

Chapter 1 – General Introduction

Invasive plants (see glossary for terms) are a major conservation concern and are one of the main factors contributing to environmental degradation. Non-native plants can have serious environmental, economic and social impacts in Australia (AWS 2006). Plant invasions can dramatically alter native habitats by changing the species diversity, trophic structure and function of communities and ecosystems (Walker & Smith 1997; Prieur-Richard 2000). There are several key ways in which plant invaders can alter native species diversity and composition: a) by competing with and displacing native species (e.g. Minchinton *et al.* 2006) b) by facilitating the movement of other invading organisms (Holway 2005) c) by changing fire regimes (e.g. Woods 1997) and d) by altering pollination syndromes (Woods 1997; Brown & Mitchell 2001; Levine *et al.* 2003; Moragues & Traveset 2005). These changes can affect organisms at higher trophic levels through the loss of food and shelter (Levine *et al.* 2003). Ecosystem function may be altered through changes in nutrient cycling (Meyerson *et al.* 2000; Walker & Smith 1997) or the hydrological regime (Walker & Smith 1997), which can further influence the rate of community recovery following disturbance (Walker & Smith 1997; Woods 1997).

Over 29,000 plant species have been introduced into Australia, accounting for 15% of the Australian flora (DAFF 2010). Approximately 2700 of these species have become naturalised, establishing self-sustaining populations in the natural environment (DAFF 2011). Around 400 introduced plants in Australia have been declared noxious or 'invasive' and are officially recognised as problem species (AWS 2006). Plants achieve this status when they have established, or have the potential to establish, significant populations with subsequent environmental and socioeconomic impacts (AWS 2006). It is also estimated that on average 10 plant species establish naturalised populations in

Australia each year and that 70% of the naturalised species in Australia are likely to have escaped from private or public gardens (Groves *et al.* 2005). Some non-native plants that have established small naturalised populations but have not yet spread widely, known as ‘sleeper weeds’, may also have the potential to spread and cause damage if suitable conditions arise (AWS 2006). Some introduced species, however, may never establish invasive populations. These non-invasive species may exploit under-utilised resources, or occupy empty ecological niches within a disturbed community with few consequences for the native components of the ecosystem (Elton 1958; Woods 1997). Alternatively, some plant introductions can have positive effects on native species (reviewed by Schlaepfer *et al.* 2011). For example non-natives can maintain higher levels of pollinator activity (Woods 1997), act as pioneers for degraded land (Ewel & Putz 2004), and provide favourable habitat for rare species (e.g. *Lantana* in Australia and *Tamarix* in the United States as a habitat for rare birds; Schlaepfer *et al.* 2001; DEC 2005; NSW Scientific Committee 2008). Not all non-native plants, therefore, may require management.

Plants that become invasive can have major economic impacts, which in Australia amounts to over \$4 billion annually in lost agricultural productivity and costs associated with control (Sinden *et al.* 2005; AWS 2006; DAFF 2010). Weeds may be detrimental to agriculture by competing with food crops for nutrients and sunlight, increasing production costs of mechanical and chemical control, reducing crop yields, harbouring pest species, contaminating crop seed, reducing foraging areas for livestock and causing stock death or reduction in animal condition (Sinden *et al.* 2005). The cost of weeds to the natural environment is difficult to calculate, but has been estimated as similar or even greater than the estimates for agriculture (AWS 2006; DSEWPC 2010). Other costs associated with plant invasions include those attributed to impacts on human health through allergy. For example, weeds such as parthenium weed, ragweed, rye grass and privet may trigger

asthma and other respiratory diseases while others may be toxic or cause skin irritation (AWS 2006). Invasive plants may also interfere with outdoor activities and alter hydrology by choking waterways (AWS 2006).

The significant ecological and economic implications of biological invasions have led to increasing research attention on trying to understand the characteristics of successful invaders (Daehler & Carino 2000). Understanding which biological traits are the best predictors of invasion success may help to identify which species should be the subject of stringent quarantine measures, as well as help to develop more effective management of existing invaders.

Several hypotheses have been proposed to explain why some species become successful invaders (for reviews see Richardson & Pyšek 2006; Pyšek & Richardson 2007; Catford *et al.* 2009) and considerable research has focused on identifying particular biological traits associated with invasion. These traits include life history characteristics, range size, and introduction history (Richardson & Pyšek 2006; Pyšek & Richardson 2007; Catford *et al.* 2009). Despite some progress in identifying the mechanisms and traits associated with invasion success for single species, the complexity of interactions between invaders and recipient communities still makes predicting patterns of invasion difficult (Lodge 1993). The research described in this thesis aims to integrate several hypotheses about determinants of invasion success. In particular, this research focuses on the roles of (1) phylogenetic relationships between the invader and recipient community (2) natural enemies in the invaded community and (3) the time taken for the invertebrate community to adapt to the invader. Each of these roles is discussed below.

Non-native plant invasion in Australia has increased greatly since European settlement (Adair & Groves 1998). Australia has a high degree of endemism resulting from a long

history of isolation and novel environmental conditions. The distribution of Australian vegetation is largely influenced by high variability in rainfall, topography and infertile soils (Turnbull 1986). The Australian environment provides us with a unique opportunity to research aspects of invasion biology, particularly because many non-native species are likely to be phylogenetically distinct from Australian native species. Biogeographic comparisons of successful non-native species to less successful non-native and native plants further provides us with an opportunity to better understand the mechanisms behind the success of invasive species in novel environments.

Role of phylogeny and natural enemies

The idea that phylogenetic relationships between species may be important in determining the naturalisation and establishment of non-native species was first put forward by Charles Darwin in the “Origin of Species” (Darwin 1859). Now termed Darwin’s ‘naturalisation’ hypothesis (Daehler 2001), this idea proposes that upon introduction, non-native species are less likely to naturalise if there are congeneric native relatives present (Daehler 2001). Unrelated species are less likely to exhibit strong competitive interactions because their environmental requirements may be more dissimilar (Daehler 2001). Unrelated species can therefore exploit under-utilised resources or empty ecological niches in their new environment. Phylogenetically unrelated non-native species may therefore be more successful as invaders than closely related species.

An alternative *mechanism* to the competitive interactions assumption predicted by the naturalisation hypothesis, may be that natural enemy attack would be lower on distantly related species, because host switching by specialised herbivores is mostly observed between closely related non-native and native species (Connor *et al.* 1980; Thomas *et al.* 1987; Keane & Crawley 2002; Carol *et al.* 2005). The Enemy Release Hypothesis (ERH)

suggests that a plant species may spread rapidly due to being liberated from co-evolved herbivores and pathogens (for reviews see Maron & Vila 2001; Colautti *et al.* 2004). This idea is integral to the theory and success of biological control programs (Keane & Crawley 2002). As herbivores can mediate plant competition (Keane & Crawley 2002) by suppressing plant growth and reproduction for example, introduced plants suffering low rates of enemy attack can thereby gain a competitive advantage over native plants. Reduced damage on introduced plants may mean that resources lost to natural enemies or used in defence against herbivores may be reallocated to growth and reproduction. This is likely to be more pronounced in species that are distantly related to the native recipient community.

Darwin's naturalisation hypothesis and the ERH tend to have been tested as separate questions although they are clearly not mutually exclusive. Niche exploitation as part of the naturalisation hypothesis could also include exploitation of enemy-free space. A few recent studies have directly linked the naturalisation hypothesis and the ERH to investigate whether relatedness of non-native plants and their natural enemies may determine invasiveness via interaction with natural enemies such as herbivores and pathogens (Cappuccino & Carpenter 2005; Ricciardi & Ward 2006; Dawson *et al.* 2009). In these studies, the species being compared were in separate genera or families. To date, only two studies that estimate evolutionary divergence have used well-resolved phylogenies to investigate the role of phylogenetic relationships in determining the likelihood of enemy release in non-native plants (Hill & Kotanen 2009; Hill & Kotanen 2010). Several studies have made comparisons between non-native and native congeneric pairs (Schierenbeck *et al.* 1994; Agrawal & Kotanen 2003; Agrawal *et al.* 2005; Cincotta *et al.* 2009; Chun *et al.* 2010). As introduced species within a genus can have a variety of impacts ranging from being relatively innocuous to highly invasive, understanding how important phylogenetic

relationships are at a sub-generic level is essential in underpinning how important release from natural enemies is as a mechanism behind the successful invasion of non-native plants.

In this study I investigate the predictive power of phylogeny to explain the level of damage suffered by invasive species. The first investigation focused on this prediction at the level of genus and above (Chapter 2), and the second investigation examined this question at the level of species within a genus (Chapter 3).

Role of time since establishment

The formation of a herbivore assemblage on a novel host plants requires a certain amount of time (Strong *et al.* 1984). As the time since introduction increases, natural enemies such as herbivores are expected to gradually accumulate, with an increasing proportion of the assemblage as a whole being specialised; the fitness of non-native plants may thus be reduced over time (Siemann *et al.* 2006; Hawkes 2007). The rate at which the invertebrate assemblage colonises non-native species may be a result of two main factors: the time since introduction and the phylogenetic relationship between the invader and native species within the invaded community (as noted above). Plant relatedness is important because host choice by insect herbivores is largely driven by plant chemistry. Closely related plant species tend to be more similar in chemistry, thus providing similar cues for feeding and oviposition (Strong *et al.* 1984; Tallamy 2004). Evidence for phylogenetic-mediated host switching has been found between closely related species (i.e. within genera), but also at higher taxonomic levels (Connor *et al.* 1980; Thomas *et al.* 1987; Keane & Crawley 2002; Palmer *et al.* 2004; Carol *et al.* 2005). The longer the time since introduction, the more opportunity there exists for invertebrates to adapt to new hosts including, presumably, species that are relatively distantly related to the native plant community. This research

investigates how long it takes for the invertebrate community to adapt to and colonise invaders. Understanding how quickly non-native species are colonised over time may be important in determining whether enemy release is limited to the early stages of invasion.

General aims of thesis

The aim of this research is to examine the role of herbivory and insect assemblages in invasion biology. My research is directed towards identifying traits that may be useful for making generalisations about the success of invasive plants. This thesis consists of three data chapters, described below. Each of these chapters has been written as stand alone papers with each prepared in a form for publication.

Chapter 2 - Australian family ties: does a lack of relatives help invasive plants escape natural enemies?

This paper investigated the importance of phylogenetic relationships for predicting herbivore and pathogen damage on invasive species. The amount and type of damage from herbivores and pathogens was compared among fourteen invasive, non-native species on the east coast of Australia. These species were selected to represent a range of phylogenetic relationships to those of the native Australian plant community and included: (1) invasive plants with native congeners (2) invasive plants that had native species in the same region within the same family (hereafter referred to as con-familial) and (3) invasive species where the family does not naturally occur in Australia (hereafter referred to as non-familial). This paper has been accepted for publication in *Biological Invasions*.

Chapter 3 - *Can phylogenetic relationships within genus indicate the likelihood of enemy release of an invader?*

This study extended the analysis of the previous chapter to examine if phylogenetic relationships at the subgeneric level in the genus *Senecio* can predict herbivore and pathogen damage. *Senecio* is an ideal genus to examine the role that insect herbivores play in affecting invasive, non-invasive and native species. The genus has 87 native and ten introduced species present in Australia. Two of the introduced species have been declared noxious in NSW (*S. madagascariensis* Poir., and *Jacobaea vulgaris* Gaertn., formerly *Senecio jacobaea* L.; Pelser *et al.* 2007), while others have become locally or rarely naturalised. The genus has been the focus of recent broad-scale phylogenetic and taxonomic treatments (Thompson 2006; Pelser *et al.* 2007). This study compares damage, and the abundance and richness of the herbivore assemblage across five native and five non-native naturalised *Senecio* species. Four of the non-native species are rarely or locally naturalised (non-invasive), having not been declared as invasive, and one is the invasive species *Senecio madagascariensis* Poir.

Chapter 4 - *Does time since introduction influence enemy release of an invasive weed?*

The rate of colonisation of exotic plants by native invertebrates (both herbivores and non-herbivores) over time was examined using *Senecio madagascariensis*. This species was first introduced into the Hunter Valley around 1918 and has since spread along the east coast of Australia, extending from south-east Queensland to Victoria (>1000 km). It has been declared a noxious weed in New South Wales, Queensland and the Australian Capital Territory (Parsons & Cuthbertson 1992). Using a space for time substitution, we sampled external and internal invertebrate herbivores and measured leaf damage at multiple sites, encompassing the current latitudinal range of *S. madagascariensis* (~1000 km), including

sites to both the north and south of the point of introduction. We also sampled herbivores and measured foliar damage on the closely-related native congener *S. pinnatifolius* var. *pinnatifolius* A. Rich. at the same sites. This species was used as a comparison for evaluating the ERH and also served as a control to investigate other factors that can influence herbivore assemblages, such as climate variation along the latitudinal gradient.

Chapter 5 - Conclusions

The final chapter summarises the major findings, describes future directions and discusses the implications for management of non-native species.

| Glossary |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Weed: a native or non-native plant requiring management to reduce its influence on the environment and economy. Weeds can also be known as invasive plants. |
| Invasive plant: a plant declared noxious or 'invasive' and officially recognised as a problem species. |
| Non-native / Exotic: an introduced species that is outside of its known native range often from human mediated transport. |
| Naturalised: a non-native plant that has established self-sustaining populations in the natural environment. |
| Sleeper weeds: non-native plants that have established small naturalised populations that have not yet spread widely but have the potential to spread and cause damage if suitable conditions arise. |
| Non-invasive: an introduced species that has not established invasive populations with few consequences for the native components of the ecosystem. |
| Darwin's naturalisation hypothesis: Introduced species that are taxonomically distinct from the recipient community may be more successful as invaders because they are less likely to compete with the native community as their environmental requirements may be more dissimilar. |
| Enemy release: a non-native species that may experience a decrease or loss of the regulation of their natural enemies (consumers, pathogens and parasites) during their invasion into new areas. This can result in an increase of abundance and/or biomass. |
| Enemy Release Hypothesis: an important mechanism suggested for the success of an invasive species. A plant species may spread rapidly upon its introduction due to a decrease in their regulation by herbivores and pathogens. |
| Host switching: specialist species attacking a new host. |
| Specialist: a natural enemy that attacks a single plant species (monophagous) or a few closely related species (oligophagous). |
| Generalist: a natural enemy that attacks a wide range of species (polyphagous). |

References

- Adair R, Groves, R (1998) Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology. Environment Australia, Canberra
- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters* 6:712-715
- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86:2979-2989
- AWS (2006) A national strategy for weed management in Australia. Australian Weeds Strategy. Natural Resource Management Ministerial Council, Australian Government Department of the Environment and Water Resources, Canberra ACT.
www.weeds.gov.au/publications/strategies/pubs/weed-strategy.pdf Accessed July 2011
- Brown BJ, Mitchell RJ (2001) Competition for pollination: Effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129:43-49
- Cappuccino N, Carpenter D (2005) Invasive exotic plants suffer less herbivory than non-invasive exotic plants. *Biology Letters* 1:435-438
- Carroll SP, Loye JE, Dingle H, Mathieson M, Famula TR, Zalucki MP (2005) And the beak shall inherit - evolution in response to invasion. *Ecology Letters* 8:944-951
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15:22-40

- Chun YJ, van Kleunen M, Dawson W (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecology Letters* 13:937-946
- Cincotta CL, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biological Invasions* 11:379-388
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-733
- Connor EF, Faeth SH, Simberloff D, Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 5:205-211
- Daehler CC, Carino DA (2000) Predicting invasive plants: prospects for a general screening system based on current regional models. *Biological Invasions* 2:93-102
- Daehler CC (2001) Darwin's naturalisation hypothesis revisited. *American Naturalist* 158: 324-330
- Darwin CR (1859) *The Origin of Species by Means of Natural Selection*. John Murray, London
- Dawson W, Burslem DFRP, Hulme PE (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions* 15:141-147
- DAFF (2010) *Weeds Management*. Department of Agriculture Fisheries and Forestry. <http://www.daff.gov.au/natural-resources/invasive/weeds> Accessed July 2011

DAFF (2011) Sleeper Weeds. Department of Agriculture Fisheries and Forestry.

<http://www.daff.gov.au/brs/land/weeds/sleeper> Accessed July 2011

DEC NSW (2005) Black-breasted Button-quail *Turnix melanogaster*. In: Threatened species: species, populations & ecological communities of NSW. Department of Environment and Conservation.

<http://www.threatenedspecies.environment.nsw.gov.au/tsprofile/profile.aspx?id=10814>

Accessed August 2011

DSEWPC (2010) Impact of Weeds. Department of Sustainability, Environment, Water, Population and Communities. <http://www.weeds.gov.au/weeds/why/impact.html> Accessed August 2011

Elton CS, (1958) The Ecology of Invasion by Animals and Plants. Methuen, London

Ewel JJ, Putz FE (2004) A place for alien species in ecosystem restoration. *Frontiers in Ecology and the Environment* 27:354-360

Groves RH, Boden R, Lonsdale WM (2005) Jumping the garden fence: invasive garden plants in Australia and their environmental and agricultural impacts. CSIRO report prepared for WWF-Australia. WWF-Australia, Sydney

Hawkes C.V (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist* 170:832-843

Hill SB, Kotanen PM (2009) Evidence that phylogenetically novel non-native plants experience less herbivory. *Oecologia* 161:581-590

- Hill SB, Kotanen PM (2010) Phylogenetically structured damage to Asteraceae: susceptibility of native and exotic species to foliar herbivores. *Biological Invasions* 12:3333-3342
- Holway DA (2005) Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation* 121:561-567
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *TRENDS in Ecology and Evolution* 17:164-170
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London* 270:775-781
- Lodge DM (1993) Biological invasions: Lessons for ecology. *TRENDS in Ecology and Evolution* 8:133-137
- Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361-373
- Meyerson LA, Saltonstall K, Windham L, Kiviat E, Findlay S (2000) A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management* 8:89-103
- Minchinton TE, Simpson JC, Bertness MD (2006) Mechanisms of exclusion of native coastal marsh plants by an invasive grass. *Journal of Ecology* 94:342-354
- Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biological Conservation* 122:611-619

- NSW Scientific Committee (2008) Bush-hen *Amaurornis olivaceus*. Review of current information in NSW. August 2008. Unpublished report arising from the Review of the Schedules of the Threatened Species Conservation Act 1995. NSW Scientific Committee, Hurstville
- Palmer WA, Day MD, Dhileepan K, Snow EL, Mackey AP (2004) Analysis of the non-target attack by the lantana sap-sucking bug, *Aconophora compressa* and its implications for biological control in Australia. In: Sindel BM, Johnson SB (eds) Proceedings of the 14th Australian Weeds Conference, Weed Society of New South Wales, Sydney, pp 341-344
- Pelser PB, Nordenstam B, Kadereit JW, Watson LE (2007) An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56:1077-1104
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: Where do we stand? In: Nentwig W (ed) Biological invasions, Ecological Studies 193. Springer-Verlag, Berlin/Heidelberg, pp 97-126
- Prieur-Richard AH, Lavorel S (2000) Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1-7
- Ricciardi A, Ward JM (2006) Comment on "Opposing effects of native and exotic herbivores on plant invasions". *Science* 313:298
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30:409-431
- Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75:1661-1672

- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conservation Biology* 25:428-437
- Siemann E, Rogers WE, Dewalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. *Proceedings of the Royal Society B-Biological Sciences* 273:2763-2769
- Sinden J, Jones R, Hester S, Odom D, Kalisch D, James R, Cacho O, Griffith G, (2005) The economic impact of weeds in Australia. *Plant Protection Quarterly* 20:25-32
- Strong DR, Lawton JH, Southwood R (1984) *Insects on Plants: Community patterns and mechanisms*. Blackwell Scientific Publications, Oxford London
- Tallamy DW (2004) Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692
- Thomas CD, Ng D, Singer MC, Mallet JLB, Parmesan C, Billington HL (1987) Incorporation of a European weed into the diet of a North American herbivore. *Evolution* 41:892-901
- Thompson IR (2006) A taxonomic treatment of tribe Senecioneae (Asteraceae) in Australia. *Muelleria* 24:51-110
- Turnbull JW (1986) Australian vegetation. In: Turnbull JW (ed) *Multipurpose Australian trees and shrubs: lesser-known species for fuelwood and agroforestry*. Canberra: Australian Centre for International Agricultural Research No. 14, pp 29-44
- Walker LR, Smith SD (1997) Impacts of invasive plants on community and ecosystem properties. In: Luken JO, Thieret JW (eds) *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, pp 69-85

Woods KD (1997) Community response to plant invasion. In: Luken JO, Thieret JW (eds)
Assessment and Management of Plant Invasions. Springer-Verlag, New York, pp 56-68

Chapter 2

Australian family ties: does a lack of relatives help invasive plants escape natural enemies?

Kerinne J. Harvey^{1*}, David A. Nipperess¹, David R. Britton², & Lesley Hughes¹

¹ Department of Biological Sciences, Macquarie University, North Ryde, NSW
Australia

² Entomology Collections, Australian Museum, Sydney, NSW, Australia

* Kerinne Harvey: Email: kerinne.harvey@gmail.com

Telephone: +612 9850 6279; Fax: +612 9850 8245.

Running headline: Relatives, insects and invasions

Accepted for publication in *Biological Invasions*

Abstract

Invasive plants may initially be released from natural enemies when introduced to new regions, but once established, natural enemies may accumulate. How closely related invasive species are to species in the native recipient community may drive patterns of herbivore and pathogen damage and therefore, may be important in understanding the success of some invasions. We compared herbivore and pathogen damage across a group of invasive species occurring in natural environments on the east coast of Australia. We examined whether the level of damage experienced by the invasive species was associated with the degree of phylogenetic relatedness between these plants and the native plants within the region. We found that phylogenetic distance to the nearest native relative was a good predictor of herbivore and pathogen damage on the invasive plants, explaining nearly 37% of the variance in leaf damage. Total leaf damage and the variety of damage types declined with increasing phylogenetic distance to the nearest native relative. In addition, as the phylogenetic distance to the nearest native relative increased, invasive species were colonised by fewer functional guilds and the herbivore assemblage was increasingly dominated by generalist species. These results suggest that invasive species that are only distantly related to those in the native invaded community may be released from specialist natural enemies. Our results indicate that the phylogenetic relatedness of invasive plants to species in native communities is a significant predictor of the rate of colonisation by the herbivore and pathogen community, and thus a useful tool to assess invasion potential.

Key words: invasive plants, enemy release hypothesis, naturalisation hypothesis, plant-insect interactions, herbivore and pathogen damage, phylogenetic relationships

Introduction

Invasion by non-native plants is a global threat to the natural environment with major economic consequences (D'Antonio & Meyerson 2002; Culliney 2005). Non-native plants can affect species diversity, trophic structure and the functioning of native communities and ecosystems (Walker & Smith 1997; Vitousek *et al.* 1997; reviewed by Prieur-Richard & Lavorel 2000). Many hypotheses have been proposed to explain the success of biological invasions (for reviews see Richardson & Pyšek 2006; Pyšek & Richardson 2007; Catford *et al.* 2009) and considerable research has focused on identifying particular plant traits associated with invasion success including life history characteristics, range size, and weed and introduction history (Richardson & Pyšek 2006; Pyšek & Richardson 2007; Catford *et al.* 2009); several of these traits are used within weed risk assessments (Weber *et al.* 2009). Despite some progress in identifying the mechanisms and traits associated with invasion success, the complexity of interactions between invaders and recipient communities makes predicting patterns of invasion difficult at a species level (Lodge 1993).

One characteristic that may be associated with invasion success is the degree to which the invader is related to other species in the invaded community. This idea was first put forward by Darwin (1859), who hypothesised that exotic species that are more closely related to native species in a newly colonised region may be less likely to become invasive. This idea, now known as the naturalisation hypothesis (Daehler 2001), is based on the notion that closely related species are less likely to become naturalised because they compete more strongly for similar resources than distantly related species (Daehler 2001). Tests of this hypothesis thus far have been equivocal. Some studies have concluded that introduced species are more successful if surrounded by plant species that were not closely related (Mack 1996; Rejmánek & Richardson 1996; Lockwood *et al.* 2001; Riccarrdi &

Atkinson 2004; Strauss *et al.* 2006), while others have found either no support (Lambdon & Hulme 2006; Ricciardi & Mottiar 2006; Lambdon 2008; Ricotta *et al.* 2010), or marginal support, depending on the introduction history (Diez *et al.* 2008), or the spatial and taxonomic scale assessed (Diez *et al.* 2008; Proches *et al.* 2008). In some communities, higher naturalisation rates in species with native congeners have occurred, suggesting that introduced congeners share some level of pre-adaptation to the conditions of the invaded region (Daehler 2001; Duncan & Williams 2002). In turn, this may outweigh the potential for strong competition between close relatives.

An alternate mechanism by which phylogeny may be important in determining the success of exotic species is through a release from natural enemies. The Enemy Release Hypothesis (ERH) suggests that upon introduction to a new region, a new plant species might spread rapidly because it is liberated from its co-evolved herbivores and pathogens (for reviews see Maron & Vila 2001; Colautti *et al.* 2004). Most tests of the ERH have either compared damage suffered by exotic plants in their native range to that in their introduced range (biogeographic comparisons), or have been community-based comparisons between invasive species and their native or non-invasive counterparts (for review see Colautti *et al.* 2004; and meta analysis by Liu & Stiling 2006). The ERH has generally been supported by biogeographic comparisons. In contrast, community-based analyses have yielded mixed results, finding evidence both for and against the ERH, or partial support depending upon seasons and years (e.g. Colautti *et al.* 2004; Liu & Stiling 2006). As host switching by specialised herbivores has been found between closely related non-native and native species (Connor *et al.* 1980; Thomas *et al.* 1987; Keane & Crawley 2002; Carol *et al.* 2005), the degree of relatedness of non-native species to co-occurring natives may be a contributing factor to whether the non-native species is released from natural enemies.

Few studies have directly linked the naturalisation hypothesis and the ERH to investigate whether phylogenetic relatedness, or the taxonomic isolation of invasive plants and their natural enemies, may assist some species to become more invasive than others. The studies that have investigated both hypotheses together have generally quantified the taxonomic isolation of non-native species based on the number of congeneric or con-familial native plants present in the recipient community, finding weak or no support (Cappuccino & Carpenter 2005; Ricciardi & Ward 2006; Dawson *et al.* 2009). Inconsistent results from different studies may be due to the fact that comparisons have been made across different spatial scales and between plants at varying stages of invasion. Few studies have used a phylogenetic approach that estimates relatedness to the nearest native relative based on their evolutionary divergence rather than taxonomic similarity (Hill & Kotanen 2010). For example, only Hill and Kotanen (2009, 2010) and Pearse and Hipp (2009) have used well-resolved phylogenies to determine whether phylogenetically distinct non-native species suffer less damage from natural enemies than closely related non-native species. Although weak trends, based on distance measures, were found in a common garden experiment (Hill & Kotanen 2009), there is still conflicting evidence as to whether release from natural enemies occurs in non-native taxa that are more phylogenetically distinct from other species in the recipient native community (Hill & Kotanen 2009; Hill & Kotanen 2010).

Interpretation of the naturalisation hypothesis should consider enemy release as a fundamental mechanism by which introduced plants become invasive. This is because closely related plants often present more similar chemical cues than those of unrelated plants, leading to the expectation that specialised herbivores and pathogens may shift onto close relatives of their host more readily than onto distantly or unrelated taxa (Connor *et al.* 1980; Strong *et al.* 1984; Weiblen *et al.* 2006; Gilbert & Webb 2007; Parker & Gilbert

2007). However, the types of damage incurred on non-native taxa closely related to the native community have not been compared to distantly related taxa. Further, the degree to which specialists, compared to generalists, colonise closely and distantly related non-native plants has received little attention. A recent review revealed that loss of fitness in specialist insects is greater than generalist insects and more pronounced with increasing phylogenetic distance from novel hosts (Bertheau *et al.* 2010).

Whether invasive plants may escape their natural enemies if they are distantly related to the plants in the invaded range may also depend on the types of insect herbivores most likely to have a suppressive impact. The success of introduced plants is attributed to escape from specialist natural enemies (Keane & Crawley 2002; Stastny *et al.* 2005), which may include endophagous insect herbivores (miners and gall formers). The invader is therefore more likely to encounter polyphagous (generalist) enemies (Maron & Vila 2001; Keane & Crawley 2002; Stastny *et al.* 2005) that are expected to have a relatively low impact and not impede growth (Stastny *et al.* 2005). While polyphagous herbivores are often the first to colonise introduced plant species, with ectophagous species being more common than endophagous (Strong *et al.* 1984; Liu & Stiling 2006), rarely do comparative studies examine the diversity, impact and type of functional damage by herbivores and pathogens (e.g. grazers, chewers, skeletonizers, sap-suckers, miners, seed feeders, gallers). To our knowledge, no previous studies have quantified both the impact and identity of the herbivore feeding guilds on introduced plants based on their level of relatedness to the recipient native community.

In this study, we compared herbivore and pathogen damage on several species of invasive plants in Australia, based on their level of relatedness to sympatric Australian native plant species. The extent of exotic plant invasion in Australia has increased greatly since European settlement, especially in areas of agricultural and urban development and

disturbance (Adair & Groves 1998). Australia's long history of isolation has resulted in a high incidence of endemism, and novel environmental conditions for non-native species. These conditions include relatively infertile soils, aridity, high evaporative water loss, and ecosystem dynamics largely driven by episodic events (Steffen *et al.* 2009). The Australian environment provides a unique opportunity to determine whether (i) invasive plants with closely related native plants suffer more damage than those with more distant relatives; (ii) the composition of damage types found on non-native species is associated with their phylogenetic relationships to Australian natives; and (iii) non-native species more closely related to the native community have a greater variety of damage types than distantly related species.

Methods

Study species

For the purpose of this study, non-native plant species were considered invasive if they have been classified as 'noxious' in one or more council divisions of New South Wales, Australia (AWC 2007). To obtain a broad spread of non-native plants for sampling, three categories of exotic plants were initially defined, based on their degree of relatedness to the native plants of Australia: (1) invasive plants with native congeners (2) invasive plants that had native species in the same region within the same family (hereafter referred to as con-familial) and (3) invasive species with no family members or congeners in Australia (hereafter referred to as non-familial) (Table 1). A total of 14 species were selected. Species chosen were predominantly distributed along the east coast of Australia and include a variety of growth forms (herbs, shrubs and vines). All introduced species chosen are known to have been present in Australia for at least 40 years according to published literature and herbarium records. Selection of species based on these broad taxonomic

groupings was then refined further by reference to published phylogenies obtained from the Angiosperm Phylogeny website (Stevens 2006) which contains regularly updated information on plant phylogenetics.

Once the choice of the 14 invasive species and their general phylogenetic relationship to Australian natives was finalised, we selected a native relative for each species that occurred sympatrically. The absolute nearest native relative was chosen based on having a similar coastal distribution to the non-native species of interest and potentially occurring in a similar habitat (Comparison 1, see Table 1). For six of the 14 species, the native partner chosen in this way was of a different growth form and/or occurred in a different habitat. For these cases we chose a second native species for comparison using criteria that included similar habitat and growth form (Comparison 2, see Table 1). Thus an invasive species that was a climber occurring in rainforest, for example, was paired with the phylogenetically closest native climber in a similar habitat. Several of the native species chosen for the first analysis are the same as for the second analysis. All plant species including non-native and native are represented in one phylogenetic tree with each comparison identified but grouped separately for analysis (Figure 1).

As genera can differ in divergence times, a phylogenetic tree was constructed using Phylomatic software to remove the assumption of equal degrees of divergence between genera and families (Webb & Donoghue 2005). The list of 14 species, including family and genus names, was submitted to the online phylogenetic query tool, which returned a phylogenetic hypothesis for the relationships among the taxa (Webb & Donoghue 2005). Species were matched to the online ‘mega-tree’, which is a phylogenetic tree containing all angiosperm families of the world, based on the consensus tree from Davies *et al.* (2004). Because the mega-tree is largely incomplete below the level of family, the relationships among genera within each family are returned as a polytomy (‘comb’ phylogeny).

Similarly, species are returned as polytomies within genera. Branch lengths for the tree were estimated using the 'BLADJ' function in Phylomatic (Version 4.0.1) (Webb *et al.* 2009). This function fixes the root node at a specified age, and fixes other angiosperm nodes aged from Wikstrom *et al.* (2001) to the tree. Undated nodes are then placed evenly between nodes of known ages (Webb *et al.* 2009). This allows approximate estimates of distances between taxa. For the purpose of this study approximate evolutionary distances are sound so long as non-native species can be accurately ranked from being closely related to a native plant of Australia, to more distantly-related, based on the approximate divergence time of each non-native species to their closest native relative.

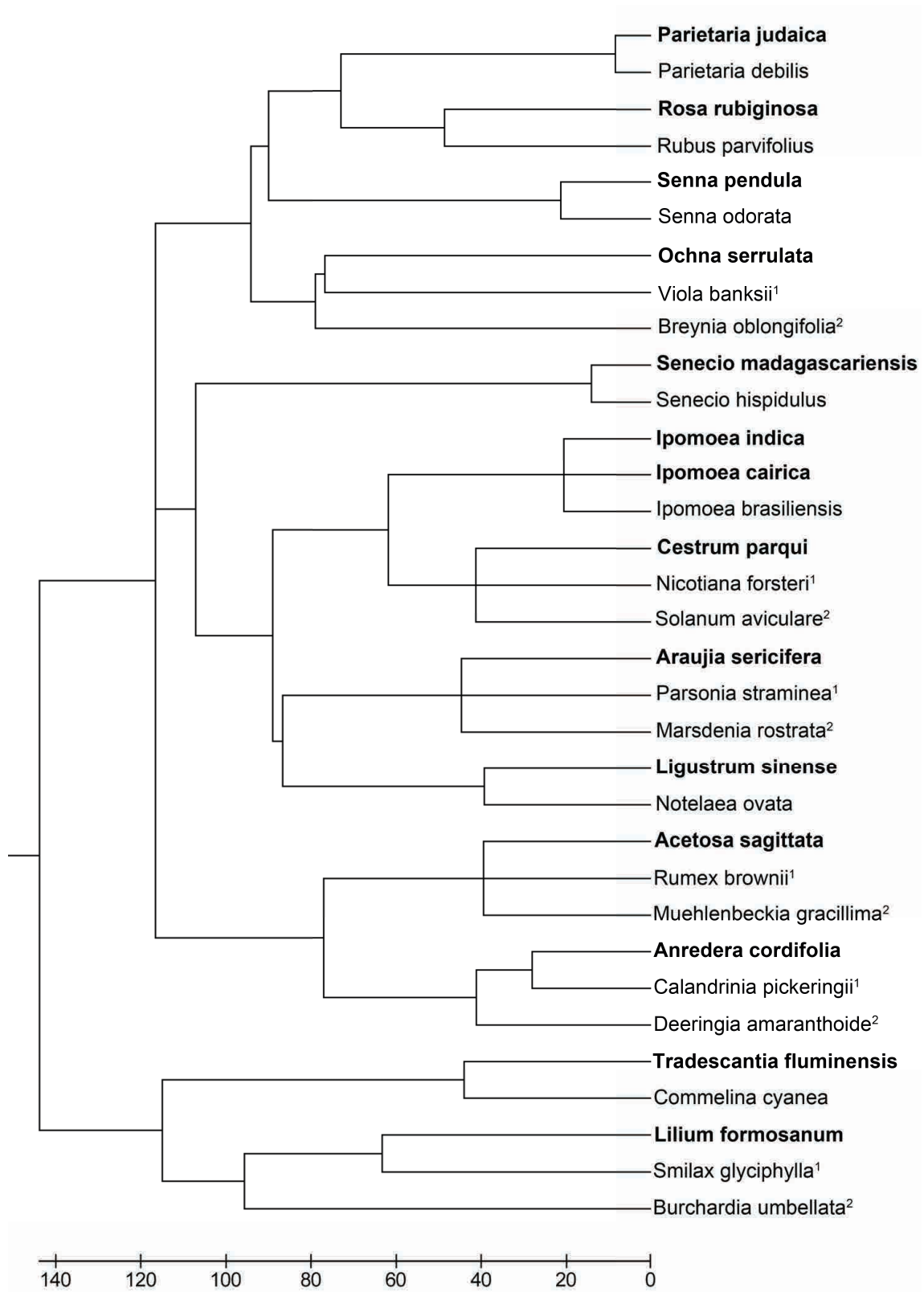
Study Sites

Sampling was conducted throughout spring (September-November) 2007 within disturbed bushland sites on the east coast of Australia. Three broad sampling regions were selected, spanning the geographic ranges of the non-native plants sampled: (1) Sydney Basin: southern region with sites included within the Wollondilly Shire, Shoalhaven and Illawarra districts (2) Sydney Basin: central and western region with sites included within several Sydney suburbs and surrounds, South Eastern Highlands, Lithgow shire and (3) North Coast: with sites included in the Grafton shire, Southeast Queensland including Brisbane suburbs, and Warwick in the Brigalow Belt (Table 1). Each invasive species was sampled at one location within each of the three regions.

