The role of non-native plants in the integration of non-native phytophagous invertebrates in native food webs

Submitted by Sally Luker, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences in August 2020.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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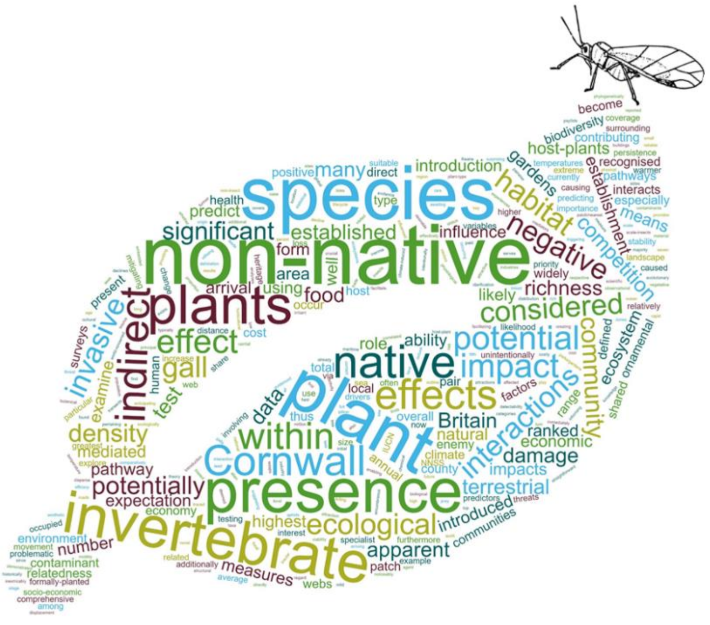

Abstract

This thesis brings together a series of studies, examining the role of non-native plants in the integration of non-native invertebrates in native food webs. I use data from comprehensive surveys of formally-planted gardens to investigate the efficacy of straightforward measures of non-native plant presence and/or landscape parameters, as reliable predictors of non-native invertebrate presence, finding that non-native invertebrate richness increases with non-native plant species richness, with invertebrates showing a clear preference for woody plants. I then use the context of metapopulation theory to explore the facilitative role of non-native plants in the ability of a non-native invertebrate to persist within a community, finding that where host-plant habitat patches are closer together, the likelihood of a patch being occupied is greater, especially if the patch is occupied but that this effect is not universal, with species-specific effects present also. I then explore the potential for apparent competition, in the form of negative indirect interactions between native and non-native plants mediated by a shared invertebrate enemy, with the indirect interactions biased by plant relatedness, finding that phylogenetically ranked pairwise native/non-native plant interactions are weakly correlated with observed shared invertebrate interactions, while a significant Mantel test result indicates a significant potential for apparent competition. Finally, I test for detectability of apparent competition in a gall wasp community, finding no evidence of apparent competition but potential evidence for the unexpected occurrence of apparent mutualism. Collectively, these findings provide original insight into how non-native plants and non-native invertebrates interact in an ecological community, and how these interactions help to structure the community. Additionally, they have implications for non-native invertebrate species management, from the practical application of ground-level planting decisions to the development of reliable predictive tools.

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Author's Declaration

This work, including data collection, analysis, interpretation and writing is my own. My supervisors have provided feedback on the structure and interpretation of all chapters.

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Chapter 1: General Introduction

1.1 Non-native species

Non-native species, or ‘alien species’, are defined as taxa which occur outside of their past/present natural range, introduced either intentionally or unintentionally via anthropogenic activity (CBD 1992; IUCN 2000). A non-native species is defined as ‘invasive’ if it becomes established or has the ability to become established, acting as an agent of change, causing damage to the environment, economy or human health, and/or threatens native biodiversity (CBD 1992; IUCN 2000; Roy *et al*. 2012, 2014). Globally, the impacts of invasive species are considered among the greatest threats to ecosystem stability, ranked in the top five drivers of biodiversity loss (Mack *et al*. 2000; Sala *et al*. 2000; Duraiappah *et al.* 2005).

Ecologically, non-native species integrate in food webs (interaction networks) as predators, prey, parasites, as vectors of disease, or as competitors for resources (e.g. Vitousek 1990; Crooks 2002; Strauss *et al.* 2006). The effect of a non-native invertebrate within a food web can be positive or negative (e.g. Simberloff & Von Holle 1999; Carlsson *et al*. 2009; Sanders & van Veen 2012; Vitule er al. 2012). Typically, negative effects occur as a consequence of biological homogenisation, caused by displacement of native communities following the arrival of a more dominant species, such as a species that has arrived without any natural enemies (e.g. Mack *et al*. 2000; Crooks 2002; White *et al.* 2006; Altieri *et al.* 2010; Helden *et al.* 2012). This, in turn, can lead to further ecosystem modification, creating cascade effects, and potentially triggering rapid evolutionary responses in native species (e.g. Strauss *et al*. 2006 and references therein but see Vellend *et al*. 2007).

As well as the ecological impacts of the arrival and potential subsequent establishment of non-native species, the economic impact of their presence is high. Economic impacts might include the financial cost of implementing chemical or bio-control measures to reduce or eliminate the species (Williams *et al*. 2010), or the direct cost of damage caused by the species’ presence, such as structural damage to buildings, and in the case of invertebrate phytophagous species, physiological damage to host plant or financially costly aesthetic damage to a horticultural display (e.g. Smith *et al.* 2007).

Whether or not the species is considered invasive, once introduced, there is a reasonable likelihood that a non-native species will establish and subsequently disperse within the environment, either through natural means or via further human-assisted movement (e.g. Kenis *et al*. 2007; Hulme *et al.* 2008), and as such, the full impact of the introduction of a non-native species might not be seen until sometime in the future (e.g. Crooks 2005; Strauss *et al*. 2006).

1.2 Non-native invertebrate species in Britain

In 2014, 1,952 non-native species were considered as established in Britain (Roy *et al*. 2014), with the annual cost of invasive species to the British economy currently given as £1.8 billion (House of Commons Environmental Audit Committee 2019). Of these established species, after higher plants, insects and non-insect invertebrates were the most numerous (combined total 502), with c.80% (399) occurring in the terrestrial environment, of which c.30% are deemed to have a negative ecological and/or socio-economic impact. While the majority of non-native species in Britain are thus not considered invasive, for those that do have a significant ecological and/or socio-economic (human) impact (notably negative economic impact or threat to human health), their presence is usually of significant encumbrance. For example, the arrival and subsequent establishment of the Harlequin Ladybird *Harmonia axyridis* in 2004 has been demonstrated as directly contributing to declines in native ladybird species (Brown & Roy 2018), while the Oak Processionary Moth *Thaumetopoea processionea* is recognised as causing severe defoliation of *Quercus* spp., reducing tree viability, and potentially contributing to oak decline, as well as being a health hazard to those who come into contact with the caterpillar's irritant hairs (Evans 2007; EFSA 2009) and/or socio-economic impact (Roy *et al*. 2012).

1.3 The role of horticulture/ornamental plant trade in the introduction and establishment of non-native terrestrial invertebrates

Anthropogenic global movement of plants and vegetative material is now widely accepted to be the principal means of introduction of non-native terrestrial invertebrate species, with many phytophagous invertebrates, especially those of low motility, such as aphids, psyllids and scale-insects, introduced unintentionally, arriving on ornamental plants, often as an undetected contaminant (Levine & D'Antonio 2003; Brockerhoff *et al.* 2006; Jones & Baker 2007; Kenis *et al.* 2007; Smith *et al.* 2005, 2007; Brasier 2008; Hulme *et al.* 2008; Roy *et al.* 2012, 2014; Bergey *et al.* 2014; Turbelin *et al*. 2016; NNSS 2019). Unsurprisingly, in their analyses of introduction pathways, NNSS (2019) found the ‘ornamental plant contaminant’ pathway to be the fifth highest out of 38 pathway categories with regard to the total number of non-native species introduced but the third highest for impact, with 9% of plant contaminants since 1950 considered ecologically and/or economically damaging. This is the highest pathway involving terrestrial invertebrates, with the ornamental plant contaminant pathway ranked first for priority pathways involving terrestrial invertebrates, and third overall in recommendations for ‘priority pathways’ management in the UK.

As an organism that feeds on one or more plants at any stage in its lifecycle, the persistence of a phytophagous invertebrate species is inextricably linked to the presence of a suitable host-plant. For a non-native phytophagous species, a particular non-native plant could be the initial means of arrival in a novel ecosystem, with the plant’s presence and/or the presence of other suitable host-plants in a community fundamental to how the invertebrate interacts within that community, and whether or not it will become established. Measures of plant presence (e.g. presence/absence, area coverage), and factors such as plant type, plant origin and relatedness to other plants present, as well as broader geographical factors (location, habitat type, distance from other plants, roads, sea, etc.), all have the potential to be used as predictors of invertebrate presence.

Here, using observational field data and utilising a number of statistical methods, I examine the role of non-native plants in both facilitating the establishment and persistence of non-native phytophagous invertebrates and as mediators in indirect interactions, using ecological communities within Cornwall, UK as study sites.

1.4 Non-native phytophagous invertebrates in Cornwall, UK

Cornwall is a long, effectively insular administrative county in the extreme southwest of the British Isles, bordered in the east by the River Tamar, which serves as both a physical and administrative boundary between Cornwall and the neighbouring county of Devon. It covers an area of 3,546 sq. km, with 697 km of coastline

The climate of Cornwall is Oceanic (maritime), meaning that it typically experiences a relatively narrow annual temperature range, with mild winters and cool summers, and with comparatively few occurrences of extreme temperatures. Hours of sunshine number more than the national average, and annual rainfall is slightly higher than average (www.metoffice.gov.uk). With its extensive coastline, Cornwall is noticeably affected by the presence of the Gulf Stream, which provides warmer waters and warmer air temperatures. Cornwall's climate, and in particular its associated microclimate, is especially conducive to the success of many non-native plant species that are unable to grow and prosper elsewhere in Britain – often unusual plants that are considered of botanical interest, desirable, attractive and/or rare (e.g. Pett 2006; Gamble 2014; Hubbard 2017). Furthermore, the effect of climate change at a local scale has been evidenced in shifting plant communities (Maclean *et al*. 2015; Kosanic *et al*. 2018), suggesting that the overall presence of non-native plants is likely to increase as a consequence of climate-induced range expansion (e.g. Clements & Ditommaso 2011).

