid-host plant association and complex life cycle: biogeographic evidence. *Science, 245*(4914), 173-175. doi: 10.1126/science.245.4914.173

Morris, R. J., & Lewis, O. T. (2002). The role of indirect interactions in structuring tropical insect communities. *Oikos, 97*(2), 308-311.

Morris, R. J., Lewis, O. T., & Godfray, H. C. J. (2004). Experimental evidence for apparent competition in a tropical forest food web. *Nature London, 428*(6980), 310-313.

Morrison, L. W. (2000). Mechanisms of interspecific competition among an invasive and two native fire ants. *Oikos, 90*(2), 238-252. doi: 10.1034/j.1600-0706.2000.900204.x

Moyle, P. B., & Light, T. Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation, 78*(1-2), 149-161. doi: Doi: 10.1016/0006-3207(96)00024-9

Muller, C. B., & Godfray, H. C. J. (1997). Apparent competition between two aphid species. *Journal of Animal Ecology, 66*(1), 57-64.

Munday, P. L., van Herwerden, L., & Dudgeon, C. L. (2004). Evidence for Sympatric Speciation by Host Shift in the Sea. *Current Biology, 14*(16), 1498-1504. doi: 10.1016/j.cub.2004.08.029

Myers, J. H., & Post, B. J. (1981). Plant Nitrogen and Fluctuations of Insect Populations: A Test with the Cinnabar Moth: Tansy Ragwort System. *Oecologia, 48*(2), 151-156.

Ness, J. H., & Bronstein, J. L. (2004). The Effects of Invasive Ants on Prospective Ant Mutualists. *Biological Invasions, 6*(4), 445-461. doi: 10.1023/B:BINV.0000041556.88920.dd

Newman, R. M., Borman, M. E., & Castro, S. W. (1997). Developmental Performance of the Weevil Euhrychiopsis lecontei on Native and Exotic Watermilfoil Host Plants. *Journal of the North American Benthological Society, 16*(3), 627-634.

Noble, I. R., & Weiss, P. W. (1989). Movement and modelling of buried seed of the invasive perennial Chrysanthemoides monilifera in coastal dunes and biological control. *Australian Journal of Ecology, 14*(1), 55-64. doi: 10.1111/j.1442-9993.1989.tb01008.x

Nosil, P., Crespi, B. J., & Sandoval, C. P. (2002). Host-plant adaptation drives the parallel evolution of reproductive isolation. [10.1038/417440a]. *Nature, 417*(6887), 440-443.

Novotný, V., Drozd, P., Miller, S. E., Kulan, M., Janda, M., Basset, Y., et al. (2006). Why are there so many species of herbivorous insects in tropical rainforests? *Science, 313,* 1115–1118.

NZPCN. (October 13, 2011). Frequently Asked Questions about New Zealand Plants Retrieved February 1, 2012, 2012, from http://nzpcn.org.nz/page.asp?help_faqs_NZ_plants

O'Dowd, D. J., Green, P. T., & Lake, P. S. (2003). Invasional "meltdown" on an oceanic island. *Ecology Letters*, 812-817.

O'Gorman, E. J., & Emmerson, M. C. (2009). Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences, 106*(32), 13393-13398. doi: 10.1073/pnas.0903682106

Oppenheim, S. J., & Gould, F. (2002). Behavioral adaptations increase the value of enemy-free space for *Heliothis subflexa*, a specialist herbivore. *Evolution, 56*(4), 679-689. doi: 10.1111/j.0014-3820.2002.tb01379.x

Orrock, J. L., & Witter, M. S. (2009). Multiple drivers of apparent competition reduce re-establishment of a native plant in invaded habitats. *Oikos, in press*.

Orrock, J. L., Witter, M. S., & Reichman, O. J. (2008). Apparent competition with an exotic plant reduces native plant establishment. *Ecology, 89*(4), 1168-1174.

Ortega, Y. K., Pearson, D. E., & McKelvey, K. S. (2004). Effects of biological control agents and exotic plant invasion on deer mouse populations. *Ecoloical Applications, 14*(1), 241-253.

Pages, J. P., & Michalet, R. (2006). Contrasted responses of two understorey species to direct and indirect effects of a canopy gap. *Plant Ecology, 187*(2), 179-187.

Parker, I. M., & Gilbert, G. S. (2004). The evolutionary ecology of novel plant-pathogen interactions. *Annual Review of Ecology and Systematics, 35*, 675-700.

Parker, I. M., & Gilbert, G. S. (2007). When there is no escape: the effects of natural enemies on native, invasive and noninvasive plants. *Ecology, 88*(5), 1210-1224. doi: doi:10.1890/06-1377

Parker, J. D., & Hay, M. E. (2005). Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters, 8*(9), 959-967. doi: 10.1111/j.1461-0248.2005.00799.x

Parker, M. A. (2001). Mutualism as a constraint on invasion success for legumes and rhizobia. *Diversity and Distributions, 7*(3), 125-136. doi: 10.1046/j.1472-4642.2001.00103.x

Pastorok, R. A. (1981). Prey vulnerability and size selection by Chaoborus larvae. *Ecology, 62*, 1311-1324.

Patrick, B. (1994). Antipodes Island Lepidoptera. *Journal of The Royal Society of New Zealand, 24*(1), 91-116.

Patrick, B. H., & Dugdale, J. S. (2000). Conservation status of the New Zealand Lepidoptera *Science for Conservation* (Vol. 136). Wellington: Department of Conservation.

Paynter, Q., Fowler, S. V., Hugh Gourlay, A., Groenteman, R., Peterson, P. G., Smith, L., et al. (2010). Predicting parasitoid accumulation on biological control agents of weeds. *Journal of Applied Ecology, 47*(3), 575-582. doi: 10.1111/j.1365-2664.2010.01810.x

Pearson, D. E., McKelvey, K. S., & Ruggiero, L. F. (2000). Indirect effects of biological control agents released to control spotted knapweed. *Oecologia, 122*, 121-128.

Pearson, D. E., & Callaway, R. M. (2003). Indirect effects of host-specific biological control agents. *Trends in Ecology & Evolution, 18*(9), 456-461. doi: 10.1016/s0169-5347(03)00188-5

Peccoud, J., Figueroa, C. C., Silva, A. X., Ramirez, C. C., Mieuzet, L., Bonhomme, J., et al. (2008). Host range expansion of an introduced insect pest through multiple colonizations of specialized clones. *Molecular Ecology, 17*(21), 4608-4618. doi: 10.1111/j.1365-294X.2008.03949.x

Pelissier, R., & Goreaud, F. (2010). ads: Spatial point patterns analysis (Version R package version 1.2-10). Retrieved from http://CRAN.R-project.org/package=ads

Pelser, P. B., de Vos, H., Theuring, C., Beuerle, T., Vrieling, K., & Hartmann, T. (2005). Frequent gain and loss of pyrrolizidine alkaloids in the evolution of Senecio section Jacobaea (Asteraceae). *Phytochemistry, 66*(11), 1285-1295. doi: 10.1016/j.phytochem.2005.04.015

`

Pelser, P. B., Nordenstam, B., Kadereit, J. W., & Watson, L. E. (2007). An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon, 56*, 1077-1104.