Table 1. Sampling design for the comparison of damage on invasive plants with native congeners¹, native con-familials² and those where the family does not naturally occur in Australia (non-familial³) across three sampling regions. Invasive plant species used in the study were compared with the nearest Australian relative (comparison 1) and nearest relative with a similar distribution, growth form and habitat (comparison 2).

| Invasive plant species | Sampling location | Comparison 1: Invasive species with nearest native relative | Comparison 2: Invasive species with nearest native relative, similar distribution, growth form and habitat |
|----------------------------------------------|------------------------------|-------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|
| <i>Parietaria judaica</i> ¹ | 34°26'15.61"S 150°53'39.56"E | <i>Parietaria debilis</i> | <i>Parietaria debilis</i> |
| | 33°47'21.96"S 151°09'53.05"E | | |
| <i>Senna pendula</i> ¹ | 27°26'47.35"S 152°56'45.57"E | <i>Senna odorata</i> | <i>Senna odorata</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 34°26'00.66"S 150°52'44.52"E | | |
| <i>Senecio madagascariensis</i> ¹ | 29°44'44.72"S 152°57'11.46"E | <i>Senecio hispidulus</i> | <i>Senecio hispidulus</i> |
| | 33°50'08.26"S 150°51'15.20"E | | |
| | 34°07'21.49"S 150°41'52.91"E | | |
| <i>Ipomoea indica</i> ¹ | 27°30'46.58"S 152°56'03.34"E | <i>Ipomoea brasiliensis</i> | <i>Ipomoea brasiliensis</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 34°26'01.70"S 150°52'28.92"E | | |
| <i>Ipomoea cairica</i> ¹ | 27°56'27.94"S 153°10'49.35"E | <i>Ipomoea brasiliensis</i> | <i>Ipomoea brasiliensis</i> |
| | 33°40'49.00"S 151°18'44.03"E | | |
| | 34°35'53.20"S 150°53'54.44"E | | |
| <i>Acetosa sagittata</i> ² | 27°56'27.94"S 153°10'49.35"E | <i>Rumex brownii</i> | <i>Muehlenbeckia grasillima</i> |
| | 33°40'49.00"S 151°18'44.03"E | | |
| | 34°26'01.70"S 150°52'28.92"E | | |
| <i>Tradescantia fluminensis</i> ² | 27°26'47.35"S 152°56'45.57"E | <i>Commelina cyanea</i> | <i>Commelina cyanea</i> |
| | 33°47'21.96"S 151°09'53.05"E | | |
| | 34°26'01.70"S 150°52'28.92"E | | |
| <i>Cestrum parqui</i> ² | 27°31'05.91"S 153°00'33.08"E | <i>Nicotiana forsteri</i> | <i>Solanum aviculare</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 34°31'49.44"S 150°52'21.81"E | | |
| <i>Araujia sericifera</i> ² | 27°56'27.94"S 153°10'49.35"E | <i>Parsonia straminea</i> | <i>Marsdenia rostrata</i> |
| | 33°39'56.70"S 151°18'04.79"E | | |
| | 34°35'53.20"S 150°53'54.44"E | | |
| <i>Ligustrum sinense</i> ² | 27°50'04.88"S 153°16'24.01"E | <i>Notelaea ovata</i> | <i>Notelaea ovata</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 34°26'00.66"S 150°52'44.52"E | | |
| <i>Rosa rubiginosa</i> ² | 27°58'32.36"S 153°18'08.04"E | <i>Rubus parvifolius</i> | <i>Rubus parvifolius</i> |
| | 33°33'36.56"S 149°55'41.07"E | | |
| | 34°07'21.49"S 150°41'52.91"E | | |
| <i>Ochna serrulata</i> ³ | 27°26'47.35"S 152°56'45.57"E | <i>Viola banksii</i> | <i>Breynia oblongifolia</i> |
| | 33°47'42.64"S 151°09'05.93"E | | |
| | 34°31'49.44"S 150°52'21.81"E | | |
| <i>Anredera cordifolia</i> ³ | 27°26'47.35"S 152°56'45.57"E | <i>Calandrinia pickeringii</i> | <i>Deeringia amaranthoide</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 34°31'49.44"S 150°52'21.81"E | | |
| <i>Lilium formosanum</i> ³ | 27°56'27.94"S 153°10'49.35"E | <i>Smilax glycyphylla</i> | <i>Burchardia umbellata</i> |
| | 33°48'40.15"S 151°08'24.64"E | | |
| | 35°01'07.60"S 150°39'52.49"E | | |

Figure 1. Phylogenetic tree from Phylomatic (Webb *et al.* 2009), displaying node labels representing divergence (million of years ago) of invasive species (in bold) from their nearest native relatives, based on their most recent common ancestors (comparison 1) and most recent common ancestor with similar distribution, habitat and morphology (comparison 2). Native species with no superscripts were used for both comparison 1 and 2. Phylocom (Webb *et al.* 2009) has complete familial representation but uses angiosperm nodes aged from Wickstrom *et al.* (2001) by running a program called 'BLADJ' to estimate aged distance at the genus and species level.



Herbivory Measurements

Damage by invertebrate herbivores and pathogens was assessed on 15 individual plants for each invasive species per sampling region. Five haphazardly selected mature leaves from each plant, totalling 75 leaves per region per species, were collected. This method of sampling provides a quick easy estimate of herbivory but underestimates total herbivory from leaves or other parts of the plant that are wholly eaten (Lowman 1984). Leaves were scanned within a week of collection using a Canoscan LiDe 20 Image Scanner in grayscale and color. Senescing leaves were not collected because distinguishing decay from herbivore damage is not possible (Lowman 1984).

Types of damage

Herbivore damage (grazing, chewing, skeletonising, sap-sucking, galling, mining) and any sign of pathogen damage (from fungus and bacteria such as leaf spotting and rust) were identified, and the area missing due to the particular damage type, relative to the total leaf area, was assessed using Image J software (Rasband 2003). Grazing, chewing and skeletonising damage result from external feeding by invertebrates with chewing mouthparts, such as caterpillars, beetles and grasshoppers. Grazing damage was identified as leaf necrosis where the scraping of the leaf surface occurred without the complete loss of photosynthetic material. The material slowly decays and in turn can cause holes within the leaf. Chewing damage was identified as holes that occurred from leaf edge surfaces and likely involved insects with cutting mouthparts such as caterpillars and grasshoppers. Direct loss of photosynthetic material and removal of the full depth of leaf lamina occurs. For leaves with damage along the edge, approximate areas were drawn relying on the symmetry of the leaf to estimate area lost (Carpenter & Cappuccino 2005). Any known

mechanical or physiological damage was removed from analysis. Any damage from unknown sources that showed signs of necrosis was included in the analysis.

The probable cause of all herbivore and pathogen damage was broadly identified using texts (Hockings 1980; McMaugh *et al.* 1985; McCarthy 1985; Jones & Elliot 1986; APPS 1997; Agrios 2004) and assistance from entomological and phytopathological experts at the Australian Museum in Sydney and the National Herbarium of NSW.

Statistical analysis

We compared (i) total foliar damage (ii) types of damage and (iii) number of damage types among the 14 invasive species.

(1) Relationship of total leaf damage and phylogenetic distance to Australian natives

Data from different sites within each species range were pooled prior to analysis because between-site variability was not the prime focus of this study. We used linear least-squares regression to test for an association between total damage and phylogenetic relatedness to the closest nearest native (Data Desk[®] 6.1). Total damage was transformed to the natural logarithm before analysis to satisfy the assumption of normality.

(2) Damage type, species identity and phylogenetic distance to Australian natives

To determine if composition of damage types is associated with species identity and their evolutionary distance to the nearest native relative, two steps were used. Firstly, the association between species identity and composition of damage types was tested by multivariate analysis, performed by the PERMANOVA+ add-on package for PRIMER v6 using Euclidean distances on data transformed to the arcsine of their square roots with 15 replicates per species (Clarke & Gorley 2006; Anderson 2001; McArdle & Anderson

2001). Second, replicates were averaged and DISTLM, which is a non-parametric, permutation procedure for multivariate multiple regression, was used to test for an association between damage type across species and phylogenetic distance to the nearest native relative (Anderson 2001; McArdle & Anderson 2001). Damage of each type for each species was standardised as a proportion of the mean total damage. Differences in damage types across non-native species were visually represented using pie charts. For visual simplicity, where distinct boundaries in evolutionary distances to the nearest native relative occurred, distances and damage types for these species were averaged.

(3) Number of damage types and phylogeny

To investigate the relationship between plant phylogeny and variety of damage types, the phylogenetic distance to the nearest native relative was plotted against the total number of damage types. The boundary test in EcoSim was then used to determine if there was a limit to the diversity of damage types found on non-native species with distantly related native plant species (Gotelli & Entsminger 2000). From the plot, an asymmetric upper right boundary was determined from the maximum and medium points of the x variable (phylogenetic distance) and y variable (number of damage types). EcoSim then evaluated the number of points that fell outside the selected boundary through randomisation of the x and y variable (Gotelli & Entsminger 2000). Ten thousand random permutations were generated using values within the minimum and maximum range of the data set. An observed and simulated test statistic was then calculated to determine if the observed number of points outside the boundary was significantly smaller than the number found for the simulated data sets. A significant boundary test would indicate that non-native species with distant native relatives are limited in the maximum number of damage types than closely related species. Distantly related species with few types of damage are therefore

likely to be colonised by specialist herbivores at a slower rate than more closely related species.

Results

Relationship of total leaf damage and phylogenetic distance to Australian natives

Leaf damage on invasive plants was generally low, ranging from an average per species of 0.41% of the total leaf area (*Lilium formosanum*) to 4.5% (*Senecio madagascariensis*).

Leaf damage on invasive plants declined with greater phylogenetic distance to the nearest native relative (Fig. 2 a, b). When phylogenetic distance was estimated between invasive plants and their nearest native relative (comparison 1), 31% of variation in damage on invasive plants was explained by phylogenetic distance ($F = 5.42$, d.f = 1, 12, $P = 0.0383$) (Fig. 2 a). When phylogenetic distance was estimated between invasive species and their nearest native relative with similar habitat and growth form (comparison 2), phylogenetic distance explained 37% of the variation in damage on invasive plants ($F = 7.01$, d.f = 1, 12, $P = 0.0213$) (Fig. 2 b).

Damage type, species identity and phylogenetic distance to Australian natives

Composition of damage type was strongly associated with species identity (PERMANOVA: $F_{13, 196} = 14.315$, $P = 0.0001$). However, the relative proportion of damage types among invasive plants was not explained by phylogenetic distance to the nearest native relative (DISTLM: $F = 0.585$, $P = 0.633$; Fig. 3). In general, endophagous insect damage (mining and galling) across invasive plant species was minimal and contributed 0.5% of the mean total damage. Damage by ectophagous insects (grazing, chewing, skeletonising and sap-sucking) contributed 86% of the mean total damage. Ectophagous damage was dominated by the impacts of grazing and chewing generalists.

Pathogenesis and unknown necrotic damage contributed minimally (12.5% and 1%) to the remainder of the mean total damage (Fig. 3).

Number of damage types and phylogenetic distance to Australian natives

There was a limit to the number of damage types invasive species with distant native relatives can have. Invasive species with a near native relative had a wider range of damage types than those with distant native relatives, as indicated by the absence of points in the top right corner of Figure 4 (observed = 0, simulated = 3.681, $p = 0.012$ EcoSim Fig. 4).

Figure 2. Relationship of leaf damage on invasive plants with the phylogenetic distance (a) to the nearest native relative and (b) to the nearest native relative with similar distribution, growth form, and habitat.

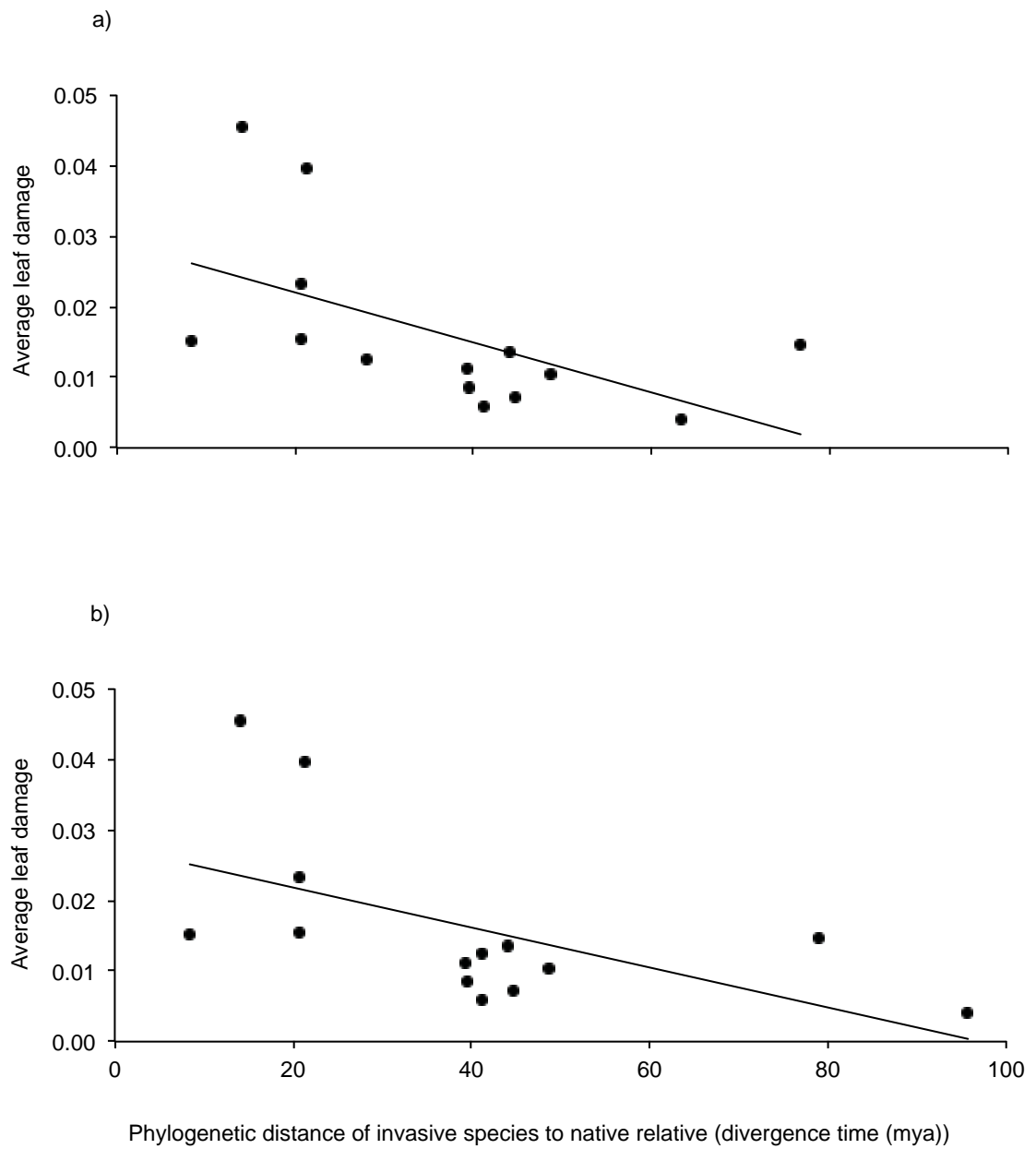


Figure 3. External (ectophagous) and internal (endophagous) damage across species that are closely related to native co-occurring species with an average divergence time of (a) 17 mya, to more distantly related to native species (b) 43 mya and with minimal to no relationship to native species (87 mya). N = the number of non-native species averaged.

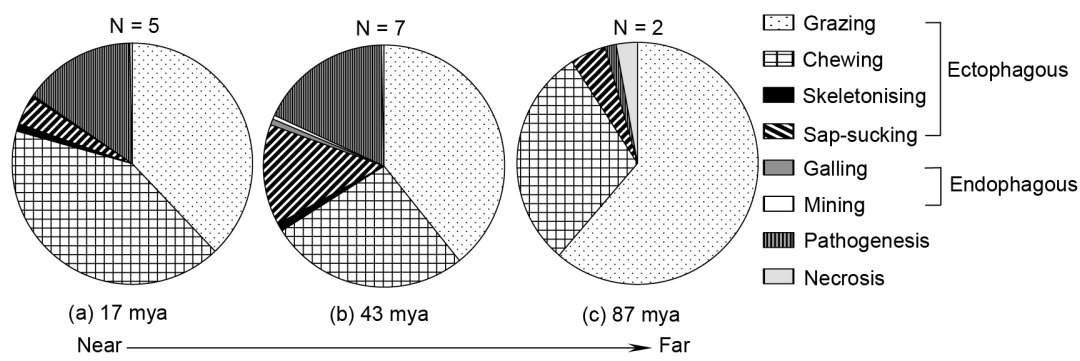
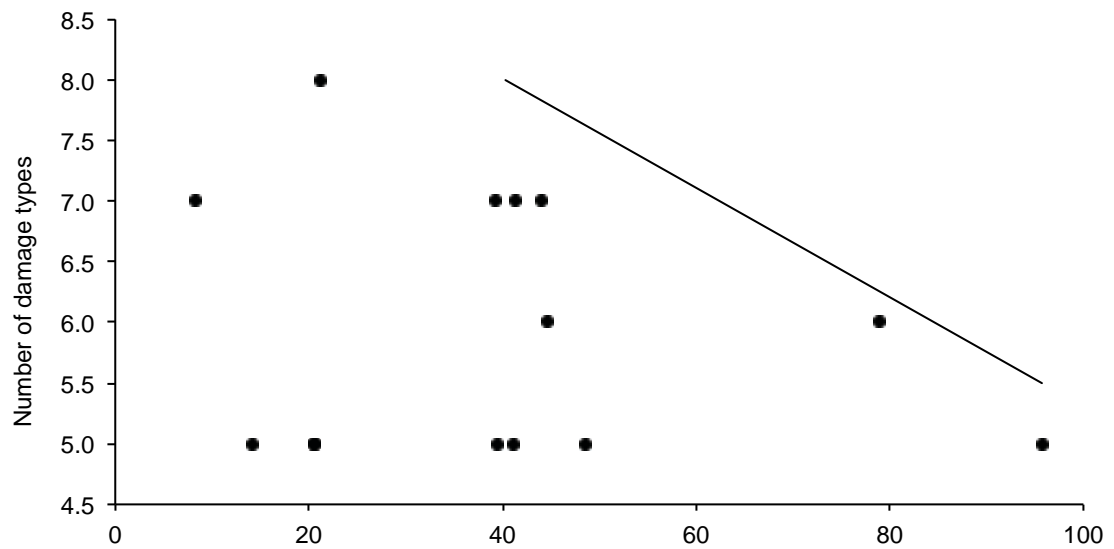


Figure 4. Relationship between the number of damage types occurring on non-native plants and the phylogenetic distance to the nearest native relative with similar distribution, habitat and morphology. The line indicates the asymmetric boundary of damage types generated by EcoSim.



Phylogenetic distance of invasive species to nearest sympatrically occurring native species with similar distribution, growth form and habitat (divergence time (mya)).
Asymmetric boundaries generated by EcoSim

Discussion

We have demonstrated that phylogenetic relatedness to sympatric plant species is a significant predictor of herbivore and pathogen damage to plant foliage on non-native plants, explaining over 30% of damage variation. Invasive species with closer phylogenetic relationships to Australian natives in the recipient community suffered more total damage, as well as being potentially exposed to a wider variety of damage types, than invasive species more distantly related to local species. These results were consistent whether we estimated phylogenetic distance based on the absolute nearest native relative of an invasive species, or the distance to the nearest relative with similar habitat and growth form. Differences in damage types were found between species, but due to the dominance of chewing and grazing herbivores on all plants, the types of damage was not significantly related to phylogenetic distance to the nearest native relative.

In general, our results support the hypothesis that herbivory is related to the taxonomic isolation of non-native species with respect to the native community. If natural enemies are important for limiting the invasion success of non-natives, our results provide support for a mechanism behind Darwin's naturalisation hypothesis, in that an invasive plant may be more successful if surrounded by plants that are not closely related (Mack 1996; Lockwood *et al.* 2001; Riccarrdi & Atkinson 2004; Strauss *et al.* 2006). Our results are consistent with findings of a common garden experiment in which non-native plants suffered less herbivory with increasing phylogenetic distance from native con-familials (Hill & Kotanen 2009). However, unlike Hill & Kotanen (2009) who did not find a relationship with phylogentic distance and damage in natural communities, we found that phylogenetic relationships within natural communities provide a useful indication of the rate of herbivore and pathogen damage that non-native plants may experience. Our results are also consistent with the finding that introduced oak species closely related to a native

oak received more herbivore damage by chewers and miners than more distantly related oaks (Pearse & Hipp 2009).

Determining the types of damage by herbivores and pathogens likely to have a suppressive impact is a crucial step for understanding whether distantly or unrelated non-native plants may be released from specialist natural enemies or share some level of pre-adaptation to natural enemies of the invaded region. In this study, not only did phylogenetically distant invasive species experience less total damage, they were subject to attack from fewer types of herbivores than those more closely related to the native community. Generalist or polyphagous feeding behaviour by grazers and chewers dominated damage on more distantly related or unrelated taxa. In contrast, invasive species that were closely related to the native community were potentially subject to a full suite of damage types by generalists and specialists that included endophagous damage by gallers and miners. Other studies have demonstrated that ectophagous species are more commonly associated with introduced species (Strong *et al.* 1984; Liu & Stiling 2006). Our finding, that chewing and grazing were the dominant feeding guilds that drove patterns of herbivore and pathogen damage across all invasive species in this study, is consistent with this idea. Although the composition of damage type was associated with species identity, dominance by chewing and grazing damage meant that no phylogenetic signal between damage type and species was found.

Our overall results indicate that taxonomically distinct exotic species are more likely to be susceptible to a wide range of generalist herbivores compared to exotic species that are more closely related to plants in their invaded community (Ricciardi & Ward 2006). This is because generalist herbivores are not as responsive to chemical defences, which are often shared between closely related plants and are important in determining the smell, taste and palatability of leaves for specialist herbivores (Tallamy 2004). However, having

found such low proportions of endophagous damage across all species in this study, our results imply that non-native species may be largely released from specialist natural enemies. Other factors, such as time since colonisation of the invader, may therefore be important for determining the accumulation of specialist herbivores (Strong *et al.* 1984; Brändle *et al.* 2008) and warrants further investigation.

The invasive potential of a plant species introduced to new environments is generally assessed by considering whether it (or its close relatives) have a history of becoming invasive elsewhere (DAFF 2010). The results of our study indicate that the phylogenetic relatedness of invasive plants to native species in the new environment may provide an additional tool for understanding and managing this global problem. Promising areas of future research could include an assessment of herbivory and the herbivore community composition at finer taxonomic scales to investigate the influence of phylogenetic relationships on functional herbivore guilds.

Acknowledgements

We greatly appreciate the help of field volunteers Kate Umbers, John Martin and Katherine McClellan. We'd also like to thank Sheldon Navie of the University of Queensland, Paul Robins of the Herbarium of Queensland, Matthew Springall from National Parks, Alexandra Stengle of Wollondilly Shire Council, and Gary Chapple of the Royal Botanic Gardens Sydney for plant location data. We also thank Edward Liew of the Royal Botanic Gardens Sydney who assisted with plant pathology identifications. We are grateful to city councils including, Sutherland, Port Macquarie, Wollongong and for the managers of Boondall Wetlands reserve QLD for sampling permits. Research was supported by Macquarie University and the Australian Museum in Sydney.

References

- Adair R, Groves, R (1998) Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology. Environment Australia, Canberra
- Agrios G (2004) Plant Pathology 5th Edition. Elsevier Academic Press, Amsterdam, Boston
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46
- APPS (1997) Plant pathogens and plant diseases. Australasian Plant Pathology Society, Rockvale Publications for the Division of Botany, School of Rural Science and Natural Resources, University of New England, Armidale, NSW, Australia
- AWC (2007) Noxious weed list for Australian States and Territories. Australian Weeds Committee <http://www.weeds.org.au/docs/weednet6.pdf> Accessed Mar 2007
- Bertheau C, Brockerhoff EG, Roux-Morabito G, Lieutier F, Jactel H (2010) Novel insect-tree associations resulting from accidental and intentional biological ‘invasions’: a meta-analysis of effects on insect fitness. *Ecology Letters* 13:506-515
- Brändle M, Kühn I, Klotz S, Belle C, Brandl R (2008) Species richness of herbivores on exotic host plants increases with time since introduction of the host. *Diversity and Distributions* 15:905-912
- Cappuccino N, Carpenter D (2005) Invasive exotic plants suffer less herbivory than non-invasive exotic plants. *Biology Letters* 1:435-438
- Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology* 93:315-321
- Carroll SP, Loe JE, Dingle H, Mathieson M, Famula TR, Zalucki MP (2005) And the beak shall inherit - evolution in response to invasion. *Ecology Letters* 8:944-951
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by

integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15:22-40

Clarke KR, Gorley RN (2006) Primer v6: In: PRIMER-E: Plymouth, UK

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-733

Connor EF, Faeth SH, Simberloff D, Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 5:205-211

Culliney TW (2005) Benefits of classical biological control for managing invasive plants. *Critical Reviews in Plant Sciences* 24:131-150

D'Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology* 10:703-713

Daehler CC (2001) Darwin's naturalisation hypothesis revisited. *American Naturalist* 158: 324-330

DAFF (2010) Weed risk assessment system In: Biosecurity Australia. Department of Agriculture Fisheries and Forestry, Australian Government
http://www.daff.gov.au/ba/reviews/weeds/system/weed_risk_assessment Accessed Dec 2010

Darwin CR (1859) *The Origin of Species by Means of Natural Selection*. John Murray, London

Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences, USA* 101:1904-1909

Dawson W, Burslem DFRP, Hulme PE (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions* 15:141-

- Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalisation conundrum: dissecting taxonomic patterns of species invasions. *Ecology Letters* 11:674-681
- Duncan RP, Williams PA (2002) Darwin's naturalisation hypothesis challenged. *Nature* 417:608-609
- Gilbert GS, Webb CO (2007) Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the United States of America* 104:4979-4983
- Gotelli NJ, Entsminger GL (2000) EcoSim: Null models software for ecology. Version 6.0. Acquired Intelligence and Kesey-Bear Inc.
<http://homepages.together.net/~gentsmin/ecosim.htm> Accessed Aug 2010
- Hill SB, Kotanen PM (2009) Evidence that phylogenetically novel non-native plants experience less herbivory. *Oecologia* 161:581-590
- Hill SB, Kotanen PM (2010) Phylogenetically structured damage to Asteraceae: susceptibility of native and exotic species to foliar herbivores. *Biological Invasions* 12:3333-3342
- Hockings FD (1980) Friends and foes of Australian gardens: including pests, diseases, parasites and predators. Reed in association with the Society for Growing Australian Plants, Sydney
- Jones DL, Elliot WR (1986) Pests, diseases and ailments of Australian plants, with suggestions for their control. Lothian, Melbourne, Australia
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *TRENDS in Ecology and Evolution* 17:164-170
- Lambdon PW (2008) Is invasiveness a legacy of evolution? Phylogenetic patterns in the

- alien flora of Mediterranean islands. *Journal of Ecology* 96:46-57
- Lambdon PW, Hulme PE (2006) How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalisation hypothesis assessed on Mediterranean islands. *Journal of Biogeography* 33:1116-1125
- Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions* 8:1535-1545
- Lockwood JL, Simberloff D, McKinney ML, Von Holle B (2001) How many, and which, plants will invade natural areas? *Biological Invasions* 3:1-8
- Lodge DM (1993) Biological invasions: Lessons for ecology. *TRENDS in Ecology and Evolution* 8:133-137
- Lowman MD (1984) An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica* 16:264-268
- Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation* 78:107-121
- Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361-373
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290-297
- McCarthy GJP, Branch QPP (1985) *A Handbook of plant diseases in colour. Vol. 2. Field crops.* Queensland Department of Primary Industries, Brisbane, Australia
- McMaugh J, Joyce R, Morison R (1985) *What garden pest or disease is that? Every garden problem solved.* Lansdowne, Sydney
- Parker IM, Gilbert GS (2007) When there is no escape: the effects of natural enemies on native, invasive, and noninvasive plants. *Ecology* 88:1210-1224
- Pearse IS, Hipp AL (2009) Phylogenetic and trait similarity to a native species predict

- herbivory on non-native oaks. *Proceedings of the National Academy of Sciences USA* 106:18097-18102
- Prieur-Richard A-H, Lavorel S (2000) Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1-7
- Proches S, Wilson JRU, Richardson DM, Rejmánek M (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography* 17:5-10
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) *Biological invasions, Ecological Studies* 193. Springer-Verlag, Berlin/Heidelberg, pp 97-126
- Rasband W (2003) Image J. 1.3. Image Processing and Analysis in Java
<http://rsb.info.nih.gov/ij/> Accessed Dec 2008
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655-1661
- Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters* 7:781-784
- Ricciardi A, Mottiar M (2006) Does Darwin's naturalisation hypothesis explain fish invasions? *Biological Invasions* 8:1403-1407
- Ricciardi A, Ward JM (2006) Comment on "Opposing effects of native and exotic herbivores on plant invasions". *Science* 313:298
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30:409-431
- Ricotta C, Godefroid S, Rocchini D (2010) Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. *Diversity and Distributions* 16:655-662

- Stastny M, Schaffner U, Elle E (2005) Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology* 93:27-37
- Steffen W, Burbidge AA, Hughes L, Kitching R, Lindenmayer D, Musgrave W, Stafford Smith M, Werner PA (2009) Australia's biodiversity and climate change. CSIRO Publishing, Collingwood
- Stevens PF (2006) Angiosperm Phylogeny Website. Version 7
<http://www.mobot.org/MOBOT/research/APweb/> Accessed Dec 2008
- Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103:5841-5845
- Strong DR, Lawton JH, Southwood R (1984) *Insects on Plants: Community patterns and mechanisms*. Blackwell Scientific Publications, Oxford London
- Tallamy DW (2004) Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692
- Thomas CD, Ng D, Singer MC, Mallet JLB, Parmesan C, Billington HL (1987) Incorporation of a European weed into the diet of a North American herbivore. *Evolution* 41:892-901
- Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant components of human-caused global change. *New Zealand Journal of Ecology* 21:1-16
- Walker LR, Smith SD (1997) Impacts of invasive plants on community and ecosystem properties. In: Luken JO, Thieret JW (eds) *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, pp 69-85
- Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181-183

- Webb CO, Ackerly DD, Kembel SW (2009) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1 http://www.phylodiversity.net/phylocom/phylocom_manual.pdf Accessed Dec 2008
- Weber J, Panetta FD, Virtue J, Pheloung P (2009) An analysis of assessment outcomes from eight years' operation of the Australian border weed risk assessment system. *Journal of Environmental Management* 90:798-807
- Weiblen GD, Webb CO, Novotny V, Basset Y, Miller SE (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87:S62-S75
- Wikstrom N, Savolainen, V, Chase MW (2001) Evolution of angiosperms: calibrating the family tree. *Proceedings of the Royal Society, Series B* 268:2211-2220

Chapter 3

Can phylogenetic relationships within genus indicate the likelihood of enemy release of an invader?

Kerinne J. Harvey^{1*}, David A. Nipperess¹, David R. Britton², & Lesley Hughes¹

¹ Department of Biological Sciences, Macquarie University, North Ryde, NSW
Australia

² Entomology Collections, Australian Museum, Sydney, NSW, Australia

* Kerinne Harvey: Email: kerinne.harvey@gmail.com

Telephone: +612 9850 6279; Fax: +612 9850 8245.

Running headline: Phylogeny and enemy release within genus

For submission to *Biological Invasions*

Abstract

Invasive plants have become a global environmental and economic problem. Understanding the mechanisms behind invasion is integral for management solutions. The enemy release hypothesis (ERH) is often invoked to explain the success of non-native plant species. The ERH suggests that upon introduction to a new region, a novel plant species may spread rapidly because it is liberated from co-evolved herbivores and pathogens. The phylogenetic relationship between a non-native plant and the native recipient community may be important in understanding the success of some non-native plants because host switching by native herbivores is more likely to occur between closely related rather than distantly related species. In this study, we tested the ERH by comparing leaf damage and herbivorous insect assemblages on the invasive species *Senecio madagascariensis* Poir. to nine congeneric species, of which five are native to the invasion sites, and four are non-native but considered non-invasive. As the closeness of the phylogenetic relationship between invasive species and other species in the recipient community has been found to play a role in determining invasiveness, we also investigated the relationship of the insect assemblage to the level of relatedness of the host plants. We found that while non-native species had less leaf damage than natives overall, there were no significant differences in the abundance, richness and diversity of herbivores among native and non-native *Senecio* L. species. The composition of the herbivore assemblages and percentage abundance of herbivore guilds differed between all *Senecio* species, but patterns were not related to whether the species was native or not. Species level differences suggested that *Senecio madagascariensis* may have a greater proportion of generalist insect damage (represented by phytophagous leaf chewers) than all other *Senecio* species. Our results indicate that predictions based on phylogenetic relationships for the success of invasive species within genus are not supported: *Senecio*

madagascariensis was not distantly related to other non-invasive or native *Senecio* species, and there was no correlation between the phylogenetic distance of *Senecio* species and the dissimilarity of herbivore assemblages. Within a plant genus, variation in escape from natural enemies does not appear to support the ERH as a mechanism for why some non-native *Senecio* species are more invasive than others. Predictions based on phylogeny of invasive behaviour through enemy release are likely to be only viable at broad phylogenetic scales.

Key words: invasive plants, enemy release hypothesis, naturalisation hypothesis, plant-insect interactions, congeners, non-invasive plants.

Introduction

Invasive plants pose one of the most serious threats to the environment with major economic consequences. Negative impacts include: displacement of native species, land degradation, reduction in farm and forest productivity, alteration of ecosystem properties, and the disruption of ecosystem function (Adair & Groves 1998; Sinden *et al.* 2005).

While our understanding of the impacts of non-native plants on native communities has grown considerably, the reasons why only some introduced plants become invasive still appear to be context dependent.

There is some evidence to suggest that introduced plants are more likely to become invasive in the absence of closely related species in the recipient native community (Mack 1996; Rejmánek & Richardson 1996, Lockwood *et al.* 2001; Riccarrdi & Atkinson 2004; Strauss *et al.* 2006; Schaefer *et al.* 2011). This is generally referred to as the naturalisation hypothesis (Darwin 1859; Daehler 2001) and rests partly on the idea that closely related species are likely to compete more strongly for similar resources. However, some studies have shown that higher naturalisation rates of non-native species with congeneric native relatives have occurred, suggesting that competition is outweighed by the importance of sharing similar environmental conditions to which non-natives may be pre-adapted to (Daehler 2001; Duncan & Williams 2002).

Phylogenetic relationships between a potential invader and co-occurring native species may also be important in relation to the impact of natural enemies. If a plant species is introduced to an area where the natural enemies from its native region are not present, the probability of successful establishment may be increased. This is termed the Enemy Release Hypothesis (ERH) (for reviews see Maron & Vila 2001; Colautti *et al.* 2004). The enemy release of non-natives may be more pronounced in species that are distantly related

to the recipient native plant community. Plants that are closely related tend to share more natural enemies than those that are distantly related (Connor *et al.* 1980; Frenzel & Brandl 2003; Ødegaard *et al.* 2005), due to sharing similar physical and chemical characteristics (Strong *et al.* 1984; Jones & Lawton 1991; Tallamy 2004). Harvey *et al.* (in press) demonstrated that with increasing phylogenetic distance from native relatives, leaf damage on invasive species declined. Similarly, a common garden experiment demonstrated that with increased phylogenetic distance from native con-familials, non-native plants suffered less herbivory (Hill & Kotanen 2009). Neither of these studies however, investigated the comparative levels of herbivory below the level of genus. The impacts of established non-native plants within a genus can range from innocuous to invasive, so understanding phylogenetic relationships at a sub-generic level in relation to levels of herbivory is necessary for predicting if release from natural enemies could be a mechanism behind successful invasion.

Several tests of the ERH have attempted to control for phylogenetic signals by comparing herbivore damage and herbivore communities between congeneric native and non-native pairs in the invaded region. Results for the ERH vary between studies (reviewed by Colautti *et al.* 2004; meta-analysis by Chun *et al.* 2010), with some showing that damage may be greater on native species compared to non-natives as predicted by the ERH (Schierenbeck *et al.* 1994; Siemann & Rogers 2003; Cincotta *et al.* 2009), while others demonstrate that non-natives can receive greater damage than native congeners (Keane & Crawley 2002 and references therein; Agrawal & Kotanen. 2003), but that this can also vary with space and over time (Agrawal *et al.* 2005). If release from natural enemies is an important mechanism behind the success of some non-native plants, we would expect that invasive species are more likely to escape natural enemies than non-invasive or innocuous non-invasive species (Liu *et al.* 2006). Therefore, tests to determine the importance of

enemy release in the success of invasive species should ideally include comparisons with non-native non-invasive congeners. The few studies that have performed such comparisons have found that less invasive or non-invasive species suffered greater herbivory than invasive species (Cappuccino & Carpenter 2005; Carpenter and Cappuccino 2005) and have accumulated more pathogens (Mitchell & Power 2003). Only a handful of studies have included three-way comparisons among congeners of native plants and introduced non-invasive and invasive plants (Carpenter & Cappuccino 2005; Liu *et al.* 2006; Liu *et al.* 2007). In two separate studies, similar levels of herbivore damage (Liu *et al.* 2007) and richness (Liu *et al.* 2006) between introduced invasive and non-invasive *Eugenia* species were recorded but herbivore damage and richness were both lower than on their native counterparts (Liu *et al.* 2006; Liu *et al.* 2007). Without including the non-invasive species, the authors would have concluded that escape from natural enemies would have been an important driving mechanism for the success of the invasive *Eugenia* species.