Tourism is an economic mainstay of Cornwall, and is considered one of the county's 'bedrock' industries, providing over 10% of the county's total Gross Value Added (GVA) – the highest ranked UK region in its importance to the local economy (Cornwall Council 2013). Playing a significant role in the local tourism industry is the county's rich, cultural heritage. Landed estates, botanically significant gardens and world-renowned attractions, many of which were borne from the results of Victorian plant hunting expeditions, play an important role in this heritage. For example, in 2018, The Eden Project was the 13th most visited paid England attraction, with over 1 million visitors (VisitEngland 2019), and 35 of Cornwall's parks/gardens are granted listed status by Historic England as being historically significant, with 2 being Grade I listed as being 'of exceptional interest' (https://historicengland.org.uk). Similarly, Cornwall is home also to many smaller public/municipal gardens, specialist plant nurseries and other related enterprises. It is therefore to be expected that a significant number of non-native phytophagous invertebrates are now present in the county, many of which are firsts for Britain (e.g. *Powellia vitreoradiata* (St. Mawes), *Plagiotrochus quercusilicis*, *Agonoscena targionii* and *Coccus viridis* (Eden Project, St. Austell), *Acanthoxyla inermis* (Treseders Nursery, Truro), and *Cacopsylla fatsiae*/*Psylla tetrapanaxae* (species awaiting clarification) (Morrab Gardens, Penzance but likely source is a nearby nursery), and all of which can be traced to the importation of plants from overseas.

1.5 Thesis outline

Given that with any non-native invertebrate, there exists the potential for a negative impact, which might or might not be immediately recognised, the ability to predict how a non-native phytophagous invertebrate interacts within an ecological community, and how these interactions might be influenced by non-native plant presence is crucial in terms of anticipating and/or mitigating any impact. With species embedded in food webs, there is potential for both direct and indirect effects to occur; however, while direct effects are widely reported, indirect effects seem less well-studied, and it is likely that their presence is potentially being overlooked (e.g. White *et al*. 2006).

Here, I seek to examine the role of non-native plants in the integration of non-native phytophagous invertebrates in native food webs, and to find evidence in support of the presence of indirect interactions, as indirect effects mediated by a non-native invertebrate.

In Chapter 2, with the expectation that phytophagous invertebrate species richness is correlated with plant species richness (e.g. Moeed & Meads 1985, 1992; Crisp *et al*. 1998; Unsicker *et al*. 2006), I investigate the efficacy of straightforward measures of non-native plant presence and/or landscape parameters, as well as surrounding land use, as reliable predictors of non-native invertebrate presence. Using data from comprehensive surveys of formally-planted gardens in West Cornwall, I test for a positive relationship between non-native plant species richness and non-native invertebrate species richness as a means of predicting non-native invertebrate richness within an ecological community. Furthermore, I explore the influence of plant type, plant area coverage and level of plant presence in predicting non-native invertebrate presence. Additionally, I examine the effects of landscape variables, such as size, age and surrounding landcover, and how they could potentially influence the non-native plant effects.

In Chapter 3, with the expectation that proximity of a habitat patch, especially if already occupied by the focal invertebrate species, will predict invertebrate species presence (e.g. MacArthur & Wilson 1967; Prugh *et al*. 2008; reviewed Prugh 2009), I use metapopulation theory to examine how non-native plants facilitate the ability of a non-native invertebrate to persist within a community, thus enabling it to potentially increase in population size to become problematic. Using data pertaining to the distribution of seven specialist non-native invertebrates and their respective host-plants (the latter as potential habitat patches) within a defined geographical area, I test if patch occupancy can be predicted using measures of nearest habitat patch/nearest occupied habitat patch, strengthened by the effect of additional habitat variables, such as distance from sea and habitat type.

In Chapter 4, with the expectation that the more closely related a plant pair, the more likely it is that they will share one or more common enemy (e.g. Gilbert & Webb 2007; Dawson *et al*. 2009; Ness *et al*. 2011), I examine the potential for apparent competition in the form of enemy-mediated negative indirect effects, by testing if phylogenetic relatedness of a native/non-native plant pair can predict the likelihood that the pair will share a natural enemy. Using data from comprehensive surveys of formally-planted gardens in West Cornwall, I correlate phylogenetically ranked pairwise native/non-native plant interactions with observed shared invertebrate interactions, thus testing for the potential for apparent competition, in the form of negative indirect interactions between native and non-native plants mediated by a shared invertebrate enemy, with the indirect interactions biased by plant relatedness.

In Chapter 5, with the expectation that in heteroecious oak Cynipid gall wasps, non-native host presence will have a positive effect on non-native gall density on a native host, and that non-native gall density will have a negative effect on native gall density (e.g. Collins *et al*. 1983; Cornell & Hawkins 1993; Schönrogge & Crawley 2000; Schönrogge *et al*. 2000; Keane & Crawley 2002; Torchin & Mitchell 2004; Naniagua *et al*. 2009; Verhoeven *et al*. 2009; Dostál *et al*. 2013), I test for the detectability of apparent competition in a gall wasp community. Using data from repeated surveys of 40 transects in which oak trees are present, by examining the ability of density measures of non-native oak host-plants to predict non-native gall density on native host-plants, I test for presence of apparent competition in the form of the negative indirect effect of a non-native plant on a native plant, mediated by a non-native gall wasp. Additionally, using density measures of non-native and native galls, I test for the presence of apparent competition in the form of the negative indirect effect of a non-native gall wasp on a native gall-wasp, potentially mediated by the modifying presence of one or more shared parasitoids.

1.6 Summary

In summary, while only a relatively small proportion of non-native species are currently recognised as invasive, in that they have a negative ecological and/or economic effect within an ecosystem, all have the potential to be problematic. With the impacts of invasive species widely acknowledged as one of the key drivers of biodiversity loss, and among the greatest threats to ecosystem stability, increased knowledge of the factors that determine and influence how a non-native species interacts within a food web is of paramount importance in contributing to the overall scientific knowledge base, informing management techniques and responsibilities, and potentially mitigating any unwanted effects.

Chapter 2: Variation in non-native phytophagous invertebrate species richness in formally-planted gardens is driven by non-native plant richness and plant type

2.1 ABSTRACT

While cultivated green spaces, such as parks and gardens, can bring benefit to an environment or to human society, they are often dominated by ornamental plantings, the latter potentially functioning in the presence of one or more potentially problematic non-native invertebrate species. Here, data from comprehensive surveys of formally-planted gardens in West Cornwall, UK is used to investigate the efficacy of straightforward measures of non-native plant presence and/or landscape parameters, as reliable predictors of non-native invertebrate presence. This study demonstrates that a high non-native plant species richness likely corresponds to a high non-native invertebrate species richness, with woody plants having a greater effect, and while the probability of any one non-native invertebrate species becoming problematic may be relatively low, a higher richness of non-native invertebrate species in a community means that the likelihood of the presence of a problem species being among them is greater also. Findings have implications for non-native species management, from the practical application of ground-level planting decisions to the development of reliable predictive tools.

2.2 INTRODUCTION

Cultivated community green spaces, such as formally-planted parks and non-domestic gardens, are an important landscape component. Socially, they can provide an aesthetically-pleasing environment, historical and/or cultural interest, and with 83.14% of the UK population living in towns or cities (World Bank 2018), a significant means of increasing valuable human contact with nature (e.g. Kazemi *et al.* 2009). Furthermore, when managed effectively, they can play a valuable ecological role in the maintenance and enhancement of biodiversity (e.g. Cornelis & Hermy 2004; Colding 2007; Helden *et al.* 2012; Salisbury *et al.* 2015a; Su *et al.* 2015); however, as largely unnatural, man-made habitats, typically dominated by non-native, ornamental plantings, they also function highly in the introduction and potential accelerated dispersal, increased propagule pressure and subsequent establishment of plant pathogens and diseases, and significantly, of non-native invertebrate species (Bradley & Altizer 2007; Brasier 2008; Goddard *et al.* 2010). Accordingly, the recent Non-native Species Secretariat (NNSS) recommendations for 'priority pathway' management to better reduce the impact of non-native species in the UK (NNSS 2019) ranks ornamental plant contaminants (invertebrate species, and to a lesser extent, plant pathogens/diseases, of which the former are often vectors (Kluth *et al*. 2002; Tack & Dicke 2013; reviewed Stout *et al*. 2006)) as the third priority pathway overall, and the first (highest) priority pathway involving terrestrial invertebrates.

Many ornamental plants arrive from overseas as seedlings, cuttings or bulbs rather than as seed (Jones & Baker 2007), and it is not uncommon for associated invertebrates from the plant's native range to arrive with the plant itself (CBI 2005; Jones & Baker 2007). As such, invertebrate contaminants are predominantly phytophagous species, those which utilise one or more plants as a food source at any stage in their lifecycle. Phytophagy comprises the following feeding types: exophytic (external/surface feeders), endophytic (internal feeders), phyllophagous (leaf/foliage feeders, phloem/xylem (sap) feeders), zoophytophagous (both plant and animal material feeders), shelter builders (e.g. leaf rollers, tent builders, webbers), casebearers, leaf/needle miners, gall-causers, root feeders, borers (bark, flowers, fruits, pods, stem, etc.). Nectar and/or pollen feeders are not considered phytophagous. Phytophagous invertebrates typically include Hemipteran phloem/xylem-feeders (Aphididae, Cicadellidae, Psyllidae, Coccidae, etc.), leaf-miners (Order: Lepidoptera, Hymenoptera, Coleoptera, Diptera), gall-causers (Order: Hemiptera, Diptera, Class: Arachnida, etc.). These can be further defined as either specialist (monophagous – species that use a single plant genus or species, or oligophagous – species that use closely-related plants from the same family/tribe), or generalist (polyphagous – species that use plants in several/many plant families).

While the majority of non-native terrestrial invertebrate species in Britain are not currently considered invasive, c.30% (116) of those known are recognised as having a negative ecological and/or socio-economic impact (Roy *et al.* 2014). A relatively small number of non-native phytophagous invertebrates are strictly monophagous specialist species, feeding only on the non-native host species with which they arrive, and as such, with exceptions, any negative impact is usually considered to be predominantly of economic/human concern, rather than ecological (Manchester & Bullock 2000; Roy *et al.* 2012, 2014; NNSS 2019); however, less strictly monophagous/oligophagous specialist species and polyphagous generalist species can be expected to feed either on closely-related plants or on any plant – native or non-native in origin – respectively, meaning that the chances of a native wild plant species or important crop species becoming a host-plant are greater in the presence of generalist invertebrate species. The potential for a generalist invertebrate to become a problem species is comparatively high, and therefore such species might be more likely to be considered as having a negative ecological impact. Examples of non-native generalist phytophagous invertebrates assessed as being of negative ecological impact include the following: Horse-chestnut Scale *Pulvinaria regalis* Canard, 1968, Potato Aphid *Macrosiphum (Macrosiphum) euphorbiae* (Thomas, 1878), and Brown Soft-scale *Coccus hesperidum* Linnaeus, 1758.