Pelser, P. B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. (2007) 56 (4): 1077–1104. (2007). An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon, 56*(4), 1077-1104.

Philpot, A. (1916). A list of the Lepidoptera of Otago. *Transactions of the Royal Society of New Zealand 49*, 195-238.

Philpott, A. (1907). Notes on protective resemblance in New Zealand moths. *Transactions and Proceedings of the New Zealand Institute, 39*, 212-219.

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics, 52*(3), 273-288. doi: DOI: 10.1016/j.ecolecon.2004.10.002

Poole, A. L., & Cairns, D. (1940). *Botanical aspects of ragwort (Senecio jacobaea L.) control* (Vol. 82). Wellington, N.Z.: E.V. Paul (Govt. Print).

Poulin, R., & Mouillot, D. (2003). Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology, 126*(5), 473-480.

Power, A. G., & Mitchell, C. E. (2004). Pathogen spillover in disease epidemics. [Journal Article]. *The American Naturalist, 164*, S79-S89.

Procheş, Ş., Wilson, J. R. U., Richardson, D. M., & Rejmánek, M. (2008). Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography, 17*(1), 5-10. doi: 10.1111/j.1466-8238.2007.00333.x

Prowse, A. J., & Goodridge, F. (2003). Experimental invasion of woodland by the alien *Impatiens glandulifera*: the role of slug herbivory. *Plant invasions: ecological threats and management solutions*.

Puente, M., Magori, K., Kennedy, G., & Gould, F. (2008). Impact of Herbivore-induced Plant Volatiles on Parasitoid Foraging Success: A Spatial Simulation of the *Cotesia rubecula, Pieris rapae* and *Brassica oleracea* System. *Journal of Chemical Ecology, 34*(7), 959-970. doi: 10.1007/s10886-008-9472-9

Pyšek, P., & Richardson, D. M. (2006). The biogeography of naturalization in alien plants. *Journal of Biogeography, 33*, 2040-2050.

Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon, 53*, 131-143.

Radcliffe, J. E. (1969). Ragwort control. *New Zealand Journal of Agriculture, 119*(1), 80-83.

`

Rand, T. A. (2003). Herbivore-mediated apparent competition between two salt marsh forbs. *Ecology, 84*(6), 1517-1526.

Rand, T. A., & Louda, S. M. (2006). Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conservation Biology, 20*(6), 1720-1729.

Rand, T. A., Russell, F. L., & Louda, S. M. (2004). Local- vs. landscape-scale indirect effects of an invasive weed on native plants. *Weed Technology, 18*(Suppl.), 1250-1254.

Rand, T. A., Russell, F. L., & Louda, S. M. (2009). Local- Vs. Landscape-Scale Indirect Effects of an Invasive Weed on Native Plants. *Weed Technology, 18*(sp1), 1250-1254. doi: 10.1614/0890-037x(2004)018[1250:lvlieo]2.0.co;2

Reitz, S. R., Funderburk, J. E., & Waring, S. M. (2006). Differential predation by the generalist predator Orius insidiosus on congeneric species of thrips that vary in size and behavior. *Entomologia Experimentalis et Applicata, 119*(3), 179-188. doi: 10.1111/j.1570-7458.2006.00408.x

Rejmanek, M. (1996). A theory of seed plant invasiveness: the first sketch. *Biological Conservation, 78*, 171-181.

Rejmanek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology, v77*(n6), p1655(1657).

Reynolds, J. D. (1988). Crayfish extinctions and crayfish plague in central Ireland. *Biological Conservation, 45*(4), 279-285. doi: Doi: 10.1016/0006-3207(88)90059-6

Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., & Rejmanek, M. (2000). Plant invasions - the role of mutualisms. *Biological Review, 75*, 65-93.

Ripple, W. J., & Beschta, R. L. (2005). Willow thickets protect young aspen from elk browsing after wolf reintroduction. *Western North American Naturalist, 65*(1), 118-122.

Rodriguez, C. F., Becares, E., Fernandez-alaez, M., & Fernandez-alaez, C. (2005). Loss of diversity and degradation of wetlands as a result of introducing exotic crayfish. *Biological Invasions, 7*(1), 75-85.

Roemer, G. W., Coonan, T. J., Garcelon, D. K., Bascompte, J., & Laughrin, L. (2001). Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation, 4*(4), 307-318. doi: 10.1017/s1367943001001366

Rogers, W. E., & Siemann, E. (2005). Herbivory Tolerance and Compensatory Differences in Native and Invasive Ecotypes of Chinese Tallow Tree (Sapium sebiferum). *Plant Ecology, 181*(1), 57-68.

Rosenthal, J., & Dirzo, R. (1997). Effects of life history, domestication and agronomic selection on plant defence against insects: Evidence from maizes and wild relatives. *Evolutionary Ecology, 11*(3), 337-355. doi: 10.1023/a:1018420504439

Rosenthal, J. P., & Kotanen, P. M. (1994). Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution, 9*(4), 145-148. doi: 10.1016/0169-5347(94)90180-5

Rossbach, A., Löhr, B., & Vidal, S. (2006a). Host shift to peas in the diamondback moth Plutella xylostella (Lepidoptera: Plutellidae) and response of its parasitoid Diadegma mollipla (Hymenoptera: Ichneumonidae). *Bulletin of Entomological Research, 96*(04), 413-419. doi: doi:10.1079/BER2006445

Rossbach, A., Löhr, B., & Vidal, S. (2006b). Parasitism of *Plutella xylostella* L. Feeding on a New Host Plant. *Environmental Entomology, 35*(5), 1350-1357.

Rott, A. S., & Godfray, H. C. J. (2000). The structure of a leafminer-parasitoid community. *Journal of Animal Ecology, 69*(2), 274-289.

Rowles, A. D., & O'Dowd, D. J. (2009). New mutualism for old: indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. *Oecologia, 158*(4), 709-716.