Phylogenetic relationships between plants within a community have been shown to be important in the make up of the co-occurring insect community. As the phylogenetic distance between co-occurring host plant species declines, greater similarities are found between the insect communities (Novotony *et al.* 2006; Ødegaard *et al.* 2005; Weiblen *et al.* 2006; Nipperess *et al.* 2012). These differences are most evident at the level of plant family (Nipperess *et al.* 2012) because differences in plant chemistry and architecture are more pronounced between the taxonomic level of family and above. Phylogenetic relationships between native and non-native species may offer important insights into compositional differences of invertebrates between native and non-native species post-invasion. Comparing insect herbivore communities between native, non-invasive and invasive plants within the same genus offers the chance to detect species that may be the

main drivers of enemy impact. It further assists in determining whether the community on the invasive species exhibits relatively little variation between plants or recruits a less diverse fauna compared to native and non-invasive species. Comparing herbivore communities allows us to determine if specialist insects are replaced by generalist insect activity in the new range as predicted by the ERH (Keane & Crawley 2002). Endophagous herbivores including miners and gall inducers may be replaced by more generalist ectophagous chewers and sap-suckers (Strong *et al.* 1984; Ando *et al.* 2010).

Endophagous herbivores are considered more specialised as they feed internally on plants (Frenzel & Brandl 1998), and research has indicated that the species richness of endophagous herbivores may be lower on introduced plants than on related native plants, whereas ectophagous insects (leaf chewing and sap-sucking herbivores) are more likely to readily colonise introduced species (Jobin *et al.* 1996). To our knowledge no prior studies have considered the phylogeny of host plants in quantifying both the impact and identity of the herbivore community and guilds between native, non-invasive and invasive species within genus.

In this study we compared invertebrate herbivore faunas among native (five species), invasive (one species; *Senecio madagascariensis* Poir.) and naturalised (four species) of *Senecio* L. growing on the east coast of Australia (Plate 1; Table 1). The *Senecio* spp. studied here included perennial shrubs, vines and annual and biannual herbs. If enemy release is important in the success of the invasive *S. madagascariensis*, we predict that:

(1) Herbivore damage will be greater on native species and non-invasive naturalised species than *S. madagascariensis*.

(2) The abundance and richness of herbivores will be greater on the native and non-invasive naturalised *Senecio* species than the invasive species *S. madagascariensis*.

(3) The composition of the insect assemblage on *S. madagascariensis* will (a) be significantly different from other native and non-invasive naturalised species (b) have a relatively larger proportion of non-specialised feeding guilds than native *Senecio* species and (c) will exhibit relatively little plant-to-plant variation compared to native and non-invasive *Senecio* species.

If phylogenetic relationships are important in determining the insect assemblage on *Senecio* spp., and explain why *S. madagascariensis* is more invasive than non-invasive naturalised *Senecio* species, we also predict that:

(1) The dissimilarity in the invertebrate herbivore assemblages found on *Senecio* species will be correlated with the evolutionary relatedness of those species.

Methods

Locations and plant species studied

Sampling of plants from the genus *Senecio* L. (Asteraceae) was conducted during spring and summer between November 2008 and February 2009 and repeated in autumn from March 2009 to May 2009 in coastal bushland, wet sclerophyll rangelands and grazing land along the east coast of Australia (Table 1; Plate 1).

Senecio is one of the largest genera of flowering plants and encompasses a wide range of perennial shrubs, vines and biannual and annual herbs (Frodin 2004). The genus is represented with 87 native species and 10 non-native species in Australia (Thompson 2006). With the exceptions of the invasive species *Senecio madagascariensis* Poir. and *Jacobaea vulgaris* Gaertn. (formerly *Senecio jacobaea* L.; Pelter *et al.* 2007), all other non-native species are either locally or rarely naturalised (Parsons & Cuthbertson 1992; Harden 2011; AWC 2011). *Senecio madagascariensis* has been declared a noxious

invasive weed in New South Wales, Queensland and the Australian Capital Territory (Parsons & Cuthbertson 1992). It is an annual or biannual herb that was first recorded in the Hunter Valley (NSW) in 1918. Originating in South Africa, it has since become a widespread and aggressive weed invading cultivated disturbed lands, pastures and roadsides of NSW extending into south-east Queensland (Parsons & Cuthbertson 1992; Holtkamp & Hosking 1993). It is of significant economic concern due to containing pyrrolizidine alkaloid, which if ingested by livestock can affect fitness and even lead to death (Parsons & Cuthbertson 1992; Sindel 2009). The range of species within the genus, in terms of the variability of invasiveness, makes *Senecio* an ideal system to examine the role that insect herbivores play in affecting invasiveness. Further, this genus has been the subject of recent broad-scale phylogenetic and taxonomic treatments (Thompson 2006; Pelser *et al.* 2007) that provide a basis for relating phylogeny to their interaction with natural enemies.

Sampling design

Sampling took place at three sites, spread across the geographic range of *Senecio madagascariensis* (Table 1). All *Senecio* species were located within 100 km of the east coast of Australia (Table 1). We sampled across seasons to ensure that a large portion of the invertebrate biodiversity was sampled and to target plants when flowering. We used within-species analyses to look at variation across sites and between summer and autumn sampling. No significant effects of sites or seasons were detected. Samples across sites and seasons were therefore pooled prior to analysis because site and seasonal variability was not our focus.

Herbivore and pathogen damage was estimated on 20 randomly chosen leaves from 10 plants for each species at each site; leaves were collected at the same time as the

invertebrate collections. Leaf damage or necrosis was scored visually on a scale of 0-100% (0 = necrosis, 100 = total necrosis). This method of sampling provides a quick easy estimate of herbivory but underestimates total herbivory from leaves or other parts of the plant that are wholly eaten (Lowman 1984).

At each site where damage levels were scored, the invertebrate assemblage was sampled on five, randomly selected plants, including flower heads, stems and leaves and roots. For larger plants including perennial shrubs, one middle branch of the plant similar in volume to *S. madagascariensis* was collected, in addition to a portion of the roots. Each plant sample collected was separated by at least 2 m for all species.

Plants were sampled using two techniques that targeted: 1) Herbivores that feed externally, such as leaf chewers and phloem feeders, which were collected by bagging whole plants; and 2) Herbivores that feed internally, and those hatching from eggs and immature stages, which were reared from the flowers, stems and leaves and the roots. Species accumulation curves were constructed to determine the number of samples that was needed to collect a representative sample of the richness of invertebrate herbivores (Colwell & Coddington 1994). The accumulation curves indicated that the sampling effort was sufficient to make comparisons across species.

Plate 1. Range of *Senecio* species architectures compared in study. Non-native species denoted by *.



*S. madagascariensis**



S. linearifolius var. *arachnoideus*



S. amygdalifolius



*S. glastifolius**



S. pinnatifolius var. *pinnatifolius*



S. angulatus



S. pterophorus

Table 1. Locations and dates of plant species sampled. Non-native species denoted by *.

| Latitude | Longitude | Dates collected | Location | Habitat |
|----------------------------------------------------------|----------------|--------------------------|---------------------------------------------------------------|--------------------|
| <u><i>S. madagascariensis</i>*</u> | | | | |
| 34°46'29.91"S | 150°40'11.14"E | 10.01.2009 23.04.2009 | Schofields Lane, Berry | Farmland |
| 32°42'58.34"S | 151°32'50.34"E | 05.02.2009 28.05.2009 | Walka Water Works, end of Waterworks Rd., Maitland | Disturbed bushland |
| 31°28'32.55"S | 152°56'12.85"E | 18.12.2009 18.05.2009 | Tacking Point Lighthouse, Port Macquarie | Disturbed bushland |
| <u><i>S. pterophorus</i>*</u> | | | | |
| 33°46'53.08"S | 151° 8'14.79"E | 02.12.2009 | Lane Cove National Park | Disturbed bushland |
| 33°45'44.87"S | 150°53'6.24"E | 10.01.2009 25.05.2009 | Reserve cnr. of Clarence & McCulloch Road, Doonside | Disturbed bushland |
| 32°51'28.24"S | 151°37'5.28"E | 05.02.2009 27.05.2009 | Pambalong Nature Reserve | Disturbed bushland |
| 33°52'38.47"S | 150°50'27.37"E | 25.05.2009 | Walgrove Rd, Cecil Pk. | Disturbed bushland |
| <u><i>S. angulatus</i>*</u> | | | | |
| 33°46'37.00"S | 150°59'48.77"E | 10.01.2009 25.05.2009 | Model Farm Reserve Northmead | Disturbed bushland |
| 33°59'3.73"S | 151°14'30.09"E | 26.11.2008 18.03.2009 | Jennifer St., Little Bay | Disturbed bushland |
| 32°56'14.00"S | 151°46'26.77"E | 05.02.2009 01.04.2009 | Nesca Park, Newcastle | Disturbed bushland |
| <u><i>S. glastifolius</i>*</u> | | | | |
| 34° 5'14.43"S | 151° 9'29.19"E | 24.11.2008 17.03.2009 | Fire break near Eric St. Royal National Park, Bundeena | Disturbed bushland |
| <u><i>S. macroglossus</i>*</u> | | | | |
| 32°47'14.07"S | 152° 6'47.61"E | 14.12.2008 28.05.2009 | Ocean Pde., Boat Harbour | Disturbed bushland |
| 28°19'39.71"S | 153°33'55.84"E | 16.05.2009 | Cabarita Beach northern end of Grevillea Ave., Cabarita Beach | Disturbed bushland |
| 36° 3'0.29"S | 150° 8'23.48"E | 22.04.2009 | Tuross Head | Hind dunes |
| <u><i>S. pinnatifolius</i> var. <i>pinnatifolius</i></u> | | | | |
| 32°10'2.50"S | 152°30'16.87"E | 15.12.2008 02.05.2009 | Tuncurry | Hind dunes |
| 31°28'32.55"S | 152°56'12.85"E | 18.12.2008 18.05.2009 | Tacking Point Lighthouse, Port Macquarie | Headland |
| 34° 2'21.13"S | 151°12'58.53"E | 24.11.2008 17.03.2009 | 400m East S end Sir Joseph Banks Drive, Kurnell | Headland |

Table 1. cont.

| Latitude | Longitude | Dates collected | Location | Habitat |
|--------------------------------------------------|----------------|--------------------------|--------------------------------------------------------------|---------------------------------------------------|
| <i>S. linearifolius</i> var. <i>arachnoideus</i> | | | | |
| 34°24'7.37"S | 150°49'39.80"E | 15.11.2008 17.03.2009 | Harry Graham Drive, Mount Keira | Roadside wet sclerophyll forest escarpment ranges |
| 31°32'51.5"S | 151°47'30.6"E | 19.01.2009 01.05.2009 | Nowendoc Rd, 7.1km E. Nowendoc | Roadside wet sclerophyll forest escarpment ranges |
| <i>S. amygdalifolius</i> | | | | |
| 31°22'17.64"S | 152° 4'10.20"E | 16.12.2008 19.05.2009 | NSW: Tobins Rd. off Oxley Hwy., Cotton-Bimbang National Park | Roadside wet sclerophyll forest escarpment ranges |
| 31°33'05.6"S | 151°48'27.9"E | 19.01.2009 01.05.2009 | Nowendoc Rd, 9km E. Nowendoc | Roadside wet sclerophyll forest escarpment ranges |
| 31°54'04.0"S | 151°37'23.1"E | 20.01.2009 02.05.2009 | Cobark Lookout, Barrington Tops | Roadside wet sclerophyll forest escarpment ranges |
| <i>S. minimus</i> | | | | |
| 31°21'55.56"S | 152° 2'29.94"E | 16.12.2008 19.05.2009 | Track off Oxley Hwy. 15km from Gingers Creek. | Roadside wet sclerophyll forest escarpment ranges |
| 31°53'50.2"S | 151°36'01.4"E | 20.01.2009 | Cobark Park, Barrington Tops | Roadside wet sclerophyll forest escarpment ranges |
| 33°42'9.56"S | 151° 4'47.98"E | 26.11.2008 | Ginger Meggs Park, Hornsby. | Disturbed bushland |
| <i>S. bippinatisectus</i> | | | | |
| 31°21'56.51"S | 152° 2'43.76"E | 16.12.2008 | Roadside, 15km from Gingers Creek, Oxley Hwy. | Roadside wet sclerophyll forest escarpment ranges |
| 31°59'59.6"S | 151°49'23.0"E | 20.01.2009 02.05.2009 | Scone Rd, Copland Tops State Forest. | Roadside wet sclerophyll forest escarpment ranges |
| 33°42'36.52"S | 151° 4'27.71"E | 26.11.2008 15.04.2009 | Reserve near Westleigh Fire Station, Westleigh | Bushland |

Each plant, including the roots (or a similar volume for shrubs and climbers based on the average plant size of *S. madagascariensis*) was collected into a bag and refrigerated for at least 2 hours before invertebrate removal. Invertebrates found externally on the stems and flowers of plants were then removed. Flower heads, stems and leaves and roots were separated and stored in clear plastic containers (1L and 1.25L) with a covering of polyester organza (Plate 2). The containers were stored in a glasshouse and checked regularly for emerging invertebrates over a four-month period. Immature stages of externally feeding invertebrates that could not be readily identified at time of collection and could not be reared on decaying vegetation were reared to adults on plants of the same species grown in a glasshouse (Plate 2). The stems and leaves, flowers and roots for each individual were then dried separately at 70°C for 12 hours and biomass recorded. Herbivores were identified to family level and then morphospecies based on available taxonomic keys (CSIRO 1973; Rentz 1996; Lawrence *et al.* 1999; Shattock 1999; Hamilton *et al.* 2005; CSIRO 2011) and personal communication with entomologists. Where individual morphospecies dominated species level analyses, genus or species level identification was made where possible (Appendix 2). Voucher specimens of the invertebrates are lodged in the Entomology collection of the Australian Museum in Sydney. Voucher specimens for plant species are lodged in the Downing Herbarium, Macquarie University, Sydney.

Senecio phylogeny

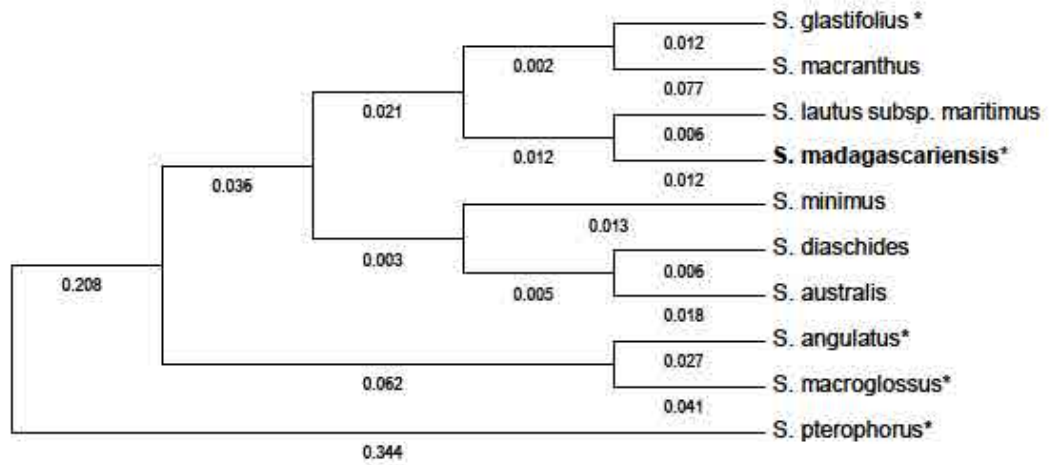
Phylogenetic relationships among *Senecio* species were determined using recent literature (Thompson 2006; Pelser *et al.* 2007) and estimated from internal transcribed spacer 1 (ITS 1) nucleotide gene sequences from a nucleotide database (Pelser *et al.* 2007; National Center for Biotechnology Information (NCBI) database www.ncbi.nlm.nih.gov) (Fig. 1; Appendix 1). All sequences were available for non-native *Senecio* species, but three (*S. linearifolius* var. *arachnoideus*, *S. amygdalifolius* and *S. bippinnatisectus*) of the five

native species were not present in the database. For these three species we used information from their taxonomic classification (Thompson 2006; Pelser *et al.* 2007) and substituted available ITS 1 gene sequences of other *Senecio* species as a reasonable indicator of phylogeny. We believe this approach is appropriate because after mapping all *Senecio* species occurring in Australia with available ITS 1 gene sequences, we found that the broad groupings of Australian *Senecio* species as determined by Thompson (2006), matched phylogenetic relationships from ITS 1 nucleotide gene sequences (Pelser *et al.* 2007). An estimate of the phylogeny of *Senecio* was constructed using neighbour joining from maximum composite likelihood and tested using the bootstrap method with 500 replicates. To investigate the association between herbivore assemblages and phylogenetic relationship between *Senecio* species, pairwise genetic distances using Nei's Genetic Distance (Nei & Kumar 2000) from the *Senecio* phylogeny were calculated. All phylogenetic analyses were performed using the software package, Molecular Evolutionary Genetics Analysis (MEGA 5; Tamura *et al.* 2011).

Plate 2. Immature stages of externally feeding invertebrates that were reared on adults of the same species grown in a glasshouse because they could not be identified at time of collection and could not be reared on decaying vegetation (a); Invertebrates reared from containers (b) and stored in a glasshouse (c).



Figure 1. Phylogenetic relationships and branch lengths within *Senecio* from nucleotide Internal transcribed spacer 1 gene sequences obtained from NCBI database <http://www.ncbi.nlm.nih.gov/nucleotide/>. Non-native species are denoted by asterisks. The invasive species *S. madagascariensis* is shown in bold.



Sampling variables

Invertebrate herbivores collected from each species were combined, pooling collections from the two sampling techniques, and from each location and season. The following parameters were calculated: (1) abundance (2) morphospecies richness, and (3) evenness (Shannon diversity index; $H' = -\sum (p_i \ln p_i)$ where p_i is the proportional abundance of the i th morphospecies). Herbivores were assigned to four trophic guilds: leaf chewers, sap-suckers, miners and gall inducers. These groupings were based on the published biology of the invertebrates at family level (CSIRO 1973; Rentz 1996; Lawrence *et al.* 1999; Shattock 1999; Hamilton *et al.* 2005; CSIRO 2011) and personal communications with entomologists.

Statistical analyses

Univariate analyses

To compare leaf damage and herbivore guilds (leaf chewers, sap-suckers, miners and gall inducers) across all the *Senecio* species we used a two factor nested Analysis of Variance (ANOVA) with category (native, non-native) and species (n=10) nested within category. All variables were considered fixed factors. Leaf damage data was transformed to $\log x + 1$ and comparisons for each herbivore guild were transformed to the arcsine of their square roots before the analysis to homogenise the variances and meet the assumption of normality.

To compare herbivore assemblages among native and non-native *Senecio* species, we used a two factor nested Analysis of Covariance (ANCOVA) with category (native or non-native), and species nested within category. To account for variation in plant sizes between species and across populations and differences in structural complexity between

species, plant biomass was fitted as a covariate. All variables were considered fixed factors. Biomass, herbivore abundance and species richness were transformed to the log (x+1) to homogenise variances and meet assumptions of normality.

Multivariate analyses

Multivariate analyses of the invertebrate herbivore assemblage were also performed using the PERMANOVA add-on statistical package (Anderson 2001; McArdle & Anderson 2001) within PRIMER (Clarke 1993; Clarke & Gorley 2006). To compare the herbivore assemblage between native and non-native *Senecio* species we used a two factor nested PERMANOVA with category (native, non-native) and species (n=10) nested within category and biomass (log x+1) for each plant as a covariate. Category and species were both considered fixed factors. We used the Bray-Curtis measure of dissimilarity on log x+1 transformed data with 9999 permutations of residuals under a reduced model and Type 1 sum of squares. Samples without herbivores present were removed prior to analysis. Differences between native and non-native *Senecio* species were also compared using non-metric, multidimensional scaling (Clarke 1993) based on Bray-Curtis dissimilarity.

Where there were clear patterns of difference in herbivore assemblages between native and non-native *Senecio* species, dominant invertebrate taxa contributing most to differences between plant species (with a cumulative cut-off of approximately 90%) were identified by SIMPER (Clarke 1993; Clarke & Gorley 2006). Dominant taxa collected from *S. madagascariensis* were also separately identified (SIMPER). Similarity Percentage analysis (SIMPER) calculates the average Bray-Curtis dissimilarity between all pairs of inter-group samples and expresses these differences in terms of the average contribution from each species (Clarke 1993).

Comparison of beta-diversity of invertebrate communities between native, non-native Senecio spp.

We used the PERMDISP function in PERMANOVA add-on statistical package (Anderson 2001; McArdle & Anderson 2001; Anderson *et al.* 2006) within PRIMER (Clarke 1993; Clarke & Gorley 2006) to compare the beta-diversity (that is, variation in composition between individual plants within a species) of herbivore communities collected from the invasive *S. madagascariensis* to that of the other *Senecio* species. PERMDISP tests for differences multivariate dispersion among groups by calculating the distances from observations to their centroids and comparing these average distances among groups (Anderson 2006). We ran PERMDISP on $\log x + 1$ herbivore abundances to find the mean deviation from the centroid across *Senecio* species with 9999 permutations using Bray-Curtis dissimilarity as the distance measure.

Phylogeny of Senecio and herbivore dissimilarity

The Bray-Curtis dissimilarity index on $\log x + 1$ transformed data was calculated on the sum of herbivore individuals collected for each plant species. The pairwise genetic distances (Nei's Genetic Distance Nei & Kumar 2000) calculated from the *Senecio* phylogeny were then matched to the dissimilarities of herbivore species using the RELATE function within PRIMER (Clarke 1993; Clarke & Gorley 2006). The RELATE function calculates the Mantel correlation between pairwise dissimilarity (Bray-Curtis) in the herbivore assemblage across *Senecio* species and pairwise genetic distances using Spearman's Rank correlation index.

Results

Leaf damage

Leaf damage from herbivores and pathogens ranged from 6 to 20% across native and non-native *Senecio* species (Fig. 2). Overall leaf damage, on average, was significantly lower on non-native species compared to native (Table 2; Fig. 2). Leaf damage on the invasive species *S. madagascariensis* was similar to the levels of damage found on other non-native *Senecio* species (Fig. 2).

Patterns of invertebrate abundance, richness and evenness

The total number of invertebrate morphospecies collected across the ten species of *Senecio* was 799 with 26% of these being herbivores. Overall, no significant differences were found in the abundance, morphospecies richness or Shannon diversity of invertebrate herbivores collected on native *Senecio* species compared to non-native species (Table 3; Fig. 3). Across *Senecio* species there were species level differences in invertebrate abundance, richness and Shannon diversity (Table 3; Fig. 3). Differences were to a large extent driven by the invasive species *S. madagascariensis* and the native *S. minimus* that supported a considerably more abundant and diverse fauna than the other *Senecio* species (Fig. 3).

Figure 2. Percentage leaf damage from herbivore and pathogen necrosis (\pm SE) across native and non-native *Senecio* species. The horizontal lines indicate the average leaf damage for native and non-native species collectively.

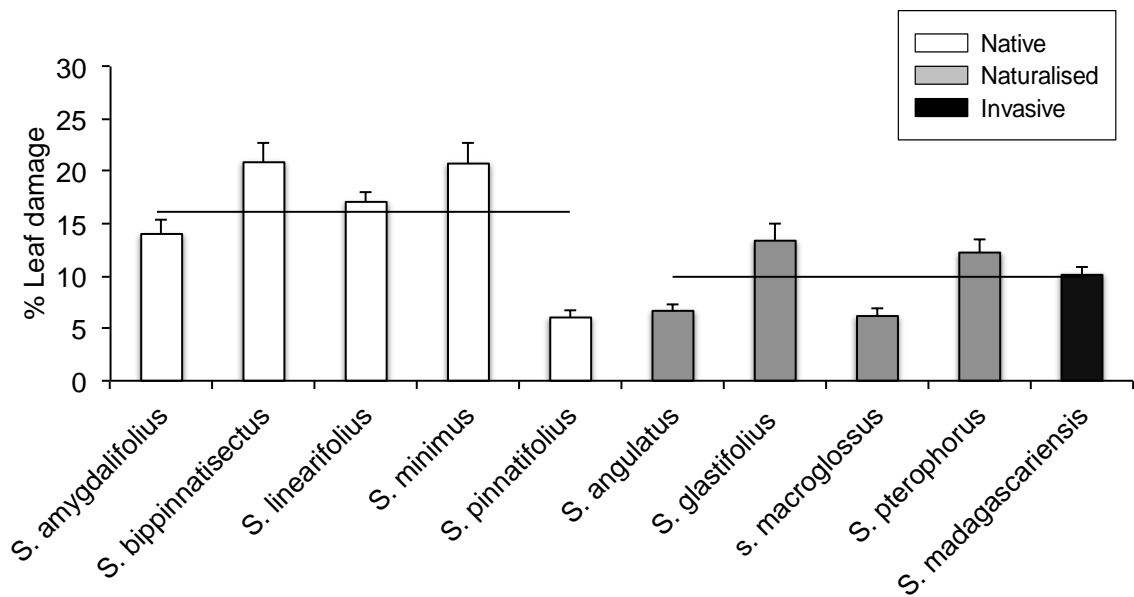


Table 2. Results of a two factor, nested analysis of variance for the effect of category (native, non-native d.f. = 1, 498) and species nested within category (d.f. = 8, 498) on the percentage leaf damage.

| <u>Variable</u> | <u>Category</u> | | <u>Species (Category)</u> | |
|------------------------|-----------------|------------------|---------------------------|------------------|
| | F | P | F | P |
| Percentage leaf damage | 58.013 | <0.001 | 24.405 | <0.001 |

Figure 3. Abundance, morphospecies richness, and Shannon diversity of herbivores (\pm SE) across native and non-native *Senecio* species. Horizontal lines indicate average values for native and non-native species collectively.

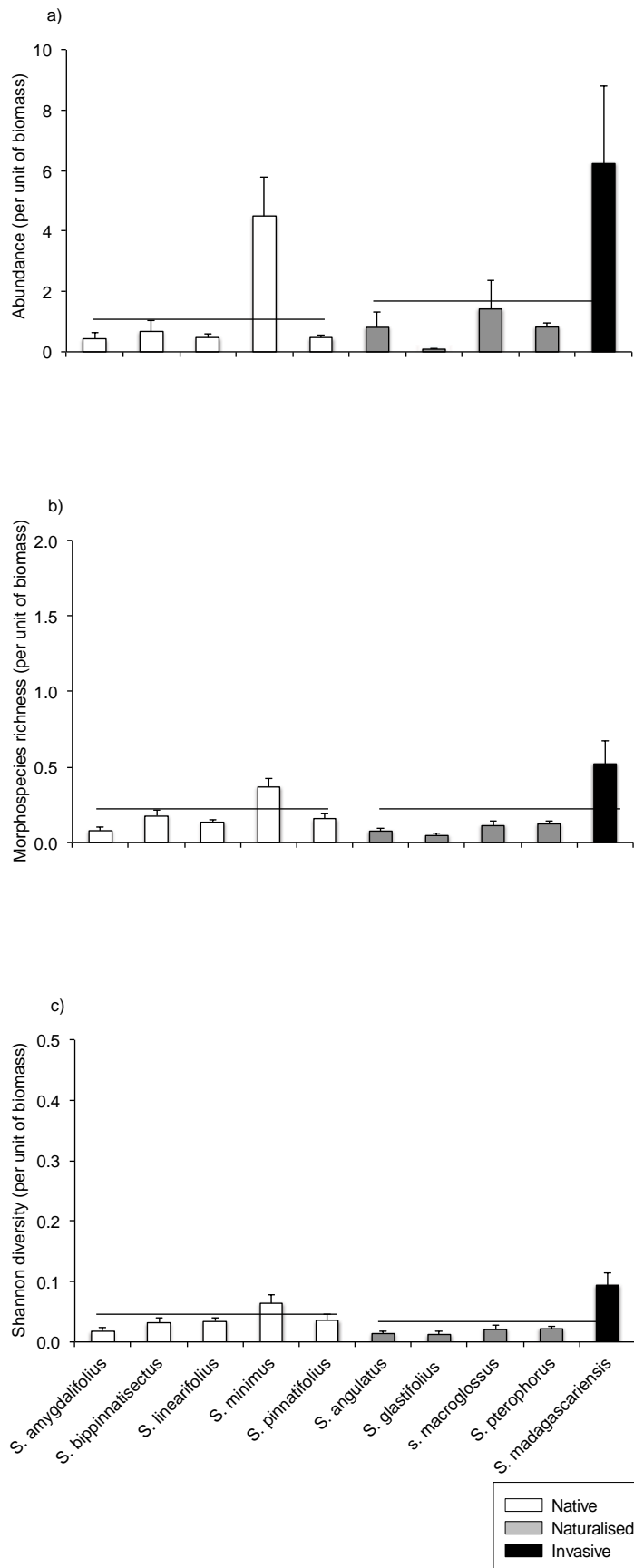


Table 3. Results of a two factor, nested analysis of covariance for the effect of category (native, non-native d.f. = 1, 244) and species nested within category (d.f = 8, 244) on invertebrate herbivore abundance, morphospecies richness and Shannon diversity after accounting for plant biomass (d.f. = 1, 244). Biomass, abundance and richness were transformed to the log (x+1).

| | <u>Biomass</u> | | <u>Category</u> | | <u>Species (Category)</u> | |
|------------------------|----------------|------------------|-----------------|-------|---------------------------|------------------|
| <u>Variable</u> | F | P | F | P | F | P |
| Abundance | 10.477 | 0.001 | 0.124 | 0.726 | 11.515 | <0.001 |
| Morphospecies richness | 12.451 | <0.001 | 1.290 | 0.257 | 11.907 | <0.001 |
| Shannon diversity | 8.423 | 0.004 | 0.472 | 0.493 | 8.640 | <0.001 |

Herbivore guilds

There was no significant difference in the abundance and richness of herbivore guilds between native and non-native *Senecio* species (Table 4; Fig. 4a,b). However, species level differences were found between plant species for the abundance of phytophagous leaf-chewers and sap-sucking invertebrates. Forty per cent of the herbivores collected on the invasive *S. madagascariensis* were leaf-chewing invertebrates and overall, this species had a greater proportion of leaf chewing invertebrates than all other *Senecio* species. The non-native species, *S. macroglossus* DC., had the greatest proportion of sap-sucking herbivores (85%) compared to all other *Senecio* species.

Herbivore species assemblage

There were marked differences in the herbivore species assemblages supported by native and non-native *Senecio* species (Fig. 5, Pseudo F = 5.874, d.f. = 1, 209, $p < 0.001$), with an average between-group species assemblage dissimilarity of 94.81% (SIMPER). Within each category (native and non-native), herbivore assemblages on individual species were also significantly different (Fig. 5, Pseudo F = 3.406, d.f. = 8, 209, $p < 0.001$), with an average between-group community dissimilarity of 93.49% (native) and 91.72 % (non-native).

SIMPER analyses indicated that most of the variation between assemblages was due to 10 herbivore species: two morphospecies of sap-sucking hemipterans (Aphididae Ap. 18, Ap. 27) predominately collected on the non-native *Senecio* species, four morphospecies of sap-sucking Hemipterans dominant on native *Senecio* species (morphospecies Het. 1

Hemiptera: Lygaeoidea; Het. 3 Hemiptera: Orsillidae: *Nysius clevelandensis* (Evans) and Au. 5 Hemiptera: Cicadellidae) and a heteropteran (Het. 2 Hemiptera: Miridae) which was dominant on non-native *Senecio* species. The other morphospecies that contributed

substantial amounts of variation between native and non-native groups all occurred in greater abundance on non-native *Senecio* species and included two leaf chewing herbivores (morphospecies L. 2 Lepidoptera: Pyraloidea and L. 20 Lepidoptera Arctiidae: *Nyctemera* sp. (Hübner)), a sap-sucking mite (morphospecies Ac. 44 Acari: Trombidiformes: Tenuipalpidae) and thrips (morphospecies T. 2 Thysanoptera: Thripidae: *Pseudanaphothrips achaetus* (Bagnall)) (Appendix 2).

Six herbivore species made up 90% of the assemblage collected on *S. madagascariensis*. This group included several of the above mentioned herbivores including the leaf chewing generalist herbivore (morphospecies L. 2 Lepidoptera: Pyraloidea) that contributed to 63% of the total abundance of herbivores collected on this host plant, sap-sucking thrips that contributed 14.5% (T. 2 Thysanoptera: Thripidae: *Pseudanaphothrips achaetus* (Bagnall)), three unknown morphospecies of aphids (morphospecies Ap. 18, Ap. 26 and Ap. 27. Hemiptera: Aphididae) and a sap-sucking heteropteran (morphospecies Het. 1 Hemiptera: Lygaeoidea) (Appendix 2).

Variation in herbivore communities between native and non-native Senecio species

Herbivore communities on non-native *Senecio* species exhibited similar among-plant variation in composition to that of the native species (PERMDISP $F = 2.372$, d.f = 1, 218, p (perm) = 0.145). However, significant differences between *Senecio* species were found (PERMDISP $F = 7.36$, d.f = 9, 210, p (perm) < 0.001). With the exception of *S. minimus*, *S. madagascariensis* on average recruited a less diverse fauna overall compared to all other native *Senecio* species, but among-plant variation on *S. madagascariensis* is similar to levels of other non-native *Senecio* species (Table 5; Fig. 6).

Phylogeny and community composition

Senecio madagascariensis is not phylogenetically isolated from the other species sampled, (Fig. 1). There was no correlation between phylogenetic distance between hosts and the dissimilarity of the herbivore assemblage collected (Fig. 7, RELATE Spearman rank correlation $Rho = 0.104$, $p = 0.325$). Overall, phylogeny does not appear to have any influence on differences in community composition between *Senecio* species.

Figure 4. Percentage abundance (a) and richness (b) (\pm SE) of herbivore guilds (leaf chewers, sap-suckers, miners and gall inducers) collected on *Senecio* species.

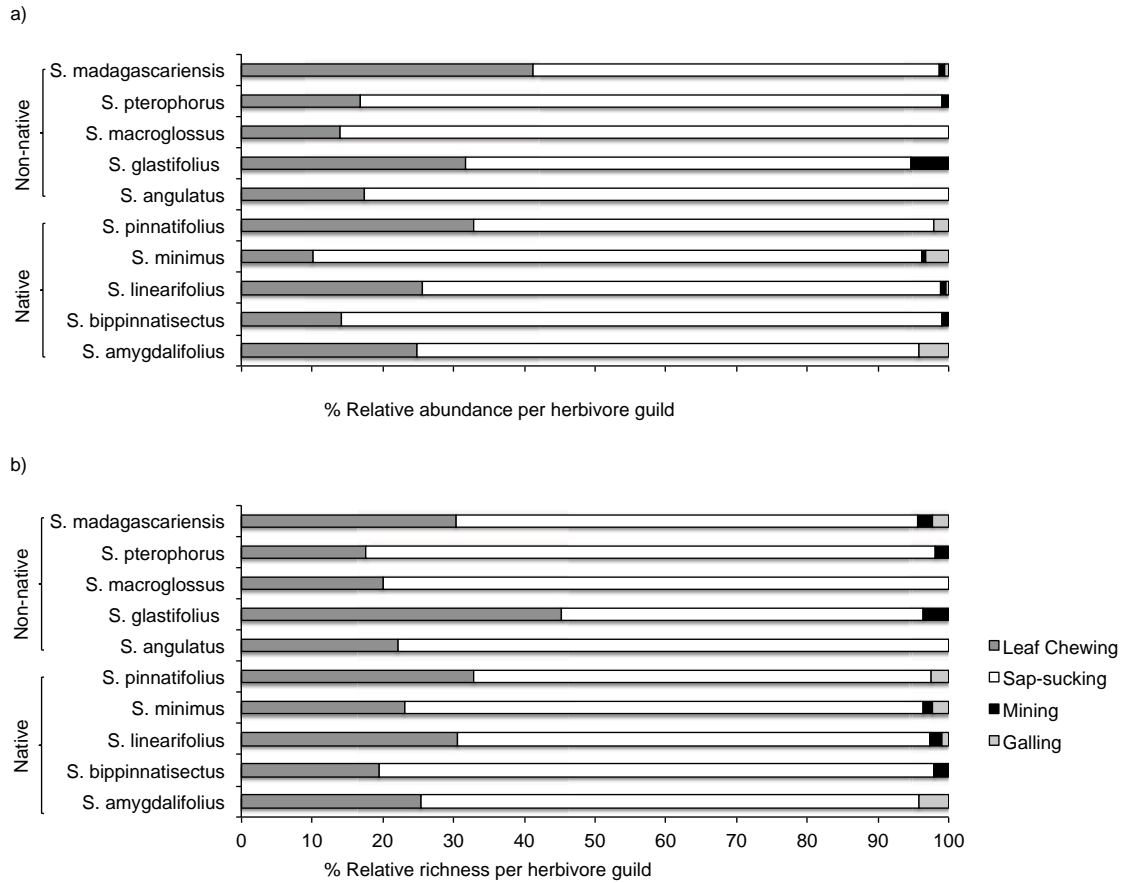


Table 4. Results of a two factor analysis of variance for the relative abundance and richness of herbivore guilds (leaf chewers, sap-suckers, miners and gall inducers) across *Senecio* species with effect of category (native, non-native d.f. = 1, 210) and species nested within category (d.f. = 8, 210).

| Variable | Category | | Species (Category) | |
|-------------------------------|----------|-------|--------------------|--------------|
| | F | P | F | P |
| Abundance | | | | |
| Chewers | 0.391 | 0.533 | 4.068 | 0.020 |
| Sap-suckers | 0.137 | 0.711 | 2.362 | 0.019 |
| Mining | 0.166 | 0.200 | 1.597 | 0.127 |
| Galling | 2.157 | 0.143 | 0.601 | 0.777 |
| Morphospecies richness | | | | |
| Chewers | 0.035 | 0.851 | 1.255 | 0.269 |
| Sap-suckers | 0.002 | 0.963 | 1.482 | 0.165 |
| Mining | 0.568 | 0.452 | 1.410 | 0.194 |
| Galling | 1.484 | 0.225 | 0.618 | 0.762 |

Figure 5. Non-metric, multidimensional scaling plot of herbivore assemblages from replicate samples (one point per plant for each species) of native and non-native *Senecio* species.