In order to maintain/improve a healthy functioning ecological community, efforts should be made to limit/reduce the presence of non-native invertebrates already recognised as having a negative ecological impact and also of those with the potential to become a problem species. As the extent of the impact of every non-native invertebrate species cannot be fully known, especially when it comes to recent arrivals, a better awareness of factors contributing to an increased level of the overall presence of non-native invertebrates is clearly advantageous in mitigating the impact of problem species, and in informing relevant decision-makers, such as garden-designers/planners. Given the potential unprecedented environmental change due to the projected impacts of climate change (latest climate change scenarios) and the current accelerated declines in biodiversity, this is now especially important, as the probability of ecological invasions will likely increase (Diez *et al*. 2012; Bellard *et al*. 2013; Hulme 2017).

2.2.1 Botanical diversity

In formally-planted gardens/parks, numerous measurable ecological and physical factors can be considered as possible explanations for variation in non-native phytophagous invertebrate diversity between sites that otherwise seem similar.

Greater botanical diversity (e.g. species richness, taxonomic diversity, plant type/growth form, area coverage) in a community is likely to provide a greater variety of feeding opportunities for phytophagous invertebrates. It is generally expected that there will be a positive relationship between the number of plant species and the number of invertebrate species present, i.e. the greater the species richness of plants present in a garden, the greater the species richness of invertebrates (e.g. Moeed & Meads 1985, 1992; Crisp *et al*. 1998; Unsicker *et al*. 2006). Accordingly, it would be assumed that the greater the species richness of non-native plants present in a garden, the greater the species richness of non-native invertebrates present.

Furthermore, genetic and physical differences in taxonomically diverse plants might allow for increased variety of niche feeding opportunities (e.g. Webb *et al*. 1984; Matsubayashi *et al*. 2010) In contrast to the small number of niches afforded by low botanical diversity being likely dominated by a correspondingly small number of invertebrate species present in high numbers, it would be expected that a greater level of botanical diversity would mean an increased opportunity for establishment of a greater number of invertebrate species, particularly of generalist species, for which the provision of potential new (and available) hosts will be more numerous. As such, it would be assumed also that the higher the taxonomic diversity in a garden, the greater the species richness of non-native invertebrates present.

Likely due to their comparative robustness, longevity and year-round presence, woody plants (trees, shrubs, etc.) constitute a disproportionately high and substantial share of imported ornamental plants (CBI 2005; APHA 2016). Likewise, the number of woody species in British non-native flora (introduced via all pathways, including established garden escapes) is disproportionately higher than that of other plant types (e.g. herbs, ferns, etc.) (Crawley *et al*. 1996; Stace 2019). Given that the availability of a year-round food source for phytophagous invertebrates is better provisioned by woody plants than by other plant types, as is increased overall niche and resource availability, such as temporal shelter for overwintering species, thus improving opportunities for an invertebrate species' establishment, it would therefore be reasonable to expect that the number of associated non-native invertebrates present in a garden community will be disproportionately high also (Smith *et al*. 2007). In their studies of garden biodiversity of 61 urban domestic gardens in Sheffield (BUGS project) Smith *et al*. (2006a,b,c, 2007) found that invertebrate species richness was greater in gardens with a greater tree presence, and that a greater proportion of the non-native invertebrates present occurred on non-native trees or shrubs than on annual/biennial herbs (forb/graminoid species), whereas that native host-plants were more likely to be herb species than woody plants. Therefore, it would be assumed that the greater the species richness and area coverage of non-native woody plants in a garden, the greater the species richness of non-native invertebrates. Furthermore, it is expected that this effect will be stronger for specialist species that have arrived with their host, with generalist species better able to utilise a wider range of host-plant.

2.2.2 Physical garden parameters

In addition to the effects of botanical diversity, research suggests that environmental/landscape parameters bear influence over community species presence, both species richness and species density, with factors such as garden size, age and surrounding land use likely to have an effect.

Island Biogeography theory (MacArthur & Wilson 1967) predicts that larger islands or habitat patches are associated with a greater species richness, therefore, it would be expected that a larger garden area would support a proportionally greater number of both plant species and invertebrate species. Likewise, smaller islands or habitat patches are predicted to support fewer species (MacArthur & Wilson 1967; Davis & Glick 1978; Bastin & Thomas 1999; Guirado *et al*. 2006). Accordingly, in urban biodiversity studies, it has been found that larger gardens exhibit greater plant species richness and greater invertebrate species richness/species density (e.g. McGeoch & Chown 1997; Miyashita *et al*. 1998). Assuming that non-native plant species richness is proportionally greater the larger the garden, it can be expected that accordingly, the larger the garden, the greater the presence of non-native invertebrates. Furthermore, greater availability of space and potential area coverage of individual plant species might allow for larger, more persistent populations of an increased number of invertebrate species.

Moreover, in a study of biodiversity of 12 bioretention basins in Melbourne, Australia, Kazemi *et al*. (2009) found that age, as well as size, was significant in explaining the diversity index of the basins. The older a garden, the greater the opportunity for non-native invertebrates to become established; this might be via direct introduction of an invertebrate or via the accumulation over time of non-native novel enemies by non-native plants. Furthermore, as woody plants in gardens will mature over time, provision of resource availability for non-native invertebrates increases also.

Wider variables, such as surrounding land use, are important when considering the impact of environment/landscape. In larger, urban settings, numerous studies have found landscape variables associated with urbanisation, such as expansive residential areas, building cover, industrial areas, etc. to be have a negative influence on biodiversity levels (reviewed McKinney 2008). For example, numerous studies indicate that while overall density of birds has been seen to increase with urbanisation, avian species richness decreases (e.g. Jokimäki 1999; Isaksson 2018; Kale *et al*. 2018). In other vertebrate groups, Germaine & Wakeling (2001), for example, found marked declines in the distribution, site occupation and assemblage of lizard species in Tucson, USA as residential density increased, and in Adelaide, Australia, Tait *et al*. (2005) found that species richness of mammals decreased as urbanisation increased.

In contrast, a number of studies have found positive associations between urbanisation and biodiversity levels, notably in the presence of non-native species. This seems to especially be the case for non-native plants; e.g. Paudel *et al*. (2017) found that on San Clemente Island, USA, as distance from a major road decreased, non-native plant cover increased and native plant cover decreased, for which a number of explanations have been posited. Plants require relatively small habitat patches to sustain a viable population (Gaston *et al*. 1998) and thus are able to successfully inhabit areas such as buildings, walls, pavements, road edges and waste ground. Of these plants, it can be expected that many will be ‘escaped’ non-native species that have been intentionally introduced in domestic gardens, or as amenity plantings/horticultural displays, etc., or inadvertently introduced via human activity, such as in garden or landscaping materials (e.g. compost, soil, timber) (CABI 2009). It is expected, therefore, that land surrounding the gardens surveyed will include varying degrees of urban/suburban habitat ecologically similar to that of the gardens themselves, such as domestic gardens, amenity planting, and/or uncultivated wasteland, consisting of a significantly large proportion of non-native plants. These habitat patches serve as a potential source for the immigration of non-native invertebrates, which might or might not already be present within the garden community. It is therefore anticipated that in gardens with a greater percentage of surrounding land classified as urban/suburban, non-native invertebrate species richness will be greater.

2.2.3 Study model/hypotheses

Drawing on the expectations posited above, by means of data acquired from in-depth plant/invertebrate surveys of seven formally-planted public gardens, the following specific hypotheses will be tested:

i. Garden-level influence of non-native plants presence/physical garden parameters

- that the greater the species richness of non-native plants present in a garden, the greater the species richness of non-native invertebrates present.
- that the greater the taxonomic diversity of non-native plants present in a garden, the greater the species richness of non-native invertebrates present.
- that the greater the species richness/area coverage of non-native woody plants (trees/shrubs) in a garden, the greater the species richness of non-native invertebrates.
- that the older the garden, the greater the species richness of non-native invertebrates.
- that the larger the garden (area m^2), the greater the species richness of non-native invertebrates.
- that the greater the proportion of surrounding land classified as urban/suburban, the greater the species richness of non-native invertebrates.

ii. Species-level influence of non-native woody plants presence

- that the greater the species-level presence of a non-native woody plant the greater the species richness of non-native invertebrates present.

2.3 METHODS

2.3.1 Overview and study location

During the period June to September 2015, seven formally-planted public gardens within a 3.5 km radius of Penzance, West Cornwall, UK were surveyed. All plants and phytophagous arthropods (insect phloem/xylem-feeders, leaf-feeders, gall-causers, leaf-miners and case-makers, and arachnid gall-causers, henceforth referred to as 'invertebrates') observed in association with the plants at the time of the survey were recorded. Recording took place via 1 to 3 visits per garden, with visits of more than 1-day duration occurring no more than 2 days apart per visit. All visits were made in warm, sunny weather conditions, thus providing a comparable temporal snapshot of all species present, invertebrate host-plant and abundance, and plant area coverage within each garden. Each garden's location, size (area), and approximate year established was noted (Fig. 2.1, Table 2.1). Gardens surveyed are each considered a separate ecological community, of varying age, size and primary function, and all are open freely to the public.