Rudgers, J., Mattingly, W., & Koslow, J. (2005). Mutualistic fungus promotes plant invasion into diverse communities. *Oecologia, 144*(3), 463-471. doi: 10.1007/s00442-005-0039-y

Ruiz, G. M., Carlton, J. T., Grosholz, E. D., & Hines, A. H. (1997). Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *American Zoology, 37*, 621-632.

Rushton, S. P., Lurz, P. W. W., Gurnell, J., & Fuller, R. (2000). Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology, 37*(6), 997-1012.

Sabelis, M. W., Janssen, A., & Kant, M. R. (2001). The enemy of my enemy is my ally. *Science, 291*, 2104-2105.

Saeed, A., Dangerfield, P. C., & Austin, A. D. (1999). Systematics and host relationships of Australasian <i>Diolcogaster</i> (Hymenoptera : Braconidae : Microgastrinae). *Invertebrate Systematics, 13*(1), 117-178. doi: doi:10.1071/IT97033

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., et al. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics, 32*(1), 305-332. doi: doi:10.1146/annurev.ecolsys.32.081501.114037

Sax, D. F., & Brown, J. H. (2000). The paradox of invasion. *Global Ecology and Biogeography, 9*(5), 363-371. doi: 10.1046/j.1365-2699.2000.00217.x

Sax, D. F., & Gaines, S. D. (2008). Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences, 105*(Supplement 1), 11490-11497. doi: 10.1073/pnas.0802290105

Sax, D. F., Gaines, S. D., & Brown, J. H. (2002). Species Invasions Exceed Extinctions on Islands Worldwide: A Comparative Study of Plants and Birds. *The American Naturalist, 160*(6), 766-783.

Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., et al. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution, 22*(9), 465-471. doi: DOI: 10.1016/j.tree.2007.06.009

Schmidl, L. (1972a). Biology & control of ragwort (Senecio jacobaea L.), in Victoria, Australia. *Weed Research, 12*, 37-45.

Schmidl, L. (1972b). Studies on the control of ragwort (Senecio jacobaea L.), with the cinnabar moth (Callimorpha jacobaeae L.) (Lepidoptera: Arctiidae) in Victoria. *Weed Research, 12*, 46-47.

Schoener, T. W. (1993). On the relative importance of direct versus indirect effects in ecological communities. In H. Kawanabe, J. E. Cohen & K. Iwasaki (Eds.), *Mutualism & Community Organisation* (pp. 365-415). Oxford: Oxford University Press.

Schoental, R. (1968). Toxicology and carcinogenic action of pyrrolizidine alkaloids. *Cancer Research, 28*, 2237-2246.

Schoonhoven, L. M., van Loon, J. A. A., & Dicke, M. (2006). *Insect-Plant Biology* (2 ed.). Oxford, UK: Oxford University Press.

Sessions, L., & Kelly, D. (2002). Predator-mediated apparent competition between an introduced grass, *Agrostis capillaris*, and a native fern, *Botrychium australe* (Ophioglossaceae), in New Zealand. *Oikos, 96*(1), 102-109.

Settle, W. H., & Wilson, L. T. (1990). Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology, 71*(4), 1461-1470.

Shannon, M. M., & Feeny, P. (2006). Chemical facilitation of a naturally occurring host shift by *Papilio machaon* butterflies (Papilionidae). *Ecological Monographs, 76*(3), 399-414.

Sher, A. A., Marshall, D. L., & Gilbert, S. A. (2000). Competition between Native *Populus deltoides* and Invasive *Tamarix ramosissima* and the Implications for Reestablishing Flooding Disturbance

Competencia Entre la Especie Nativa *Populus deltoides* y la Invasiva *Tamarix ramosissima* y las Implicaciones para Reintegrar Perturbaciones Causadas por Inundaciones. *Conservation Biology, 14*(6), 1744-1754. doi: 10.1111/j.1523-1739.2000.99306.x

Shirai, Y., & Morimoto, N. (1999). A host shift from wild blue cohosh to cultivated potato by the phytophagous ladybird beetle, Epilachna yasutomii (Coleoptera, Coccinellidae). *Researches on Population Ecology, 41*(2), 161-167.

Simberloff, D. (1995). Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science, 49*(1), 87-97.

Simberloff, D., & Stiling, P. (1996). Risk of species introduced for biological control. *Biological Conservation, 78*, 185-192.

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions, 1*, 21-32.

Simmonds, F. J., & Bennett, F. D. (1966). Biological control of *Opuntia* spp. by *Cactoblastis cactorum* in the Leeward Islands (West Indies). *Entomophaga, 11*, 183-189.

Simon, K. S., Townsend, C. R., Biggs, B. J. F., Bowden, W. B., & Frew, R. D. (2004). Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. *Ecosystems, 7*(8), 777-792.

Singer, M. S., & Stireman, J. O. (2005). The tri-trophic niche concept and adaptive radiation of phytophagous insects. *Ecology Letters, 8*(12), 1247-1255. doi: 10.1111/j.1461-0248.2005.00835.x

Singh, P., & Mabbett, F. E. (1976). Note on the life history of the magpie moth, *Nyctemera annulata* (Lepidoptera: Arctiidae). *New Zealand Journal of Zoology, 3*, 277-278.

Smith, W. W. (1893). Notes on *Nyctemera annulata*. *Entomologist, 26*, 220-221.

Snyder, W. E., Clevenger, G. M., & Eigenbrode, S. D. (2004). Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia, 140*(4), 559-565. doi: 10.1007/s00442-004-1612-5

Soler, R., Harvey, J. A., Kamp, A. F. D., Vet, L. E. M., Van der Putten, W. H., Van Dam, N. M., et al. (2007). Root herbivores influence the behaviour of an aboveground parasitoid through changes in plant-volatile signals. *Oikos, 116*(3), 367-376. doi: 10.1111/j.0030-1299.2007.15501.x

Spiller, D. M., & Wise, K. A. J. (1982). A catalogue (1860-1960) of New Zealand insects and their host plants. (Vol. Bulletin 231). Wellington: Department of Scientific and Industrial Research.

Stables, R. (1983). *Ragwort*. Christchurch: Whitcoulls.

`

Stachowicz, J. J., & Byrnes, J. E. (2006). Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Marine Ecology Progress Series, 311*, 251-262.

Stadler, B., Müller, T., & Orwig, D. (2006). The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology, 87*(7), 1792-1804. doi: doi:10.1890/0012-9658(2006)87[1792:TEOEAN]2.0.CO;2

Stamp. (2001). Enemy-free space via host plant chemistry and dispersion: assessing the influence of tri-trophic interactions. *Oecologia, 128*(2), 153-163. doi: 10.1007/s004420100679

Strauss, S. Y. (2006). *Exotic taxa less related to native species are more invasive.* Paper presented at the Proceedings of the National Academy of Sciences of the United States of America.