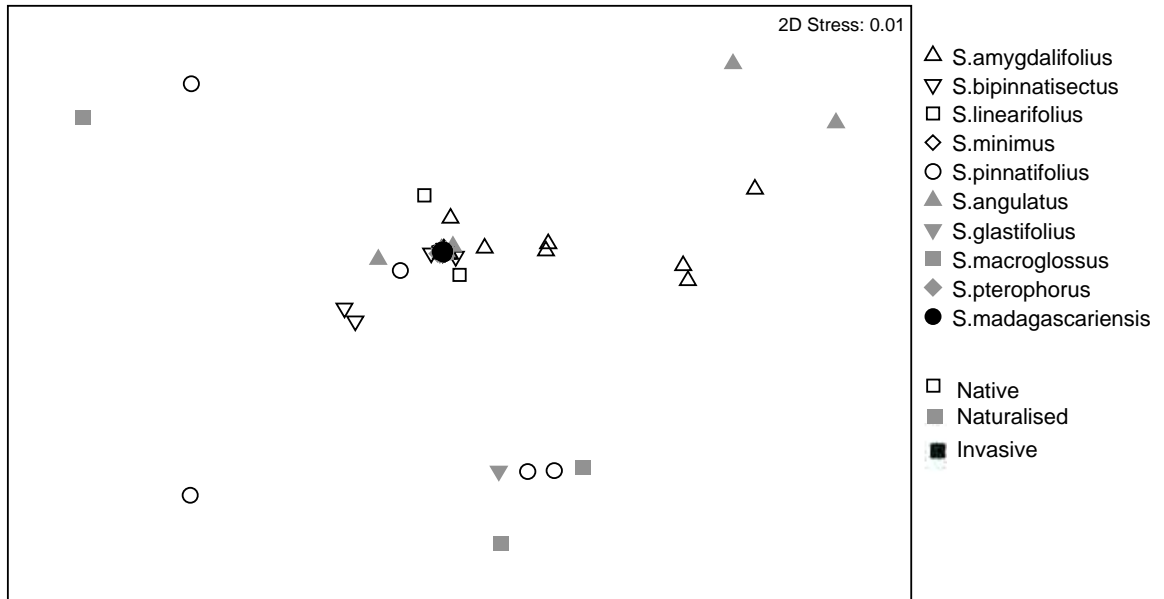


Figure 6. Average distance (\pm SE) for distance-based multivariate dispersion among native and non-native *Senecio* species.

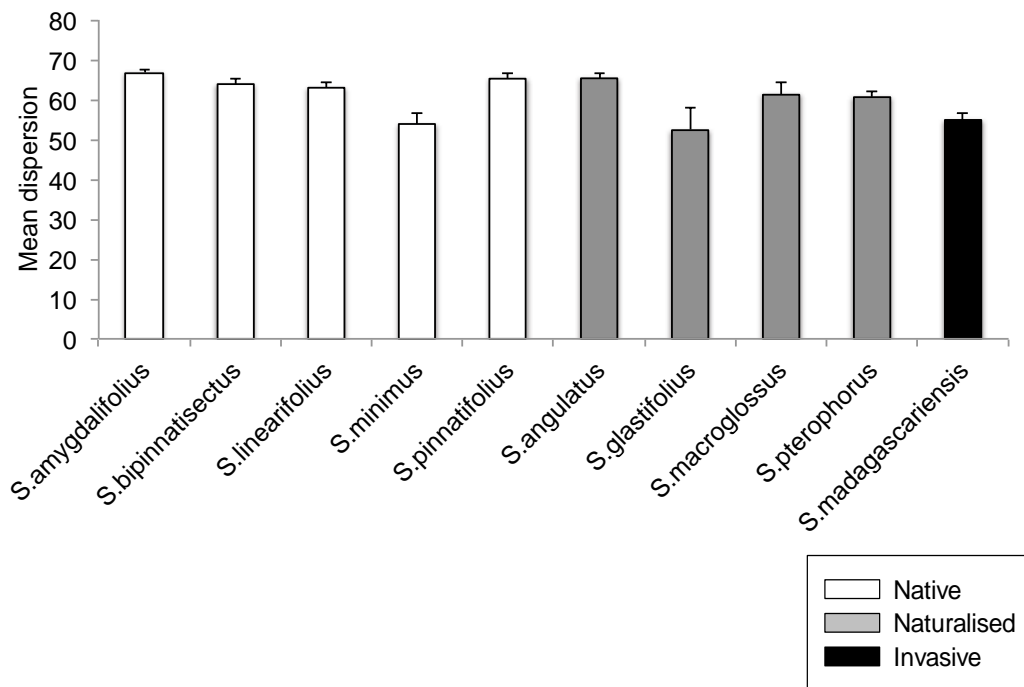
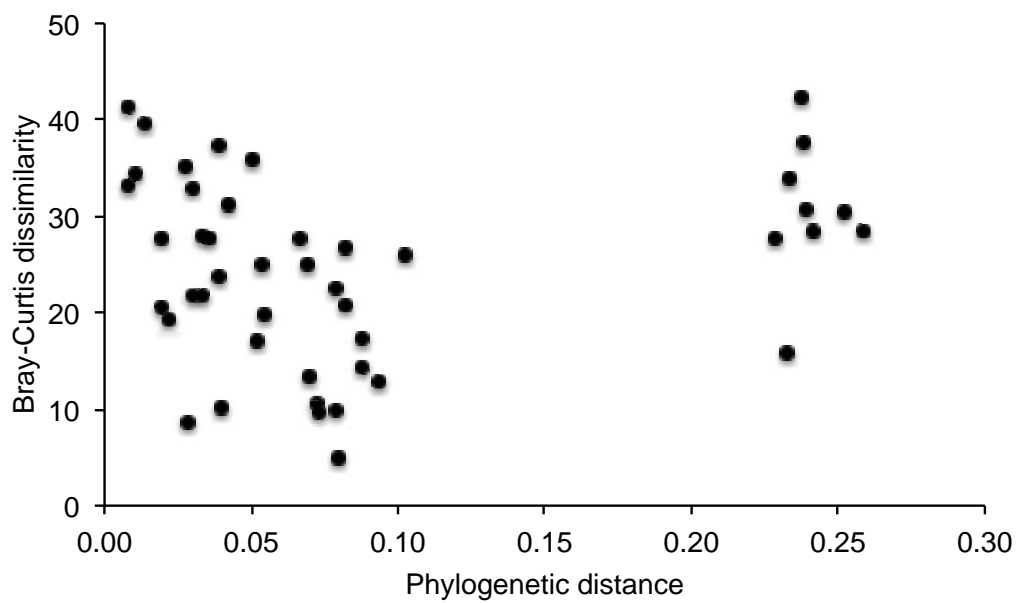


Table 5. Results of PERMDISP for differences in dispersion for *S. madagascariensis* compared to native and non-native *Senecio* species. Non-native *Senecio* species denoted by asterisks.

| Variable | Pairwise comparisons | |
|---------------------------------------------------|----------------------|------------------|
| | t | p |
| <i>S. madagascariensis</i> | | |
| <i>S. pterophorus</i> * | 2.330 | 0.033 |
| <i>S. glastifolius</i> * | 0.558 | 0.640 |
| <i>S. angulatus</i> * | 4.402 | <0.001 |
| <i>S. macroglossus</i> * | 1.780 | 0.136 |
| <i>S. amygdalifolius</i> | 5.422 | <0.001 |
| <i>S. bipinnatisectus</i> | 3.575 | 0.002 |
| <i>S. linearifolius</i> var. <i>arachnoideus</i> | 3.450 | 0.002 |
| <i>S. pinnatifolius</i> var. <i>pinnatifolius</i> | 4.536 | <0.001 |
| <i>S. minimus</i> | 0.334 | 0.761 |

Figure 7. Scatter plot of Bray-Curtis dissimilarity of herbivore composition with phylogenetic distance between native and non-native *Senecio* species.



Discussion

This study sought to determine the extent of enemy release and the importance of phylogenetic relationships in predicting invasion success among species within a single genus. As a mechanism of invasion, the enemy release hypothesis (ERH) predicts that non-native species may be successful as invaders due to being released from co-evolved natural enemies. Total damage, abundance, richness and Shannon diversity of herbivores, the proportional abundance and richness of herbivore guilds and the composition of the herbivore assemblage were compared between native, non-invasive and an invasive *Senecio* species (*Senecio madagascariensis* Poir.). The results provide very little support for the ERH, with non-native *Senecio* species receiving less leaf damage than native counterparts, but with similar levels of invertebrate herbivore abundance, richness and Shannon diversity and a similar proportional abundance and richness of feeding guilds compared to native *Senecio* species. Contrary to predictions, damage levels on the invasive species *S. madagascariensis* were similar to non-invasive species, and greater than on the closely related native *S. pinnatifolius* var. *pinnatifolius*. Overall, *S. madagascariensis* had a greater abundance and richness of herbivores than all other *Senecio* species. Herbivore communities were considerably different in composition between native and non-native *Senecio* species. *Senecio madagascariensis* did not have a reduced subset of the native herbivore community as indicated by a similar variation in composition among plants to other non-native species, but may be accumulating a more generalist assemblage indicated by a greater abundance of chewing herbivores than all other *Senecio* species. Phylogenetic distance between *Senecio* species could not explain the differences in the herbivore assemblages. Further, as the phylogeny of *Senecio* species does not indicate the phylogenetic isolation of non-natives including *S. madagascariensis*

(Thompson 2006; Pelser *et al.* 2007), the results overall suggest that enemy release is not an immediate contributing factor to the success of *S. madagascariensis*.

The majority of published studies on herbivore damage and the accumulation of the herbivore community have focused either on herbivory alone, or on herbivore abundance and richness, with few studies considering both. In two separate studies on native, non-invasive and invasive *Eugenia* spp. (Myrtaceae), Liu *et al.* (2006, 2007) found that while herbivore damage was lower on non-native species, non-invasive species sustained similar levels of herbivore damage to the invasive *Eugenia* species. Further, herbivore richness was similar between the native, non-invasive and invasive *Eugenia* species (Liu *et al.* 2007). These studies are consistent with our results. If we did not include the non-invasive *Senecio* species when comparing herbivore damage, we may have concluded that release from the insect herbivores may be an important factor in the success of *S. madagascariensis*.

The enemy release hypothesis further predicts that non-native species are more likely to be released from specialist herbivores in their new range but are more susceptible to generalist insect activity (Keane & Crawley 2002). As internal feeding niches (miners and gall inducers) are often associated with specialised diets (Frenzel and Brandl 1998), non-native plants may be more susceptible to attack by generalist ectophagous herbivores (leaf chewers and sap-sucking herbivores). In this study, we found that the proportion of feeding guilds across *Senecio* species did not vary between native and non-native species. Interestingly, very few endophagous herbivores were collected on *Senecio* species; the assemblages were dominated by leaf chewing and sap-sucking herbivores. Categorising ectophagous insects as generalists in this study, however, is unlikely to be sufficient for determining whether non-natives are released from specialist herbivores and more susceptible to damage by generalist insect activity. While some studies have found

success in categorising ectophagous insects as generalists (Frenzel and Brandl 1998; Liu *et al.* 2007; Frenzel & Brandl 2003), species level identifications are required in our case because it is probable that several of these leaf chewing and sap-sucking herbivores may be specialists. Unfortunately, there is insufficient information on feeding preferences available for the majority of Australian insects to confidently categorise most as either specialists or generalists. Further investigation into herbivore feeding rates, host plant choice and the impacts and performance of herbivores across the range of non-native *Senecio* species is required for a greater understanding of whether non-native species may be released from specialist natural enemies.

Contrary to our predictions, *S. madagascariensis* had a greater abundance, richness and Shannon diversity of herbivores than all other *Senecio* species sampled. Other workers have also found high densities of herbivores on non-native species with levels similar to, or greater, than native plants (French & Eardly 1997; Viejo 1999; Hedge & Kriwoken 2000; Petillion *et al.* 2005). Greater density and diversity of herbivores collected from this invasive species compared to native species may not necessarily translate to greater enemy attack, but may be attributed to herbivores using this plant for oviposition sites, nesting and reproduction.

Senecio madagascariensis has rapidly accumulated a generalist herbivore assemblage but may also have developed a specialist assemblage, which may explain why there are greater abundances and richness of herbivores overall collected on this species compared to the other non-native species sampled. A greater density and diversity of herbivores on this species compared to the other non-invasive species may be in part attributed to *S. madagascariensis* being present on the east coast of NSW for a longer period of time or having a larger geographical range (species area effect; Connor & McCoy 1979; Southwood 1961) compared to the other non-native species. *Senecio madagascariensis*

was first recorded in the Hunter Valley in 1918 and, according to NSW herbarium records, occurrences for all other non-native species in eastern NSW are no earlier than 1957.

Moreover, the species area effect, suggests that plants with large geographical ranges or those that are in larger densities with a greater biomass per unit area have more species of associated insects than those with smaller geographical ranges or smaller densities (Southwood 1961; Strong 1979). Indeed, herbarium records indicate that *S. madagascariensis* has a greater range (in terms of occurrence records) than the other non-native species throughout Australia. Future research focusing on the taxonomy, impacts of herbivores and community development would give insight into how specialised the community has developed over time and the role herbivores play in utilising *S. madagascariensis*.

Although there were some herbivore species in common across *Senecio* species, herbivore communities overall differed markedly among *Senecio* species. Large differences in community composition were particularly evident when the native species as a group were compared to the group of non-native species. Corresponding differences in plant structure or architecture; and/or differences in the nutritional value or chemical composition and biomass per unit area across sites may account for the differences in the herbivore assemblage between *Senecio* species. The *Senecio* species sampled included a variety of herbs, shrubs and vines for both the native and non-native species groups. It is likely that variations in plant architecture (Lawton & Schroeder 1977), that may include differences in the size, growth form and types of aboveground and belowground structures, may provide different microhabitats that influence the colonisation of insect herbivores. Past studies have indicated that differences in microhabitats created by non-native species are associated with variation in the invertebrate assemblage (Hedge & Kriwoken 2000; Petillion *et al.* 2005) through causing variation in light penetration, protection from abiotic

stresses and predators and suitability for resting, feeding, reproduction and nest building (Strong *et al.* 1984). The nutritive value including chemical composition and water content, and other variables such as trichome density and mechanical properties can vary greatly between even closely related species and have been shown to influence host plant selection, palatability and the demography and population dynamics of many insect taxa (Crawley 1983, Strong *et al.* 1984; Agrawal *et al.* 2005). For example, the Richmond birdwing butterfly (*Ornithoptera richmondia*) requires the native plant species of *Aristolochia* and *Pararistolochia* for breeding, but can mistakenly oviposit on the highly invasive Dutchman's Pipe vine - *Aristolochia elegans*, which is highly toxic for the larvae (Braby 2000). *Senecio* species are known to contain pyrrolizidine alkaloids, which can vary within and among species, across their ranges and overall influence herbivore host choice (Hol 2011; Langal *et al.* 2011). By minimizing variation in plant biomass in our sampling and by comparing congeneric species, we have attempted to control for at least some of these potential confounding factors that may contribute to variation in our data.

In summary we did not find evidence to support the hypothesis that enemy release explains the success of the invasive plant *S. madagascariensis*. The results of this study indicate that for closely related species, enemy release may not be important as a mechanism for the success of some invasive species. Areas of future research could include understanding how time may be important for propagules to spread and the populations to increase. Future research focusing on the taxonomy and impacts of herbivores and the development of the community from its point of introduction to its invasion fronts would give insight into the development of a specialist and generalist assemblage on *S. madagascariensis* and give a better indicator of the role of natural enemies in invasion biology over time.

Acknowledgements

We thank fieldwork volunteers, Kate Umbers, Katy Wilkins, John Martin, Hayley Given, Laurel Harvey and William Harvey. Thank you to Katy Wilkins for laboratory assistance. Invertebrate collection methods were based on the work of John Hosking and Royce Holtcamp of the NSW Department of Primary Industries. We would also like to thank Paul Robins of the Herbarium of Queensland, Frank Hemmings of John T. Waterhouse Herbarium University of New South Wales, Gary Chapple of the Royal Botanic Gardens Sydney, Belinda Pellow of Janet Kosh Herbarium University of Wollongong, also John Hosking and Royce Holtkamp of the NSW Department of Primary Industries, Paul O'Connor from Hastings City Council, Ross Rapmund from Hornsby Shire Council, Mathew Misdale of Wollongong City Council and Matthew Springall of Lane Cove National Park for plant location data. Thank you to Alison Downing of the Downing Herbarium Macquarie University for plant identifications and Muhammad Masood for support in the glasshouse. We are grateful to city councils including Wollongong, Great Lakes and Hastings for sampling permits. Research was supported by Macquarie University, the Australian Museum in Sydney and the Wildlife Preservation Society of Australia. A special thanks to taxonomists Dr Laurence Mound and Bruce Halliday of CSIRO Ecosystem Sciences, Canberra, for species identification of Thysanoptera and Acarina. Assistance with the phylogeny of *Senecio* was given by Michelle Power, Nikolai Tatarnic, Vincenzo Repaci and Kate Umbers.

References

- Adair R, Groves R (1998) Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology. Environment Australia, Canberra
- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a

phylogenetically controlled experiment. *Ecology Letters* 6:712–715

Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005)

Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86:2979-2989

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance.

Austral Ecology 26:32-46

Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions.

Biometrics 62:245-253

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of

beta diversity. *Ecology Letters* 9:683-693

Ando Y, Utsumi S, Ohgushi T (2010) Community structure of insect herbivores on

introduced and native *Solidago* plants in Japan. *Entomologia Experimentalis et*

Applicata 136:174-183

AWC (2011) Noxious weed lists for Australian States and Territories. Prepared by the

Australian Weeds Committee Last Update: Mar 2011 Version: 23.00

www.weeds.org.au/docs/weednet6.pdf Accessed May 2011

Braby MF (2000) Butterflies of Australia: Their Identification, Biology and Distribution.

CSIRO, Melbourne, Australia

Cappuccino N, Carpenter D (2005) Invasive exotic plants suffer less herbivory than non-

invasive exotic plants. *Biology Letters* 1:435-438

Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the

- invasiveness of exotic plants. *Journal of Ecology* 93:315-321
- Chun YJ, van Kleunen M, Dawson W (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecology Letters* 13:937-946
- Cincotta CL, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biological Invasions* 11:379-388
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143
- Clarke KR, Gorley RN (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-733
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society, Series B* 345:101-118
- Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *American Naturalist* 113:791-833
- Connor EF, Faeth SH, Simberloff D, Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 5:205-212
- Crawley MJ (1983) *Herbivory: The Dynamics of Animal-Plant Interactions*. Blackwell

Scientific, Oxford, UK

CSIRO (1973) *The Insects of Australia: A Textbook for Students and Research Workers.*

Vol 1 & 2. Melbourne University Press, Melbourne

CSIRO (2011) *What bug is that? The guide to Australian Insect Families*

<http://anic.ento.csiro.au/insectfamilies> Accessed May 2011

Daehler CC (2001) Darwin's naturalization hypothesis revisited. *American Naturalist*

158:324-330

Darwin CR (1859) *The Origin of Species by Means of Natural Selection.* John Murray,

London

Duncan RP, Williams PA (2002) Ecology - Darwin's naturalization hypothesis challenged.

Nature 417:608-609

French K, Eardley K (1997) The impact of weed infestations on litter invertebrates in

coastal vegetation. In: Klomp N, Lunt I (eds) *Frontiers in Ecology.* Elsevier

Science, London, pp 89-102

Frenzel M, Brandl R (1998) Diversity and composition of phytophagous insect guilds on

Brassicaceae. *Oecologia* 113:391-399

Frenzel M, Brandl R (2003) Diversity and abundance patterns of phytophagous insect

communities on alien and native host plants in the Brassicaceae. *Ecography*

26:723-730

Frodin DG (2004) History and concepts of big plant genera. *Taxon* 53:753-776

Hamilton JR, Yeates DK, Hastings A, Colless DH, McAlpine DK, Bickel D, Cranston PS,

- Schneider MA, Daniels G, Marshall S (2005) On The Fly: The Interactive Atlas and Key to Australian Fly Families, Beta Version 0.9. Australian Biological Resources Study and CSIRO, Canberra
- Harden GJ (2011) Genus *Senecio*. In: PlantNET - The Plant Information Network System of The Royal Botanic Gardens and Domain Trust, Sydney, Australia
<http://plantnet.rbgsyd.nsw.gov.au/cgi-bin/NSWfl.pl?page=nswfl&lvl=gn&name=Senecio> Accessed July 2011
- Harvey KJ, Nipperess DA, Britton DR, Hughes L (in press) Australian family ties: does a lack of relatives help invasive plants escape natural enemies? Biological Invasions
- Hedge P, Kriwoken LK (2000) Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport estuary, Tasmania. Austral Ecology 25:150-159
- Hill SB, Kotanen PM (2009) Evidence that phylogenetically novel non-native plants experience less herbivory. Oecologia 161:581-590
- Hol WHG (2011) The effect of nutrients on pyrrolizidine alkaloids in *Senecio* plants and their interactions with herbivores and pathogens. Phytochemistry Reviews 10:119-126
- Holtkamp RH, Hosking JR (1993) Insects and Diseases of Fireweed, *Senecio madagascariensis*, and the closely related *Senecio* Lautus Complex In: Swarbrick JT, Henderson CWL, Jettre RJ, Streit L, Walker SR (eds) Proceedings of the Tenth Australian and 14th Asian Pacific Weed Science Society Conference Weeds Society of Queensland. Brisbane, pp 104-106

- Jobin A, Schaffner U, Nentwig W (1996) The structure of the phytophagous insect fauna on the introduced weed *Solidago altissima* in Switzerland. *Entomologia Experimentalis et Applicata* 79:33-42
- Jones CG, Lawton JH (1991) Plant chemistry and insect species richness of British umbellifers. *Journal of Animal Ecology* 60:767-777
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17:164-170
- Langel D, Ober D, Pelser PB (2011) The evolution of pyrrolizidine alkaloid biosynthesis and diversity in the Senecioneae. *Phytochemistry Reviews* 10:3-74
- Lawrence JF, Hastings HM, Dallawite MJ, Paine TA, Zurcher EJ (1999) *Beetles of the World* CSIRO Publishing, Canberra
- Lawton JH, Schroder D (1977) Effects of plant type size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* 265:137-140
- Liu H, Stiling P, Pemberton RW, Pena J (2006) Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: implications for the Enemy Release Hypothesis. *The Florida Entomologist* 89:475-484
- Liu H, Stiling P, Pemberton RW (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* 9:773-781
- Lockwood JL, Simberloff D, McKinney ML, Von Holle B (2001) How many, and which, plants will invade natural areas? *Biological Invasions* 3:1-8

- Lowman MD (1984) An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica* 16:264-268
- Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation* 78:107-121
- Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361-373
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290-297
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421:625-627
- Nei M & Kumar S (2000) *Molecular Evolution and Phylogenetics*. Oxford University Press, New York
- Nipperess DA, Beattie AJ, Faith DP, Ginn SG, Kitching RL, Reid CAM, Russell T, Hughes L (2012) Plant phylogeny as a surrogate for turnover in beetle assemblages. *Biodiversity and Conservation* 21:323-342
- Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115-1118
- Ødegaard F, Diserud OH, Ostbye K (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters* 8:612-617
- Parsons WT, Cuthbertson EG (1992) *Noxious Weeds of Australia*. Inkata Press, Sydney
- Pelser PB, Nordenstam B, Kadereit JW, Watson LE (2007) An ITS phylogeny of tribe

Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. Taxon 56:1077-1104

Petillon J, Ysnel F, Canard A, Lefeuvre JC (2005) Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. Biological Conservation 126:103-117

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655-1661

Rentz D (1996) Grasshopper Country: The Abundant Orthopteroid Insects of Australia. University of NSW Press, Sydney

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7:781-784

Schaefer H, Hardy OJ, Silva L, Barraclough TG, Savolainen V (2011) Testing Darwin's naturalisation hypothesis in the Azores. Ecology Letters 14:389-396

Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology 75:1661-1672

Shattuck SO (1999) Australian Ants, Their Biology and Identification. Monographs on Invertebrate Taxa, Vol. 3. CSIRO Publishing, Victoria

Siemann E, Rogers WE (2003) Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84:1489-1505

Sindel B (2009) Fireweed in Australia: Directions for future research. Report for the Bega

Valley Fireweed Association

www.ruralfutures.une.edu.au/fireweed/resources/0901_Sindel.pdf Accessed May 2011

Sinden J, Jones R, Hester S, Odom D, Kalisch D, James R, Cacho O, Griffith G, (2005)

The economic impact of weeds in Australia. *Plant Protection Quarterly* 20:25-32

Southwood TRE (1961) The number of species of insect associated with various trees.

Journal of Animal Ecology 30:1-8

Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103:5841-5845

Strong DR (1979) Biogeographical dynamics of insect-host plant communities. *Annual Review of Entomology* 24:89-119

Strong DR, Lawton JH, Southwood R (1984) *Insects on Plants: Community patterns and mechanisms*. Blackwell Scientific Publications, Oxford, London

Tallamy DW (2004) Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* doi: 10.1093/molbev/msr121

Thompson IR (2006) A taxonomic treatment of tribe Senecioneae (Asteraceae) in Australia. *Muelleria* 24:51-110

Viejo RM (1999) Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany* 64:131-149

Weiblen GD, Webb CO, Novotny V, Basset Y, Miller SE (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87:S62-S75

Chapter 4

Does time since introduction influence enemy release of an invasive weed?

Kerinne J. Harvey^{1*}, David A. Nipperess¹, David R. Britton², & Lesley Hughes¹

¹ Department of Biological Sciences, Macquarie University, North Ryde, NSW
Australia

² Entomology Collections, Australian Museum, Sydney, NSW, Australia

*Kerinne Harvey: Email: kerinne.harvey@gmail.com

Telephone: +612 9850 6279; Fax: +612 9850 8245

Running headline: Time since introduction and enemy release

For submission to *Oecologia* or *Oikos*

Abstract

Release from natural enemies is considered to potentially play an important role in the initial establishment and potential success of introduced plants. With time, the species richness of herbivores using non-native plants has been found to increase, providing the community is not already saturated (known as the species-time relationship). During this time herbivores and their hosts may develop closer physiological or co-evolutionary associations. Time since introduction may affect the amount of enemy release experienced by an invader, resulting in its rate of spread being potentially reduced as herbivores adapt to it over time. In this study, we investigated whether the amount of enemy release experienced by an invader may be limited to the early stages of its invasion. Substituting space for time, we sampled invertebrates and measured leaf damage on the invasive species *Senecio madagascariensis* Poir. This species has extensive historical data detailing its known point of introduction and spread on the east coast of Australia. We sampled at multiple sites that encompassed the current latitudinal range of *S. madagascariensis* (~1000 km) and included sites to both the north and south of the point of introduction. Invertebrate communities were collected from the plants in the field, as well as being reared from collected plant tissue over several months post-collection. Because the sites are located along a latitudinal gradient, and therefore differ in climate as well as in time since introduction, we also sampled invertebrates and estimated damage on the closely related native congener *S. pinnatifolius* var. *pinnatifolius* A. Rich. at the same sites. This species therefore served as a control to help account for environmental factors but also as a comparison for evaluating the enemy release hypothesis (ERH). Our results provided no support for the enemy release hypothesis but did provide partial support for the species-time relationship. Greater damage and herbivore abundances and richness were found on *S. madagascariensis* than its native congener, *S. pinnatifolius*, in contrast to predictions of

the enemy release hypothesis. Invertebrates decreased in abundance, richness and Shannon diversity from the point of introduction to the invasion front, supporting the species-time relationship. Leaf damage showed the opposite trend, with highest damage levels at invasion fronts. Greater herbivore abundance, richness and Shannon diversity of reared herbivores (as opposed to external collections) were found on the invasive species at the point of introduction compared with sites further from this region, indicating that closer physiological associations in plant-herbivore interactions may have developed with increasing time since introduction. Our results suggest that there is a complex relationship between the invader and the response of the invertebrate community over time. There is the potential that *S. madagascariensis* may be undergoing rapid changes at its invasion fronts in response to environmental and herbivore pressure, which may in turn be influencing these plant-herbivore interactions.

Key words: species-time relationship, invasive plants, enemy release hypothesis, congeners, plant-insect interactions, evolution of increased compatibility hypothesis.

Introduction

The enemy release hypothesis (ERH) predicts that when non-native plant species are introduced to a new region with few or no co-evolved specialist herbivores from their native habitat, they suffer only minimal damage from generalist polyphagous herbivores and thereby gain a competitive advantage over native plants (e.g. Keane & Crawley 2002). Understanding how rapidly both specialist and generalist insects adapt to and colonise non-native invasive plants is integral to understanding the basis of the ERH as a mechanism behind successful invasions.

Studies in which the densities and damage by herbivores and pathogens on non-native species within their introduced range compared to that of their native range have generally found support for the enemy release hypothesis (reviewed by Colautti *et al.* 2004; meta-analysis by Liu & Stiling 2006). In contrast, comparisons of non-native species in their introduced range with co-occurring native species have yielded mixed results (reviewed by Colautti *et al.* 2004; meta-analysis by Chun *et al.* 2010), with some cases showing that greater herbivory is found on non-native compared to native species (Agrawal & Kotanen 2003). Although damage levels on non-native species may be generally lower in their country of origin compared to the area of introduction, native herbivores do adapt to and colonise non-native species. The complexity and unpredictability in patterns of damage and densities of herbivores between native and non-native species may be the result of complex interactions between the time since a plant's introduction, the phylogenetic relatedness of the invader and other species within the invaded community, and the influence of a variety of abiotic factors.

The observation that species richness of herbivores on introduced plants accumulates through time was first noted by Preston (1960). This pattern is referred to as the species-

time relationship (STR) and describes how the species richness of a community increases with time, provided the community is not already saturated (*sensu* Preston 1960). This relationship is analogous to the species-area relationship whereby richness increases with the local abundance and area of habitat sampled (Arrhenius 1921; Preston 1960). For non-native species, time since introduction may be an important determinant of herbivore and pathogen accumulation and therefore the potential pressure they may exert on the success of the invader (Strong *et al.* 1984; Siemann *et al.* 2006; Mitchell *et al.* 2010). If herbivores adapt to and colonise the non-native species gradually over time, enemy release may be limited to the early stages of invasion (Siemann *et al.* 2006; Hawkes 2007). Moreover, while time has been suggested to be important for insects and pathogens to adapt to non-native species (Strong *et al.* 1984), different rates of accumulation can occur across herbivore species. Some non-native species have been found to support similar insect communities to natives within a few hundred years (Strong *et al.* 1984), while rapid evolution of specific herbivores to non-native species may occur in as little as 50 years (Carroll *et al.* 2005).

There is conflicting evidence for the importance of time in the success of invasive species (Carpenter & Cappuccino 2005; Siemann *et al.* 2006). It is likely that differences in the extent of species geographic ranges (Strong 1974; Strong 1979; Neuvonen & Niemela 1981), variation in growth forms (Lawton & Schroeder 1977) and the phylogenetic relationships of species with respect to the native community (Conner *et al.* 1980; Lawton & Strong 1981; Strong *et al.* 1984), may mask the role of time in the accumulation of natural enemies on non-native species. Some of these confounding factors can be accounted for by including measures of plant biomass and by comparing herbivory and herbivores on the invader with that of a co-occurring congeneric native species.

Most species of phytophagous insects are specialised to feed on just a few host plant

species (Bernays & Graham 1988). When a non-native plant invades a new habitat, it generally leaves behind its co-evolved herbivores and pathogens (Keane & Crawley 2002). These specialist insects and pathogens are replaced by generalists in the new range (Keane & Crawley 2002). This implies that the longer a plant species has been established within a community, the more specialised the herbivore assemblage it supports (Andow & Imura 1994). Indeed a review of arthropod communities on 24 annual crop species found that the proportion of specialists was greater than generalists on plant species that had been in Japan for longer periods of time (Andow & Imura 1994). This indicates that closer physiological associations may occur between an invader and its natural enemies over time. The overall impact of herbivores and pathogens may thus be determined by the net effect of escaping specialists and acquiring new natural enemies over time.

By comparing rates of herbivore accumulation and damage in newly colonised regions to older sites of invasion, it should be possible to gain insight into the role time plays in adaptation of herbivores to invasive species. In this study, our focus was the invasive species *Senecio madagascariensis* Poir. (Fireweed). This species provides an ideal system to study the process of natural enemy accumulation due to historical data that details its known point of introduction in the Hunter Valley, NSW (1918) and steady spread for over 90 years to the north and south of this region. We investigated how rapidly *S.*

madagascariensis has been colonised by invertebrates by comparing the assemblages on *S. madagascariensis* from sites where it was first introduced, to other sites, to both the north and south. Our general aim was to assess whether the relationship between this invasive species and its natural enemies has changed over time. We made the following predictions:

- (1) In accordance with the 'Enemy Release Hypothesis' (ERH), the total damage and abundance of invertebrates including non-herbivores would be less on *S. madagascariensis*

than on a closely related congener *S. pinnatifolius* var. *pinnatifolius* A. Rich. at the same sites.

(2) In accordance with the ‘Species-Time Relationship’ (STR), damage, herbivore abundance, and species richness would decrease on *S. madagascariensis* from its point of introduction to the invasion fronts.

By comparing herbivore accumulation and damage impacts over time, we specifically investigated whether enemy release may be limited to the early stages of its invasion. We further identified herbivores that contributed to differences across the range of *S. madagascariensis* to correlate damage with herbivore identity.

Our sampling encompassed both herbivores and the general invertebrate assemblage. Assessing the invertebrate assemblage as a whole assists in investigating whether changes in predator prey interactions, in addition to disturbance by non-herbivorous invertebrates, may contribute to facilitating the establishment and spread of non-native species over time. Therefore, we made the further prediction that:

(3) In accordance with the ‘Species-Time Relationship’ (STR), the total invertebrate abundance including non-herbivores would decrease on *S. madagascariensis* from its point of introduction to invasion fronts.

We also investigated how the types of herbivores on the plant varied from the introduction point to the invasion fronts. Internal feeders, such as gallers, stem borers and leaf miners and those species that oviposit into the plant tissue, may have developed more specialised associations with the plant than herbivores collected externally. A higher proportion of herbivores reared from internal plant tissues at the introduction point compared to the invasion fronts would indicate that, over time, closer physiological associations may occur

between an invader and its natural enemies. Therefore, we further predicted that:

(4) The number of herbivores reared from internal tissues compared to those collected from external sampling of *S. madagascariensis* would increase from its introduction point to the invasion fronts.

For all predictions we compared the damage and invertebrate assemblage on the congeneric native *S. pinnatifolius* var. *pinnatifolius*. This species has a similar distribution to *S. madagascariensis* on the east coast of Australia and they commonly co-occur together. *Senecio pinnatifolius* var. *pinnatifolius* was used as a community based comparison of the ERH, in addition to serving as a control to account for the invertebrate community being influenced by other factors including latitude (Rosenzweig 1995; reviewed by Moles *et al.* 2011).

Methods

Plant species

Senecio madagascariensis Poir. is an aggressive annual or biennial herbaceous weed that invades pastures and disturbed areas of eastern Australia (Holtkamp & Hosking 1993) and is of significant concern due to its toxicity to domestic livestock (Sindel 1986). The species has been declared a noxious weed in New South Wales, Queensland and the Australian Capital Territory (Parsons & Cuthbertson 1992). It was introduced from the KwaZulu-Natal province on the east coast of South Africa (Radford *et al.* 2000), and was first recorded in the lower Hunter Valley, NSW in 1918 (32°43'0"S, 151°49'60"E) (Fig. 1). It has since become prevalent along the east coast of Australia (Holtkamp & Hosking 1993; Radford & Cousens 2000), extending from south-east Queensland into Victoria, a latitudinal distance of over 1000 km (Parsons & Cuthbertson 1992). Herbarium records

indicate a steady invasion front along the coast to the north and south of the introduction point (NSW Collections database, National Herbarium of New South Wales). Recent evidence from nuclear microsatellite data indicates an augmentation of the population in far north-eastern NSW occurred in the mid 1950s (E. Dormontt *pers. comm.* 2011). This introduction was from the same genetic stock as the Hunter Valley region and is likely to have originated from crop seed used in industries such as turf farming (E. Dormontt *pers. comm.* 2011).

The invertebrate community on a single host plant, when sampled at different sites, may be influenced by factors other than time since colonisation, such as latitude (Rosenzweig 1995; reviewed by Moles *et al.* 2011). To control for the potential role of latitude in influencing the assemblage sampled on the invasive species, we also sampled a native senecio species, *S. pinnatifolius* var *pinnatifolius* A. Rich., at the same sites or nearby. *Senecio pinnatifolius* var. *pinnatifolius* is an herbaceous sprawling or prostrate annual or short-lived perennial that has a similar geographic range and appearance to *S. madagascariensis* in eastern Australia. It occurs in scattered populations in dry hills, coastal dunes, forest, woodland and scrubland throughout south-east Queensland, extending south into Victoria (Thompson 2005).