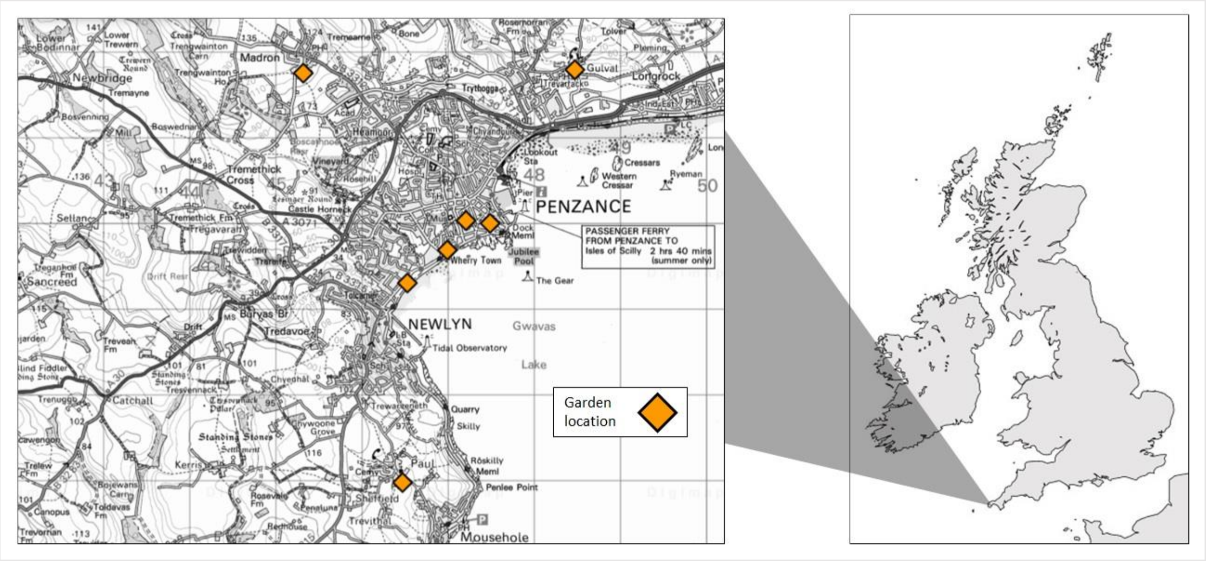


Fig. 2.1. Location of seven formally-planted public gardens within a 3.5 km radius of Penzance, West Cornwall, UK – gardens were surveyed for plant and phytophagous arthropod presence. Source: https://digimap.edina.ac.uk(a)

Table 2.1. Details of gardens surveyed, including location, size (area, excluding mapped buildings/similar structures, etc.), approximate year of establishment, primary use of garden.

Garden name	Full name	OS Nat. Grid Ref. (centre)	Area (m^2)	Year est. (approx.)	Primary use
Alexandra	Alexandra Grounds	SW4698929686	3457.4	1903	Landscaped children's playground (equipped)
Bolitho	Bolitho Gardens	SW4656429342	14563.1	1924	Pleasure gardens
Gulval	Gulval Churchyard	SW4846531763	5965.5	1882 (grounds extended; consecrated 1336)	Landscaped churchyard
Madron	Madron War Memorial Garden/Garden of Remembrance	SW4531831756	647.6	1918	Memorial garden
Morrab	Morrab Gardens	SW4722429986	15512.8	1841	Municipal gardens
Paul	Paul Peace Garden	SW4647626972	4176.8	1850	Landscaped churchyard
St. Mary's	St. Mary's Churchyard	SW4749229991	6014.1	1832 (church built)	Landscaped churchyard

Cornwall's most westerly major town, Penzance, is located within the 90 sq. km. geographic area of West Penwith (also known as the Land's End Peninsula), a Natural England designated National Character Area (NCA) and Environmentally Sensitive Area (ESA), with Heritage Coast status, much of which lies within the Cornwall Area of Outstanding Natural Beauty (AONB) (https://www.cornwall-aonb.gov.uk/). Penzance is the 6th largest town/city in Cornwall, covering an area of c.28 km^2, and with a 2018 population estimate of 17,965 (estimate for West Penwith is 39,300) (ONS 2019).

With its extensive Atlantic coastline, Cornwall's climate is affected by the presence of the Gulf Stream, which provides warmer waters and warmer air temperatures. Arriving first in the far southwest of the British Isles, these warmer temperatures mean that West Penwith experiences a sub-tropical microclimate. Planting choices typically reflect the climate, with many sub-tropical and hardy, coastal species common to all gardens surveyed.

2.3.2 Data collection

All vascular plants – those that were intentionally planted and those that arrived of their own accord – present within each garden at the time of the visit were recorded. Plants were identified to a minimum of genus level but to species level wherever possible.

Each identified plant was subsequently allocated to a designated ‘Plant Taxonomic Unit’ (PTU), consisting of either a single species or a group of congeners of the same native or non-native status and plant type (e.g. small shrub, large tree, etc.); exceptions to this are 4 PTUs where 1 or more of the former congeners has subsequently undergone a taxonomic change or where a single species has subsequently been split into several novel genera (Table 2.2). Where known and where both were present, recognised cultivars/varieties were recorded as a separate PTU from the originating species – the reason being that potential differences in feeding preferences between the two by phytophagous invertebrates could be better highlighted.

The abundance of each Plant Taxonomic Unit (PTU) was estimated by first recording the number of ‘Designated Plant Units’ (DPU) per PTU per m2. The DPU was chosen to be a relatively constant unit of vegetation appropriate to the PTU, such as an individual plant (e.g. small, herbaceous species), a single leaf (e.g. large-leaved plants), 25cm2 of a ground-covering plant, or a single branch of a tree. An estimate of abundance of each PTU (as m2) per garden was then made based on the number of DPU’s present per PTU. DPUs are used only in the process of data collection as an aid to plant recording, and no data pertaining specifically to this measure is presented.

At the same time as plant presence/area coverage was measured, an inventory of phytophagous invertebrates present on each PTU was created. A minimum of 20 DPUs or all units present per Plant Taxonomic Unit (PTU), whichever was smallest, per garden were visually inspected, up to a maximum of 300 where circumstances allowed (mean no. of DPUs inspected = 29.97, median = 20, mode = 20). All visible parts of the plant were examined: foliage, stems, trunks, bark, flowers, etc.; however, for consistency and practicality, visual inspection only was used to assess invertebrate presence, i.e. no beating, digging of roots, dissection of stems or similar was performed. Where there was more than one occurrence of a PTU within a garden, a similar proportion of each occurrence was inspected. For practical reasons and to standardise methodology, only foliage up to approx. 3m from the ground was inspected.

Any individual exhibiting phytophagy was noted. Casual/incidental visitors were noted but disregarded for analysis purposes. Due to difficulties in ensuring estimates of invertebrate density levels that would allow for meaningful comparison between contrasting species (e.g. those exhibiting large differences in body size, or those whose presence is based on the presence of galling, mines, etc. only), presence/absence only of invertebrate species was noted. Invertebrates were identified to species level where possible, and life-stage was noted also. Leaf-miners, case-bearers and gall-causers were identified mostly based on host-plant and mine/gall morphology, with identification of cryptic species confirmed by rearing.

2.3.3 Additional data

Post-survey, additional data were sought for each Plant Taxonomic Unit (PTU) and each invertebrate, as follows:

Up-to-date plant nomenclature/taxonomic classification was determined using primarily Stace (2019) and POWO (2019) (plants), and individual sources (invertebrates), supplemented by Catalogue of Life: 2018 Annual Checklist (Roskov *et al.* 2018). Post-survey changes have subsequently been incorporated, and noted accordingly, as have disputed/ambiguous names (Appendix I, Appendix II).

Native/non-native status of each PTU/invertebrate was established using the Non-native Species Secretariat (NNSS) GB Non-native Species Information Portal (NNSIP) (http://www.nonnativespecies.org/) as the primary authority, supplemented by interrogation of POWO (2019) for additional detail (plants), and consultation of individual sources for data-deficient invertebrate species.

Each PTU was placed in one of the following plant type categories: fern/horsetail, herb, tree/shrub (woody). A numerical measure of phylogenetic plant diversity per garden was created by finding the mean value of a matrix of pairwise interactions of ranked relatedness between a) all PTUs present, and b) all non-native PTUs present. The higher the mean value, the greater the diversity. Rank values are as follows: same Subspecies = 0, same Species = 1, same Genus = 2, same Family = 3, same Order = 4, same Superorder = 5, same Subclass = 6, same Class = 7, same Kingdom = 8.

Each invertebrate was further defined as monophagous, oligophagous or polyphagous – for species that host-switch, feeding type corresponding to plant on which it was recorded was used. Whether the invertebrate is a vascular feeder (case-bearers, gall-causers, leaf-miners, phloem/xylem (sap)-feeders) or non-vascular feeder (general leaf/vegetation-feeders) at the stage it was recorded was also noted. (Appendix II)

Garden parameters: area, perimeter, etc. were measured using Digimap measuring tools (https://digimap.edina.ac.uk(a)). Area coverage was calculated as the entire garden area minus man-made/built buildings and structures present on the map (scale 1: 500). Land cover use for the 12 ha area (the minimum that encompasses the entirety of the largest study site (Bolitho)) in radius from approximate centre of each garden was calculated using the 2015 Land Cover Map (LCM2015) (released April 2017), produced by the Centre for Ecology & Hydrology (CEH), and accessed via Digimap (https://digimap.edina.ac.uk(b)). The area coverage of land classified as urban/was manually calculated using Digimap.

2.3.4 Data analysis

All statistical analyses and descriptive statistics were performed using R (v 3.6.1) (R Core Team 2019).

Sequential stepwise selections of Generalised Linear Models (GLMs) were performed to produce Minimum Adequate Models (MAMs) addressing the above hypotheses. Significance of effects and model differences were evaluated using ANOVA Chi-squared (χ^2) test, and further assessed using AIC values and percentage deviance provided by the model, the latter calculated as: (null deviance – residual variance)/null deviance.

i. Garden-level influence of non-native plant presence/physical garden parameters

For garden-level tests, due to the power of analysis limited by a low number of replicates (n=7), the response variable Species Richness of All non-native invertebrates only was used. To test for the effect of non-native plants' presence on species richness of non-native invertebrates, four explanatory variables were used: non-native PTU richness, non-native PTU phylogenetic diversity, non-native woody PTU richness, non-native woody PTU area coverage, while to test for the effect of physical garden parameters, three explanatory variables were used: garden age, garden size and proportion of surrounding urban/suburban land.

Due to the low number of replicates (n=7), there were insufficient df to test all variables in a combined model; therefore, non-native plant presence was addressed first, and the effects of physical garden parameters added to the resultant MAM until the best-performing model was achieved.

ii. Species-level influence of non-native woody plant presence

Using the full dataset of combined survey data, to test for the effect of woody PTU (trees/shrubs) presence on the presence/absence of non-native invertebrates, the following three explanatory variables were used: woody/non-woody PTU, PTU native status, no. of gardens in which PTU is present. All three explanatory variables were entered into a binomial occupancy Generalised Linear Model (GLM) and tested for interaction effects, with presence/absence of all non-native invertebrate species (ALL), of generalist non-native invertebrate species (GEN), and of specialist non-native invertebrate species (SPEC) per PTU as response variables.