Strauss, S. Y., & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution, 14*(5), 179-185. doi: 10.1016/s0169-5347(98)01576-6

Strauss, S. Y., Lau, J. A., & Carroll, S. P. (2006). Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters, 9*, 357-374.

Strauss, S. Y., & Murch, P. (2004). Towards an understanding of the mechanisms of tolerance: compensating for herbivore damage by enhancing a mutualism. *Ecological Entomology, 29*(2), 234-239. doi: 10.1111/j.0307-6946.2004.00587.x

Stromberg, J. C., Lite, S. J., Marler, R., Paradzick, C., Shafroth, P. B., Shorrock, D., et al. (2007). Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography, 16*(3), 381-393. doi: 10.1111/j.1466-8238.2007.00297.x

Strong, D. R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology, 73*, 747-757.

Strong, D. R., Lawton, J. H., & Southwood, T. R. E. (1984). *Insects on Plants: Community Patterns and Mechanisms.* Oxford, UK: Blackwell Scientific.

Strong, D. R., Whipple, A. V., Child, A. L., & Dennis, B. (1999). Model selection for a subterranean trophic cascade: root-feeding caterpillars and entomopathogenic nematodes. *Ecology, 80*(8), 2750-2761.

Styrsky, J. D., & Eubanks, M. D. (2007). Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the Royal Society B: Biological Sciences, 274*(1607), 151-164. doi: 10.1098/rspb.2006.3701

Suarez, A. V., Holway, D. A., & Ward, P. S. (2005). The role of opportunity in the unintentional introduction of nonnative ants: National Academy of Sciences.

Sullivan, J. J. (2006). *Senecio* species in New Zealand Retrieved 29 August 2010, 2010, from http://www.mollivan.com/science/senecios/nzsenecios.php

Sullivan, J. J., Williams, P. A., Timmins, S. M., & Smale, M. C. (2009). Distribution and spread of environmental weeds along New Zealand roadsides. *New Zealand Journal of Ecology 33*(2), 190-204.

Sullivan, J. J., Winks, C. J., & Fowler, S. V. (2008). Novel host associations and habitats for *Senecio*-specialist herbivorous insects in Auckland. *New Zealand Journal of Ecology, 32*(2), 219-224.

Sutherland, R. D., Betteridge, K., Fordham, R. A., Stafford, K. J., & Costall, D. A. (2000). Rearing Conditions for Lambs May Increase Tansy Ragwort Grazing. *Journal of Range Management, 53*(4), 432-436.

Syrett, P. (1983). Biological control of ragwort in New Zealand - a review. *Australian Weeds, 2*, 96-101.

Syrett, P., Briese, D. T., & Hoffmann, J. H. (2002). Success in Biological Control of Terrestrial Weeds by Arthropods. In G. Gurr & S. Wratten (Eds.), *Biological control: measures of success*: Springer.

Syrett, P., Grindell, J. M., Hayes, L. M., & Winks, C. J. (1991). *Distribution and establishment of two biological control agents for ragwort in New Zealand.* Paper presented at the New Zealand Weed and Pest Control Conference.

Syrett, P., Scheele, S. M., & Philip, B. A. (1983). *Renewed activities in biological control of ragwort.* Paper presented at the Proceedings of the 37th NZ Weed and Pest Control Conference, Hastings, NZ.

Taniguchi, Y., Fausch, K. D., & Nakano, S. (2002). Size-structured Interactions between Native and Introduced Species: Can Intraguild Predation Facilitate Invasion by Stream Salmonids? *Biological Invasions, 4*(3), 223-233. doi: 10.1023/a:1020915416559

Team, R. D. C. (2010). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Tentelier, C., & Fauvergue, X. (2007). Herbivore-induced plant volatiles as cues for habitat assessment by a foraging parasitoid. *Journal of Animal Ecology, 76*(1), 1-8. doi: 10.1111/j.1365-2656.2006.01171.x

`

Thomas, C. D., Ng, D., Singer, M. C., Mallet, J. L. B., Parmesan, C., & Billington, H. L. (1987). Incorporation of a European Weed Into the Diet of a North American Herbivore. *Evolution, 41*(4), 892-901.

Thompson, G. M. (1922). *The Naturalisation of Animals & Plants in New Zealand.* Cambridge: Cambridge University Press.

Thomson, G. M. (1909). *A New Zealand naturalist's calendar*. Dunedin: R.J. Stark & Co.

Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C., et al. (2010). Resolving Darwin’s naturalization conundrum: a quest for evidence. *Diversity and Distributions, 16*(3), 461-475. doi: 10.1111/j.1472-4642.2010.00645.x

Tickner, D. P., Angold, P. G., Gurnell, A. M., & Mountford, J. O. (2001). Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Progress in Physical Geography, 25*(1), 22-52. doi: 10.1177/030913330102500102

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America, 101*(30), 10854-10861. doi: 10.1073/pnas.0403458101

Tompkins, D. M., Draycott, R. A. H., & Hudson, P. J. (2000). Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters, 3*(1), 10-14.

Tompkins, D. M., White, A. R., & Boots, M. (2003). Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters, 6*(3), 189-196. doi: 10.1046/j.1461-0248.2003.00417.x

Toppel, G., Witte, L., Riebesehl, B., Borstel, K. v., & Hartmann, T. (1987). Alkaloid patterns and biosynthetic capacity of root cultures from some pyrrolizidine alkaloid producing *Senecio* species. *Plant Cell Reports, 6*(6), 466-469. doi: 10.1007/bf00272784

Tscharntke, T., Rand, T. A., & Bianchi, F. (2005). The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici, 42,* 421-432.

Tscheulin, T., Petanidou, T., & Settele, J. (2009). Invasive weed facilitates incidence of Colorado potato beetle on potato crop. *International Journal of Pest Management, 55*(2), 165 - 173.

Tsutsui, N. D., & Suarez, A. V. (2003). The Colony Structure and Population Biology of Invasive Ants

Estructura de una Colonia y Biología Poblacional de Hormigas Invasoras. *Conservation Biology, 17*(1), 48-58. doi: 10.1046/j.1523-1739.2003.02018.x

Turchin, P. (2003). *Complex Population Dynamics*. Princeton, N.J.: Princeton University Press.

Ueno, H., Fujiyama, N., Yao, I., Sato, Y., & Katakura, H. (2003). Genetic architecture for normal and novel host-plant use in two local populations of the herbivorous ladybird beetle, Epilachna pustulosa. *Journal of Evolutionary Biology, 16*(5), 883-895.