Survey design

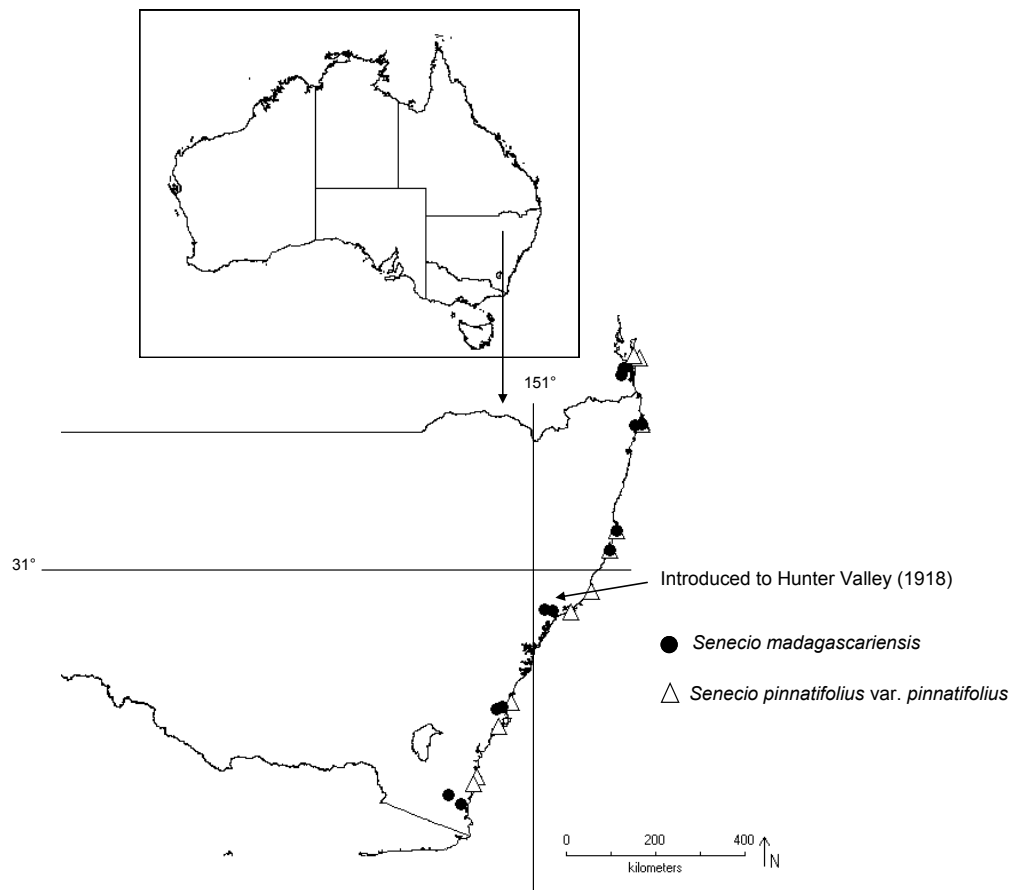
The study was conducted between March and May 2009 in coastal bushland and grazing land along the east coast of Australia extending from south-eastern New South Wales (NSW) to south-eastern Queensland (QLD). Plants were sampled in flowering periods only. Survey sites were divided into six latitudinal bands of 10°, covering the latitudinal distribution of *S. madagascariensis* ((1) 36-37°; (2) 34-36°; (3) 32-34°; (4) 30-32°; (5) 28-30°; (6) 27-28°). The northern-most site sampled was 584 km from the Hunter Valley

introduction region and the southern-most was 484 km south of the introduction region (Fig. 1). The distance between each latitudinal band was approximately 200 km. Sites north and south of the Hunter Valley were then grouped into four bands in terms of the distance from the introduction point to the invasion fronts ignoring latitude (0-100: 101-300: 301-500 and 501-700 in kilometres). Two sampling sites within each of the 6 latitudinal bands were selected in which *S. madagascariensis* and *S. pinnatifolius* var. *pinnatifolius* co-occurred. Where the species did not co-occur, *S. pinnatifolius* var. *pinnatifolius* was sampled at the closest site to where *S. madagascariensis* had invaded (Fig.1). At each site, insect assemblages were sampled once on 5 randomly selected similar sized plants of each plant species. Each plant sampled was separated by at least 2 m from all other plants on the site.

Plants were sampled for invertebrates using two techniques: direct external collections and rearing from plant material. Each plant, including above and belowground biomass was collected and placed into a plastic bag, which was then refrigerated. Invertebrates found externally on the stems, flowers and among the soil from the roots of plants were then removed. Immature stages of externally feeding invertebrates that could not be readily identified at time of collection and could not be reared on decaying vegetation were reared to adults on plants of the same species grown in a glasshouse. The plants were then separated into (1) flowers, (2) stems and leaves and (3) roots, and stored in clear plastic containers with a covering of polyester organza. The containers were stored in a glasshouse and checked regularly for emerging invertebrates over a four-month period. To account for variation in plant sizes between species and across populations, the flowers, stems and leaves, and roots for each individual were dried separately at 70°C for 12 hours and the biomass (expressed per gram of dry plant weight) was recorded.

Invertebrates were identified to family level and then morphospecies, using the published biology of the invertebrates at family level (CSIRO 1973; Rentz 1996; Lawrence *et al.* 1999; Shattock 1999; Hamilton *et al.* 2005) and personal communications with entomologists (Appendix 3). Invertebrate collections are lodged in the entomology collection at the Australian Museum, Sydney and voucher specimens for both plant species collected at each site are lodged in the Downing Herbarium, Macquarie University, Sydney.

Figure 1. Map of the locations of the non-native species *Senecio madagascariensis* and native congener *S. pinnatifolius* var. *pinnatifolius* sampled in this study.



To assess herbivore and pathogen damage, 20 leaves randomly chosen from each of 10 individual plants from both *S. madagascariensis* and *S. pinnatifolius* var. *pinnatifolius* were collected at the same time as the invertebrate collections. Necrosis or leaf damage on each leaf was visually scored on a scale of 0 – 100%. While this method of sampling provides a quick easy estimate of herbivory, it underestimates total herbivory from leaves or other parts of the plant that are wholly eaten (Lowman 1984).

Statistical analysis

Data from the two sampling techniques (external collections plus reared invertebrates) was combined to estimate: (i) abundance of individuals (ii) morphospecies richness and (iii) the Shannon diversity index ($H' = -\sum (p_i \ln p_i)$ where p_i is the proportional abundance of the i th morphospecies). These parameters were estimated for the total invertebrate assemblage to gain insight into colonisation of the whole invertebrate community in addition to the herbivores alone. Data from each of the sampling techniques was then separated into external and reared herbivores and the (i) abundance (ii) morphospecies richness and (iii) Shannon diversity was estimated for each.

Two comparisons were made: (1) invertebrate assemblages, leaf damage and external and reared herbivores associated with the invasive *S. madagascariensis* and the native *S. pinnatifolius* var. *pinnatifolius* were compared among sites with increasing distance from the introduction point in the Hunter Valley to the invasion front north and south of this region. Using a space for time substitution, this comparison served to examine how the invertebrate community changes from its point of introduction to invasion fronts while ignoring latitudinal direction; (2) invertebrate assemblages, leaf damage and external and reared feeding herbivores associated with the invasive and native plants were compared among sites across six latitudes. This second comparison served to examine changes in the

invertebrate community over a latitudinal gradient, in particular to examine differences between the point of introduction and invasion fronts. As there was no between site variability for each species, samples from the two sites per species were pooled prior to analysis. Comparisons were made for each of the sampling variables by univariate analyses. Biomass, abundance and richness were transformed to the $\log(x+1)$ to improve the homogeneity of variance and to meet assumptions of normality.

For the first comparison, with the exception of leaf damage, a two-factor (plant species, distance) mixed model analysis of covariance (ANCOVA) was used. Plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*) and distance from the introduction region were considered fixed factors. Plant biomass for each plant was fitted as a covariate. The same analysis was used for the second comparison, but with six latitudinal bands instead of distance. For leaf damage, the same comparisons were made as above except biomass was removed as a covariate and the comparison became a two-factor mixed model analysis of variance (ANOVA). Where there were significant interactions between species and distance or species and latitude for *S. madagascariensis*, results were further analysed using Fisher's Least Significant Difference (LSD) post hoc multiple comparisons tests to determine the location of differences among means.

Multivariate analyses of the invertebrate herbivore assemblage using untransformed individual morphospecies abundance data was also performed using the Similarity Percentage analysis (SIMPER) in the PRIMER statistical package, to determine which taxa contributed most to the differences in the herbivore assemblage. SIMPER calculates the average Bray-Curtis dissimilarity between all pairs of inter-group samples and expresses these differences in terms of the average contribution from each species. A cumulative cut-off of approximately 90% was identified by SIMPER (Clarke 1993; Clarke & Gorley 2006).

Results

Relationship of total leaf damage and number of invertebrates between the native and non-native invader

Leaf damage was generally low and ranged between ~5 and 15% for both the invasive *S. madagascariensis* and the native *S. pinnatifolius* var. *pinnatifolius* (Fig 2.) Contrary to predictions of the enemy release hypothesis (ERH), damage was significantly greater on the invasive species than the native (Table 1; Fig. 2).

A total of 5,408 invertebrates were collected from *S. madagascariensis*, comprising 309 morphospecies (54% of which were only recorded once) (Appendix 3). The total number of invertebrates collected from *S. pinnatifolius* var. *pinnatifolius* was approximately half that number (2,530) and comprised 215 morphospecies (34% of which were only recorded once). Of the total number of invertebrates collected, *S. madagascariensis* had a greater proportion of herbivores (65%) than the native congener (39%).

Patterns of herbivore damage, abundance, richness, Shannon diversity and composition

Support for the species-time relationship (STR) was found for herbivore loads (abundance, richness & Shannon diversity), which declined on *S. madagascariensis* with increasing distance from the point of introduction, with significant differences apparent for the abundance and Shannon diversity of herbivores from the point introduction to a sampling distance of 300-500 km (Table 2; Fig. 3). No support for the STR was found for leaf damage (Table 1; Fig. 2a). Damage on *S. madagascariensis* did not significantly increase on plants with increasing distance from the introduction region (Table 1; Fig 2a). Damage analyses show that *S. madagascariensis* was not released from natural enemies in its early stage of invasion. Levels of damage on *S. madagascariensis* were significantly lower at

the introduction origin and area of population augmentation in northern NSW compared to invasion fronts at the northern and southern boundary (Table 1; Fig. 2b).

Herbivore loads on *S. madagascariensis* across latitudes were in contrast to damage analyses, with a significantly greater richness and Shannon diversity of herbivores in the area of introduction compared to the southern-most location and a non significant trend towards an increase in herbivore richness and Shannon diversity in the area of introduction compared to the northern-most location (Table 3; Fig. 3). Although herbivore abundance appears to be greater at the area of introduction compared to the southern most and northern most invasion fronts no significant interaction was found between species and latitude (Table 3; Fig. 3). Northern locations had a significantly greater richness and Shannon diversity of herbivores and a marginally significant increase in abundances compared to the southernmost locations (Table 3; Fig.3). There was a decline in herbivore abundance, richness and Shannon diversity on *S. madagascariensis* in far north-eastern NSW at the region where augmentation of the population occurred, compared to the introduction origin, but these differences were only significant for Shannon diversity (Table 3; Fig. 3d, e, f). From this point of augmentation, there was a sharp increase in the richness and Shannon diversity of herbivores collected at the Queensland sites in the north but this increase was not significant (Table 3; Fig. 2).

Minimal variation in leaf damage, herbivore abundance, richness and Shannon diversity between latitudes was found for the native control species *S. pinnatifolius* var. *pinnatifolius* (Figs. 2, 3).

Most of the variation among the herbivore assemblages from point of introduction to invasion fronts was due to sap-sucking and chewing herbivores (SIMPER analysis). At sites in the area of introduction, five morphospecies of sap-sucking herbivores from the

family Aphididae dominated 88% of the total herbivore assemblage, with a sap-sucker *Nysius clevelandensis* Evans (Orsillidae) contributing 4% to the herbivore assemblage. At the invasion front in the south, a leaf-feeding moth (Morphospecies L.2, Lepidoptera: Pyraloidea) comprised 88% of the herbivores with a heteropteran (morphospecies Het.2, Heteroptera: Miridae) contributing 8%. At the invasion front to the north, two morphospecies of Aphididae comprised 50% of the assemblage. The same leaf-feeding moth (Lepidoptera: Pyraloidea) that was collected at the invasion front in the south contributed to 7% of the herbivores in the north in addition to leaf-feeding thrips (morphospecies T.3, Thysanoptera: Panchaetothripinae: *Bhattithrips* sp.), contributing 15% of the herbivores. Other morphospecies of aphids and leaf- and flower-feeding thrips (Thripidae: *Pseudanaphothrips achaetus* Bagnell) contributed the remaining 90%. The herbivore assemblage in the area on the north coast of NSW where *S. madagascariensis* underwent augmentation in the 1950's was 90% dissimilar to the introduction region. Most of the variation was due to 5 morphospecies of Aphids (65% morphospecies Ap. 18, Ap. 24, Ap.26, Ap.27 Ap.28 Aphididae) that were all in greater densities at the introduction origin compared to the region of augmentation, with the exception of Ap. 18. For the region of population augmentation, 39% of the herbivore assemblage was dominated by a sap-sucker (Hemiptera: morphospecies Het. 2, Heteroptera: Miridae) and an Aphid (Ap.18) added 29% of the remaining herbivores (Appendix 3).

Table 1. Results of a two-factor, analysis of variance and Fisher's Least Significant Difference (LSD) post hoc tests for total leaf damage on *S. madagascariensis*, with the effect of (a) plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. = 1, 228), distance from introduction site of *S. madagascariensis* (d.f. = 5, 228) and their interaction (d.f. = 5, 228); and (b) plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. = 1, 228), latitude (bands 1-6; d.f. = 5, 228) and their interaction (d.f. = 5, 228). Total leaf damage was transformed to the log (x+1).

| Leaf damage | | | F | P | | |
|-------------------------------------------------|------|------|--------|--------|------|------|
| Plant species | | | 62.291 | <0.001 | | |
| Distance | | | 7.927 | <0.001 | | |
| Species × Distance | | | 1.026 | 0.382 | | |
| Plant species | | | 72.399 | <0.001 | | |
| Latitude | | | 8.284 | <0.001 | | |
| Species × Latitude | | | 5.484 | <0.001 | | |
| LSD post hoc tests - <i>S. madagascariensis</i> | | | | | | |
| | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 |
| Lat1 | | | | | | |
| Lat2 | *** | | | | | |
| Lat3 | *** | ns | | | | |
| Lat4 | ns | ** | ** | | | |
| Lat5 | *** | ns | ns | *** | | |
| Lat6 | ns | *** | *** | ns | *** | |

ns = not significant; * < 0.05; ** < 0.01; *** < 0.001

Note: Latitudes 1-6 (southern most point 1; northern most 6; introduction region 3 and population augmentation 5)

Figure 2. Leaf damage on *S. madagascariensis* and *S. pinnatifolius* var. *pinnatifolius* with a) distance from introduction region to the invasion fronts for *S. madagascariensis* and b) across latitudes 1-6 (southern most point 1; northern most 6; introduction region 3 and population augmentation 5).

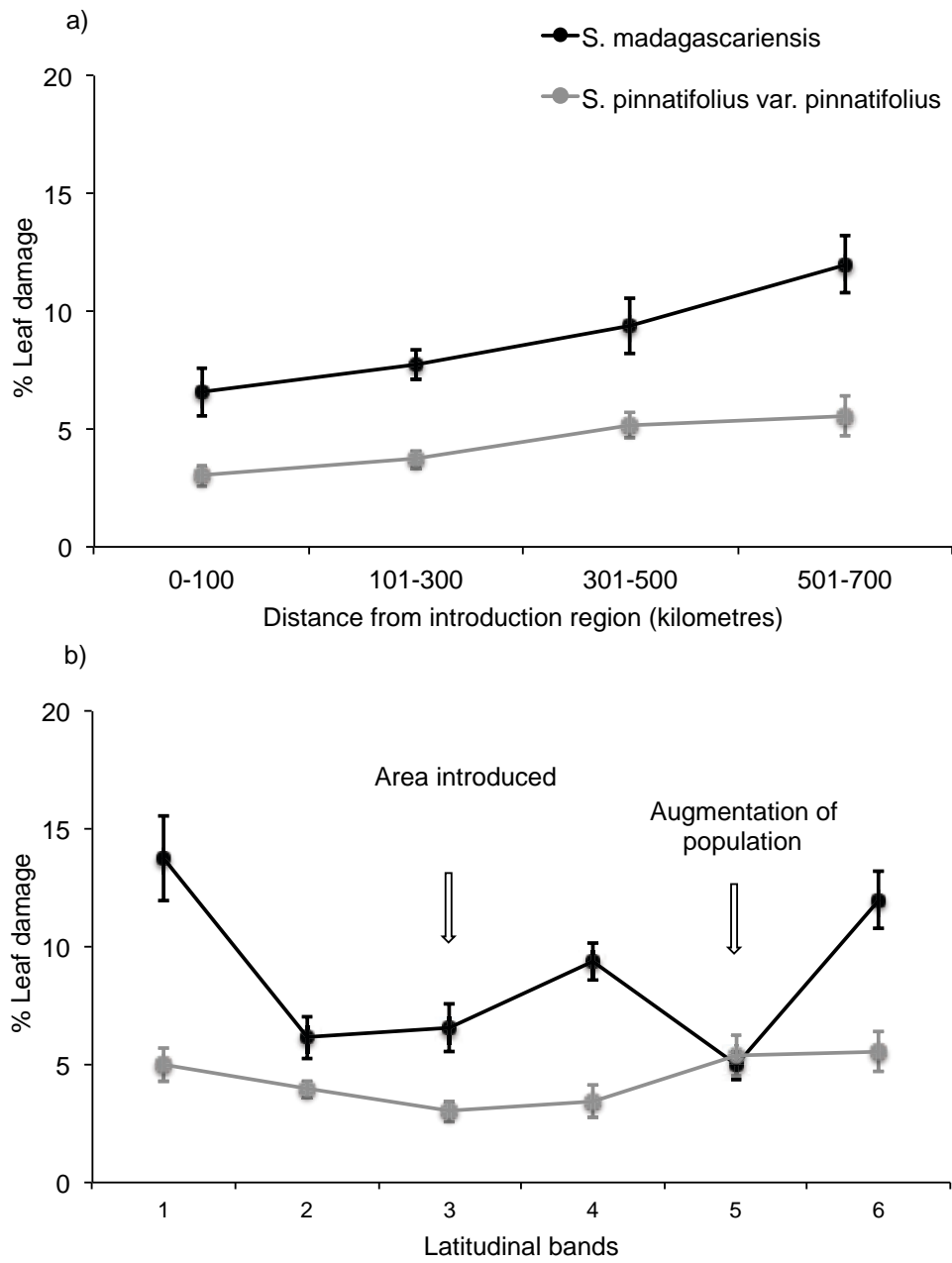


Figure 3. Abundance, morphospecies richness and Shannon diversity of herbivores collected on the non-native species *Senecio madagascariensis* and the native *S. pinnatifolius* var. *pinnatifolius* with distance from where *S. madagascariensis* was first introduced (a,b,c) and across latitudes 1-6 (d,e,f), (southern most point 1; northern most 6; introduction region 3 and population augmentation 5). Response variables are standardised by dividing by the dry weight (biomass) of the individual plants. Data points are means. Error bars are standard errors.

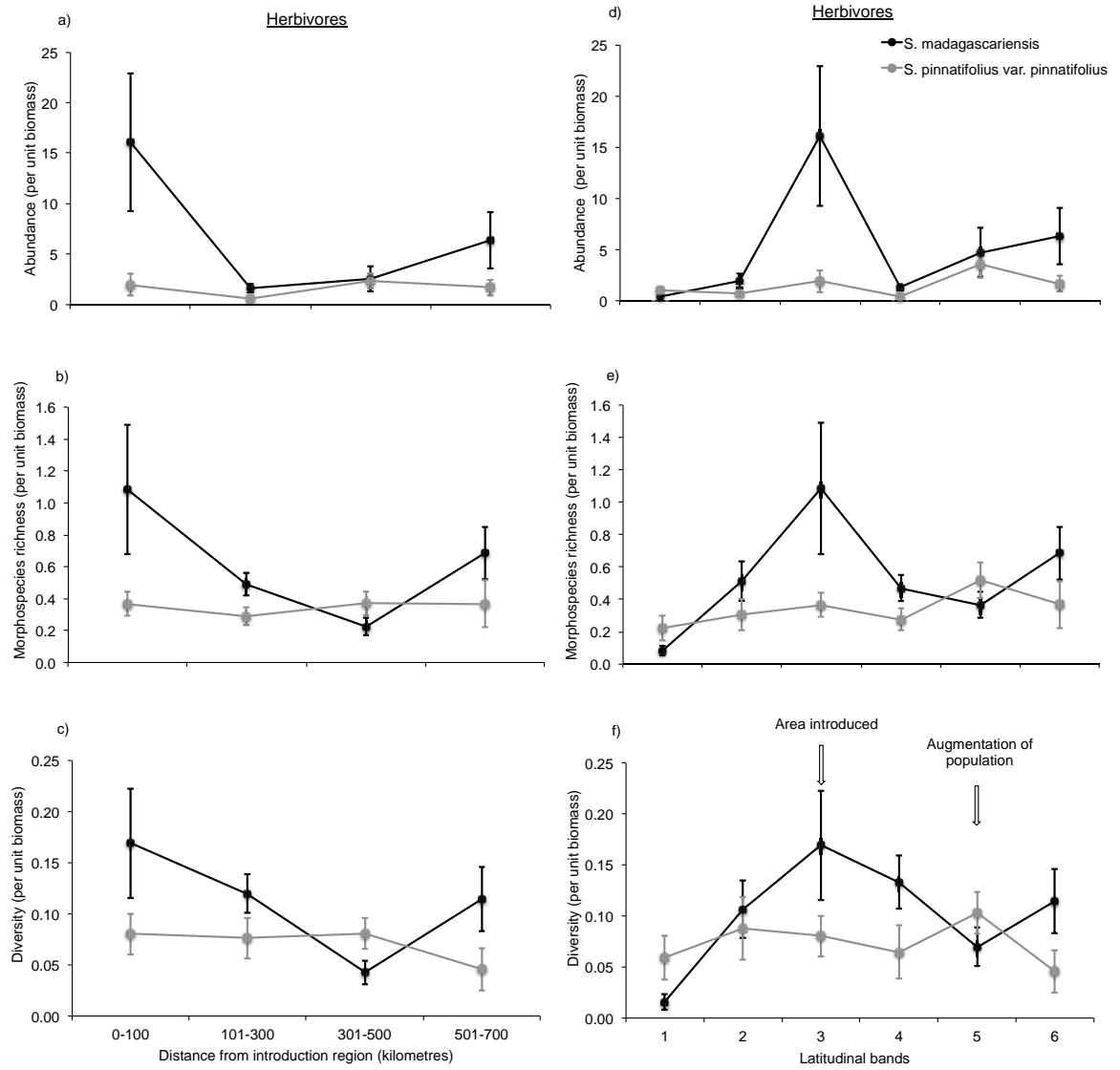


Table 2. Results of a two-factor analysis of covariance and Fisher's Least Significant Difference (LSD) post hoc tests for the effect of plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. = 1, 111), distance from introduction site of *S. madagascariensis* (0-100; 101-300; 301-500 and 501-700 km; d.f. = 3, 111) and their interaction (d.f. = 3, 111) on the abundance, morphospecies richness and Shannon diversity of invertebrate herbivores and total invertebrates. Dried plant mass (biomass) was fitted as a covariate (d.f. = 1, 111). Biomass, abundance and richness were transformed to the log (x+1).

| | <u>Biomass</u> | | <u>Plant species</u> | | <u>Distance</u> | | <u>Species × Distance</u> | |
|--------------------------------------------------------|----------------|------------------|----------------------|------------------|-----------------|------------------|---------------------------|--------------|
| <u>Variable</u> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> |
| Abundance | | | | | | | | |
| Herbivores | 0.783 | 0.378 | 10.946 | 0.001 | 2.297 | 0.082 | 2.838 | 0.041 |
| Invertebrates | 6.181 | 0.014 | 8.636 | 0.004 | 2.243 | 0.087 | 1.803 | 0.151 |
| Richness | | | | | | | | |
| Herbivores | 0.902 | 0.345 | 12.149 | <0.001 | 2.191 | 0.093 | 5.107 | 0.002 |
| Invertebrates | 6.786 | 0.010 | 9.457 | 0.003 | 1.635 | 0.185 | 3.438 | 0.019 |
| Diversity | | | | | | | | |
| Herbivores | 2.076 | 0.152 | 11.631 | <0.001 | 2.264 | 0.085 | 5.142 | 0.002 |
| Invertebrates | 3.177 | 0.077 | 7.552 | 0.007 | 1.626 | 0.187 | 3.905 | 0.011 |
| <u>LSD post hoc tests - <i>S. madagascariensis</i></u> | | | | | | | | |
| Herbivores | | Abundance | | | | Richness | | |
| | 0-100 | 101-300 | 301-500 | 501-700 | 0-100 | 101-300 | 301-500 | 501-700 |
| 0-100 | | | | | | | | |
| 101-300 | ns | | | | ns | | | |
| 301-500 | * | ns | | | ns | ns | | |
| 501-700 | ns | ns | ns | | ns | ns | ns | |
| Herbivores | | Diversity | | | | | | |
| | 0-100 | 101-300 | 301-500 | 501-700 | | | | |
| 0-100 | | | | | | | | |
| 101-300 | ns | | | | | | | |
| 301-500 | ** | * | | | | | | |
| 501-700 | ns | ns | * | | | | | |
| Invertebrates | | Richness | | | | Diversity | | |
| | 0-100 | 101-300 | 301-500 | 501-700 | 0-100 | 101-300 | 301-500 | 501-700 |
| 0-100 | | | | | | | | |
| 101-300 | ns | | | | ns | | | |
| 301-500 | * | * | | | ns | ** | | |
| 501-700 | ns | ns | ns | | ns | ns | ns | |

ns = not significant; * <0.05 ; ** <0.01 ; *** <0.001

Note: Distance in kilometres from introduction region

Table 3. Results of a two-factor analysis of covariance and Fisher's Least Significant Difference (LSD) post hoc tests for the effect of plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. = 1, 107), latitude (bands 1-6; d.f. = 5, 107) and their interaction (d.f. = 5, 107) on the abundance, morphospecies richness and Shannon diversity of invertebrate herbivores and total invertebrates. Dried plant mass (biomass) was fitted as a covariate (d.f. = 1, 107). Biomass, abundance and richness were transformed to the log (x+1).

| | Biomass | | Plant species | | Latitudinal band | | Species × Latitude | | | | | | |
|-------------------------------------------------|---------|--------------|---------------|--------------|------------------|--------------|--------------------|--------------|------|------|------|------|------|
| Variable | F | P | F | P | F | P | F | P | | | | | |
| Abundance | | | | | | | | | | | | | |
| Herbivores | 1.600 | 0.208 | 8.323 | 0.005 | 2.261 | 0.053 | 1.926 | 0.096 | | | | | |
| Invertebrates | 7.917 | 0.006 | 6.515 | 0.012 | 3.832 | 0.003 | 2.101 | 0.071 | | | | | |
| Richness | | | | | | | | | | | | | |
| Herbivores | 2.137 | 0.147 | 9.133 | 0.003 | 2.694 | 0.025 | 3.220 | 0.010 | | | | | |
| Invertebrates | 9.216 | 0.003 | 8.201 | 0.005 | 2.921 | 0.016 | 2.797 | 0.021 | | | | | |
| Diversity | | | | | | | | | | | | | |
| Herbivores | 3.453 | 0.066 | 8.435 | 0.004 | 2.522 | 0.034 | 3.268 | 0.009 | | | | | |
| Invertebrates | 4.742 | 0.032 | 5.605 | 0.020 | 1.694 | 0.142 | 2.524 | 0.036 | | | | | |
| LSD post hoc tests - <i>S. madagascariensis</i> | | | | | | | | | | | | | |
| Herbivores | | Richness | | | | Diversity | | | | | | | |
| | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 | | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 |
| Lat1 | | | | | | | | | | | | | |
| Lat2 | ** | | | | | | | ** | | | | | |
| Lat3 | *** | ns | | | | | | *** | ns | | | | |
| Lat4 | * | ns | ns | | | | | ** | ns | ns | | | |
| Lat5 | * | ns | ns | ns | | | | ns | ns | * | ns | | |
| Lat6 | ** | ns | ns | ns | ns | | | ** | ns | ns | ns | ns | |
| Invertebrates | | Richness | | | | Diversity | | | | | | | |
| | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 | | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 |
| Lat1 | | | | | | | | | | | | | |
| Lat2 | *** | | | | | | | ** | | | | | |
| Lat3 | *** | ns | | | | | | * | ns | | | | |
| Lat4 | * | ns | ns | | | | | ** | ns | ns | | | |
| Lat5 | ** | ns | ns | ns | | | | ns | ns | ns | ns | | |
| Lat6 | ** | ns | ns | ns | ns | | | * | ns | ns | ns | ns | |

ns = not significant; * < 0.05; ** < 0.01; *** < 0.001

Note: Latitudes 1-6 (southern most point 1; northern most 6; introduction region 3 and population augmentation 5)

Patterns of total invertebrate abundance, richness and Shannon diversity

For *S. madagascariensis* the total invertebrate assemblage may be driven by the time in which invertebrates adapt to and colonise the invader, as indicated by the sharp decline in invertebrate abundance, richness and Shannon diversity from the point of introduction to latitudes to the north (580km) and south (480km) of this point (Fig. 4). However, substantial variation in invertebrate abundance among replicate samples within and between latitudes meant that only morphospecies richness and Shannon diversity were found to be significantly affected by an interaction between species and distance from introduction region and between species and latitude (Table 2; Table 3). For the native control *S. pinnatifolius* var. *pinnatifolius* latitude played a minor role in the abundance, richness and Shannon diversity of invertebrates, as indicated by minimal variation in the invertebrate communities across the range (Fig. 4d, e, f). In the region where an augmentation of the population of *S. madagascariensis* occurred, the richness and Shannon diversity was lower than the introduction origin but this trend was not significant (Fig. 4d, e, f).

External herbivore collections and reared herbivores

Overall, the total abundance, richness and Shannon diversity of herbivores reared from *S. madagascariensis* decreased with increasing distance from the point of introduction, with significant differences for richness and Shannon diversity evident at a distance of 301-500km from the point of introduction (Table 4; Fig. 5a, b, c). Although somewhat lower than at the introduction site, levels of reared herbivores increased at the furthest distance from introduction origin, due to higher levels at northern-most locations (Fig. 5,d, e, f). Herbivore richness and Shannon diversity from external collections varied little across distance from the point of introduction whereas external abundances were slightly greater

at the point of introduction (Table 4; Fig. 5a,b,c). At the point of introduction, the richness and Shannon diversity of reared herbivores were greater on *S. madagascariensis* compared to all other latitudes including sites where the population was augmented in the 1950's, with significant differences apparent between the introduction origin and the southern-most latitude (Table 5; Fig. 5). Northern-most sites had a greater richness and Shannon diversity of reared herbivores on *S. madagascariensis* compared to the southern-most sites (Table 5; Fig. 5). Minimal variation in the abundance, richness and Shannon diversity of reared herbivores and external collections occurred in the native *S. pinnatifolius* var. *pinnatifolius* (Fig. 5).

Table 4. Results of a two-factor, analysis of covariance and Fisher's Least Significant Difference (LSD) post hoc tests for the effect of plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. =1, 111), distance from introduction region of *S. madagascariensis* (0-100; 101-300; 301-500 and 501-700 km; d.f. = 3, 111) and their interaction (d.f. = 3, 111) on the abundance, morphospecies richness and Shannon diversity of external collections and reared invertebrate herbivores. Dried plant biomass was fitted as a covariate (d.f = 1, 111). Biomass, abundance and richness were transformed to the log (x+1).

| | <u>Biomass</u> | | <u>Plant species</u> | | <u>Distance</u> | | <u>Species × Distance</u> | | |
|--------------------------------------------------------|----------------|------------------|----------------------|--------------|-----------------|-----------------------------|---------------------------|--------------|---------|
| <u>Variable</u> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> | |
| Abundance | | | | | | | | | |
| External collections | 0.153 | 0.696 | 10.903 | 0.001 | 6.473 | <0.001 | 3.129 | 0.029 | |
| Reared | 0.344 | 0.559 | 11.480 | 0.001 | 2.946 | 0.036 | 2.803 | 0.043 | |
| Richness | | | | | | | | | |
| External collections | 0.590 | 0.444 | 11.082 | 0.001 | 2.859 | 0.040 | 1.637 | 0.185 | |
| Reared | 0.194 | 0.660 | 11.011 | 0.001 | 2.713 | 0.048 | 5.163 | 0.002 | |
| Diversity | | | | | | | | | |
| External collections | 2.942 | 0.089 | 10.507 | 0.002 | 4.495 | 0.005 | 1.242 | 0.298 | |
| Reared | 1.258 | 0.264 | 8.034 | 0.006 | 2.550 | 0.059 | 5.638 | 0.001 | |
| <u>LSD post hoc tests - <i>S. madagascariensis</i></u> | | | | | | | | | |
| Reared Herbivores | | Abundance | | | | Richness | | | |
| | 0-100 | 101-300 | 301-500 | 501-700 | | 0-100 | 101-300 | 301-500 | 501-700 |
| 0-100 | | | | | | | | | |
| 101-300 | ns | | | | | ns | | | |
| 301-500 | ns | ns | | | | * | ns | | |
| 501-700 | ns | ns | ns | | | ns | ns | ns | |
| Reared Herbivores | | Diversity | | | | External Collections | | | |
| | 0-100 | 101-300 | 301-500 | 501-700 | | 0-100 | 101-300 | 301-500 | 501-700 |
| 0-100 | | | | | | | | | |
| 101-300 | ns | | | | | *** | | | |
| 301-500 | * | * | | | | *** | ns | | |
| 501-700 | ns | ns | * | | | * | ns | * | |

ns = not significant; * <0.05 ; ** <0.01 ; *** <0.001

Note: Distance in kilometres from introduction region

Table 5. Results of a two-factor, analysis of covariance and Fisher's Least Significant Difference (LSD) post hoc tests for the effect of plant species (*S. madagascariensis* or *S. pinnatifolius* var. *pinnatifolius*; (d.f. =1, 107), latitude (bands 1-6; d.f. = 5, 107) and their interaction (d.f. = 5, 107) on the abundance, morphospecies richness and Shannon diversity of external collections or reared invertebrate herbivores. Dried plant biomass was fitted as a covariate (d.f = 1, 107). Biomass, abundance and richness were transformed to the log (x+1).

| | <u>Biomass</u> | | <u>Plant species</u> | | <u>Latitudinal band</u> | | <u>Species × Latitude</u> | | | | | | |
|--------------------------------------------------------|----------------|-----------------|----------------------|--------------|-------------------------|------------------|---------------------------|--------------|------|------|------|------|------|
| <u>Variable</u> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> | F | <i>P</i> | | | | | |
| Abundance | | | | | | | | | | | | | |
| External collections | 0.845 | 0.360 | 6.287 | 0.014 | 4.352 | 0.001 | 2.029 | 0.080 | | | | | |
| Reared | 0.909 | 0.343 | 10.156 | 0.002 | 2.524 | 0.034 | 1.844 | 0.110 | | | | | |
| Richness | | | | | | | | | | | | | |
| External collections | 2.102 | 0.150 | 7.459 | 0.007 | 2.546 | 0.032 | 1.202 | 0.313 | | | | | |
| Reared | 0.605 | 0.438 | 10.363 | 0.002 | 2.556 | 0.032 | 3.142 | 0.011 | | | | | |
| Diversity | | | | | | | | | | | | | |
| External collections | 3.318 | 0.071 | 7.708 | 0.006 | 2.770 | 0.022 | 0.807 | 0.547 | | | | | |
| Reared | 1.618 | 0.206 | 6.795 | 0.010 | 2.359 | 0.045 | 3.472 | 0.006 | | | | | |
| <u>LSD post hoc tests - <i>S. madagascariensis</i></u> | | | | | | | | | | | | | |
| Reared Herbivores | | Richness | | | | Diversity | | | | | | | |
| | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 | | Lat1 | Lat2 | Lat3 | Lat4 | Lat5 | Lat6 |
| Lat1 | | | | | | | | | | | | | |
| Lat2 | * | | | | | | | * | | | | | |
| Lat3 | ** | ns | | | | | | ** | ns | | | | |
| Lat4 | ns | ns | ns | | | | | * | ns | ns | | | |
| Lat5 | ns | ns | ns | ns | | | | ns | ns | ns | ns | | |
| Lat6 | * | ns | ns | ns | ns | | | * | ns | ns | ns | ns | |

ns = not significant; * <0.05 ; ** <0.01 ; *** <0.001

Note: Latitudes 1-6 (southern most point 1; northern most 6; introduction region 3 and population augmentation 5)

Figure 4. Abundance, morphospecies richness and Shannon diversity of total invertebrates collected on the non-native species *Senecio madagascariensis* and the native *S. pinnatifolius* var. *pinnatifolius* with distance from where *S. madagascariensis* was first introduced (a,b,c) and across latitudes 1-6 (d,e,f), (southern most point 1; northern most 6; introduction region 3 and population augmentation 5). Response variables are standardised by dividing by the dry biomass of the individual plants. Data points are means. Error bars are standard errors.