2.4 RESULTS

2.4.1 Descriptive statistics

Plants

A total of 410 individual PTUs were recorded (Appendix I), comprising a combined planted area of 80,865 m^2. Efforts were made to identify all plants present at the time of the garden visit(s); however, 22 of the 410 PTUs remain unidentified or only partially-identified. Fully/partially-identified PTUs (n=408) represent 318 distinct genera and 4 indistinct (mixed) genera (the above-mentioned exceptions), in 113 families within 46 orders and 6 classes (Table 2.2).

Table 2.2. Breakdown of Plant Taxonomic Units (PTUs) (n=410) by native status according to identification level. Total single species and total multiple species are provided, with the respective percentage of the total PTUs per native status category.

Category	Total	Native	Non-native	Unknown
Species (single known species)	288	103	185	-
Genus (single unknown species)	21	4	17	-
Genus (multiple known species)	21	16	5	-
Genus (mixed known species/unknown species)	4	-	4	-
Genus (multiple unknown species)	51	1	50	-
Genera (mixed genera)	3	1	2	-
Unknown (Genus/species unknown)	22	-	7	15
Total	**410**	**125**	**270**	**15**
Total single species	331 (81%)	107 (86%)	209 (77%)	15 (100%)
Total multiple species	79 (19%)	18 (14%)	61 (23%)	0 (0%)

Of the total 410 PTUs, 66% are non-native (n=270), representing 34% of total plant coverage (27,276 m^2), while 30% are native (n=125), representing 66% of total plant coverage (53,403 m^2), and <1% are of unknown native status (n=15), representing <1% of total plant coverage (236 m^2); 49% are herbs (n=201), representing 63% of total plant coverage (51,198 m^2), while 48% are trees/shrubs (n=197), representing 36% of total plant coverage (29,482 m^2), 2% are ferns/horsetails (n=8), representing < 1% of total plant coverage (224 m^2), and 1% are unknown plant types (n=4), representing < 1% of total plant coverage (11 m^2).

Of the 125 native PTUs, 73% are herbs (n=91), representing 83% of total native plant coverage and 55% of total plant coverage (44,434 m^2), while 22% are trees/shrubs (n=27), representing 16% of total native plant coverage and 11% of total plant coverage (8,763 m^2), and the remaining 5% are ferns/horsetails (n=7), representing <1% of both total native plant coverage and total plant coverage (206 m^2).

Of the 270 non-native PTUs, 58% are trees/shrubs (n=157), representing 75% of total non-native plant coverage and 25% of total plant coverage (20,491 m^2), while 41% are herbs (n=110), representing 25% of total non-native plant coverage and 8% of total plant coverage (6,764 m^2), and the remaining 1% consisting of ferns/horsetails (n=1) and unknown PTUs (n=2), representing <1% of both total native plant coverage and total plant coverage (21 m^2).

PTUs of unknown native status consist of trees/shrubs (n=13) and unknown plant types (n=2).

Mean overall PTU richness per garden is 123 (±SE 26.74), with the greatest PTU richness recorded in Morrab (n=268, 65% of total PTU richness), and the lowest PTU richness recorded in Madron (n=62, 15% of total PTU richness). Mean native PTU richness is 51 (±SE 4.23), with the greatest native PTU richness recorded in Bolitho (n=62, 50% of total native PTU richness), and the lowest native PTU richness recorded in Alexandra (n=30, 24% of total native PTU richness). Mean non-native PTU richness is 70 (±SE 22.71), with the greatest non-native PTU richness recorded in Morrab (n=197, 73% of total non-native PTU richness), and the lowest non-native PTU richness recorded in Madron (n=20, 7% of total non-native PTU richness).

Garden level PTU data are depicted in Fig. 2.2.

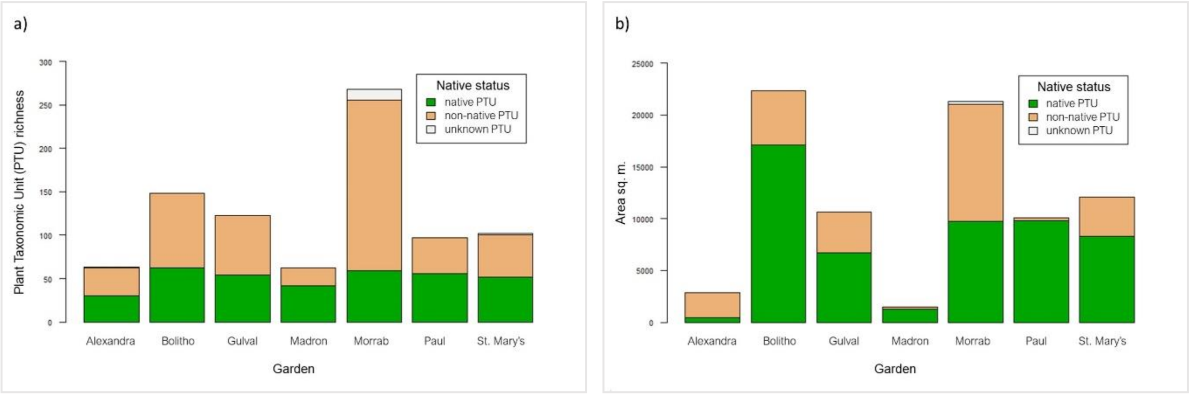


Fig. 2.2a. PTU native status (native, non-native, unknown) by garden, as PTU richness.

Fig. 2.2b. PTU native status (native, non-native, unknown) by garden, as PTU area coverage m^2.

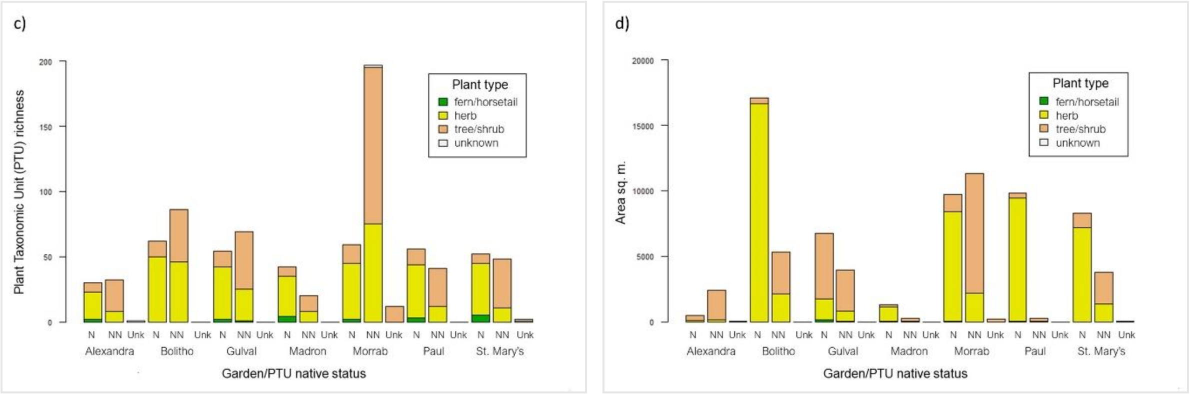


Fig. 2.2c. Plant type by garden/native status (N = native, NN = non-native, Unk = unknown), as PTU richness.

Fig. 2.2d. Plant type by garden/native status (N = native, NN = non-native, Unk = unknown), as PTU area coverage m^2.

Fig. 2.2. Garden level depictions of Plant Taxonomic Unit (PTU) data, as species richness and as area coverage, according to a) and b) PTU native status and c) and d) plant type/native status.

Pairwise interactions between PTUs were assigned a rank value according to their relatedness: same subspecies = 0, same species = 1, same Genus = 2, same Family = 3, same Order = 4, same Superorder = 5, same Subclass = 6, same Class = 7, same Kingdom = 8. Mean values of pairwise interactions of ranked PTU phylogenetic relatedness for all PTUs and for all non-native PTUs per garden ranged from 6.50 to 6.82 (all PTUs) and 6.25 to 6.86 (non-native PTUs) (Table 2.3).

Table 2.3. Total Plant Taxonomic Unit (PTU) pairs, sum and mean ranked relatedness values for all PTUs and non-native PTUs per garden. The higher the mean value, the greater the phylogenetic diversity present.

		Total PTU pairs		**Sum ranked relatedness values**		**Mean ranked relatedness value**	
		All PTUs	**Non-native PTUs**	**All PTUs**	**Non-native PTUs**	**All PTUs**	**Non-native PTUs**
Garden	**Alexandra**	1891	528	12391	3408	6.55	6.45
	Bolitho	10878	3741	72075	25154	6.63	6.72
	Gulval	7503	2346	50488	15922	6.73	6.79
	Madron	1891	190	12582	1295	6.65	6.82
	Morrab	31375	18528	213826	127172	6.82	6.86
	Paul	4753	820	30892	5126	6.50	6.25
	St. Mary's	4851	1128	32827	7546	6.77	6.69

Invertebrates

A total of 115 invertebrate species were recorded, 106 identified to species level, and 3 identified to genus only, while 6 remain only partially-identified. Fully/partially-identified invertebrates (n=115) represent 72 distinct genera, in 27 families within 6 Orders and 2 Classes. 85 invertebrate species are native, 23 non-native and 7 of unknown native status (Appendix II).

Of the total 115 invertebrate species, 74% are native (n=85), 20% are non-native (n=23), and 6% are of unknown native status (n=7); 96% are insects (n=110) (3% Coleoptera (n=4), 23% Diptera (n=26), 49% Hemiptera (n=56), 5% Hymenoptera (n=6), 15% Lepidoptera (n=17), 1% Unknown (n=1)), and 4% are arachnids (n=5); 24% are generalist feeders (polyphagous) (n=28), 70% are specialist feeders (monophagous or oligophagous) (n=80), and for 6% feeding type is unknown (n=7); 93% are vascular feeders (n=107), and 7% are non-vascular feeders (n=8).

Of the 85 native invertebrate species, 95% are insects (n=81) (4% Coleoptera (n=3), 31% Diptera (n=26), 39% Hemiptera (n=33), 6% Hymenoptera (n=5), 16% Lepidoptera (n=14)), and 5% are arachnids (n=4), 24% are generalist feeders (polyphagous) (n=20), 76% are specialist feeders (monophagous or oligophagous) (n=65); 93% are vascular feeders (n=79), and 7% are non-vascular feeders (n=6).

Of the 23 non-native invertebrate species, 96% are insects (n=22) (78% Hemiptera (n=18), 4% Hymenoptera (n=1), 13% Lepidoptera (n=3)), and 4% are arachnids (n=1), 35% are generalist feeders (polyphagous) (n=8) and 65% are specialist feeders (monophagous or oligophagous) (n=15); 96% are vascular feeders (n=22), and 4% are non-vascular feeders (n=1).