Unsicker, S. B., Kunert, G., & Gershenzon, J. (2009). Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. *Current Opinion in Plant Biology, 12*(4), 479-485. doi: DOI: 10.1016/j.pbi.2009.04.001

Valentine, E. (1967). *A list of the hosts of entomophagous insects of New Zealand* (Vol. 10). Wellington: Department of Scientific and Industrial Research.

Valiente-Banuet, A., & Verdú, M. (2008). Temporal shifts from facilitation to competition occur between closely related taxa. *Journal of Ecology, 96*(3), 489-494. doi: 10.1111/j.1365-2745.2008.01357.x

Valladares, G. R., Salvo, A., & Godfray, H. C. J. (2001). Quantitative food webs of dipteran leaf miners and their parasitoids in Argentina. *Ecological Research, 16*(5), 925-939.

van der Meijden, E., De Boer, N. J., & van der Veen-van Wijk, C. A. M. (2000). Pattern of storage and regrowth in ragwort. *Evolutionary Ecology, 14*, 439-455.

van der Meijden, E., & van der Waals-kooi, R. R. (1979). The population ecology of *Senecio jacobaea* in the Netherlands sand dune system. I. Reproductive strategy and the biennial habit. *Journal of Ecology, 67*, 131-154.

Van der Putten, W. H. (2009). A multitrophic perspective on functioning and evolution of facilitation in plant communities. *Journal of Ecology, 97*, 1131-1138.

van Rhijn, P., & Vanderleyden, J. (1995). The *Rhyzobium*-plant symbiosis. *Microbiological Reviews, 59*(1), 124-142.

Van Valen, L. (1974). Molecular evolution as predicted by natural selection. *Journal of Molecular Evolution, 3*(2), 89-101. doi: 10.1007/bf01796554

van Veen, F. J. F., Morris, R. J., & Godfray, H. C. J. (2006). Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, 187-208.

Velasco, L. R. I., & Walter, G. H. (1993). Potential of Host-Switching in *Nezara viridula* (Hemiptera: Pentatomidae) To Enhance Survival and Reproduction. *Environmental Entomology, 22*, 326-333.

Verhoeven, K. J. F., Biere, A., Harvey, J. A., & van der Putten, W. H. (2009). Plant invaders and their novel natural enemies: who is naive? *Ecology Letters, 12*(2), 107-117.

`

Vet, L. E. M., & Dicke, M. (1992). Ecology of Infochemical Use by Natural Enemies in a Tritrophic Context. *Annual Review of Entomology, 37*(1), 141-172. doi: doi:10.1146/annurev.en.37.010192.001041

Via, S. (1990). Ecological Genetics and Host Adaptation in Herbivorous Insects: The Experimental Study of Evolution in Natural and Agricultural Systems. *Annual Review of Entomology, 35*(1), 421-446. doi: doi:10.1146/annurev.en.35.010190.002225

Vitousek, P. M., D'antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology, 21*(1), 1-16.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996). Biological invasion as global environmental change. *American Scientist, 84*, 468-478.

Von Holle, B., and D. Simberloff. (2005). Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology, 86*(12), 3212-3218.

Wardle, D. A. (1987). The ecology of ragwort (Senecio jacobaea L.) - a review. *New Zealand Journal of Ecology, 10*, 67-76.

Wardle, D. A., Nicholson, K. S., & Rahman, A. (1995). Ecological effects of the invasive weed species Senecio jacobaea L. (ragwort) in a New Zealand pasture. *Agriculture, Ecosystems & Environment, 56*(1), 19-28. doi: Doi: 10.1016/0167-8809(95)00636-2

Watt, M. N. (1914). Contributions to the Study of New Zealand Entomology, from an Economical and Biological Standpoint: No.1 - Plusia chalcites Esp.; No. 2 - Nyctemera annulata Boisd.; No. 3 - Venusia verriculata Feld. (Lepidoptera). *Study of New Zealand Entomology* (pp. 245-274): Transactions of The New Zealand Institute.

Webb, C. J., Sykes, W. R., & Garnock, J. P. J. (1988). Naturalised pteridophytes, gymnosperms, dicotyledons *Flora of New Zealand* (Vol. IV). Christchurch, New Zealand: Botany Division, Department of Scientific and Industrial Research.

Weis, A. E. (1992). Plant variation and the evolution of phenotypic plasticity in herbivore performance. In R. S. Fritz & E. L. Simms (Eds.), *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics* (pp. 140-177): University of Chicago Press.

White, E. M., Sims, N. M., & Clarke, A. R. (2008). Test of the enemy release hypothesis: the native magpie moth prefers a native fireweed (*Senecio pinnatifolus*) to its introduced congener (*S. madagascariensis*). *Austral Ecology, 33*, 110-116.

White, E. M., Wilson, J. C., & Clarke, A. R. (2006). Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions, 12*, 443-455.

White, E. P. (1969). Alkaloids of some herbaceous *Senecio* species in New Zealand. *New Zealand Journal of Science, 12*, 165.

White, J. A., & Andow, D. A. (2006). Habitat modification contributes to associational resistance. *Oecologica, 148,* 482-490.

White, J. A., & Whitham, T. G. (2000). Associational susceptibility of cottonwood to a box elder herbivore. *Ecology, 81*(7), 1795-1803.

White, P. S., & Allison, E. S. (1998). Where Do We Go from Here? The Challenges of Risk Assessment for Invasive Plants. *Weed Technology, 12*(4), 744-751.

Williams, R. J., Berlow, E. L., Dunne, J. A., Barabasi, A. L., & Martinez, N. D. (2002). Two degrees of seperation in complex food webs. *Proceedings of The National Academy of Sciences, 99*(20), 12913-12916.

Williamson, M. (1999). Invasions. *Ecography, 22*(1), 5-12. doi: 10.1111/j.1600-0587.1999.tb00449.x

Williamson, M., & Fitter, A. (1996). The Varying Success of Invaders. *Ecology, 77*(6), 1661-1666.

Willis, A. J., & Memmott, J. (2005). The potential for indirect effects between a weed, one of its biocontrol agents and native herbivores: A food web approach. *Biological Control, 35*(3), 299-306. doi: DOI: 10.1016/j.biocontrol.2005.07.013

Willis, S. G., & Hulme, P. E. (2002). Does temperature limit the invasion of Impatiens glandulifera and Heracleum mantegazzianum in the UK? *Functional Ecology, 16*(4), 530-539. doi: 10.1046/j.1365-2435.2002.00653.x

Wise, M. J., & Abrahamson, W. G. (2005). Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos, 109*(3), 417-428. doi: 10.1111/j.0030-1299.2005.13878.x

Woodward, D. R. (1984). *Insect-plant interactions between magpie moth (Nyctemera annulata) and four species of Senecio.* Master of Science, University of Canterbury, Christchurch.