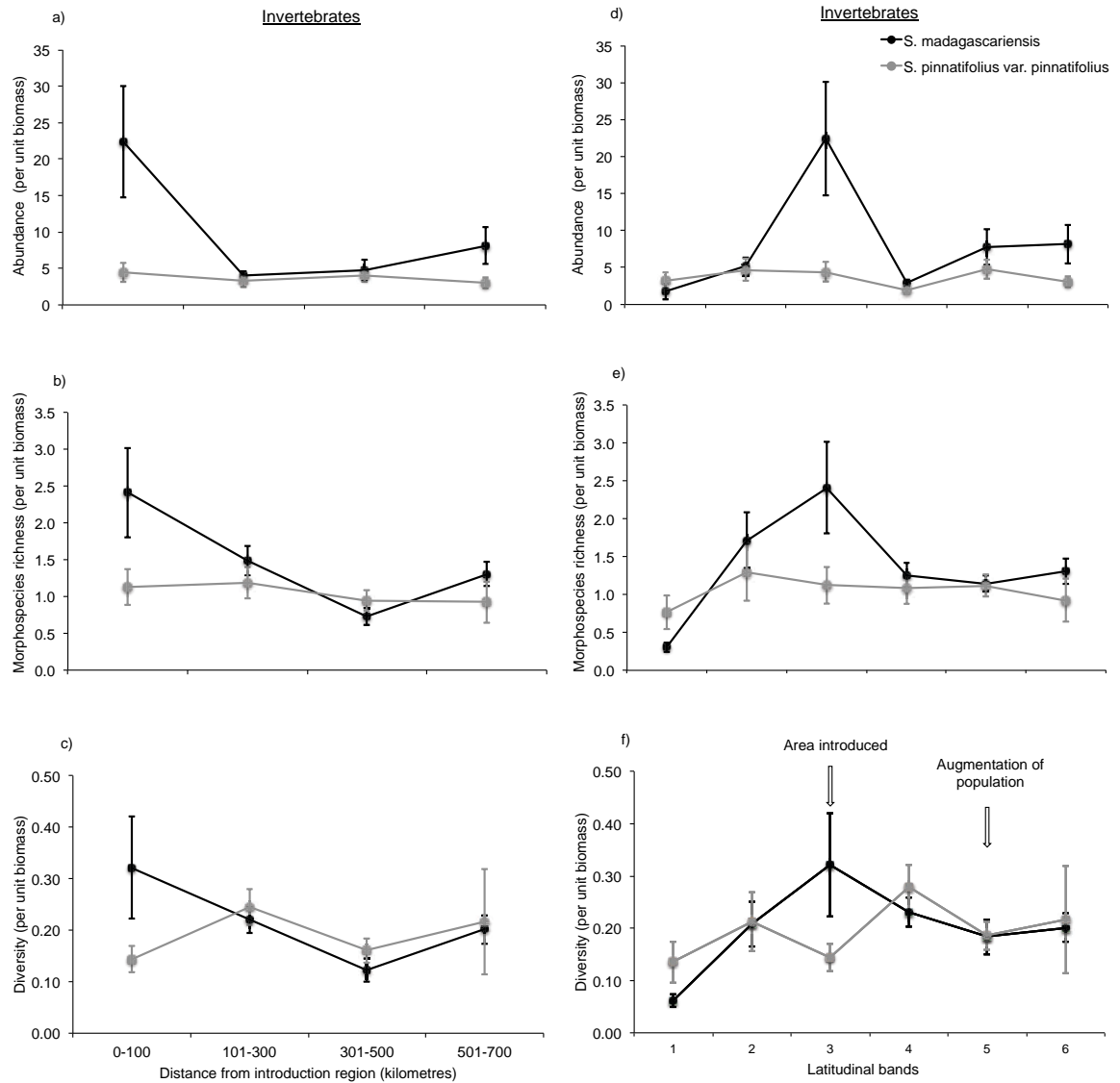
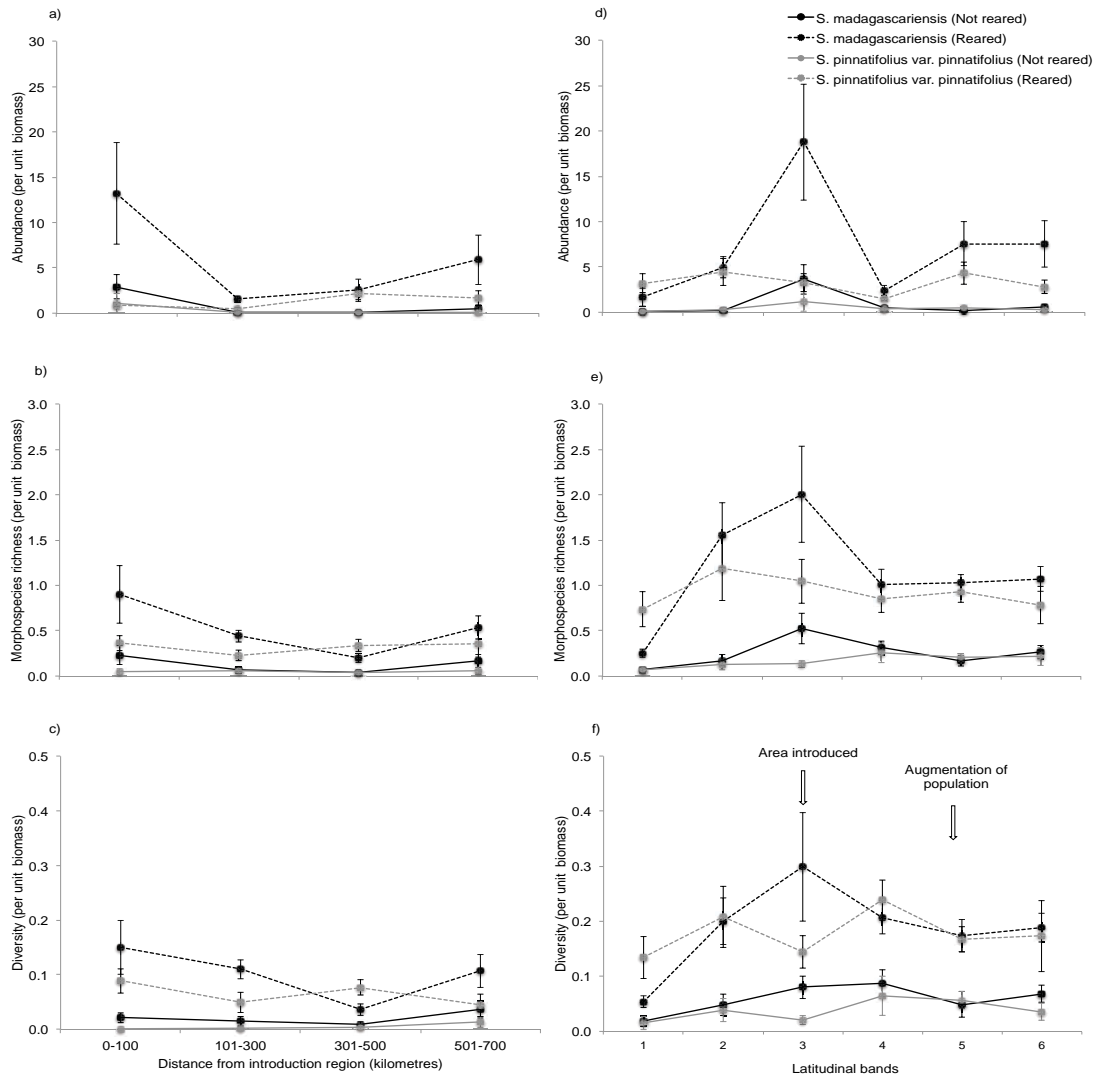


Figure 5. Abundance, morphospecies richness and Shannon diversity of total invertebrates reared versus collected externally from the non-native species *Senecio madagascariensis* and the native *S. pinnatifolius* var. *pinnatifolius* with distance from where *S. madagascariensis* was first introduced (a,b,c) and across latitudes 1-6 (d,e,f), (southern most point 1; northern most 6; introduction region 3 and population augmentation 5). Response variables are standardised by dividing by the dry weight (biomass) of the individual plants. Data points are means. Error bars are standard errors.



Discussion

We used a space for time substitution to evaluate the relationship between an invasive species and its natural enemies since establishment. As herbivory is considered to play a potentially important role in the initial success of introduced species via release from natural enemies, we also compared leaf damage as a surrogate for fitness loss to determine whether herbivores may have reduced the fitness of a non-native species. Using *Senecio madagascariensis* Poir. as our focal species, we found the opposite results to what would be predicted from the enemy release hypothesis (ERH) (for reviews see Maron & Vila 2001; Colautti *et al.* 2004), but partial support for the species-time relationship (STR) (*sensu* Preston 1960; Strong *et al.* 1984). Contrary to expectations of the ERH, greater herbivore and invertebrate loads (abundance, richness and Shannon diversity) were found on the invasive species than on the native “control” *S. pinnatifolius* var. *pinnatifolius*; this difference was particularly evident in samples collected at sites in the region of introduction. Supporting the STR, herbivore abundance, richness and Shannon diversity declined on *S. madagascariensis* from its point of introduction in the Hunter Valley NSW, to both its invasion fronts to the north in Queensland and south in southern NSW. The results for the invertebrate assemblages as a whole mirrored that of the herbivores, declining in loads (abundance, richness, Shannon diversity) from the introduction point to the invasion fronts. Also consistent with the STR, there were more herbivores reared from *S. madagascariensis* at the area of introduction compared to all other locations, indicating that herbivores may be adapting over time and increasing their ability to feed on *S. madagascariensis*.

In direct contrast to these results, leaf damage on *S. madagascariensis* did not decrease from its point of introduction to the invasion fronts. At the invasion fronts we found high leaf damage on *S. madagascariensis* despite the fact that total herbivore loads were low,

whereas at the point of introduction, damage levels were low and herbivore loads were high. In the region where the population was augmented in the 1950's on the far north coast of NSW, damage levels and herbivore loads were both low compared to the invasion fronts in the north and south. Results from the damage analysis indicated that the potential for enemy release is not limited to the early stages of invasion or presumably linked to the success of this species as an invader. Minimal variation across latitudes in our control species *S. pinnatifolius* var. *pinnatifolius*, confirmed that the patterns observed in our invasive species are not likely to be driven by environmental variation along the latitudinal gradient.

Several studies have shown reduced herbivory on invasive plants, which may have been a contributing factor to their subsequent invasion and spread into native habitats (Vila *et al.* 2005; Carpenter & Cappuccino 2005). By contrast, our results directly contradict the ERH as greater damage and herbivore loads were found on the invasive species compared to the co-occurring close relative *S. pinnatifolius* var. *pinnatifolius*. Our results are consistent with studies that have found greater rates of herbivory on non-native compared to native species (Keane & Crawley 2002 and references therein; Agrawal & Kotanen 2003).

Greater rates of damage on non-native plants may be attributed to being closely related to a co-occurring native congener as well as being evolutionarily naive to natural enemies in their new environment. Closely related plants often share similar classes of secondary metabolic compounds that determine their smell, taste and toxicity for phytophagous insects (Tallamy 2004). This may explain some of the similarities in the abundance and richness of the invertebrate assemblage observed, as native insects are more likely to be able to feed on a close relative of the native plant species than on a plant from a different family (Strong *et al.* 1984; Tallamy 2004). Greater enemy attack on non-native plants may occur because non-natives are unlikely to have developed defences against enemy impact

which is often compounded through invasion bottlenecks (e.g. ‘increased susceptibility hypothesis’ Colautti *et al.* 2004).

Our results indicate that for *Senecio* in Australia, there is no simple relationship between the time over which herbivore species can be accumulated on non-native plants and the herbivore community complexity on an invader. In studies by Siemann *et al.* (2006) and Hawkes (2007) it was demonstrated that the enemy release of a non-native species was limited to the early stages of its invasion. Greater herbivory was found at sites where the Chinese tallow tree (*Sapium sebiferum*) had been present for longer compared to more recent sites of introduction (Siemann *et al.* 2006). We found the opposite result - areas where *S. madagascariensis* was recently introduced had greater damage than older sites of introduction (i.e. point of introduction and where the population was augmented in the 1950’s on the far north coast of NSW). Inconsistent patterns between the relevance of time and herbivore or pathogen community accumulation has emerged across studies, with some demonstrating strong relationships between time and herbivore accumulation or rates of herbivory on non-native species (Birks 1980; Siemann *et al.* 2006; Brändle *et al.* 2008) or weak or no relationships (Strong *et al.* 1977; Carpenter & Cappuccino 2005).

Differences among studies may be due to variation in range size, growth form, the taxonomic affiliation of non-native species to the native community, and the interaction of other abiotic and biotic factors (Mitchell *et al.* 2006). After controlling for at least some of the potential confounding factors, by accounting for differences in biomass and by comparing herbivores and herbivory on a congeneric species, our results also show inconsistent patterns between rates of herbivory and herbivore loads. In this study, some support was found for the STR with respect to herbivore loads (in terms of abundance, richness, Shannon diversity) which declined on *S. madagascariensis* from its point of introduction to its invasion fronts, but inconsistent for damage levels.

There may be several explanations for the lack of correlation between damage and the number and variety of herbivores. Different herbivore species vary in the relative amount of damage they inflict, due to differences in their size, or feeding mode. Generalist defoliators such as the moth in the superfamily Pyraloidea found at the invasion fronts may cause considerably more conspicuous and easily measurable damage per plant than more numerous sap-suckers which occurred at the point of introduction. The effects of chewers or defoliators are often more obvious than those of sap-suckers where damage can be relatively subtle unless damage from sap-sucking insects is exacerbated by them acting as vectors of plant pathogens (Gullan & Cranston 2010). Moreover, surveying for the removal of plant biomass by sap-suckers is often problematic and only possible through controlled experiments.

Greater damage levels at the invasion fronts where low herbivore loads were recorded may not be just a stochastic element or an artefact of the damage inflicted by generalist defoliators. The net impacts of losing natural enemies from its native range and acquiring a new assemblage in the new range may be influenced by several non-mutually exclusive factors. For example, rates of herbivory may be influenced by evolutionary changes that a plant may undergo in its new environment. Non-native plant species may reallocate resources to growth and reproduction rather than defence due to the release from natural enemies in their new environment, a hypothesis known as the evolution of increased competitive ability (EICA) (Blossey & Notzold 1995). Evidence for the EICA has been demonstrated in *Sapium sebiferum*, which has evolved to be faster growing and less herbivore resistant in its new range (Zou *et al.* 2008).

Alternatively, changes in abiotic and biotic conditions may in turn increase the nutritional value of the plant tissue or bring about other physiological changes that can influence herbivore feeding. For example, natural and human disturbances including changes in

salinity, water stress and patterns of weather, can result in an increase in nutrients such as nitrogen in plant tissues that may in turn lead to an increase in feeding by herbivores (e.g. White 1984). A reduction in plant silicon content from environmental stress, for example, may increase feeding in herbivores. Alternatively, the silicon content may change in response to herbivores whereby the cell wall is reinforced acting as a physical defence against herbivore attack (Epstein 2009; Reynolds *et al.* 2009). Although little is known for herbaceous plants, higher levels of silicon have been found to deter feeding on grasses (Massey *et al.* 2007; Reynolds *et al.* 2009) and subsequently high levels of silicon can reduce the efficiency with which nitrogen can be absorbed by herbivores (Massey & Hartley 2009).

There is some evidence to suggest that *S. madagascariensis* may be undergoing physiological changes in its new environment, which is likely to influence its interaction with herbivores. *Senecio* species are known to contain pyrrolizidine alkaloids, which can play a role in defence against herbivores (Parsons & Cuthbertson 1992; Sindel 2009). Although changes in chemical defences have not been measured in *S. madagascariensis*, the genes potentially associated with defence against insect herbivores are more switched on in their native range of South Africa than in Australia (Prentis *et al.* 2010). Preliminary research indicates that *S. madagascariensis* may be allocating more resources to reproduction and growth at the range edges as indicated by a larger pappus and moderately larger achene than at non-edges (S. Bonser *pers. comm.*). Higher germination rates, faster growth rates and reproduction at the range edges compared to non-edges have also been found (S. Bonser *pers. comm.*). Greater growth rates and damage has also been found in the invasive *Jacobaea vulgaris* Gaertn. (formerly *Senecio jacobaea* L.; Pelter *et al.* 2007) compared to native populations (Stastny *et al.* 2005), and partial support for increased

dispersal in invasive populations of *S. inaequidens* has also been found (Monty & Mahy 2010).

An extension of the ERH predicts that when a non-native plant is introduced it leaves behind its co-evolved specialist herbivores, which are then replaced by generalist polyphagous herbivores (e.g. Keane & Crawley 2002). Generalists have been found to be replaced by a more specialised assemblage over time (Andow & Imura 1994). Our results may be consistent with this idea, as the herbivores collected on *S. madagascariensis* may be widening their niche to include this invasive weed, potentially developing a stronger physiological link with the host plant. The proportion of reared herbivores, dominated by aphids, at the area of introduction on *S. madagascariensis* was greater than all other regions including where the population was augmented in far northern NSW in the 1950's. Aphids are predominately monophagous (Carver 1959; Eastop 1973) and food selection is based on complex behavioural patterns that test for chemical structure, surface properties and nutrients (Niemeyer 1990). Aphids may be developing specialised associations with the plant, by utilising the plant for oviposition and and/or sequestering toxins for defence against parasites. At the invasion fronts, generalist defoliators, dominated by a moth species in the superfamily Pyraloidea, were the main herbivores present and are likely to be the main drivers of herbivory and damage levels seen in this study.

This study has shown that time since introduction is a factor affecting the composition of the invertebrate assemblage in terms of increasing in density, richness and potential specialisation but these changes in the herbivore community were not associated with the damage suffered by the invading species. Due to high leaf damage at invasion fronts on the invader compared to the native species, the low level of herbivory on this non-native species does not appear to be an important mechanism underlying its apparent invasion success. High damage levels and invertebrate loads on this invader may be due to *S.*

madagascariensis being a closely related congener and evolutionary naive in its new range. Further investigation of two possible non-mutually exclusive ideas may explain why we found greater damage at the invasion fronts compared to point of introduction. These include exploring the relationship between herbivores and the damage they inflict on plants. For example, by determining whether the generalist herbivores present at the invasion fronts are doing most of the damage, or whether the damage and herbivore loads observed are unpredictable in time and space. Research is also needed into understanding whether non-natives may become better defended against herbivores over time. For example, a comparison of in defence and growth at the invasion fronts with that at the older sites of introduction could test whether *S. madagascariensis* may be undergoing physiological changes that may increase or decrease its tolerance to herbivory. It is likely that abiotic and biotic interactions may prevail in understanding the success of species that are closely related to the native community. By better understanding the mechanisms behind the plasticity of this species it may be possible to gain clearer insight into the naturalisation and success of other non-native species.

Acknowledgements

We greatly appreciate the help of field volunteers Kate Umbers, John Martin, Katy Wilkins, Laurel Harvey and William Harvey. Thank you to Katy Wilkins for laboratory assistance. Invertebrate collection methods were based on the work of John Hosking and Royce Holtcamp of the NSW Department of Primary Industries. We would also like to thank Paul Robins of the Herbarium of Queensland, Frank Hemmings of the John T. Waterhouse Herbarium at the University of New South Wales, Gary Chapple of the Royal Botanic Gardens Sydney, Belinda Pellow of Janet Kosh Herbarium University of Wollongong, John Hosking and Royce Holtkamp of the NSW Department of Primary Industries, Graham Harding of Eurobodalla Council also Paul O'Connor from Hastings

City Council for plant location data. Thank you to Alison Downing of the Downing Herbarium Macquarie University for plant identifications and Muhammad Masood for support in the glasshouse. We are grateful to councils including Bega, Eurobodalla, Wollongong, Great Lakes, Port Macquarie and Ballina for sampling permits. Thank you also to the Department of Environment and Resource Management, North Stradbroke Island Queensland and Biosecurity Queensland for sampling permits. A special thanks to taxonomists Dr Laurence Mound and Bruce Halliday of CSIRO Ecosystem Sciences Canberra for species identification of Thysanoptera and Acarina. This research was supported by Macquarie University, the Australian Museum in Sydney and the Wildlife Preservation Society of Australia.

References

- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters* 6:712-715
- Andow DA, Imura O (1994) Specialization of phytophagous arthropod communities on introduced plants. *Ecology* 75:296-300
- Arrhenius O (1921) Species and area. *Journal of Ecology* 9:95-99
- Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886-892
- Birks HJB (1980) British trees and insects: a test of the time hypothesis over the last 13,000 Years. *The American Naturalist* 115:600-605
- Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83:887-889

- Brändle M, Kuhn I, Klotz S, Belle C, Brandl R (2008) Species richness of herbivores on exotic host plants increases with time since introduction of the host. *Diversity and Distributions* 14:905-912
- Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology* 93:315-321
- Carroll SP, Loefer JE, Dingle H, Mathieson M, Famula TR, Zalucki MP (2005) And the beak shall inherit - evolution in response to invasion. *Ecology Letters* 8:944-951
- Carver (1959) Aphididae. In: CSIRO The Insects of Australia: A textbook for students and research workers, Vol 1. Melbourne University Press, Melbourne, pp 452-456
- Chun YJ, van Kleunen M, Dawson W (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecology Letters* 13:937-946
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:17-143
- Clarke KR, Gorley RN (2006) Primer v6: In: PRIMER-E: Plymouth, UK
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-733
- Connor EF, Faeth SH, Simberloff D, Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 5:205-211
- CSIRO (1973) The Insects of Australia: A Textbook for Students and Research Workers,

Vol. 1 & 2. Melbourne University Press, Melbourne

Eastop VF, (1973) Deductions from the present day host plants of aphids and related species. *Symposia of the Royal Entomological Society of London* 6:157-177

Epstein E (2009) Silicon: its manifold roles in plants. *Annals of Applied Biology* 155:155-160

Gullan PJ, Cranston PS (2010) *The Insects: An Outline of Entomology*. 4th edn. Wiley-Blackwell, United Kingdom

Hamilton JR, Yeates DK, Hastings A, Colless DH, McAlpine DK, Bickel D, Cranston PS, Schneider MA, Daniels G, Marshall S (2005) *On The Fly: The Interactive Atlas and Key to Australian Fly Families*, Beta Version 0.9. Australian Biological Resources Study and CSIRO, Canberra

Hawkes C.V (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist* 170:832-843

Holtkamp RH, Hosking JR (1993) Insects and Diseases of Fireweed, *Senecio madagascariensis*, and the closely related *Senecio* Lautus Complex. In: Swarbrick JT, Henderson CWL, Jettre RJ, Streit L, Walker SR (eds) *Proceedings of the Tenth Australian and 14th Asian Pacific Weed Science Society Conference* Weeds Society of Queensland, Brisbane, pp 104-106

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17:164-170

Lawrence JF, Hastings HM, Dallwitz MJ, Paine TA, Zurcher EJ (1999) *Beetles of the*

World CSIRO Publishing, Canberra

- Lawton JH, Schroder D (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* 265:137-140
- Lawton JH, Strong DR (1981) Community patterns and competition in folivorous insects *American Naturalist* 118:317-338
- Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions* 8:1535-1545
- Lowman MD (1984) An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica* 16:264-268
- Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361-373
- Massey FP, Ennos AR, Hartley SE (2007) Herbivore specific induction of silica-based plant defences. *Oecologia* 152:677-683
- Massey FP, Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *Journal of Animal Ecology* 78:281-291
- Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vázquez DP (2006) Biotic interactions and plant invasions. *Ecology Letters* 9:726-740
- Mitchell CE, Blumenthal D, Jarosik V, Puckett EE, Pyšek P (2010) Controls on pathogen species richness in plants' introduced and native ranges: roles of residence time,

- range size and host traits. *Ecology Letters* 13:1525-1535
- Moles AT, Bonser SP, Poore AGB, Wallis IR, Foley WJ (2011) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25:380-388
- Monty AGM, Mahy G (2010) Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). *Oikos* 119:1563-1570
- Neuvonen S, Niemela P (1981) Species richness of macrolepidoptera on Finnish deciduous trees and shrubs. *Oecologia* 51:364-370
- Niemeyer HM (1990) The role of secondary plant compounds in aphid-host interactions. In: Campbell RK, Eikenbary RD (eds) *Aphid-plant genotype interactions*. Elsevier, Amsterdam
- Parsons WT, Cuthbertson EG (1992) *Noxious Weeds of Australia*. Inkata Press, Sydney
- Pelser PB, Nordenstam B, Kadereit JW, Watson LE (2007) An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1114.
- Prentis PJ, Woolfit M, Thomas-Hall SR, Oritz-Barrientos D, Pavasovic A, Lowe AJ, Schenk PM (2010) Massively parallel sequencing and analysis of expressed sequence tags in a successful invasive plant. *Annals of Botany* 106:1009-1017
- Preston FW (1960) Time and space and the variation of species. *Ecology* 41:611-627
- Radford IJ, Cousens RD (2000) Invasiveness and comparative life-history traits of exotic and indigenous *Senecio* species in Australia. *Oecologia (Berlin)* 125:531-542

- Radford IJ, Muller P, Fiffer S, Michael PW (2000) Genetic relationships between Australian fireweed and South African and Madagascan populations of *Senecio madagascariensis* Poir. and closely related *Senecio* species. Australian Systematic Botany 13:409-23
- Rentz D (1996) Grasshopper Country: The Abundant Orthopteroid Insects of Australia. University of NSW Press, Sydney
- Reynolds OL, Keeping MG, Meyer JH (2009) Silicon-augmented resistance of plants to herbivorous insects: a review. Annals of Applied Biology 155:171-186
- Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge
- Shattuck SO (1999) Australian Ants, Their Biology and Identification. Monographs on Invertebrate Taxa, Vol. 3. CSIRO Publishing, Victoria
- Siemann E, Rogers WE, Dewalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. Proceedings of the Royal Society B-Biological Sciences 273:2763-2769
- Sindel BM (1986) The ecology and control of fireweed *Senecio madagascariensis* Poir. Plant Protection Quarterly 1:163-172
- Sindel BM (2009) Fireweed in Australia: Directions for future research. Report for the Bega Valley Fireweed Association PO Box 79 Bega NSW 2550, Armidale <http://thebegavalley.org.au/fireweed.html> Accessed August 2011
- Stastny M, Schaffner U, Elle E (2005) Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? Journal of Ecology 93:27-37

- Strong DR (1974) Nonasymptotic species richness models and insects of British trees.
Proceedings of the National Academy of Sciences of the United States of America
71:2766-2769
- Strong DR, McCoy ED, Rey JR (1977) Time and the number of herbivore species-pests of
sugarcane. Ecology 58:167-175
- Strong DR (1979) Biogeographic dynamics of insect-host plant communities. Annual
Review of Entomology 24:89-119
- Strong DR, Lawton JH, Southwood TRE (1984) Insects on Plants: Community Patterns
and Mechanisms. Blackwell Scientific, Oxford, England
- Tallamy DW (2004) Do alien plants reduce insect biomass? Conservation Biology
18:1689-1692
- Thompson IR (2005) Taxonomic studies of Australian *Senecio* (Asteraceae): 5. the *S.*
pinnatifolius/*S. lautus* complex. Muelleria 21:23-76
- Vila M, Maron JL, Marco L (2005) Evidence for the enemy release hypothesis in
Hypericum perforatum. Oecologia 142:474-479
- White TCR (1984) The abundance of invertebrate herbivores in relation to the availability
of Nitrogen in stressed food plants. Oecologia 63:90-105
- Zou J, Rogers WE, Siemann E (2008) Increased competitive ability and herbivory
tolerance of the invasive plant *Sapium sebiferum*. Biological Invasions 10:291-302

Chapter 5 - Conclusions

Invasive plants can have devastating consequences on both natural and agricultural systems via their impact of native species assemblages, disturbance regimes, primary productivity, stability and ecosystem function (Walker & Smith 1997; Prieur-Richard & Laval 2000). In Australia, the economic costs of lost agricultural productivity and weed management are estimated to be over \$4 billion per year (Sinden *et al.* 2005; AWS 2006; DAFF 2008); the costs for natural ecosystems are far more difficult to quantify. By understanding which biological traits are characteristic of successful invasive species we can improve quarantine procedures and provide a better basis for management decisions.

Elton (1958) in *The Ecology of Invasions by Animals and Plants* noted that predicting the success of introduced species would be a major aim in ecological research in the future. Since this publication there has been considerable research into characteristics associated with successful invasive behaviour (Williamson 1996; Goodwin *et al.* 1999; Rejmánek & Richardson 1996; reviewed by Richardson & Pyšek 2006), with several of these traits used for the risk assessment of weeds (Weber *et al.* 2009). Theory suggests that the success of invasive species may depend upon the evolutionary relationships between the invader and the native community to which it invades. Charles Darwin (1859) was the first to recognise the potential importance of evolutionary relationships in the naturalisation of non-native species. Introduced species that are phylogenetically distinct from the native community are more likely to be successful invaders than closely related species for two main reasons. Firstly, phylogenetically distinct non-native invaders may be relatively free from competition with closely related species and are therefore more likely to exploit under-utilised niches (i.e. Darwin's Naturalisation Hypothesis). Secondly, non-native plants with close native relatives are more likely to suffer more damage from natural

enemies in the native community (i.e. Enemy Release Hypothesis) than species with few co-occurring relatives. This is because host choice in insect herbivores is generally determined by plant relatedness and host switching has been found between closely related non-native and native species. During this process the time taken for the insect herbivore community and the associated assemblage to develop may be important in determining whether an invader is immediately released from natural enemies upon its introduction, or if the herbivore community readily colonises and hinders its spread and invasive ability.

This study investigated patterns of plant-insect interactions on non-native and native plants with the aim of understanding the relative importance of phylogenetic relationships between the invader and the native community with respect to the likelihood of a species becoming colonised and damaged by natural enemies. In a series of field surveys on the east coast of Australia I explored these ideas at a variety of taxonomic levels. Chapter 2 examined the degree and kinds of damage fourteen invasive plants sustained based on how closely related they were to native species. Chapter 3 used *Senecio* L. as a case study to explore how important phylogenetic relationships are on a finer taxonomic scale. The amount of damage and the herbivore assemblages was compared across native and non-native, invasive and non-invasive *Senecio* species. This chapter specifically addressed the likelihood of enemy release being associated with the success of the invasive species *Senecio madagascariensis* (Poir.). Chapter 4 tested the importance of time since introduction in relation to the accumulation of the herbivore species on *Senecio madagascariensis* Poir. This chapter aimed at determining whether the herbivore community on *S. madagascariensis* quickly colonised and damaged this host potentially playing a role in reducing its invasive ability.

I found that phylogenetic distance to the nearest native relative at the genus level and higher was a good predictor of herbivore and pathogen damage on the invasive plants, explaining nearly 37% of the variance in leaf damage. As phylogenetic distance to the nearest native relative increased the total leaf damage decreased. These invasive species were colonised by fewer functional herbivore guilds and were dominated by apparent generalist natural enemies. My results suggest that those invasive species that are distantly related to the native community may be released from specialist natural enemies. The results supported expectations generated by both Darwin's Naturalisation and the Enemy Release hypotheses. The phylogenetic relationship between non-native and native communities may therefore be a useful tool for assessing the invasive potential of different species with respect to colonisation by the herbivore and pathogen community.

On a finer taxonomic scale within the genus of *Senecio*, my results indicate that phylogenetic relationships and enemy release may be less important for determining the invasiveness of an introduced species. Damage levels and invertebrate abundance and richness on *S. madagascariensis* were similar to the native and other non-native non-invasive *Senecio* species. There was no correlation between the genetic distance of different *Senecio* species and the herbivore assemblage. *Senecio madagascariensis* does not appear sufficiently phylogenetically distant from native and naturalised non-native *Senecio* species to be released from native herbivore assemblages. At this level there appears to be no support for enemy release in the case of the invasive species *S. madagascariensis*, unless the enemy release relates to specialist herbivores from its native range, which was not investigated in this study.

Over the time since introduction, the invertebrate community on *S. madagascariensis* has increased in abundance and richness and become apparently more specialised, as defined

by the number of herbivores reared from plant samples. These herbivores are more likely to have stronger physiological associations with their host plants than do external feeding herbivores, which were more abundant and diverse at the point of introduction than at invasion fronts. Leaf damage showed the opposite trend, with the highest damage levels at the invasion fronts compared to introduction point. Compared to its native congener *S. pinnatifolius* var. *pinnatifolius* A. Rich., *S. madagascariensis* sustained higher levels of herbivore damage, invertebrate abundance and diversity. Due to *S. madagascariensis* having many closely related species in the recipient community to which it has invaded, many herbivores and pathogens appear to be pre-adapted to using it as a source for food and site for reproduction.

Overall these results have significant implications for current research in invasion biology and for how invertebrate communities on non-native species change over time. This research has shown that phylogenetic relationships may play an important role in predictions of invasiveness for non-natives but is dependent on the taxonomic level assessed. Predictions of invasive potential based on non-native species being released from natural enemies for introductions above the level of genus may be successful. At a finer taxonomic scale (within genus), complex biotic interactions between an invader and the recipient native community make predictions of invasion success much more unreliable.

Management implications

Results from the findings of this thesis could be directly applied to the weed risk assessment process used in Australia, or similarly, in other quarantine systems used globally for screening plants for proposed introductions or for detection of high risk accidental introductions including “sleeper weeds”. Results can also be applied to

targeting existing non-native plants for management and control that have been imported prior to the stringent quarantine methods used today.

The Australian Weeds Risk Assessment (WRA) process, developed on a system-based model by Pheloung (1995), is a scientifically-based quarantine risk analysis tool used to identify whether a plant proposed for import may become a serious weed (DAFF 2008). The WRA has been adopted by the Australian Quarantine Inspection Service (AQIS) in 1997 and has since become internationally recognised and modified for use in other countries, including Japan (Kato *et al.* 2006), Hawaii (Daehler & Carino 2000), Florida (Gordon *et al.* 2008), the Czech Republic (Křivánek & Pyšek 2006), and the Pacific Islands (Daehler *et al.* 2004). To evaluate the invasive potential of a plant suggested for import, a part of the WRA utilises a questionnaire that includes information on a plant species biology, climatic preferences, reproductive and dispersal methods and proven weed history of congeneric taxa (Steinke 1999). Each of the 49 questions generates a score and the combined total evaluates the outcome of whether a plant is accepted for importation, rejected or prohibited pending further evaluation (Steinke 1999). A plant unsuitable for importation generates a high score from the questionnaire and is rejected for importation.

At present the WRA system utilises no known information about a species' phylogenetic relationship to the local environment. With global databases emerging on plant phylogenetics (e.g. Angiosperm phylogeny and Phylomatic (Stevens 2001; Webb & Donaghue 2005; Webb *et al.* 2009) it is now possible to incorporate phylogenetic relationships in weed risk assessments. Generating phylogenetic distances from scratch for weed risk assessments is too time consuming and impractical for use in a questionnaire but incorporating basic knowledge on a plants' taxonomic similarity to the native community will be possible in many cases. Online regional databases such as Flora of Australia

Online and the Australian Plants Name Index (APNI) or comparable databases in other countries can supply information on phylogenetic relationships, which in turn could be incorporated into the WRA process. The Flora of Australia and APNI are online databases that give access to taxonomic and biological information on plants, both native and weedy which currently occur in Australia. Simple searches could be conducted to ascertain whether a proposed plant species for import has family members present in the region of introduction or congeners present. Under the assumption that phylogenetically distant plant species are likely to be released from natural enemies, which may contribute to their initial success as invaders, the questionnaire could include a few extra steps that indicate the phylogenetic relationship of the plant in question to existing native plants in Australia. Questions could include: (1) Is the plant family present in Australia? (2) If the plant family is present, are congeneric native species present? If the proposed species has no congeneric native relatives present or no family members present in Australia, a higher score would be given to each, indicating a higher risk of enemy release. If there are native congeners present, my research findings suggest that further evaluation based on other weed risk assessment characteristics such as life history traits are required to determine its invasive potential.

There have been many plants introduced to Australia before stringent quarantine measures were in place, such as those used in the nursery industry. Many weeds start as innocuous “sleeper weeds”, with as many as 150 years elapsing between naturalisation and achieving significant weed status (Caley *et al.* 2008). Applying the WRA process to these existing non-native species present in Australia using phylogenetic relationships may enable informed decisions prior to the species becoming a serious pest. For example, *Hieracium aurantiacum* L., which has no native congeners present in Australia, is currently listed as a sleeper weed with the potential to become a serious pest (Groves 1999). Similarly,

Mimosa pigra L. (Fabaceae) (past sleeper weed now currently listed as a ‘Weed of National Significance’) is from a family that is represented in Australia but has no native congeners present. It was first recorded in 1891 in the Northern Territory and was naturalised in the Darwin area as a sleeper weed until 1952 when it was relocated and subsequently increased its population size to become a serious invader (Groves 2006). The invasive plant *Anredera cordifolia* from the family Basellaceae, represented in Chapter 2 as one of the declared noxious invasive species, is from a family with no native family representatives in Australia. It was introduced as a garden ornamental from South America and is now widespread and common in all Australian states with the exception of South Australia (Groves *et al.* 2005). It is a serious climbing weed invading margins of rainforests, inland watercourses and bushland. It can smother small trees and shrubs and produces thousands of aerial tubers along its stem (Harden 1990). At present it is still listed as a species available for sale throughout Australia with the exception of some council regions in Queensland and NSW (Groves *et al.* 2005).

Application of a phylogenetic component in weeds risk assessments could also be applied to many of the current species listed as ‘Weeds of National Significance’ (WONs) in Australia (Table 1). Most of the WONs have family representatives in Australia but 75% of the species are from a novel genus. A further two species *Tamarix aphylla* and *T. ramosissima* are from the family Tamaricaceae, which is not represented in Australia by any native relatives (Table 1).