Invertebrate species of unknown native status are insects (n=7), consisting of Coleoptera (n=1), Hemiptera (n=5), and Unknown (n=1), for which feeding type is unknown, 6 of which are vascular feeders and 1 a non-vascular feeder.

Mean overall invertebrate species richness per garden is 27 (SE ±4.75), with the greatest invertebrate species richness recorded in Morrab (n=54, 47% of total invertebrate species richness), and the lowest invertebrate species richness recorded in Alexandra (n=17, 15% of total invertebrate species richness). Mean native invertebrate species richness is 18 (SE ±2.91), with the greatest native invertebrate species richness recorded in Morrab (n=35, 41% of total native invertebrate species richness), and the lowest native invertebrate species richness recorded in Alexandra (n=11, 13% of total native invertebrate species richness). Mean non-native invertebrate species richness is 7 (SE ±1.70), with the greatest non-native invertebrate species richness recorded in Morrab (n=16, 70% of total non-native invertebrate species richness), and the lowest non-native invertebrate species richness recorded in both Madron and Paul (n=3, 13% of total non-native invertebrate species richness).

Garden level invertebrate data are depicted in Fig. 2.3.

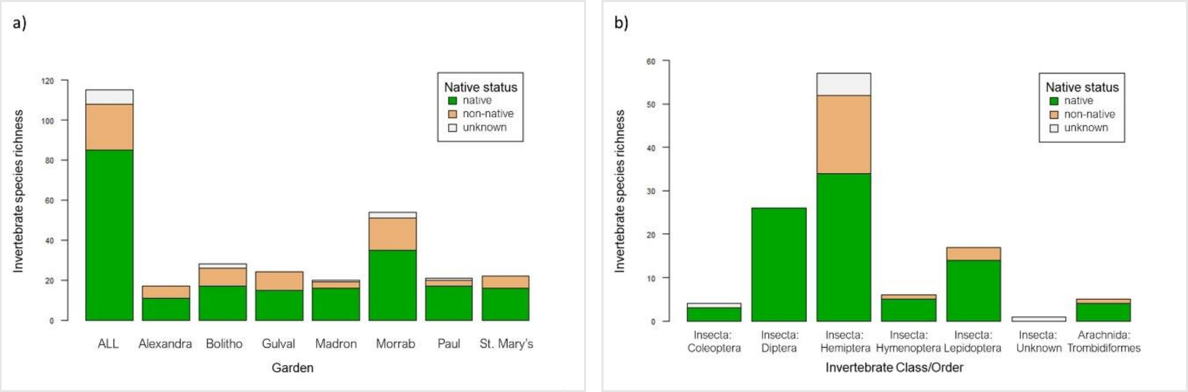


Fig. 2.3a. Species richness and native status of all invertebrates present and per garden.

Fig. 2.3b. Species richness and native status of all invertebrates by Class/Order.

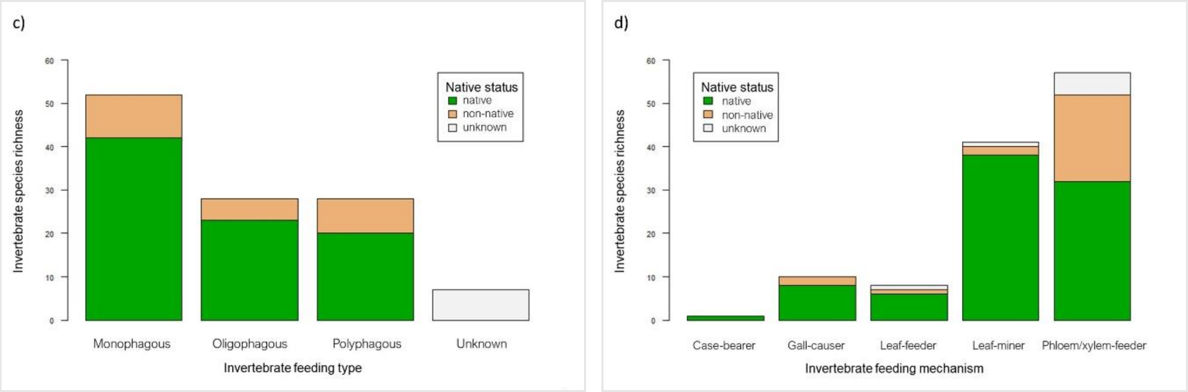


Fig. 2.3c. Species richness and native status of all invertebrates by feeding type.

Fig. 2.3d. Species richness and native status of all invertebrates present by feeding mechanism.

Fig. 2.3. Garden level depictions of invertebrate species richness according to native status, as a) total presence per garden, b) by Class/Order, c) feeding type, and d) feeding mechanism.

2.4.2 Statistical analyses

i. Garden level influence of non-native plants presence/physical garden parameters on non-native invertebrate species richness

Testing for the significance of non-native plants' presence, both non-native woody PTU richness and non-native phylogenetic diversity were non-significant, and thus removed from the model. Significant positive effects were observed for both non-native PTU richness (GLM: ANOVA $\chi^2_{1,5}$: p < .001) and for non-native woody PTU area coverage (GLM: ANOVA $\chi^2_{1,4}$: p = 0.017). The resultant MAM is as follows: non-native PTU richness + non-native woody PTU area coverage (GLM: df 6, resid. df 4, null dev. 121.7143, resid. dev. 4.4394), with 96% deviance explained by the model. When tested independently, a significant positive effect was observed for the effect of garden size (GLM: ANOVA $\chi^2_{1,5}$: $p < .001$); however, following addition of the physical garden parameters effects to the non-native plants presence MAM, no significant effects were observed for any of the additional variables, therefore, non-native PTU richness + non-native woody PTU area coverage was confirmed as the best-performing MAM (Fig. 2.4). Further tests revealed garden size to be significantly positively correlated with PTU richness (GLM: ANOVA $\chi^2_{1,5}$: $p < .001$).

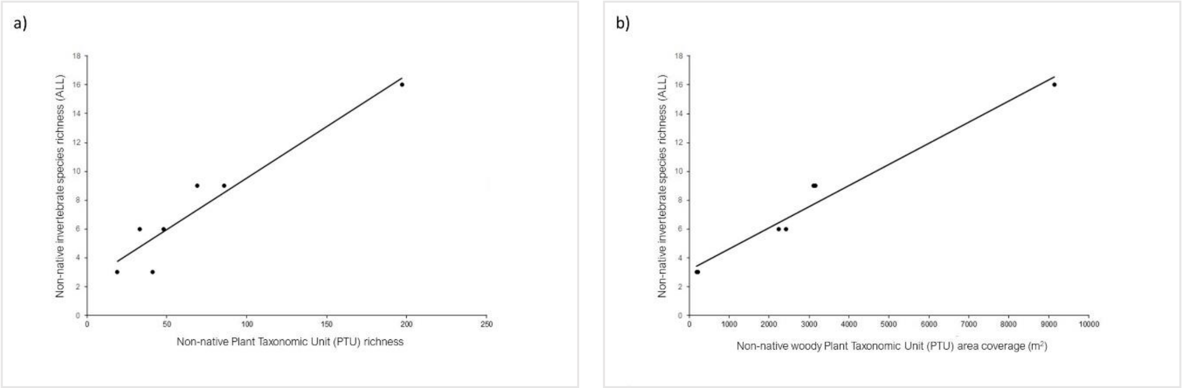


Fig. 2.4. Significant main effects of a) non-native Plant Taxonomic Unit (PTU) species richness ($p < .001$) and b) non-native woody PTU area coverage ($p = 0.017$) (with linear regression) in predicting non-native invertebrate species richness.

ii. Species-level influence of non-native woody plants presence

All non-native invertebrates

For the response variable ‘ALL non-native invertebrate presence/absence’, PTU native status was not significant as a main or as an interaction effect, and was removed from the model. As independent variables, a significant effect was observed for woody/non-woody PTU (GLM: ANOVA $\chi^2_{1,408}$ $p < .001$) and for no. of gardens in which PTU is present (GLM (binom): ANOVA $\chi^2_{1,407}$ $p < .001$). A significant effect was observed also for woody/non-woody PTU and no. of gardens in which PTU is present as a 2-way interaction (GLM (binom): ANOVA $\chi^2_{1,406}$ $p = 0.009$). Thus, MAM (ALL) is as follows: woody/non-woody PTU X no. of gardens in which PTU is present (GLM: df 409, resid. df 406, null dev. 262.15, resid. dev. 203.41), with 22% deviance explained by the model.

Generalist non-native invertebrates

For the response variable ‘GEN non-native invertebrate presence/absence’, PTU native status was not significant as a main or as an interaction effect, and was removed from the model. As independent variables, a significant effect was observed for woody/non-woody PTU (ANOVA $\chi^2_{1,408}$ $p < .001$) and for no. of gardens in which PTU is present (GLM (binom): ANOVA $\chi^2_{1,407}$ $p < .001$). A significant effect was observed also for woody/non-woody PTU and no. of gardens in which PTU is present as a 2-way interaction (GLM (binom): ANOVA $\chi^2_{1,406}$ $p = 0.016$). Thus, MAM (ALL) is as follows: woody/non-woody PTU X no. of gardens in which PTU is present (GLM: df 409, resid. df 406, null dev. 199.08, resid. dev. 152.89), with 23% deviance explained by the model.

Specialist non-native invertebrates

For the response variable ‘SPEC non-native invertebrate presence/absence’, PTU native status was not significant as a main or as an interaction effect, and was removed from the model. As independent variables, a significant effect was observed for woody/non-woody PTU (GLM (binom): ANOVA $\chi^2_{1,408}$ $p = 0.001$) and for no. of gardens in which PTU is present (GLM (binom): $\chi^2_{1,407}$ $p = 0.011$). No significant effect was observed also for woody/non-woody PTU and no. of gardens in which PTU is present as a 2-way interaction. Thus, MAM (ALL) is as follows: woody/non-woody PTU + no. of gardens in which PTU is present (GLM: df 409, resid. df 407, null dev. 147.73, resid. dev. 131.12), with 11% deviance explained by the model.