Woodward, G., & Hildrew, A. G. (2001). Invasion of a stream food web by a new top predator. *Journal of Animal Ecology, 70*(2), 273-288.

Wootton, J. T. (1994a). The nature & consequences of indirect effects in ecological communities. *Annual Review of Ecological Systematics, 25,* 443-466.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., et al. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science, 314*(5800), 787-790. doi: 10.1126/science.1132294

Zalba, S. M., Sonaglioni, M. I., Compagnoni, C. A., & Belenguer, C. J. (2000). Using a habitat model to assess the risk of invasion by an exotic plant. *Biological Conservation, 93*(2), 203-208. doi: Doi: 10.1016/s0006-3207(99)00146-9

Zamora, R. (2000). Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. *Oikos, 88*(2), 442-447. doi: 10.1034/j.1600-0706.2000.880222.x

Zangerl, A. R., Huang, T., McGovern, J. L., & Berenbaum, M. R. (2002). Paradoxical host shift by *Depressaria pastinacella* in North America: is enemy-free space involved? *Oikos, 98*(3), 431-436.

Zedler, J. B., & Kercher, S. (2004). Causes and Consequences of Invasive Plants in Wetlands: Opportunities, Opportunists, and Outcomes. *Critical Reviews in Plant Sciences, 23*(5), 431 - 452.

Zou, J., Rogers, W., & Siemann, E. (2008). Increased competitive ability and herbivory tolerance in the invasive plant Sapium sebiferum. *Biological Invasions, 10*(3), 291-302.

Zwölfer, H., & Harris, P. (1971). Host Specificity Determination of Insects for Biological Control of Weeds. *Annual Review of Entomology, 16*(1), 159-178. doi: doi:10.1146/annurev.en.16.010171.001111

Zwölfer, H., & Harris, P. (1984). Biology and host specificity of *Rhinocyllus conicus* (Fröl.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans* L. *Zeitschrift Fuer Angewanate Entomologie, 97*, 36-62.

Appendix A

Senecio Data Sources (Chapter 3)

A.1 Overview

In this section I want to convey my appreciation to the entities and individuals that allowed me to use their *Senecio* collection data in my Ph.D. project. The *Senecio* and *J. vulgaris* records that I used in Chapter 3 came from the herbarium (A.2) and vegetation survey (A.3) sources listed below. All data sets used from the public access (A.3.1.1) and restricted access (A.3.1.2) lists of the National Vegetation Survey Database are listed as well, with specific acknowledgement of the custodial entities and individuals that granted permission to use their restricted access data (A.3.1.3)

A.2 Herbarium Data Sources

The Allen Herbarium (**CHR**), The Auckland University Herbarium (**AK**), National Forestry Herbarium (**NZFRI**), Museum of New Zealand/TePapa Tongarewa Herbarium (**WELT**), Lincoln University Herbarium (**LINC**), University of Waikato Herbarium (**WAIK**), Dame Ella Campbell Herbarium (**MPN**), The British Museum (**BM**).

A.3 Vegetation Survey Databases

Department of Conservation BioWEB Database (**BWEB**), National Vegetation Survey Database (**NVS**).

A.3.1 NVS Data Soures by Individual Study Name

A.3.1.1 Public Access Data Sets

AORANGI FOREST PARK FOREST 1979-1980, AORANGI FOREST PARK FOREST 1983-1984, AORANGI FOREST PARK FOREST 1985-1986, ASHLEY/PUKETERAKI FOREST 1984, BIG BUSH FOREST 1983, BIRCHWOOD WETLAND 2009-2009, BLUE MOUNTAIN EXCLOSURES FOREST 1980-1980, CAMP CREEK FOREST 1982-1983, CAMP CREEK FOREST 1983-1984, CDRP EARNCLEUGH STATION 2008-2008, COBB FOREST 1986, COLERIDGE FOREST 1987-1988, DUNSTAN FOREST 1984-1985, ERUA STATE FOREST EXCLOSURES FOREST 1984, FAREWELL SPIT 2008-2008, FIORDLAND NTH FOREST 1969-1970, FOX RIVER FOREST 1982, FYFFE-MOUNT FOREST 1980, GRANITE HILL FOREST 1983, HOHONU FOREST 1973-1974,

`

HOKITIKA FOREST 1971-1972, HOKITIKA FOREST 1985-1986, HOKITIKA RIVER FOREST 1983-1986, HOWARD ECOLOGICAL AREA FOREST 1983-1984, HOWLONG - IKAWHENUA RANGE FOREST 1997, HOWLONG - MATEMATEAONGA FOREST 1996-2004, HUNDALEE FOREST 1997, HURUNUI SOUTH FOREST 1986-1987, KAIKOURA FOREST 1966-1967, KAIKOURA FOREST 1983, KAIMAI EXCLOSURES FOREST 1980-1981, KAIMAI FOREST 1974, KAIMANAWA/WAIPAKAHI FOREST 1983-1984, KAIMANAWA/WINDFALL FOREST 1983-1984, KARAMEA FOREST 1984-1985, KAWEKA - MANGATAINOKA EXCL FOREST 1982, KAWEKA MIXED 1981-1982, KNOBS FLAT 2008-2008, LONGWOOD FOREST 1977-1978, MARATOTO FOREST 1982, MCKENZIE MIXED 1984, NELSON - MURCHISON EXCL FOREST 2000, NGAUMU FOREST 1983-1984, NORTHLAND/WAIKARE E.A. FOREST 1984, NYDIA SADDLE - MAHOE FOREST 1994, OLD MAN FOREST 1983-1985, OXFORD-MOUNT FOREST 1985-1986, PAKAHI FOREST 1985-1986, PAPAROA FOREST 1985, PELORUS FOREST 1983, POULTER FOREST 1984, PUREORA EXCLOSURES FOREST 1986, PUREORA FOREST 1982-1983, PUREORA FOREST 1986, RAKAIA/MATHIAS FOREST 1986-1987, RAUKUMARA EXCLOSURES FOREST 1985, RIMUTAKA FOREST 1984, RIMUTAKA FOREST 1985-1986, ROCKY HILLS FOREST 1984, ROTOEHU FOREST 1979-1980, ROTORUA LAKES FOREST 1983-1984, ROTORUA LAKES FOREST 1999, RUAHINE (TUKITUKI) FOREST 1983, RUAHINE NORTH/KAWEKA RUAHINE FOREST 1983, RUAHINE-NORTH FOREST 1983, RUAHINE-POHANGINA FOREST 1983, RUAHINE-POHANGINA FOREST 1996, S. W. M. E. P. FOREST 1983-1985, S. W. M. E. P. MAHITAHI RIVER FOREST 1984-1985, S. W. M. E. P. MOERAKI FOREST 1985, S. W. M. E. P. PARINGA-OTOKO FOREST 1984-1985, STEWART ISLAND EXCLOSURES FOREST 1979, STEWART ISLAND EXCLOSURES FOREST 1980, STEWART ISLAND NORTH (STEWRT) 2008-2009, TAIPO RIVER FOREST 1983-1984, TAKITIMU MIXED 1961-1962, TARAMAKAU FOREST 1968-1969, TARAMAKAU FOREST 1978-1979, TARAMAKAU FOREST 1992, TARANAKI-NORTH FOREST 1983-1984, TARARUA FOREST 1974-1975, TARARUA FOREST 1983-1984, TARARUA FOREST 1984-1985, TAWARAU EXCLOSURES FOREST 1993-1994, THREE KINGS ISLANDS FOREST 1996, TONGARIRO FOREST 1983-1984, UREWERA EXCLOSURES FOREST 1980-1981, UREWERA-SOUTH FOREST 1980-1981, UREWERA-SOUTH FOREST 1981-1982, UREWERA/WAIKARE FOREST 1980-1981, WAIAU FOREST 1980-1981, WAIMAKARIRI FOREST 1983-1984, WAIMANGARARA FOREST 1985-1986, WAIPAPA MIXED 1983-1984, WAIPORI FOREST 1978, WAIPOUA FOREST 1984-1985, WAITAANGA FOREST 1994, WAITAKI