At present, application of the WRA system results in rejection of approximately 90% of known invasive species (Gorden *et al.* 2008) and economic assessment indicates that it only takes a few species to cause significant environmental damage with large associated economic costs (Keller *et al.* 2007). Considering that the WRA has demonstrated

considerable bioeconomic benefits within a few years of implementation (Keller *et al.* 2007), any additional tools that improve the WRA may further reduce the risk of plants present in ecosystems from becoming weeds and prevent the importation of potential new weed species.

Closing remarks

The research outlined in this thesis provides evidence that phylogenetic distance between non-native species and the native recipient community is a useful tool that could be incorporated in weed risk assessment modules. Results suggest that the interaction between non-native and native plants and their natural enemies has a phylogenetic component. This phylogenetic component is only evident at taxonomic scales above the level of genus. Below this level, predictions for invasive potential based on phylogenetic relationships are weak. Incorporating phylogeny into current weeds risk assessments for potential imports or for targeting present non-native species for management has the potential to improve upon our current predictive power for assessing likely invaders. Presently the weeds risk assessment process has been successful in identifying 90% of known invasive weeds. A further 10% of non-native plants potentially slip through quarantine procedures with the risk of becoming serious invasive weeds. Improvements to current weeds risk assessment processes such as the application of a phylogenetic component has significant environmental and economic benefits on a local and global scale.

Table 1. Weeds of National Significance (WONs) and their phylogenetic relationship to Australian natives. Native relative present ✓ or absent ✗

| WONS | Family | Novel Family | Novel Genus |
|----------------------------------------------------------------------------------------------------------------------------------------------|---------------|--------------|-------------|
| <i>Acacia nilotica</i> (L.) Willd. Ex Delile | Fabaceae | ✗ | ✗ |
| <i>Alternanthera philoxeroides</i> (Mart.) Griseb. | Amaranthaceae | ✗ | ✗ |
| <i>Annona glabra</i> L. | Annonaceae | ✗ | ✓ |
| <i>Asparagus asparagoides</i> (L.) Druce | Asparagaceae | ✗ | ✗ |
| <i>Cabomba caroliniana</i> A. Gray | Cabombaceae | ✗ | ✓ |
| <i>Chrysanthemoides monilifera</i> (L.) Norl subsp. <i>monilifera</i> <i>Chrysanthemoides monilifera</i> (DC.) Norl. subsp. <i>Rotundata</i> | Asteraceae | ✗ | ✓ |
| <i>Cryptostegia grandiflora</i> R. Br. | Apocynaceae | ✗ | ✓ |
| <i>Hymenachne amplexicaulis</i> (Rudge) Nees | Poaceae | ✗ | ✗ |
| <i>Lantana camara</i> L. | Verbenaceae | ✗ | ✓ |
| <i>Mimosa pigra</i> L. | Fabaceae | ✗ | ✓ |
| <i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth | Poaceae | ✗ | ✓ |
| <i>Nassella trichotoma</i> (Nees) Hack. Ex Arechav | Poaceae | ✗ | ✓ |
| <i>Parkinsonia aculeate</i> L. | Fabaceae | ✗ | ✓ |
| <i>Parthenium hysterophorus</i> L. | Asteraceae | ✗ | ✓ |
| <i>Prosopis</i> L. spp. | Fabaceae | ✗ | ✓ |
| <i>Rubus fruticosus</i> L. aggregate | Rosaceae | ✗ | ✗ |
| <i>Salix</i> L. spp. except <i>S. babylonica</i> , <i>S. x calodendron</i> & <i>S. x reichardtiji</i> | Salicaceae | ✗ | ✓ |
| <i>Salvinia molesta</i> D.S. Mitch | Salviniaceae | ✗ | ✓ |
| <i>Tamarix aphylla</i> (L.) H. Karst. <i>Tamarix ramosissima</i> Ledeb. | Tamaricaceae | ✓ | ✓ |
| <i>Ulex europaeus</i> L. | Fabaceae | ✗ | ✓ |

References

- Australian Plant Name Index, IBIS database, Centre for Australian National Biodiversity Research, Australian Government, Canberra
<http://www.cpbr.gov.au/cgi-bin/apni> accessed August 2011
- AWS (2006) A national strategy for weed management in Australia. Australian Weeds Strategy. Natural Resource Management Ministerial Council, Australian Government Department of the Environment and Water Resources, Canberra ACT
www.weeds.gov.au/publications/strategies/pubs/weed-strategy.pdf Accessed July 2011
- Caley P, Groves RH, Barker R (2008) Estimating the invasion success of introduced plants. *Diversity and Distributions* 14:196-203
- Daehler CC, Carino DA (2000) Predicting invasive plants: prospects for a general screening system based on current regional models. *Biological Invasions* 2:93-102
- Daehler CC, Denslow JS, Ansari S, Kuo H (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific islands. *Conservation Biology* 18:360-368
- Darwin CR (1859) *The Origin of Species by Means of Natural Selection*. John Murray, London
- DAFF (2008) Development of the Weed Risk Assessment System. In: Biosecurity Australia. Australian Government. Department of Agriculture Fisheries and Forestry <http://www.daff.gov.au/ba/reviews/weeds/development> Accessed July 2011

Elton CS (1958) *The Ecology of Invasion by Animals and Plants*. London, Methuen

Flora of Australia Online. Australian Biological Resources Study, Canberra

<http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/index.html> accessed August 2011

Goodwin BJ, McAllister AJ, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology* 13:422-426

Gordon DR, Onderdonk DA, Fox AM, Stocker RK, Gantz C (2008) Predicting Invasive Plants in Florida using the Australian Weed Risk Assessment. *Invasive Plant Science and Management* 1:178-195

Groves RH (1999) Sleeper weeds. In: Bishop AC, Boersma M, Barnes CD (eds) *Proceedings of the 12th Australian Weeds Conference*, Tasmanian Weed Society, Hobart, pp 632-636

Groves RH, Boden R, Lonsdale WM (2005) *Jumping the Garden Fence: Invasive Garden Plants in Australia and their environmental and agricultural impacts*. CSIRO report prepared for WWF-Australia. WWF-Australia, Sydney

Groves RH (2006) Are some weeds sleeping? Some concepts and reasons. *Euphytica* 148:111-120

Harden GJ (1990) *Anredera cordifolia* (Ten.) Steenis. In: *PlantNET - The Plant Information Network System of The Royal Botanic Gardens and Domain Trust*, Sydney, Australia <http://plantnet.rbgsyd.nsw.gov.au/cgi-bin/NSWfl.pl?page=nswfl&lvl=sp&name=Anredera~cordifolia> Accessed August 2011

- Kato H, Hata K, Yamamoto H, Yoshioka T (2006) Effectiveness of the weed risk assessment system for the Bonin Islands. In: Koike F, Clout M, Kawamichi M, De Poorter M, Iwatsuki K (eds) Assessment and control of biological invasion risk (eds) Shoukadoh Book Sellers, Kyoto, Japan and IUCN, Gland, Switzerland, pp 65-72
- Keller RP, Lodge DM, Finnoff DC (2007) Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences USA* 104:203-207
- Křivánek, M. & Pyšek, P. (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). *Diversity and Distributions* 12:319-327
- Pheloung PC (1995) Determining the weed potential of new plant introductions to Australia. A report to the Standing Committee on Agriculture and Resource Management, Australia
- Prieur-Richard AH, Lavorel S (2000) Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1-7
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655-1661
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30:409-431
- Sinden J, Jones R, Hester S, Odom D, Kalisch D, James R, Cacho O, Griffith G (2005) The

economic impact of weeds in Australia. *Plant Protection Quarterly* 20:25-32

Steinke E (1999) The Australian Quarantine and Inspection Service Weed Risk Assessment System for new plant imports: its development and implementation. In: Bishop AC (ed) 12th Australian Weeds Conference, Papers and Proceedings, Tasmanian Weed Society

Stevens PF (2001) Angiosperm Phylogeny Website. Version 9, June 2008
<http://www.mobot.org/MOBOT/research/APweb/> Accessed July 2011

Walker LR, Smith SD (1997) Impacts of invasive plants on community and ecosystem properties. In: Luken JO, Thieret JW (eds) *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, pp 69-85

Weber J, Panetta FD, Virtue J, Pheloung P (2009) An analysis of assessment outcomes from eight years' operation of the Australian border weed risk assessment system. *Journal of Environmental Management* 90:798-807

Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181-183

Webb CO, Ackerly DD, Kembel SW (2009) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1
http://www.phylodiversity.net/phylocom/phylocom_manual.pdf Accessed Dec 2008

Williamson M (1996) *Biological Invasions*. Chapman and Hall, London

Appendix 1

| Species | ITS availability | Replacement species | Where collected | Group | Sequence | Reference |
|-------------------------------------------------------------------------------------------------------------|------------------|----------------------|-----------------|------------|------------|--------------------------------------|
| <i>S. madagascariensis</i> | Yes | | Australia | Lautusoid | U93198.1 | Scott <i>et al.</i> (1998) |
| <i>S. glastifolius</i> | Yes | | New Zealand | Exotic | EF538340.1 | Pelser <i>et al.</i> 2007 |
| <i>S. pterophorus</i> | Yes | | South Africa | Exotic | AF085188.1 | Vincent & Getliffe (1992) |
| <i>S. macroglossus</i> | Yes | | Southern Africa | Exotic | DQ915881.1 | Sombra Staeheli <i>et al.</i> unpub. |
| <i>S. angulatus</i> | Yes | | Unknown | Exotic | AF459953.1 | Pelser <i>et al.</i> (2002) |
| <i>S. minimus</i> | Yes | | New Zealand | Disciform | EU331119.1 | Gardner <i>et al.</i> unpub. |
| <i>S. lautus</i> subsp. <i>maritimus</i> (synonym of <i>S. pinnatifolius</i> var. <i>pinnatifolius</i>) | Yes | | Australia | Lautusoid | U93203.1 | Scott <i>et al.</i> (1998) |
| <i>S. linearifolius</i> var. <i>arachnoideus</i> | No | <i>S. australis</i> | Australia | Odoratus | EF538302.1 | Pelser <i>et al.</i> 2007 |
| <i>S. amygdalifolius</i> | No | <i>S. macranthus</i> | Australia | Macranthus | EF538358.1 | Pelser <i>et al.</i> 2007 |
| <i>S. bipinnatisectus</i> | No | <i>S. diaschides</i> | Australia | Disciform | EF538328.1 | Pelser <i>et al.</i> 2007 |

References – (for nucleotide gene sequences from nucleotide database, National Center for Biotechnology Information (NCBI) database <http://www.ncbi.nlm.nih.gov/>).

Gardner RC, Keeling J, de Lange PJ, Wright SD, Cameron EK (unpublished) A New Zealand biodiversity database

Scott LJ, Congdon C, Playford J (1998) Molecular evidence that fireweed (*Senecio madagascariensis*, Asteraceae) is of South African origin. *Plant Systematics and Evolution* 213:251-257

Sombra Staeheli D, Eggli U, Nyffeler R (unpublished) Molecular phylogenetics and comparative anatomy of succulent species of *Senecio*

Pelser PB, Gravendeel B, van der Meijden R (2002) Tackling speciose genera: species composition and phylogenetic position of *Senecio* sect. *Jacobaea* (Asteraceae) based on plastid and nrDNA sequences. *American Journal of Botany* 89:929-939

Pelser PB, Nordenstam B, Kadereit JW, Watson LE (2007) An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1114.

Vincent PLD, Getliffe FM (1992) Elucidative studies on the generic concept of *Senecio* (Asteraceae). *Botanical Journal of the Linnean Society* 108:55-81

Appendix 2: Can phylogenetic relationships within genus indicate the enemy release of an invader?

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|-------------------|-------------------------|---------------------------------|---------|-------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Acarina | Acarina 44 | Tenuipalpidae | | Sap-sucker | 3 | 0 | 0 | 0 | 0 |
| Coleoptera | Coleoptera 1 | Brentidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 9 | Chrysomelidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 18 | Curculionidae | | Leaf chewer | 0 | 0 | 3 | 0 | 0 |
| | Coleoptera 20 | Curculionidae: Scolytinae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 39 | Curculionidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Coleoptera 41 | Chrysomelidae | | Leaf chewer | 0 | 0 | 2 | 0 | 0 |
| | Coleoptera 52 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Coleoptera 54 | Chrysomelidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Coleoptera 55 | Cerambycidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Coleoptera 58 | Chrysomelidae | | Leaf chewer | 0 | 4 | 0 | 0 | 0 |
| | Coleoptera 61 | Chrysomelidae: Cryptocephalinae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Coleoptera 63 | Aderidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 65 | Brentidae | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Coleoptera 66 | Brentidae | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Coleoptera 67 | Curculionidae | | Leaf chewer | 0 | 0 | 2 | 0 | 0 |
| | Larvae 24 | Curculionidae | | Leaf chewer | 3 | 0 | 3 | 0 | 0 |
| | Larvae 25 | Curculionidae | | Leaf chewer | 6 | 0 | 0 | 0 | 0 |
| | Larvae 32 | Curculionidae | | Leaf chewer | 0 | 0 | 76 | 0 | 0 |
| | Lep. Coleoptera 56 | Cerambycidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 73 | Cerambycidae | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Lep. Coleoptera 80 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| Diptera | Diptera 5 | Agromyzidae | | Miner | 0 | 0 | 0 | 0 | 0 |
| | Diptera 41 | Agromyzidae | | Miner | 0 | 4 | 3 | 0 | 2 |
| | Col: Auchenorrhyncha 45 | Membracidae | | Sap-sucker | 0 | 1 | 0 | 0 | 1 |
| Hemiptera | Dip: Sternorrhyncha 82 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Aphididae 1 | Aphididae | | Sap-sucker | 0 | 6 | 0 | 0 | 0 |
| | Aphididae 10 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 11 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 13 | Aphididae | | Sap-sucker | 0 | 3 | 0 | 0 | 0 |
| | Aphididae 14 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |

Note: *pin.* – *Senecio pinnatifolius* var. *pinnatifolius*; *min.* – *S. minimus*; *lin.* – *S. linearifolius* var. *arachnoideus*; *amy.* – *S. amygdalifolius*; *bip.* – *S. bippinnatisectus*.

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|----------------------------|-------------------|-------------------------------|--------------------------|------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Hemiptera cont. | Aphididae 18 | Aphididae | | Sap-sucker | 6 | 110 | 8 | 233 | 58 |
| | Aphididae 2 | Aphididae | | Sap-sucker | 0 | 6 | 0 | 12 | 1 |
| | Aphididae 20 | Aphididae | | Sap-sucker | 0 | 1 | 1 | 3 | 6 |
| | Aphididae 21 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 23 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 24 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 25 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 26 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 27 | Aphididae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Aphididae 28 | Aphididae | | Sap-sucker | 2 | 2 | 0 | 13 | 0 |
| | Aphididae 29 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 30 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 31 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 34 | Aphididae | | Sap-sucker | 0 | 1 | 0 | 1 | 1 |
| | Aphididae 35 | Aphididae | | Sap-sucker | 0 | 2 | 0 | 0 | 0 |
| | Aphididae 36 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 38 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 39 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 40 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 41 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 42 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 43 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 44 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 45 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 46 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 48 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 49 | Aphididae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Aphididae 50 | Aphididae | | Sap-sucker | 0 | 0 | 2 | 0 | 0 |
| | Aphididae 51 | Aphididae | | Sap-sucker | 0 | 16 | 1 | 8 | 1 |
| | Aphididae 52 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 3 | 0 |
| | Auchenorrhyncha 4 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Auchenorrhyncha 5 | Cicadellidae | | Sap-sucker | 18 | 4 | 45 | 3 | 1 |
| | Auchenorrhyncha 7 | Cicadellidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 8 | Cicadellidae: Deltocephalinae | <i>Attenuipyga minor</i> | Sap-sucker | 0 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|----------------------------|--------------------|---------------|----------------------------|------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Hemiptera cont. | Au: Heteroptera 9 | Fulgoroidea | | Sap-sucker | 9 | 0 | 1 | 1 | 0 |
| | Auchenorrhyncha 15 | Delphacidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 16 | Fulgoroidea | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 17 | Cicadellidae | | Sap-sucker | 2 | 0 | 2 | 1 | 0 |
| | Auchenorrhyncha 18 | Flatidae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 19 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 8 |
| | Auchenorrhyncha 20 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 21 | Flatidae | | Sap-sucker | 0 | 1 | 63 | 2 | 0 |
| | Auchenorrhyncha 22 | Cicadellidae | | Sap-sucker | 0 | 5 | 37 | 1 | 1 |
| | Auchenorrhyncha 23 | Cicadellidae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Auchenorrhyncha 24 | Cicadellidae | | Sap-sucker | 0 | 0 | 9 | 0 | 0 |
| | Auchenorrhyncha 25 | Cicadellidae | | Sap-sucker | 0 | 0 | 1 | 1 | 0 |
| | Auchenorrhyncha 27 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Auchenorrhyncha 28 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Auchenorrhyncha 29 | Cixiidae | | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Auchenorrhyncha 30 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Auchenorrhyncha 31 | Unknown | | Sap-sucker | 0 | 0 | 0 | 2 | 2 |
| | Auchenorrhyncha 32 | Ricaniidae | <i>Scolypopa australis</i> | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Auchenorrhyncha 33 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Auchenorrhyncha 34 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 2 |
| | Auchenorrhyncha 35 | Cicadellidae | | Sap-sucker | 0 | 0 | 12 | 0 | 0 |
| | Auchenorrhyncha 36 | Cicadellidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 37 | Aphrophoridae | | Sap-sucker | 0 | 2 | 0 | 0 | 0 |
| | Auchenorrhyncha 38 | Cicadellidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 39 | Cicadellidae | | Sap-sucker | 0 | 3 | 0 | 0 | 0 |
| | Auchenorrhyncha 40 | Cixiidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 41 | Cicadellidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 42 | Cicadellidae | | Sap-sucker | 0 | 2 | 0 | 0 | 0 |
| | Auchenorrhyncha 43 | Flatidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 44 | Flatidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 45 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Auchenorrhyncha 46 | Fulgoroidea | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Auchenorrhyncha 47 | Cicadellidae | | Sap-sucker | 0 | 0 | 2 | 0 | 0 |
| | Auchenorrhyncha 48 | Issidae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|----------------------------|------------------------|-----------------------------------|------------------------------|------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Hemiptera cont. | Auchenorrhyncha 50 | Cixiidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 51 | Cicadellidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 52 | Cicadellidae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Heteroptera 1 | Lygaeoidea | | Sap-sucker | 135 | 994 | 135 | 2 | 97 |
| | Heteroptera 2 | Miridae | | Sap-sucker | 1 | 14 | 23 | 0 | 0 |
| | Heteroptera 3 | Orsillidae | <i>Nysius clevelandensis</i> | Sap-sucker | 32 | 37 | 22 | 0 | 15 |
| | Heteroptera 4 | Miridae | <i>Creontiades</i> sp. | Sap-sucker | 0 | 1 | 1 | 0 | 0 |
| | Het: Sternorrhyncha 14 | Coccoidea | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Heteroptera 16 | Miridae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Het: Sternorrhyncha 17 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 18 | Miridae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Heteroptera 19 | Miridae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Heteroptera 20 | Coreidae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Heteroptera 21 | Pentatomidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Heteroptera 24 | Pentatomidae | | Sap-sucker | 0 | 0 | 0 | 0 | 5 |
| | Heteroptera 26 | Rhyparochromidae: Rhyparochominae | | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Heteroptera 27 | Miridae | | Sap-sucker | 0 | 0 | 0 | 2 | 0 |
| | Heteroptera 28 | Coreidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Heteroptera 29 | Pentatomidae | | Sap-sucker | 0 | 3 | 0 | 0 | 0 |
| | Heteroptera 30 | Rhyparochromidae | | Sap-sucker | 0 | 2 | 0 | 1 | 0 |
| | Heteroptera 32 | Miridae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 33 | Miridae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Heteroptera 34 | Lygaeidae | | Sap-sucker | 0 | 2 | 0 | 0 | 0 |
| | Heteroptera 35 | Lygaeidae | <i>Nysius vinator</i> | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 36 | Miridae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 38 | Aleyrodidae | | Sap-sucker | 0 | 0 | 0 | 2 | 0 |
| | Heteroptera 39 | Piesmatidae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Heteroptera 40 | Lygaeidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Unknown 21 | Coccoidea | | Sap-sucker | 4 | 0 | 0 | 0 | 0 |
| | Unknown 31 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Unknown 32 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Unknown 44 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Unknown 52 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Unknown 53 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 2 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|--------------------|------------------|--------------------------|---------------------------------|-------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Hemiptera | Unknown 58 | Coccoidea | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | M.1. Hemiptera 1 | Derbidae | | Sap-sucker | 0 | 0 | 0 | 2 | 0 |
| Hymenoptera | Hymenoptera 15 | Torymidae: Megastigminae | <i>Megastigmus</i> sp. | Galling | 2 | 9 | 1 | 2 | 0 |
| Lepidoptera | Larvae 26 | Unknown: pupae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 1 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 2 | Pyraloidea | | Leaf chewer | 81 | 7 | 7 | 0 | 2 |
| | Lepidoptera 5 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 6 | | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 13 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 15 | Tortricidae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 20 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 6 | 7 | 12 | 8 | 1 |
| | Lepidoptera 24 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Leaf chewer | 0 | 2 | 1 | 4 | 3 |
| | Lepidoptera 30 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 1 | 0 | 0 | 0 | 1 |
| | Lepidoptera 31 | Tortricidae | | Leaf chewer | 5 | 0 | 0 | 0 | 0 |
| | Lepidoptera 32 | Pyraloidea | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 36 | Pyraloidea | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 37 | Cosmopterigidae | <i>Pyroderces</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 38 | Gelechiidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 39 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 40 | Geometridae | | Leaf chewer | 0 | 0 | 11 | 0 | 4 |
| | Lepidoptera 41 | Geometridae | | Leaf chewer | 0 | 0 | 5 | 0 | 1 |
| | Lepidoptera 42 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 43 | Cosmopterigidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 44 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 2 |
| | Lepidoptera 46 | Tortricidae | | Leaf chewer | 0 | 1 | 0 | 0 | 1 |
| | Lepidoptera 49 | Tortricidae | | Leaf chewer | 0 | 0 | 1 | 1 | 0 |
| | Lepidoptera 50 | Arctiidae | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Lepidoptera 52 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Lepidoptera 53 | Arctiidae | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Lepidoptera 54 | Geometridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 55 | Pterophoridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 58 | Noctuidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 59 | Gelechioidea | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 61 | Geometridae | <i>Phrissogonus laticostata</i> | Leaf chewer | 0 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|------------------------------|-----------------|------------------------|--------------------------|-------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Lepidoptera cont. | Lepidoptera 62 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 66 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 67 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 68 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 69 | Oecophoridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 70 | Gelechiidae | | Leaf chewer | 0 | 0 | 3 | 1 | 0 |
| | Lepidoptera 72 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Lepidoptera 74 | Geometridae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 75 | Pyraloidea | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 76 | Geometridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 78 | Geometridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 79 | Gelechioidea | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 81 | Noctuidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 82 | Arctiidae: Ctenuchinae | <i>Amata sp.</i> | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 83 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 84 | Gelechioidea | | Leaf chewer | 2 | 0 | 0 | 0 | 0 |
| | Lepidoptera 85 | Gelechioidea | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 86 | Pyraloidea | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 87 | Pyraloidea | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 88 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 89 | Pyralidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| Orthoptera | Lepidoptera 90 | Gelechioidea | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Orthoptera 4 | Acrididae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Orthoptera 6 | Tettigoniidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Orthoptera 9 | Tettigoniidae | | Leaf chewer | 0 | 1 | 1 | 0 | 1 |
| Thysanoptera | | | <i>Pseudanaphothrips</i> | | | | | | |
| | Thysanoptera 1 | Thripidae: Thripinae | <i>achaetus</i> | Sap-sucker | 3 | 0 | 1 | 0 | 0 |
| | Thysanoptera 23 | Thripidae: Thripinae | <i>Thrips imaginis</i> | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | | | <i>Pseudanaphothrips</i> | | | | | | |
| | Thysanoptera 2 | Thripidae: Thripinae | <i>achaetus</i> | Sap-sucker | 6 | 3 | 3 | 0 | 1 |
| | Thysanoptera 3 | Panchaetothripinae | <i>Bhattithrips</i> sp. | Sap-sucker | 22 | 1 | 1 | 0 | 1 |
| | Thysanoptera 25 | Thripidae | Larvae | Sap-sucker | 0 | 0 | 4 | 0 | 0 |
| | Thysanoptera 35 | Thripidae: Thripinae | <i>Thrips</i> sp. | Sap-sucker | 1 | 0 | 19 | 0 | 0 |
| | Thysanoptera 37 | Thripidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Native <i>Senecio</i> spp. | | | | |
|-------------------------------|-----------------|----------------------|-------------------------------------------|------------|----------------------------------------|-------------|-------------|-------------|-------------|
| | | | | | <i>pin.</i> | <i>min.</i> | <i>lin.</i> | <i>amy.</i> | <i>bip.</i> |
| Thysanoptera cont. | Thysanoptera 39 | Thripidae | Larvae | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Thysanoptera 47 | Thripidae | Larvae | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Thysanoptera 50 | Panchaetothripinae | <i>Bhattithrips</i> larvae | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | | Phlaeothripidae: | | | | | | | |
| | Thysanoptera 51 | Phlaeothripinae | <i>Haplothrips</i> sp. | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | | Phlaeothripidae: | | | | | | | |
| | Thysanoptera 52 | Phlaeothripinae | <i>Haplothrips</i> sp. | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Thysanoptera 53 | Thripidae: Thripinae | <i>Thrips imaginis</i> & <i>T. tabaci</i> | Sap-sucker | 0 | 0 | 0 | 0 | 1 |

Appendix 2: Can phylogenetic relationships within genus indicate the enemy release of an invader?

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|-------------------|-------------------------|---------------------------------|---------|-------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Acarina | Acarina 44 | Tenuipalpidae | | Sap-sucker | 5 | 9 | 66 | 0 | 116 |
| Coleoptera | Coleoptera 1 | Brentidae | | Leaf chewer | 2 | 0 | 0 | 0 | 0 |
| | Coleoptera 9 | Chrysomelidae | | Leaf chewer | 2 | 0 | 0 | 0 | 0 |
| | Coleoptera 18 | Curculionidae | | Leaf chewer | 0 | 1 | 0 | 1 | 0 |
| | Coleoptera 20 | Curculionidae: Scolytinae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Coleoptera 39 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 41 | Chrysomelidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 52 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 54 | Chrysomelidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 55 | Cerambycidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 58 | Chrysomelidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 61 | Chrysomelidae: Cryptocephalinae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 63 | Aderidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Coleoptera 65 | Brentidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 66 | Brentidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Coleoptera 67 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Larvae 24 | Curculionidae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Larvae 25 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Larvae 32 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lep. Coleoptera 56 | Cerambycidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 73 | Cerambycidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lep. Coleoptera 80 | Curculionidae | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| Diptera | Diptera 5 | Agromyzidae | | Miner | 1 | 0 | 0 | 0 | 0 |
| | Diptera 41 | Agromyzidae | | Miner | 8 | 0 | 7 | 3 | 0 |
| Hemiptera | Col: Auchenorrhyncha 45 | Membracidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Dip: Sternorrhyncha 82 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 1 | Aphididae | | Sap-sucker | 0 | 0 | 34 | 0 | 0 |
| | Aphididae 10 | Aphididae | | Sap-sucker | 11 | 0 | 0 | 0 | 0 |
| | Aphididae 11 | Aphididae | | Sap-sucker | 0 | 0 | 55 | 0 | 0 |
| | Aphididae 13 | Aphididae | | Sap-sucker | 11 | 0 | 0 | 0 | 0 |
| | Aphididae 14 | Aphididae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |

Note: *mad.* – *Senecio madagascariensis*; *ang.* – *S. angulatus*; *ptero.* – *S. pterophorus*; *glast.* – *S. glastifolius*; *mac.* – *S. macroglossus*.

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|----------------------------|-------------------|-------------------------------|--------------------------|------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Hemiptera cont. | Aphididae 18 | Aphididae | | Sap-sucker | 240 | 327 | 439 | 0 | 1 |
| | Aphididae 2 | Aphididae | | Sap-sucker | 0 | 0 | 12 | 0 | 0 |
| | Aphididae 20 | Aphididae | | Sap-sucker | 17 | 4 | 34 | 0 | 1 |
| | Aphididae 21 | Aphididae | | Sap-sucker | 35 | 0 | 0 | 0 | 0 |
| | Aphididae 23 | Aphididae | | Sap-sucker | 34 | 0 | 0 | 0 | 0 |
| | Aphididae 24 | Aphididae | | Sap-sucker | 268 | 0 | 2 | 0 | 0 |
| | Aphididae 25 | Aphididae | | Sap-sucker | 32 | 0 | 0 | 0 | 0 |
| | Aphididae 26 | Aphididae | | Sap-sucker | 298 | 0 | 0 | 0 | 0 |
| | Aphididae 27 | Aphididae | | Sap-sucker | 126 | 34 | 98 | 0 | 196 |
| | Aphididae 28 | Aphididae | | Sap-sucker | 135 | 42 | 37 | 0 | 22 |
| | Aphididae 29 | Aphididae | | Sap-sucker | 20 | 0 | 0 | 0 | 0 |
| | Aphididae 30 | Aphididae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Aphididae 31 | Aphididae | | Sap-sucker | 12 | 0 | 0 | 0 | 0 |
| | Aphididae 34 | Aphididae | | Sap-sucker | 0 | 0 | 5 | 0 | 1 |
| | Aphididae 35 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 36 | Aphididae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Aphididae 38 | Aphididae | | Sap-sucker | 9 | 0 | 0 | 0 | 0 |
| | Aphididae 39 | Aphididae | | Sap-sucker | 8 | 0 | 0 | 0 | 0 |
| | Aphididae 40 | Aphididae | | Sap-sucker | 3 | 0 | 0 | 0 | 0 |
| | Aphididae 41 | Aphididae | | Sap-sucker | 3 | 0 | 0 | 0 | 0 |
| | Aphididae 42 | Aphididae | | Sap-sucker | 30 | 0 | 0 | 0 | 0 |
| | Aphididae 43 | Aphididae | | Sap-sucker | 15 | 0 | 0 | 0 | 0 |
| | Aphididae 44 | Aphididae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Aphididae 45 | Aphididae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Aphididae 46 | Aphididae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Aphididae 48 | Aphididae | | Sap-sucker | 0 | 0 | 9 | 0 | 0 |
| | Aphididae 49 | Aphididae | | Sap-sucker | 0 | 0 | 2 | 0 | 0 |
| | Aphididae 50 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Aphididae 51 | Aphididae | | Sap-sucker | 0 | 1 | 2 | 0 | 0 |
| | Aphididae 52 | Aphididae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 4 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 5 | Cicadellidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 7 | Cicadellidae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 8 | Cicadellidae: Deltocephalinae | <i>Attenuipyga minor</i> | Sap-sucker | 1 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|----------------------------|--------------------|---------------|----------------------------|------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Hemiptera cont. | Au: Heteroptera 9 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 15 | Delphacidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 16 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 17 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 18 | Flatidae | | Sap-sucker | 0 | 1 | 5 | 0 | 0 |
| | Auchenorrhyncha 19 | Cicadellidae | | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 20 | Cicadellidae | | Sap-sucker | 17 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 21 | Flatidae | | Sap-sucker | 0 | 0 | 2 | 5 | 0 |
| | Auchenorrhyncha 22 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 23 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 24 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 25 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 27 | Cicadellidae | | Sap-sucker | 0 | 0 | 8 | 0 | 0 |
| | Auchenorrhyncha 28 | Cicadellidae | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Auchenorrhyncha 29 | Cixiidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 30 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 31 | Unknown | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 32 | Ricaniidae | <i>Scolypopa australis</i> | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 33 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 34 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 35 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 36 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 37 | Aphrophoridae | | Sap-sucker | 0 | 0 | 3 | 0 | 0 |
| | Auchenorrhyncha 38 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 39 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 40 | Cixiidae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Auchenorrhyncha 41 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 42 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 43 | Flatidae | | Sap-sucker | 0 | 0 | 4 | 0 | 0 |
| | Auchenorrhyncha 44 | Flatidae | | Sap-sucker | 0 | 2 | 0 | 0 | 0 |
| | Auchenorrhyncha 45 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 46 | Fulgoroidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 47 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 48 | Issidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|----------------------------------|------------------------|------------------------------------|------------------------------|------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Hemiptera cont. | Auchenorrhyncha 50 | Cixiidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 51 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Auchenorrhyncha 52 | Cicadellidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 1 | Lygaeoidea | | Sap-sucker | 263 | 3 | 13 | 3 | 0 |
| | Heteroptera 2 | Miridae | | Sap-sucker | 3 | 8 | 106 | 0 | 0 |
| | Heteroptera 3 | Orsillidae | <i>Nysius clevelandensis</i> | Sap-sucker | 4 | 0 | 15 | 15 | 0 |
| | Heteroptera 4 | Miridae | <i>Creontiades</i> sp. | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Het: Sternorrhyncha 14 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 16 | Miridae | | Sap-sucker | 1 | 0 | 0 | 0 | 0 |
| | Het: Sternorrhyncha 17 | Coccoidea | | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Heteroptera 18 | Miridae | | Sap-sucker | 7 | 0 | 1 | 0 | 0 |
| | Heteroptera 19 | Miridae | | Sap-sucker | 4 | 0 | 0 | 0 | 0 |
| | Heteroptera 20 | Coreidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 21 | Pentatomidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 24 | Pentatomidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 26 | Rhyparochromidae: Rhyparochrominae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 27 | Miridae | | Sap-sucker | 0 | 0 | 8 | 0 | 0 |
| | Heteroptera 28 | Coreidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 29 | Pentatomidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 30 | Rhyparochromidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 32 | Miridae | | Sap-sucker | 0 | 0 | 2 | 0 | 0 |
| | Heteroptera 33 | Miridae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Heteroptera 34 | Lygaeidae | | Sap-sucker | 0 | 0 | 0 | 0 | 6 |
| | Heteroptera 35 | Lygaeidae | <i>Nysius vinator</i> | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Heteroptera 36 | Miridae | | Sap-sucker | 0 | 0 | 1 | 0 | 0 |
| | Heteroptera 38 | Aleyrodidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 39 | Piesmatidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Heteroptera 40 | Lygaeidae | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Unknown 21 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 1 | 0 |
| | Unknown 31 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Unknown 32 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| | Unknown 44 | Coccoidea | | Sap-sucker | 0 | 0 | 4 | 0 | 19 |
| | Unknown 52 | Coccoidea | | Sap-sucker | 0 | 97 | 1 | 0 | 0 |
| | Unknown 53 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|--------------------|------------------|--------------------------|---------------------------------|-------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Hemiptera | Unknown 58 | Coccoidea | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | M.1. Hemiptera 1 | Derbidae | | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| Hymenoptera | Hymenoptera 15 | Torymidae: Megastigminae | <i>Megastigmus</i> sp. | Galling | 4 | 0 | 0 | 0 | 0 |
| Lepidoptera | Larvae 26 | Unknown: pupae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 1 | Pyraloidea | | Leaf chewer | 0 | 1 | 1 | 0 | 0 |
| | Lepidoptera 2 | Pyraloidea | | Leaf chewer | 221 | 1 | 12 | 2 | 2 |
| | Lepidoptera 5 | Pyraloidea | | Leaf chewer | 2 | 0 | 0 | 0 | 0 |
| | Lepidoptera 6 | | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 13 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 15 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 20 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 17 | 0 | 77 | 1 | 0 |
| | Lepidoptera 24 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 30 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 0 | 0 | 0 | 3 | 0 |
| | Lepidoptera 31 | Tortricidae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 32 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 36 | Pyraloidea | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 37 | Cosmopterigidae | <i>Pyroderces</i> sp. | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 38 | Gelechiidae | | Leaf chewer | 0 | 0 | 0 | 3 | 0 |
| | Lepidoptera 39 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 1 | 0 |
| | Lepidoptera 40 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 41 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 42 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 2 |
| | Lepidoptera 43 | Cosmopterigidae | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Lepidoptera 44 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 46 | Tortricidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 49 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 50 | Arctiidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 52 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 53 | Arctiidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 54 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 55 | Pterophoridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 58 | Noctuidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 59 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 61 | Geometridae | <i>Phrissogonus laticostata</i> | Leaf chewer | 0 | 0 | 4 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|------------------------------|-----------------|------------------------|-----------------------------------|-------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Lepidoptera cont. | Lepidoptera 62 | Tortricidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 66 | Tortricidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 67 | Geometridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 68 | Tortricidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 69 | Oecophoridae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| | Lepidoptera 70 | Gelechiidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 72 | Tortricidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 74 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 75 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 76 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 78 | Geometridae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 79 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 81 | Noctuidae | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Lepidoptera 82 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Lepidoptera 83 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 1 |
| | Lepidoptera 84 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 85 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 86 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 87 | Pyraloidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Lepidoptera 88 | Tortricidae | | Leaf chewer | 0 | 0 | 1 | 0 | 0 |
| | Lepidoptera 89 | Pyralidae | | Leaf chewer | 1 | 0 | 0 | 0 | 0 |
| | Lepidoptera 90 | Gelechioidea | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| Orthoptera | Orthoptera 4 | Acrididae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Orthoptera 6 | Tettigoniidae | | Leaf chewer | 0 | 0 | 0 | 0 | 0 |
| | Orthoptera 9 | Tettigoniidae | | Leaf chewer | 0 | 1 | 0 | 0 | 0 |
| Thysanoptera | Thysanoptera 1 | Thripidae: Thripinae | <i>Pseudanaphothrips achaetus</i> | Sap-sucker | 7 | 0 | 4 | 0 | 0 |
| | Thysanoptera 23 | Thripidae: Thripinae | <i>Thrips imaginis</i> | Sap-sucker | 0 | 1 | 0 | 0 | 0 |
| | Thysanoptera 2 | Thripidae: Thripinae | <i>Pseudanaphothrips achaetus</i> | Sap-sucker | 31 | 12 | 8 | 0 | 3 |
| | Thysanoptera 3 | Panchaetothripinae | <i>Bhattithrips</i> sp. | Sap-sucker | 7 | 0 | 0 | 0 | 0 |
| | Thysanoptera 25 | Thripidae | Larvae | Sap-sucker | 2 | 0 | 0 | 0 | 0 |
| | Thysanoptera 35 | Thripidae: Thripinae | <i>Thrips</i> sp. | Sap-sucker | 0 | 8 | 10 | 0 | 1 |
| | Thysanoptera 37 | Thripidae | | Sap-sucker | 0 | 3 | 0 | 0 | 0 |
| | Thysanoptera 39 | Thripidae | Larvae | Sap-sucker | 24 | 0 | 0 | 0 | 0 |
| | Thysanoptera 47 | Thripidae | Larvae | Sap-sucker | 32 | 0 | 0 | 0 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundances: Non-native <i>Senecio</i> spp. | | | | |
|---------------------|-----------------|----------------------|-------------------------------------------|------------|--------------------------------------------|-------------|---------------|---------------|---------------|
| | | | | | <i>mad.</i> | <i>ang.</i> | <i>ptero.</i> | <i>glast.</i> | <i>macro.</i> |
| Thysanoptera | Thysanoptera 50 | Panchaetothripinae | <i>Bhattithrips</i> larvae | Sap-sucker | 0 | 0 | 0 | 0 | 1 |
| cont. | Thysanoptera 51 | Phlaeothripidae: | <i>Haplothrips</i> sp. | Sap-sucker | 0 | 0 | 0 | 0 | 0 |
| | Thysanoptera 52 | Phlaeothripidae: | <i>Haplothrips</i> sp. | Sap-sucker | 0 | 0 | 2 | 0 | 0 |
| | Thysanoptera 53 | Thripidae: Thripinae | <i>Thrips imaginis</i> & <i>T. tabaci</i> | Sap-sucker | 0 | 1 | 20 | 0 | 0 |
| | | | | | | | | | |

Appendix 3: Does time since colonisation influence enemy release of an invasive weed?