For all response variables, a significant amount of variation is explained by the woody/non-woody distinction, with the mean $\bar{x}$ presence of invertebrates being higher for woody (Fig. 2.5). For non-woody plant types (n=213), ALL: $\bar{x} = 0.03$ ±SE 0.01 (n=6); GEN: $\bar{x} = 0.02$ ±SE 0.01 (n=4); SPEC: $\bar{x} = 0.01$ ±SE 0.01 (n=3). For woody plant types, ALL: $\bar{x} = 0.17$ ±SE 0.03 (n=34); GEN: $\bar{x} = 0.12$ ±SE 0.02 (n=23); SPEC: $\bar{x} = 0.08$ ±SE 0.02 (n=15). Native/non-native PTU status was not significant for any response variable, thus separate means for native PTUs and non-native PTUs are not shown.

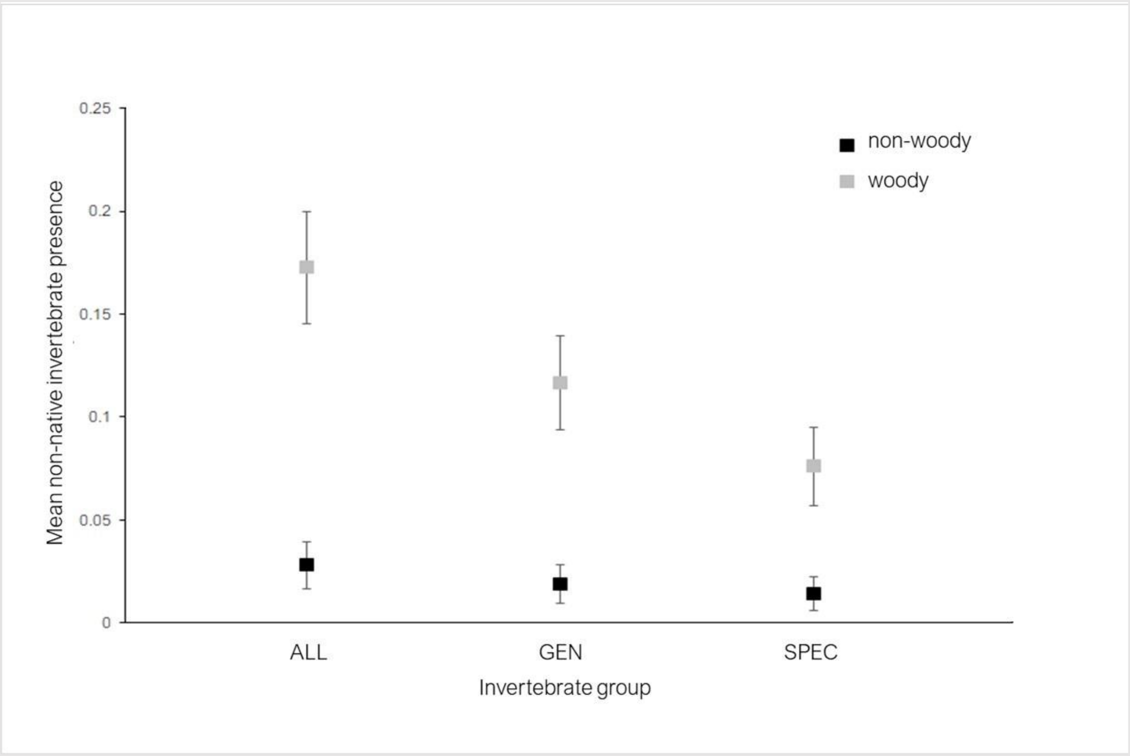


Fig. 2.5. Mean ±SE presence of non-native invertebrate species observed in association with non-woody/woody Plant Taxonomic Units (PTUs). Mean presence of invertebrates is higher for woody PTUs than for non-woody PTUs

For ALL and GEN invertebrates, significant 2-way interaction effects between woody/non-woody PTU and no. of gardens in which PTU is present were observed. Plots are provided showing presence/absence of non-native invertebrate species observed in association with non-woody/woody PTUs according to the number of gardens in which the host-PTU is present, with fitted lines for both woody and non-woody PTUs, showing a significant positive interaction for ALL invertebrates and for GEN invertebrates, and a non-significant positive interaction for SPEC invertebrates (Fig. 2.6).

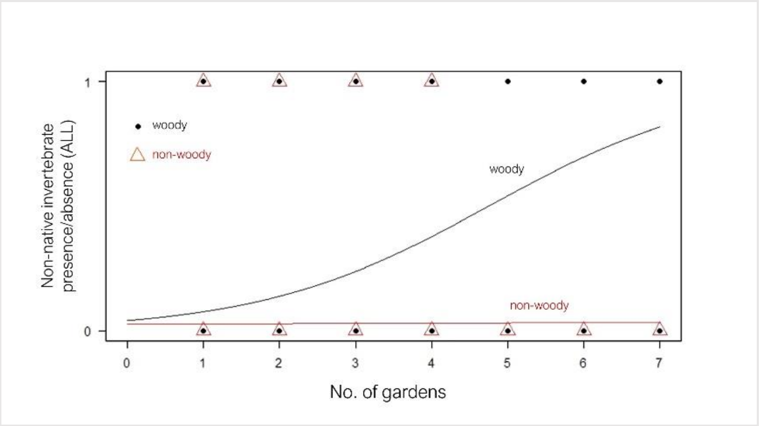


Fig. 2.6a. All non-native invertebrates (ALL) – significant interaction

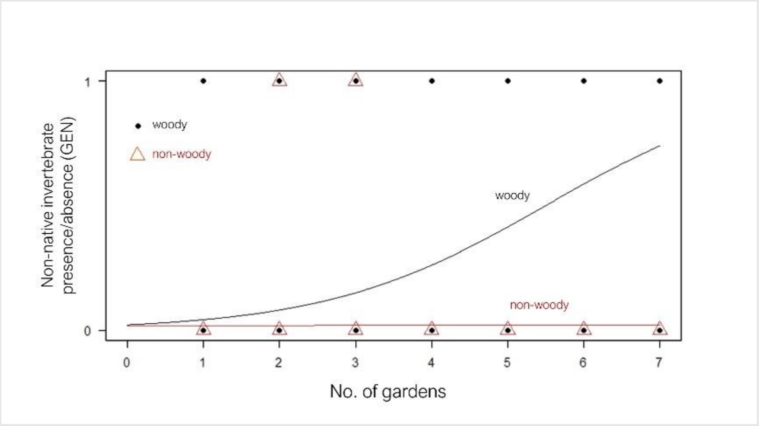


Fig. 2.6b. Generalist non-native invertebrates (GEN) – significant interaction

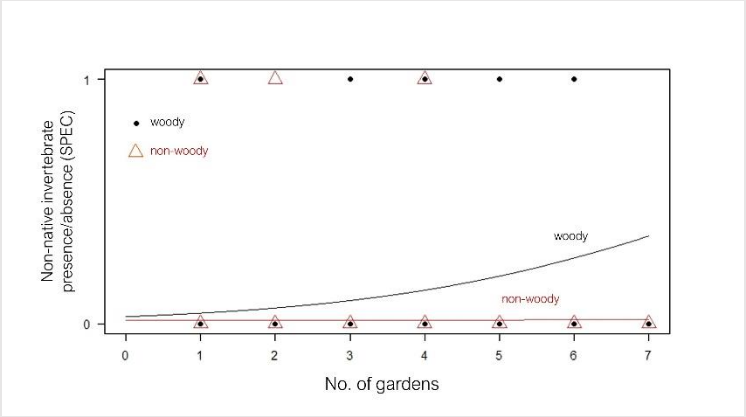


Fig. 2.6c. Specialist non-native invertebrates (SPEC) – non-significant interaction

Fig. 2.6. Non-native invertebrate species observed in association with non-woody/woody Plant Taxonomic Units (PTUs) according to presence(1)/absence(0) per no. of gardens in which the host-PTU is present, with fitted lines for woody and non-woody PTUs for **a)** all (ALL), **b)** generalist (GEN) invertebrates, and **c)** specialist (SPEC) invertebrates, showing a significant interaction in ALL and GEN models.

2.5 DISCUSSION

Expected results were garden level effects of non-native plant species richness, taxonomic diversity, species richness/area coverage of woody plants, garden age, garden size, and surrounding land classification, and a species level effect of non-native woody plant presence. Significant results were observed for the garden level effect of plant species richness and area coverage of woody plants, and for the species level effect of non-woody plant presence, thus providing partial support for the hypotheses.

At species level, a greater presence of non-native invertebrates was observed on woody plants than on non-woody plants, irrespective of PTU native status. Accordingly, at garden level, greater area coverage of non-native woody plants is associated with greater non-native invertebrate species richness, as is greater non-native PTU richness. There was an effect of garden size but its addition to a model already containing non-native PTU richness did not improve the model. Due to the presence of a strong correlation between the two variables, with a larger garden size meaning a greater PTU richness (e.g. MacArthur & Wilson 1967; Davis & Glick 1978; Bastin & Thomas 1999; Guirado *et al*. 2006) McGeoch & Chown 1997; Miyashita *et al*. 1998), it is presumed that the garden size effect was caused by the PTU richness effect. No significant effects were observed for the effects of non-native woody PTU richness, non-native PTU phylogenetic diversity, garden age and proportion of surrounding land classified as urban/suburban.

The expectation that non-native invertebrate species richness would be greater the greater the presence of non-native woody plants was partially met, in that at garden level, area coverage of non-native woody plants was significant as an effect but non-native woody PTU richness was not. This suggests that density of non-native woody plants is more important here than diversity. This finding is in agreement with Smith *et al*. (2006a,b,c, 2007), who found that invertebrate species richness was greater in gardens with a greater tree presence. Furthermore, at species level, more woody PTUs than non-woody PTUs were host to one or more non-native invertebrates but here, unlike the findings of Smith *et al*. (2006a,b,c, 2007), the native status of the plant was not significant. Thus, it is presumed that woody area coverage *per se* would be significant at garden level, and that native status is not of particular importance.

Examining differences between generalist invertebrates and specialist invertebrates, using species level data, contrary to the expectation that the effect of woody plant presence (richness and/or area coverage), notably that of non-native woody plant presence, would be stronger for specialist non-native invertebrates (e.g. Smith *et al*. (2006a,b,c, 2007), due to their having arrived with the host with reduced opportunity to utilise a wider range of host-plant than generalist species, this was not the case; however, while the general trend shown by both generalists and specialists was similar, with mean presence higher on woody PTUs than on non-woody PTUs for both groups, there was a greater difference between the woody/non-woody mean presence values for generalist non-native invertebrates than for specialist non-native invertebrates (0.10 and 0.07 respectively). Given that the combined presence of non-native generalist invertebrates, as measured by number of PTUs on which one or more invertebrate was present (27 PTUs (23 woody, 4 non-woody)), was greater than the corresponding presence of non-native specialist invertebrates (18 PTUs (15 woody, 3 non-woody)) (despite a greater number of individual specialist species (15) than generalist species (8)), it is presumed that this variation is likely a consequence of specialist invertebrate plant-host presence being comparatively lower in number, rather than anything of particular note.