`

FOREST 1973-1974, WAITAKI FOREST 1985-1986, WAITAKI GRASSLAND 1985-1986, WANGANUI N.P. FOREST 1986-1987, WANGANUI RIVER FOREST 1983, WELLINGTON LND DISTRICT FOREST 2003-2004, WELLINGTON LND DISTRICT FOREST 2004-2005, WHIRINAKI FOREST 1979-1980, WOODHILL FOREST 1983-1984.

A.3.1.2 Restricted Access Data Sets

ADAPTIVE MANAGEMENT OF DEER (DOC) FOREST 2006, ARROWSMITH FOREST 1985, AVOCA KANUKA MIXED 2008, BANKS PENINSULA OUTCROPS MIXED 2001, BLENHEIM ECOLOGICAL DISTRICT PNAP SURVEY MIXED 2001, BOUNDARY STREAM EXCLOSURES FOREST 1997, BOUNDARY STREAM SCENIC RESERVE FOREST 1999, CAPE JACKSON BIODIVERSITY ASSESSMENT MIXED 2007, CAPLES/GREENSTONE FOREST 1997, CARNEY'S CREEK MIXED 1991, CASS FOREST 1988, CHEVIOT SCRUB 1994, COLERIDGE FOREST 1987-1988, CRAIGIEBURN FOREST 1987-1989, DANSEY FOREST 1989-1990, DUNSTAN FOREST 1984-1985, EBEX - HINEWAI SCRUB 2005, EBEX AUDIT - KURUNUI SCRUB 2006, FIORDLAND NTH FOREST 1998, FLAXBOURNE ECOLOGICAL DISTRICT PNA SURVEY MIXED 2001-2002, FOXTON FOREST 1989-1991, FYFFE-MOUNT FOREST 2007-2008, GLENHOPE (TOPPINGS PROPERTY) FOREST 1996, GRASMERE ECOLOGICAL DISTRICT PNAP SURVEY MIXED 2001, HAAST/ARAWATA FOREST 1998-2000, HAKATERE FOREST 1984-1985, HARATA-MOUNT FOREST 1988, HILLERSDEN ECOLOGICAL DISTRICT PNAP SURVEY MIXED 2002-2003, HUNDALEE FOREST 1997, HUXLEY FOREST 1987-1988, KAIKOURA FLOODPLAIN SUCCESSION STUDY MIXED 2001, KAIMANAWA-NORTH FOREST 1987-1988, KAKAHU FOREST 2002, KAWEKA - LOTKOW EXCL FOREST 2001, KAWEKA FOREST 1998-2000, KOKATAHI MIXED 1999, LINDIS MIXED 1984-1985, MANAWATU PLAINS FOREST 1993, MANORBURN GRASSLAND 1989, MATAITAI ECOMONITORING FOREST 2002-2003, MATEMATEAONGA FOREST 1995, MATHIAS FOREST 1989, MCKENZIE MIXED 1984, MOLESWORTH MIXED 1987, MOTU FOREST 1983-1984, MOTUNAU SCRUB 1994, MT HUTT FOREST 1988-1989, NELSON-WEST MIXED 1982-1983, NELSON-WEST/ALPINE GRASSLAND 1982-1983, NELSON-WEST/MATIRI SLIPS MIXED 1982-1983, NELSON-WEST/PERMANENT FOREST 1982-1983, NELSON-WEST/VALLEY GRASSLAND 1982-1983, OLD MAN FOREST 1983-1985, PAHIATUA FOREST 1991, PENCARROW FOREST 2004-2005, PISA FOREST 1984-1985, PUKEAMARU FOREST 1964-1985, PUREORA EXCLOSURES FOREST 1993, PUREORA FOREST 1993, RANGITIKEI FOREST 1993,

`

ROCKY HILLS AND REWA BUSH FOREST 2005, ROWALLAN BIRD FOREST 1983, RUAHINE STATE FOREST EXCL FOREST 1996, SECRETARY ISLAND FOREST 2003-2004, SOUTH ISLAND COASTAL MIXED 1997-1998, TARANAKI, NORTH FOREST 1985-1986, TARINGATURA FOREST 1996, TE HOE FOREST 2002, TIMARU MIXED 1998-1999, TURANGA FOREST 1990, TURNBULLS BUSH FOREST 2003, TWO THUMB FOREST 1985, UPPER WAITAKI BASIN RIVERBED GRASSLAND 2002-2003, UREWERA EXCLOSURES FOREST 1997, WAIPORI FOREST 1991, WAITUTU FOREST 1996-1998, WANAKA FOREST 1984, WHAKAPAPA ISLAND HABITAT INVENTORY FOREST 2006-2007, WHANGANUI NAT. PARK: MANGAWAITI EAST FOREST 2006, WITHER HILLS ECOLOGICAL DISTRICT PNAP SURVEY MIXED 2002, WOODSIDE FOREST 2000.