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|---------|---------------|----------------------------------|---------------------------------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Acarina | Acarina 1 | | | Unknown | 1 | 0 |
| | Acarina 10 | | | Fungivore | 268 | 0 |
| | Acarina 11 | Ascidae and Histiostomatidae mix | | Unknown | 9 | 1 |
| | Acarina 12 | | | Unknown | 1 | 0 |
| | Acarina 13 | | | Unknown | 6 | 18 |
| | Acarina 2 | Ascidae | | Fungivore | 2 | 0 |
| | Acarina 3 | | | Fungivore | 12 | 23 |
| | Acarina 4 | | | Unknown | 1 | 0 |
| | Acarina 5 | | Unknown | 1 | 4 | |
| | Acarina 6 | Acaridae and other Oribatida mix | <i>Acaridae: Tyrophagus</i> sp. | Unknown | 1 | 8 |
| | Acarina 7 | | | Unknown | 89 | 54 |
| | Acarina 8 | Erythraeidae | | Predator | 1 | 0 |
| | Acarina 9 | | | Fungivore | 2 | 15 |
| | Acarina 14 | | | Unknown | 1 | 0 |
| | Acarina 15 | Ologamasidae | | Predator | 34 | 10 |
| | Acarina 16 | Phthiracaridae | | Detritivore | 6 | 2 |
| | Acarina 17 | | | Unknown | 5 | 0 |
| | Acarina 18 | | | Unknown | 1 | 0 |
| | Acarina 19 | | | Fungivore | 14 | 1 |
| | Acarina 20 | | Unknown | 1 | 0 | |
| | Acarina 21 | Acaridae | <i>Tyrophagus</i> sp. | Fungivore | 8 | 2 |
| | Acarina 22 | | | Predator | 2 | 5 |
| | Acarina 24 | Acaridae | <i>Tyrophagus putrescentiae</i> | Fungivore | 9 | 99 |
| | Acarina 25 | Bdellidae | | Predator | 1 | 1 |
| | Acarina 26 | | | Unknown | 1 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|---------------|---------------|---------------|--------------------------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Acarina cont. | Acarina 27 | Anystidae | <i>Anystis baccarum</i> | Unknown | 5 | 0 |
| | Acarina 28 | | | Unknown | 1 | 0 |
| | Acarina 29 | | | Unknown | 2 | 0 |
| | Acarina 30 | | | Unknown | 1 | 0 |
| | Acarina 31 | | | Predator | 1 | 4 |
| | Acarina 32 | | | Unknown | 2 | 1 |
| | Acarina 33 | | | Unknown | 3 | 0 |
| | Acarina 35 | | | Unknown | 1 | 0 |
| | Acarina 36 | | | Fungivore | 18 | 138 |
| | Acarina 37 | | | Fungivore | 5 | 7 |
| | Acarina 38 | Bdellidae | | Unknown | 1 | 0 |
| | Acarina 39 | | | Predator | 2 | 3 |
| | Acarina 40 | | | Unknown | 1 | 0 |
| | Acarina 41 | | | Unknown | 1 | 0 |
| | Acarina 42 | | | Fungivore | 5 | 4 |
| | Acarina 43 | Tenuipalpidae | | Unknown | 1 | 0 |
| | Acarina 44 | | | Herbivore | 1 | 3 |
| | Acarina 45 | | | Unknown | 2 | 0 |
| | Acarina 46 | | | Unknown | 1 | 0 |
| | Acarina 47 | Ascidae | <i>Proctolaelaps</i> sp. | Unknown | 1 | 0 |
| | Acarina 48 | | | Fungivore | 1 | 1 |
| | Acarina 49 | | | Unknown | 1 | 0 |
| | Acarina 50 | | | Unknown | 0 | 2 |
| | Acarina 51 | | | Unknown | 0 | 2 |
| | Acarina 52 | | | Unknown | 0 | 16 |
| | Acarina 53 | | | Unknown | 0 | 1 |
| | Acarina 54 | | | Unknown | 0 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|----------------------|---------------|--------------|---------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Acarina cont. | Acarina 55 | Ologamasidae | | Unknown | 0 | 1 |
| | Acarina 56 | | | Unknown | 0 | 1 |
| | Acarina 57 | | | Predator | 0 | 2 |
| | Acarina 58 | | | Unknown | 0 | 2 |
| | Acarina 59 | | | Unknown | 0 | 3 |
| | Acarina 60 | | | Unknown | 0 | 1 |
| | Acarina 61 | Neoliodidae | | Fungivore | 0 | 1 |
| | Acarina 62 | | | Unknown | 0 | 7 |
| | Acarina 63 | | | Predator | 0 | 1 |
| | Acarina 64 | | | Fungivore | 0 | 1 |
| | Acarina 65 | | | Unknown | 0 | 1 |
| | Acarina 66 | | | Unknown | 0 | 1 |
| Araneida | Araneida 1 | Araneidae | | Predator | 1 | 0 |
| | Araneida 2 | Araneidae | | Predator | 2 | 0 |
| | Araneida 3 | Araneidae | | Predator | 1 | 0 |
| | Araneida 4 | Araneidae | | Predator | 1 | 7 |
| | Araneida 5 | Araneidae | | Predator | 1 | 0 |
| | Araneida 6 | Araneidae | | Predator | 1 | 0 |
| | Araneida 7 | Araneidae | | Predator | 1 | 0 |
| | Araneida 8 | Araneidae | | Predator | 1 | 0 |
| | Araneida 9 | Araneidae | | Predator | 1 | 0 |
| | Araneida 10 | Araneidae | | Predator | 1 | 0 |
| | Araneida 11 | Araneidae | | Predator | 1 | 0 |
| | Araneida 12 | Araneidae | | Predator | 1 | 0 |
| | Araneida 13 | Araneidae | | Predator | 1 | 0 |
| | Araneida 14 | Araneidae | | Predator | 1 | 0 |
| | Araneida 15 | Araneidae | | Predator | 0 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-------------------------|--------------------|------------------------|---------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Araneida cont. | Araneida 16 | Araneidae | | Predator | 0 | 1 |
| | Araneida 17 | Araneidae | | Predator | 0 | 2 |
| | Araneida 18 | Araneidae | | Predator | 0 | 1 |
| | Araneida 19 | Araneidae | | Predator | 0 | 1 |
| Pseudoscorpiones | Pseudoscorpiones 1 | | | Predator | 2 | 0 |
| Amphipoda | Amphipoda 1 | Talitridae | | Unknown | 1 | 0 |
| | Amphipoda 2 | Talitridae | | Unknown | 0 | 41 |
| Annelida | Unknown 24 | | | Unknown | 3 | 3 |
| Blattaria | Blattaria 1 | | | Omnivore | 1 | 0 |
| Coleoptera | Coleoptera 1 | Brentidae | | Herbivore | 1 | 0 |
| | Coleoptera 2 | Corylophidae | | Fungivore | 18 | 19 |
| | Coleoptera 3 | Carabidae | | Detritivore | 3 | 0 |
| | Coleoptera 4 | Corylophidae | | Fungivore | 5 | 1 |
| | Coleoptera 5 | Curculionidae | | Herbivore | 1 | 0 |
| | Coleoptera 6 | Coccinellidae | | Predator | 1 | 3 |
| | Coleoptera 7 | Latridiidae | | Fungivore | 1 | 11 |
| | Coleoptera 9 | Chrysomelidae | | Herbivore | 2 | 0 |
| | Coleoptera 10 | Staphylinidae | | Unknown | 1 | 0 |
| | Coleoptera 11 | Corylophidae | | Fungivore | 1 | 3 |
| | Coleoptera 12 | Latridiidae | | Fungivore | 0 | 18 |
| | Coleoptera 13 | Staphylinidae | | Unknown | 0 | 2 |
| | Coleoptera 14 | Curculionidae | | Herbivore | 0 | 1 |
| | Coleoptera 15 | Tenebrionidae | | Scavenger | 0 | 1 |
| | Coleoptera 16 | Tenebrionidae | | Scavenger | 0 | 1 |
| | Coleoptera 17 | Scarabidae: Aphodiinae | | Dung | 0 | 2 |
| | Coleoptera 18 | Curculionidae | | Herbivore | 0 | 1 |
| | Coleoptera 19 | Curculionidae | | Herbivore | 0 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-------------------------|---------------------|---------------------------|---------|--------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Coleoptera cont. | Coleoptera 20 | Curculionidae: Scolytinae | | Wood boorers | 0 | 3 |
| | Coleoptera 72 | Latridiidae | | Fungivore | 0 | 1 |
| | Larvae 1 | Curculionidae | | Herbivore | 1 | 0 |
| | Larvae 24 | Curculionidae | | Herbivore | 0 | 6 |
| | Larvae 25 | Curculionidae | | Herbivore | 0 | 20 |
| | L.7: Coleoptera 72 | | | Unknown | 2 | 5 |
| | L.8: Coleoptera 73 | Staphylinidae | | Unknown | 1 | 0 |
| | L.10: Coleoptera 74 | | | Unknown | 1 | 0 |
| | L.18: Coleoptera 75 | | | Unknown | 0 | 1 |
| | L.21: Coleoptera 76 | Chrysomelidae | | Herbivore | 0 | 54 |
| | L.28: Coleoptera 77 | | | Unknown | 0 | 1 |
| | L.57: Coleoptera 78 | | | Unknown | 0 | 1 |
| | Unknown 10 | | | Unknown | 1 | 0 |
| | Unknown 12 | | | Unknown | 1 | 8 |
| | Unknown 14 | Corylophidae | | Fungivore | 6 | 6 |
| | Unknown 20 | Melyridae | Pupae | Predator | 2 | 4 |
| | Unknown 25 | | | Unknown | 2 | 22 |
| | Unknown 27 | Carabidae/Staphylidae | | Predator | 0 | 1 |
| Collembola | Collembola 1 | | | Detritivore | 2 | 1 |
| | Collembola 2 | | | Detritivore | 1 | 0 |
| | Collembola 3 | | | Detritivore | 1 | 0 |
| | Collembola 4 | | | Detritivore | 10 | 0 |
| | Collembola 5 | | | Detritivore | 1 | 0 |
| | Collembola 6 | | | Detritivore | 1 | 2 |
| | Collembola 7 | | | Detritivore | 1 | 0 |
| | Collembola 8 | | | Detritivore | 1 | 0 |
| | Collembola 9 | | | Detritivore | 2 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-----------------------|---------------|---------------|---------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Colombola cont | Collembola 10 | | | Detritivore | 2 | 0 |
| | Collembola 11 | | | Detritivore | 0 | 1 |
| | Collembola 12 | | | Detritivore | 0 | 1 |
| | Larvae 19 | | | Detritivore | 0 | 3 |
| | Unknown 7 | | | Detritivore | 1 | 0 |
| | Unknown 9 | | | Detritivore | 1 | 0 |
| | Unknown 23 | | | Detritivore | 1 | 0 |
| Diplura | Unknown 8 | Diplura | | Predator | 1 | 0 |
| | Unknown 11 | Diplura | | Predator | 1 | 13 |
| Diptera | Diptera 2 | Psychodidae | | Non-feeding | 1 | 0 |
| | Diptera 1 | Lauxaniidae | | Unknown | 1 | 0 |
| | Diptera 10 | Chloropidae | | Unknown | 1 | 0 |
| | Diptera 11 | Tephritidae | | Unknown | 4 | 13 |
| | Diptera 12 | | | Unknown | 1 | 0 |
| | Diptera 14 | Phoridae | | Detritivore | 1 | 0 |
| | Diptera 4 | Cecidomyiidae | | Unknown | 11 | 3 |
| | Diptera 5 | Agromyzidae | | Herbivore | 1 | 0 |
| | Diptera 6 | Tephritidae | | Herbivore | 1 | 0 |
| | Diptera 7 | Phoridae | | Detritivore | 1 | 0 |
| | Diptera 8 | Cecidomyiidae | | Unknown | 4 | 0 |
| | Diptera 9 | Cecidomyiidae | | Unknown | 1 | 1 |
| | Diptera 13 | Lauxaniidae | | Unknown | 1 | 0 |
| | Diptera 15 | | | Unknown | 1 | 0 |
| | Diptera 16 | Cecidomyiidae | | Unknown | 1 | 0 |
| | Diptera 17 | Sciaridae | | Detritivore | 1 | 0 |
| | Diptera 18 | Chironomidae | | Unknown | 1 | 0 |
| | Diptera 19 | Psychodidae | | Non-feeding | 4 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|----------------------|---------------|---------------|---------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Diptera cont. | Diptera 20 | Cecidomyiidae | | Unknown | 3 | 0 |
| | Diptera 21 | Lauxaniidae | | Unknown | 1 | 13 |
| | Diptera 22 | Chloropidae | | Unknown | 1 | 38 |
| | Diptera 23 | Cecidomyiidae | | Unknown | 7 | 2 |
| | Diptera 24 | Chironomidae | | Unknown | 2 | 1 |
| | Diptera 25 | Phoridae | | Detritivore | 1 | 0 |
| | Diptera 26 | Milichiidae | | Unknown | 0 | 10 |
| | Diptera 27 | Chloropidae | | Unknown | 0 | 14 |
| | Diptera 28 | Chloropidae | | Unknown | 0 | 2 |
| | Diptera 29 | Lauxaniidae | | Unknown | 0 | 3 |
| | Diptera 30 | Empididae | | Unknown | 0 | 1 |
| | Larvae 2 | Cecidomyiidae | | Unknown | 4 | 3 |
| | Larvae 3 | Cecidomyiidae | | Unknown | 417 | 44 |
| | Larvae 4 | Cecidomyiidae | | Unknown | 431 | 41 |
| | Larvae 6 | Cecidomyiidae | | Unknown | 15 | 0 |
| | Larvae 7 | Cecidomyiidae | | Unknown | 1 | 0 |
| | Larvae 8 | | | Unknown | 1 | 0 |
| | Larvae 10 | Cecidomyiidae | | Bacteria | 1 | 0 |
| | Larvae 13 | Syrphidae | | Unknown | 2 | 0 |
| | Larvae 14 | | | Unknown | 1 | 0 |
| | Larvae 15 | | | Unknown | 0 | 1 |
| | Larvae 16 | Cecidomyiidae | | Unknown | 0 | 3 |
| | Larvae 17 | Stratiomyidae | | Unknown | 0 | 73 |
| | Larvae 23 | Syrphidae | | Predator | 0 | 1 |
| | Diptera 31 | Nematocera | | Unknown | 2 | 0 |
| | Unknown 18 | Cecidomyiidae | | Unknown | 20 | 0 |
| Gastropoda | Gastropoda 1 | | | Unknown | 5 | 5 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-------------------------|---------------|-----------|---------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Gastropoda cont. | Gastropoda 2 | | | Unknown | 5 | 2 |
| | Gastropoda 3 | | | Unknown | 0 | 50 |
| | Gastropoda 4 | | | Unknown | 0 | 1 |
| Hemiptera | Aphididae 1 | Aphididae | | Herbivore | 5 | 109 |
| | Aphididae 10 | Aphididae | | Herbivore | 18 | 0 |
| | Aphididae 11 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 12 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 13 | Aphididae | | Herbivore | 16 | 66 |
| | Aphididae 14 | Aphididae | | Herbivore | 3 | 0 |
| | Aphididae 15 | Aphididae | | Herbivore | 2 | 1 |
| | Aphididae 16 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 17 | Aphididae | | Herbivore | 2 | 1 |
| | Aphididae 18 | Aphididae | | Herbivore | 704 | 72 |
| | Aphididae 19 | Aphididae | | Herbivore | 32 | 0 |
| | Aphididae 2 | Aphididae | | Herbivore | 4 | 0 |
| | Aphididae 20 | Aphididae | | Herbivore | 32 | 1 |
| | Aphididae 21 | Aphididae | | Herbivore | 108 | 15 |
| | Aphididae 22 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 23 | Aphididae | | Herbivore | 37 | 0 |
| | Aphididae 24 | Aphididae | | Herbivore | 269 | 10 |
| | Aphididae 25 | Aphididae | | Herbivore | 249 | 1 |
| | Aphididae 26 | Aphididae | | Herbivore | 676 | 25 |
| | Aphididae 27 | Aphididae | | Herbivore | 334 | 36 |
| | Aphididae 28 | Aphididae | | Herbivore | 307 | 23 |
| | Aphididae 29 | Aphididae | | Herbivore | 22 | 0 |
| | Aphididae 3 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 30 | Aphididae | | Herbivore | 12 | 6 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|------------------------|-------------------|---------------|---------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Hemiptera cont. | Aphididae 31 | Aphididae | | Herbivore | 18 | 8 |
| | Aphididae 32 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 33 | Aphididae | | Herbivore | 2 | 19 |
| | Aphididae 34 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 35 | Aphididae | | Herbivore | 16 | 2 |
| | Aphididae 36 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 37 | Aphididae | | Herbivore | 1 | 7 |
| | Aphididae 38 | Aphididae | | Herbivore | 14 | 0 |
| | Aphididae 41 | Aphididae | | Herbivore | 14 | 4 |
| | Aphididae 47 | Aphididae | | Herbivore | 0 | 9 |
| | Aphididae 4 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 5 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 6 | Aphididae | | Herbivore | 17 | 0 |
| | Aphididae 7 | Aphididae | | Herbivore | 16 | 0 |
| | Aphididae 8 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 9 | Aphididae | | Herbivore | 1 | 0 |
| | Aphididae 39 | Aphididae | | Herbivore | 12 | 0 |
| | Aphididae 40 | Aphididae | | Herbivore | 12 | 0 |
| | Aphididae 42 | Aphididae | | Herbivore | 48 | 0 |
| | Aphididae 43 | Aphididae | | Herbivore | 15 | 0 |
| | Aphididae 44 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 45 | Aphididae | | Herbivore | 2 | 0 |
| | Aphididae 46 | Aphididae | | Herbivore | 1 | 0 |
| | Au: Heteroptera 1 | Tropiduchidae | | Herbivore | 1 | 0 |
| | Auchenorrhyncha 2 | Cicadellidae | | Herbivore | 1 | 0 |
| | Auchenorrhyncha 3 | Cicadellidae | | Herbivore | 1 | 0 |
| | Auchenorrhyncha 4 | Cicadellidae | | Herbivore | 2 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-----------------|------------------------|------------------|------------------------------|------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Hemiptera cont. | Auchenorrhyncha 5 | Cicadellidae | | Herbivore | 4 | 3 |
| | Au: Heteroptera 9 | Fulgoroidea | | Herbivore | 1 | 4 |
| | Au: Heteroptera 10 | Flatidae | | Herbivore | 0 | 2 |
| | Au: Heteroptera 11 | Flatidae | | Herbivore | 0 | 1 |
| | Au: Heteroptera 12 | Fulgoroidea | | Herbivore | 0 | 2 |
| | Au: Heteroptera 7 | Delphacidae | | Herbivore | 1 | 7 |
| | Auchenorrhyncha 8 | Cicadellidae | | Herbivore | 1 | 11 |
| | Heteroptera 1 | Lygaeoidea | | Herbivore | 106 | 88 |
| | Heteroptera 2 | Miridae | | Herbivore | 87 | 5 |
| | Heteroptera 3 | Orsillidae | <i>Nysius clevelandensis</i> | Herbivore | 6 | 0 |
| | Heteroptera 4 | Miridae | <i>Creontiades</i> sp. | Herbivore | 1 | 0 |
| | Heteroptera 5 | Miridae | | Herbivore | 2 | 0 |
| | Heteroptera 8 | Reduviidae | | Generalist | 1 | 0 |
| | Heteroptera 10 | Thaumastocoridae | | Tourist | 1 | 0 |
| | Het: Sternorrhyncha 12 | Coccoidea | | Herbivore | 0 | 1 |
| | Het: Sternorrhyncha 14 | Coccoidea | | Herbivore | 0 | 7 |
| | Heteroptera 15 | Reduviidae | | Predator | 0 | 1 |
| | Heteroptera 16 | Miridae | | Herbivore | 0 | 2 |
| | Het: Sternorrhyncha 17 | Coccoidea | | Herbivore | 0 | 1 |
| | Hy. Hemiptera 37 | Psyllidae | | Herbivore | 0 | 1 |
| | Unknown 1 | Aphididae | | Herbivore | 1 | 0 |
| | Unknown 13 | Cicadellidae | | Herbivore | 3 | 5 |
| | Unknown 15 | | | Herbivore | 1 | 8 |
| | Unknown 17 | | | Unknown | 4 | 0 |
| | Unknown 21 | | | Herbivore | 1 | 5 |
| | Unknown 30 | | | Herbivore | 0 | 2 |
| | Unknown 31 | | | Herbivore | 0 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|---------------|-----------------|--------------------------|------------------------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Unknown cont. | Unknown 32 | | | Herbivore | 0 | 1 |
| Hymenoptera | Hymenoptera D.3 | Braconidae | | Parasite | 0 | 1 |
| | Hymenoptera 1 | Eulophidae | | Unknown | 1 | 0 |
| | Hymenoptera 2 | Braconidae | | Parasite | 4 | 0 |
| | Hymenoptera 3 | Mymaridae | | Parasite | 2 | 0 |
| | Hymenoptera 5 | Scelionidae | | Parasite | 1 | 0 |
| | Hymenoptera 6 | Braconidae | | Parasite | 1 | 0 |
| | Hymenoptera 7 | Pteromalidae | | Parasite | 2 | 0 |
| | Hymenoptera 8 | Platygasteridae | | Parasite | 2 | 3 |
| | Hymenoptera 9 | Eurytomidae | | Unknown | 6 | 1 |
| | Hymenoptera 11 | Mymaridae | | Parasite | 1 | 0 |
| | Hymenoptera 12 | Braconidae | | Parasite | 1 | 0 |
| | Hymenoptera 13 | Braconidae | | Parasite | 1 | 0 |
| | Hymenoptera 14 | Diapriidae | | Parasite | 2 | 0 |
| | Hymenoptera 15 | Torymidae: Megastigminae | <i>Megastigmus</i> sp. | Herbivore | 3 | 0 |
| | Hymenoptera 16 | Braconidae | | Parasite | 3 | 1 |
| | Hymenoptera 17 | Eulophidae | | Parasite | 1 | 0 |
| | Hymenoptera 18 | Eulophidae | | Unknown | 1 | 0 |
| | Hymenoptera 19 | Eulophidae | | Unknown | 1 | 0 |
| | Hymenoptera 20 | Mymaridae | | Parasite | 1 | 0 |
| | Hymenoptera 21 | Eulophidae | | Unknown | 1 | 0 |
| | Hymenoptera 23 | Platygastridae | | Parasite | 2 | 0 |
| | Hymenoptera 24 | Braconidae | | Parasite | 1 | 0 |
| | Hymenoptera 25 | Mymaridae | | Parasite | 1 | 0 |
| | Hymenoptera 26 | Mymaridae | <i>Mymar</i> sp. | Parasite | 1 | 0 |
| | Hymenoptera 27 | Figitidae | | Parasite | 1 | 0 |
| | Hymenoptera 28 | Braconidae | | Parasite | 6 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|------------------------------------|-----------------|-----------------|--------------------------|------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Hymenoptera cont. | Hymenoptera 29 | Braconidae | | Parasite | 1 | 0 |
| | Hymenoptera 30 | Aphelinidae | | Parasite | 1 | 0 |
| | Hymenoptera 32 | Pteromalidae | | Parasite | 1 | 0 |
| | Hymenoptera 33 | Pteromalidae | | Parasite | 1 | 1 |
| | Hymenoptera 34 | Braconidae | | Parasite | 1 | 1 |
| | Hymenoptera 35 | Eulophidae | | Unknown | 2 | 0 |
| | Hymenoptera 36 | Eupelmidae | | Parasite | 0 | 1 |
| | Hymenoptera 38 | Encyrtidae | | Parasite | 0 | 2 |
| | Hymenoptera 39 | Pteromalidae | | Parasite | 0 | 3 |
| | Hymenoptera 40 | Scelionidae | | Parasite | 0 | 1 |
| | Hymenoptera 41 | Scelionidae | | Parasite | 0 | 3 |
| | Hymenoptera 42 | Mymaridae | | Parasite | 0 | 2 |
| | Hymenoptera 43 | Platygasteridae | | Parasite | 0 | 2 |
| | Hymenoptera 44 | Eulophidae | | Unknown | 0 | 19 |
| | Hymenoptera 59 | Ichneumonidae | | Parasite | 1 | 0 |
| | Hymenoptera 106 | Encyrtidae | | Parasite | 1 | 0 |
| | Formicidae 1 | Myrmicinae | <i>Solenopsis</i> sp. | Omnivore | 1 | 16 |
| | Formicidae 2 | Ponerinae | <i>Rhytidoponera</i> sp. | Omnivore | 1 | 0 |
| | Formicidae 3 | Myrmicinae | <i>Pheidole</i> sp. | Omnivore | 1 | 0 |
| | Formicidae 4 | Dolichoderinae | <i>Ochetellus</i> sp. | Predator | 2 | 24 |
| | Formicidae 5 | Formicinae | <i>Paratrechina</i> sp. | Generalist | 3 | 0 |
| | Formicidae 6 | Dolichoderinae | <i>Ochetellus</i> sp. | Predator | 1 | 6 |
| | Formicidae 7 | Dolichoderinae | <i>Ochetellus</i> sp. | Predator | 1 | 1 |
| | Formicidae 8 | Ponerinae | <i>Rhytidoponera</i> sp. | Omnivore | 2 | 0 |
| | Formicidae 9 | Myrmicinae | <i>Pheidole</i> sp. | Omnivore | 1 | 1 |
| | Formicidae 10 | Myrmicinae | <i>Pheidole</i> sp. | Omnivore | 0 | 1 |
| | Formicidae 11 | Myrmicinae | <i>Pheidole</i> sp. | Omnivore | 0 | 1 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|------------------------------|----------------|------------------------|--------------------------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Hymenoptera cont. | Formicidae 12 | Myrmicinae | <i>Crematogaster</i> sp. | Predator | 0 | 1 |
| | Formicidae 13 | Myrmicinae | <i>Metanopius</i> sp. | Scavenger | 0 | 2 |
| | Formicidae 14 | Myrmicinae | <i>Monomorium</i> sp. | Omnivore | 0 | 2 |
| | Formicidae 15 | Dolichoderinae | <i>Tapinoma</i> sp. | Scavenger | 0 | 1 |
| | Formicidae 16 | Dolichoderinae | <i>Tapinoma</i> sp. | Scavenger | 0 | 1 |
| | Formicidae 17 | Myrmicinae | <i>Pheidole</i> sp. | Omnivore | 0 | 3 |
| | Larvae 5 | Pupae | | Unknown | 1 | 0 |
| | Larvae 9 | Scelionidae | | Parasite | 2 | 0 |
| | Larvae 11 | Hymenoptera | | Unknown | 1 | 0 |
| | Larvae 12 | Hymenoptera | | Parasite | 2 | 0 |
| | Larvae 21 | Scelionidae | | Parasite | 0 | 3 |
| | Larvae 38 | Braconidae | | Parasite | 0 | 0 |
| | Unknown 28 | | | Parasite | 0 | 1 |
| Isopoda | Isopoda 1 | Isopoda:Oniscidea | | Detritivore | 6 | 1 |
| | Isopoda 2 | Isopoda:Oniscidea | | Detritivore | 5 | 0 |
| | Isopoda 3 | Isopoda:Oniscidea | | Detritivore | 3 | 0 |
| Isopoda cont. | Isopoda 4 | Isopoda:Oniscidea | | Detritivore | 0 | 28 |
| Lepidoptera | Lepidoptera 1 | Pyraloidea | | Herbivore | 1 | 47 |
| | Lepidoptera 2 | Pyraloidea | | Herbivore | 145 | 73 |
| | Lepidoptera 3 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Herbivore | 1 | 1 |
| | Lepidoptera 4 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Herbivore | 2 | 0 |
| | Lepidoptera 5 | Pyraloidea | | Herbivore | 1 | 0 |
| | Lepidoptera 6 | Lepidoptera | | Herbivore | 1 | 0 |
| | Lepidoptera 13 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Herbivore | 1 | 0 |
| | Lepidoptera 14 | Noctuidae | | Herbivore | 1 | 0 |
| | Lepidoptera 15 | Tortricidae | | Herbivore | 1 | 0 |
| | Lepidoptera 16 | Tortricidae | | Herbivore | 1 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|--------------------------|-------------------|-------------------------|-----------------------------------|-------------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Lepidoptera cont. | Lepidoptera 17 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Herbivore | 0 | 1 |
| | Lepidoptera 20 | Arctiidae: Arctiinae | <i>Nyctemera</i> sp. | Herbivore | 0 | 20 |
| | Lepidoptera 22 | Pyraloidea | | Herbivore | 0 | 6 |
| | Lepidoptera 23 | Tortricidae | | Herbivore | 0 | 1 |
| | Lepidoptera 24 | Arctiidae: Ctenuchinae | <i>Amata</i> sp. | Herbivore | 0 | 12 |
| | Lepidoptera 26 | Pyralidae: Phycitinae | | Herbivore | 0 | 2 |
| | Unknown 19 | | Pupae | Herbivore | 1 | 0 |
| Myriopoda | L.12: Myriapoda 1 | Myriapoda | | Unknown | 1 | 0 |
| | L.25: Myriapoda 2 | Diplopoda | | Detritivore | 0 | 3 |
| | Larvae 22 | Diplopoda | | Detritivore | 0 | 1 |
| Neuroptera | C: Neuroptera 8 | Neuroptera | | Predator | 1 | 0 |
| | Unknown 2 | Hemerobiidae | | Predator | 1 | 0 |
| | Unknown 3 | Hemerobiidae | | Predator | 1 | 0 |
| Orthoptera | Orthoptera 1 | Acrididae: Catantopinae | | Herbivore | 2 | 0 |
| | Orthoptera 2 | Gryllacrididae | | Omnivore | 1 | 0 |
| Pscoptera | Pscoptera 1 | | | Detritivore | 1 | 3 |
| | Pscoptera 2 | | | Detritivore | 1 | 4 |
| | Pscoptera 3 | | | Detritivore | 2 | 4 |
| | Pscoptera 4 | | | Detritivore | 0 | 11 |
| | Unknown 5 | | | Detritivore | 3 | 0 |
| | Unknown 6 | | | Detritivore | 3 | 0 |
| | Unknown 29 | | | Detritivore | 0 | 2 |
| Thysanoptera | Thysanoptera 1 | Thripidae: Thripinae | <i>Pseudanaphothrips achaetus</i> | Herbivore | 13 | 10 |
| | Thysanoptera 10 | | Neso larvae | Unknown | 1 | 31 |
| | Thysanoptera 11 | | Neso larvae | Unknown | 100 | 296 |
| | Thysanoptera 12 | Thripidae: Thripinae | <i>Psudonathothrips</i> sp. | Herbivore | 1 | 0 |
| | Thysanoptera 13 | | | Unknown | 3 | 0 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-----------------------|-----------------|--------------------------------------------|-----------------------------------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Thysanoptera cont. | Thysanoptera 14 | Phlaeothripidae: Idolothripinae | <i>Nesothrips</i> sp. | Fungivore | 1 | 0 |
| | Thysanoptera 15 | | | Unknown | 1 | 0 |
| | Thysanoptera 16 | | | Unknown | 3 | 0 |
| | Thysanoptera 17 | | Neso larvae | Unknown | 2 | 5 |
| | Thysanoptera 18 | | Neso larvae | Unknown | 14 | 25 |
| | Thysanoptera 19 | Phlaeothripidae: Phlaeothripinae | | Fungivore | 1 | 0 |
| | Thysanoptera 20 | | | Unknown | 1 | 0 |
| | Thysanoptera 21 | | | Unknown | 2 | 0 |
| | Thysanoptera 22 | Phlaeothripidae: Idolothripinae:Nesothrips | | Fungivore | 1 | 4 |
| | Thysanoptera 23 | Thripidae: Thripinae | <i>Thrips imaginis</i> | Herbivore | 2 | 11 |
| | Thysanoptera 2 | Thripidae: Thripinae | <i>Pseudanaphothrips achaetus</i> | Herbivore | 57 | 116 |
| | Thysanoptera 3 | Panchaetothripinae | <i>Bhattithrips</i> sp. | Herbivore | 29 | 8 |
| | Thysanoptera 4 | | | Unknown | 1 | 0 |
| | Thysanoptera 5 | | | Unknown | 8 | 0 |
| | Thysanoptera 6 | | Larvae | Unknown | 3 | 0 |
| | Thysanoptera 7 | | | Unknown | 2 | 0 |
| | Thysanoptera 8 | | | Unknown | 9 | 0 |
| | Thysanoptera 9 | | Neso larvae | Unknown | 12 | 0 |
| | Thysanoptera 24 | | | Unknown | 1 | 0 |
| | Thysanoptera 25 | Thripidae | Larvae | Herbivore | 2 | 0 |
| | Thysanoptera 26 | | | Unknown | 2 | 0 |
| | Thysanoptera 27 | | | Unknown | 1 | 0 |
| | Thysanoptera 28 | | | Unknown | 3 | 0 |
| | Thysanoptera 29 | | | Unknown | 1 | 0 |
| | Thysanoptera 30 | | | Unknown | 1 | 0 |
| | Thysanoptera 31 | | | Unknown | 1 | 0 |
| | Thysanoptera 32 | Phlaeothripidae: Idolothripinae | <i>Nesothrips</i> sp. | Fungivore | 5 | 9 |

| Group | Morphospecies | Family | Species | Guild | Abundance | |
|-------------------------------|-----------------|---------------------------------|--------------------------------------------|-----------|----------------------------|-------------------------|
| | | | | | <i>S. madagascariensis</i> | <i>S. pinnatifolius</i> |
| Thysanoptera cont. | Thysanoptera 33 | Thripidae | Pupae | Unknown | 1 | 1 |
| | Thysanoptera 34 | | Neso larvae | Unknown | 0 | 7 |
| | Thysanoptera 35 | Thripidae: Thripinae | <i>Thrips</i> sp. | Herbivore | 0 | 7 |
| | Thysanoptera 36 | Phlaeothripidae: Idolothripinae | <i>Nesothrips</i> sp. | Fungivore | 0 | 10 |
| | Thysanoptera 37 | Thripidae | | Herbivore | 0 | 3 |
| | Thysanoptera 38 | Phlaeothripidae: Idolothripinae | <i>Nesothrips</i> sp. | Fungivore | 0 | 18 |
| | Thysanoptera 39 | Thripidae | Larvae | Herbivore | 0 | 3 |
| | Thysanoptera 40 | | | Unknown | 0 | 2 |
| | Thysanoptera 41 | | | Unknown | 0 | 2 |
| | Thysanoptera 42 | Panchaetothripinae | <i>Bhattithrips</i> sp. Larvae late instar | Herbivore | 0 | 4 |
| | Thysanoptera 43 | | | Unknown | 0 | 2 |
| | Unknown 16 | | | Unknown | 1 | 9 |
| Unknown | Heteroptera 7 | Unknown | | Unknown | 1 | 0 |
| | L.9: Unknown 33 | Unknown | | Unknown | 4 | 0 |