A.3.1.3 Restricted Access Data Acknowledgements

Peter Bellingham, *Landcare Research* (KAIKOURA FLOODPLAIN SUCCESSION STUDY 2001 MIXED, KOKATAHI 1999 MIXED); **Robert Miller** and **Alan Griffths**, *MAF* (GLENHOPE (TOPPINGS PROPERTY) 1996 FOREST); **George Ledgard**, *Landcare Research* (FIORDLAND NTH 1998 FOREST, SECRETARY ISLAND 2003-04 FOREST, TARINGATURA 1996 FOREST, TURNBULLS BUSH 2003 FOREST, WAITUTU 1996-98 FOREST); **Glenn Stewart**, *NZRCUE* (MOUNT HARATA 1988 Forest); **Clare Veltman**, *DOC* (ADAPTIVE MANAGEMENT OF DEER (DOC) FOREST 2006); **Owen Spearpoint**, *Greater Wellington Regional Council* (PENCARROW FOREST 2004-2005); **Alan Rose**, *MAF* (NELSON, WEST MIXED 1982-1983, AWATERE 1993 FOREST); **Alana Lawrence** and **Nicola Ethridge**, *Tongariro Taupo Conservancy* (KAIMANAWA, NORTH FOREST 1987-1988, WHAKAPAPA ISLAND HABITAT INVENTORY FOREST 2006-2007); **Jenny Hurst**, *Landcare Research* (FYFFE, MOUNT 2007-2008); **Colin Meurk**, *Landcare Research* (TIMARU 1998-99 MIXED); **John Lyall**, *DOC West Coast Tai Poutini Conservancy* (HAAST/ARAWATA 1998-00 FOREST); **Bruce Kyle**, *DOC Otago Conservancy* (CAPLES/GREENSTONE 1997 FOREST, DUNSTAN 1984-85 FOREST, LINDIS 1984-85 MIXED, MANORBURN 1989 GRASSLAND, NOKOMAI 1986-87 FOREST, OLD MAN 1983-85 FOREST, PISA 1984-85 FOREST, UMBRELLA 1985-86 FOREST, WAIPORI 1991 FOREST, WANAKA 1984 FOREST); **Simon Moore**, *DOC Nelson-Marlborough Conservancy* (BLENHEIM ECOLOGICAL DISTRICT PNAP SURVEY 2001, FLAXBOURNE ECOLOGICAL DISTRICT PNA SURVEY 2001-02, GRASMERE ECOLOGICAL DISTRICT PNAP SURVEY 2001, HILLERSDEN ECOLOGICAL DISTRICT PNAP SURVEY 2002-03, MOLESWORTH 1987 MIXED,

`

WITHER HILLS ECOLOGICAL DISTRICT PNAP SURVEY 2002, HUNDALEE FOREST 1997); **Robin Dunn**, *Marlborough District Council* (WITHER HILLS 2000-01 MIXED, WITHER HILLS 2001-02 MIXED); **Andrew Grant**, *DOC Canterbury Conservancy* (ARROWSMITH 1985 FOREST, CASS 1988 FOREST, CHEVIOT 1994 SCRUB, COLERIDGE 1987-88 FOREST, CRAIGIEBURN 1987-89 FOREST, HAKATERE 1984-85 FOREST, HURUNUI 2000-01 FOREST, HUXLEY 1987-88 FOREST, MATHIAS 1989 FOREST, MCKENZIE 1984 MIXED, MOTUNAU 1994 SCRUB, MT HUTT 1988-89 FOREST, TWO THUMB 1985 FOREST, UPPER WAITAKI BASIN RIVERBED 2002-03 GRASSLAND); **Caroline Thompson**, *Landcare Research* (CARNEY'S CREEK 1991 MIXED); **Susan Wiser**, *Landcare Research* and **private landowners** (BANKS PENINSULA OUTCROPS 2001 MIXED, LILLBURN 1998 FOREST, TUHOE RIMU REMOVAL STUDY FOREST 2004); **Eric Spurr**, *Landcare Research* (ROWALLAN BIRD 1983 FOREST); **Robert Allen**, *Landcare Research* (WOODSIDE 2000 FOREST, HARPER/AVOCA FOREST 1985-1986, HARPER/AVOCA FOREST 1993-1994, HARPER/AVOCA FOREST 1999-2000, MATIERE FOREST FOREST 1999); **Brendon Christensen**, *DOC East Coast/Bay of Plenty Conservancy* (MOTU FOREST 1983-1984, PUKEAMARU FOREST 1964-1985, TE HOE FOREST 2002, TURANGA FOREST 1990, UREWERA EXCLOSURES FOREST 1997), **Alicia Warren**, *DOC Auckland Conservancy* (MATAITAI ECOMONITORING FOREST 2002-2003); **Geoff Rogers**, *DOC* (SOUTH ISLAND COASTAL MIXED 1997-1998), **Andrea Brandon**, *MFE* (MFE CARBON TRANSECT MIXED 1998-1999, NZICMS: MAIN 2000, NZICMS: MAIN 2002-2007, NZICMS: OTHER 2002-2007, NZICMS: RESTRICTED 2002-2007, MOAWHITU CNPS CARBON SEQUESTRATION SITE D'URVILLE ISLAND 2008-2008, OXFORD CNPS CARBON SEQUESTRATION SITE 2008-2009); **Ron Marriott,** *Queen Charlotte Wilderness Park* and **Fiona Carswell**, *Landcare research* (CAPE JACKSON BIODIVERSITY ASSESSMENT 2007); **James Griffiths**, *DOC Wellington-Hawke's Bay Conservancy* (BOUNDARY STREAM EXCLOSURES FOREST 1997, BOUNDARY STREAM SCENIC RESERVE FOREST 1999, KAWEKA - LOTKOW EXCL FOREST 2001, KAWEKA FOREST 1998-2000, PAHIATUA FOREST 1991, ROCKY HILLS AND REWA BUSH FOREST 2005, RUAHINE STATE FOREST EXCL FOREST 1996); **Oliver Gansell**, *DOC Waikato Conservancy* (PUREORA EXCLOSURES FOREST 1993, PUREORA FOREST 1993); **Bill Fleury**, *DOC Wanganui Conservancy* (FOXTON FOREST 1989-1991, MANAWATU PLAINS 1993, ATEMATEAONGA FOREST 1995, RANGITIKEI FOREST 1993, TARANAKI, NORTH FOREST 1985-1986, WHANGANUI NATIONAL PARK: MANNGAWAIITI EAST FOREST 2006); **Ian Dickie**, *Landcare*

`

Research (AVOCA KANUKA MIXED 2008); **John Talbot**, *South Canterbury Conservation Trust* (KAKAHU FOREST 2002).