Additionally, for all and generalist species, the presence of one or more non-native invertebrates on a woody PTU increased as the number of gardens in which the host-plant is present increased. This might be due to an overall greater presence of the host-plant within the survey area contributing to a larger and/or more stable metapopulation of the invertebrate, as a consequence of more closely-linked habitat patches (Levins 1969; reviewed Hanski 1999), or it might be representative of the plant being more frequently imported, thus increasing the likelihood of the direct introduction of a non-native invertebrate (Levine & D'Antonio 2003; Brockerhoff *et al.* 2006; Jones & Baker 2007; Kenis *et al.* 2007; Smith *et al.* 2005, 2007; Brasier 2008; Hulme *et al.* 2008; Roy *et al.* 2012, 2014; Bergey *et al.* 2014; Turbelin *et al*. 2016; NNSS 2019). Any similar effect in non-woody plants is negligible, suggesting that proximity of woody plants is potentially key to maintaining an effective non-native invertebrate metapopulation structure, while non-native invertebrates on non-woody plants persist in more isolated patches. It could therefore be argued that the longevity of invertebrate species on non-woody plants might be shorter than that of those on woody plants, and as a further study, it would be interesting to measure comparative density levels of non-native invertebrates on woody/non-woody plants as a means of assessing potential damage levels, to see if isolated non-woody plant patches support a greater number of individuals of a single species, to 'compensate' for reduced longevity.

While the range of this study is limited, consisting of data from only 7 gardens located within a relatively small area, what it might lack in terms of geographic coverage and sample size, it makes up for in intensity of sampling effort, while also avoiding the potentially problematic confounding effects of additional variables, such as geographic variation, climate/microclimate effects, local flora/fauna differences that would be present in a wider-ranging design. This allows for fine-scale, comprehensive datasets as a consequence of intensive, whole garden surveys, without the need to control for additional variables to those being evaluated. Results are therefore considered to be suitably reliable and of particular relevance to the study locality. Given the susceptibility of the region to the negative/potentially negative presence of non-native species from multiple taxonomic groups (e.g. Jones 2003; Williams *et al*. 2010; Turner *et al*. 2018), the advantages of obtaining superior knowledge specific to a particular, localised area is paramount in the ability to make better-informed, targeted decisions regarding management approaches, mitigation efforts, etc. Thus, despite the limited geographic range of the study, there are clear benefits to maintaining a local focus. Furthermore, the implications of the study findings have applications within both the local arena and further afield, and it would be interesting to extend the study to encompass more formally planted gardens/landscape over a wider geographical area, and to observe the whether or not results are consistent, or if other trends can be detected. Moreover, given its south-westerly location within the Gulf Stream, as well as via human-assisted introduction pathways, Cornwall is particularly prone to colonisation by non-native species due to climate-induced range-shifts (Parmesan & Yohe 2003; Hickling *et al*. 2006; Parmesan 2006; Chen *et al*. 2011; Cook *et al*. 2013; Kosanic *et al*. 2018), and, as such, it is hoped that significant findings from this study have the potential to be transferable globally as predictors in similar ecological communities in locations experiencing a warming climate.

Implications of these study findings are manifold, from an improved awareness of what non-native invertebrates are present in formally-planted gardens and how they interact with both native and non-native plants present, to the development of better-informed integrated management tools designed to help mitigate the potentially negative consequences of the presence of problematic non-native invertebrates, such as a targeted planting recommendations based on a more informed consideration of the effect of increasing plant species richness within a garden and/or of multiple plantings of the same species in nearby locations, and alternatives to chemical control of problematic species; however, it is advised that caution be heeded in the application of a blanket approach to managing non-native invertebrates, particularly those that are already present. Given that the presence of a non-native species is not always negative or cause for concern (e.g. Manchester & Bullock 2000; Davis *et al*. 2011; Salisbury *et al*. 2015a), the effect of its removal (in this case either directly or by means of host-plant removal) could be more detrimental than beneficial (e.g. Zavaleta *et al*. 2001; Bergstrom *et al*. 2009; Ballari *et al*. 2016). As such, assessment of the individual impact of a species' presence is always favourable, and, as always, the key goal is the persistence of a healthy, functioning ecological community. What the findings of this study especially contribute to is an improved awareness of the factors associated with an increased non-native invertebrate presence, which is key to better/effective monitoring, etc. For example, simple approaches such as focused examination/monitoring of woody plants could prove particularly beneficial in enabling long-term assessments of the overall impact of non-native invertebrates.

In conclusion, 23 non-native phytophagous invertebrate species, representing 20% of all phytophagous invertebrates species observed, were recorded from seven formally-planted gardens in and around Penzance, Cornwall, with the invertebrates showing a clear preference for woody plants over non-woody plants. This study demonstrates that a high non-native plant species richness likely corresponds to a high non-native invertebrate species richness, with woody plants having a greater effect. Thus, while the probability of any one non-native invertebrate species becoming problematic may be relatively low, a higher richness of non-native invertebrate species in a community means that the likelihood of the presence of a problem species being among them is greater also. As a preventative measure, it could perhaps be argued that a planting focus on non-woody native species over non-native plants should be encouraged; however, given the potentially positive attributes of non-native plant presence, realistically, the solution is unlikely to be straightforward.

Chapter 3: Nearest Source and habitat variables as predictors of patch occupancy in non-native invertebrate metapopulations

3.1 ABSTRACT

Understanding factors which enable a non-native species to persist in an ecological community is paramount to the development of effective management techniques that would contribute to mitigation of any negative effects. Persistence of a phytophagous invertebrate species relies on the availability of a suitable host-plant. In the context of metapopulation theory, the facilitative role of non-native plants in the ability of a non-native invertebrate to persist within a community is tested. As expected, where host-plant habitat patches are closer together, it is found that the likelihood of a patch being occupied is greater, especially if the patch is occupied; however, this effect is not universal, with species-specific effects present also. The potential exists for a non-native invertebrate to become problematic, especially as its level of presence increases. With particular regard to non-native species management, the role of metapopulation theory, including the use of simple Nearest Neighbour measures, in predicting how host-plant presence influences a non-native species' ability to persist within an ecological community, is discussed.

3.2 INTRODUCTION

Persistence of a phytophagous invertebrate species relies on the availability of suitable habitat, which, in the case of the monophagous or narrowly oligophagous species, consists of a single suitable host-plant or small group of closely-related plants. Furthermore, such invertebrates are predominantly static feeders, such as leaf-miners, gall-causers or scale-insects, and in more active feeders, such as aphids and psyllids, although wings are often present in adult forms, their dispersal capabilities are generally accepted as being limited by weak flight capabilities (e.g. Arakawa & Mivamolo 2007; Reynolds & Reynolds 2009; Döring 2014). As a consequence, many phytophagous invertebrate species rely on passive dispersal mechanisms for inter-habitat movement (see Reynolds & Reynolds 2009). This means that close proximity of the nearest host-plant is especially important in maintaining healthy populations, facilitating (re)colonisation following events such as disease, local habitat loss, etc., as well as enabling effective immigration/emigration between populations. In an urban/suburban environment, monophagous and oligophagous non-native invertebrates will largely be restricted to formal and domestic gardens containing their non-native plant-hosts. As such, gardens represent distinct habitat patches, and the non-native invertebrate species are likely to exhibit a metapopulation structure.

With the presence of a non-native species having the potential to have a negative effect on an ecological community, understanding factors which enable such species to persist is paramount to the development of effective management techniques that would contribute to mitigation of any negative effects. By studying the factors that influence patch occupancy within these metapopulations, our understanding of the conditions under which non-native species can spread and persist in a novel environment can thus be improved.

3.2.1 Metapopulation theory and population viability analysis

A metapopulation is a group of connected but spatially isolated populations of the same species (Levins 1969; reviewed Hanski 1999) that facilitates the species' persistence. In a defined area, suitable habitat will support a number of distinct populations, and unoccupied suitable habitat will be present also. The structure of metapopulations varies, e.g. a large/stable population might act as source of recruits for smaller, satellite populations (mainland-island structure), there might be several populations of a similar same size/stability (classical structure), or there might be a mix of variously-sized populations (patchy structure). Interactions occur between the populations, such as immigration and emigration, while individual populations might be subject to stochastic events that could trigger changes in stability, leading to colonisation/re-colonisation of new habitats, or local extinctions (e.g. Hanski 1989). Such events will have a knock-on effect on other populations, thus potentially modifying a pre-existing structure. According to classical metapopulation theory (Levins 1969), while individual populations are subject to local extinction, as long as there is equilibrium in the form of a balance between extinction/colonisation, the metapopulation itself will remain stable; however, if extinction of local populations exceeds colonisation, a metapopulation will eventually become extinct.

Population viability analysis (PVA) utilises various tools to predict population dynamics, allowing assessment of the probability of extinction risk. Such tools include species-specific biological and or ecological knowledge, theoretical models and statistical analysis. Applications of PVA include but are not limited to informing the appropriate management of habitats for one or more focal species, informing the prioritising of conservation effort, and landscape design. Metapopulation theory is fundamental to PVA, and in more recent years, simulation models/computer-based packages, such as the incidence function model (IFM), originally proposed by Hanski (1994) (see also Moilanen & Hanski 1998; Moilanen 1999), stochastic patch occupancy models (SPOM) (e.g. Harrison *et al*. 2011; Sutherland *et al*. 2014; Graham *et al*. 2015; reviewed Moilanen 2004), and stochastic ecological network occupancy (SENO) models (e.g. Lafferty & Dunne 2010) have been developed, which utilise a range of ecological data to model scenarios under various conditions/events, thus enabling better-informed predictions to be made regarding metapopulation stability and likelihood of extinction. Likewise, robust statistical methods have been developed to better account for potential error caused by imperfect detection and/or by misapplied knowledge/misinterpretation of ecological relationships (evaluated Bini *et al*. 2009; Hawkins 2012).

3.2.2 Predicting patch occupancy – population dispersal

Forming the basis of all PVA techniques are simple occupancy models, such as the Nearest Neighbour measure. Despite the development and popularity of more sophisticated modelling means, techniques such as these can be useful conservation tools in their own right, especially in that they are comparatively simple to apply, and assessment of their efficacy is relatively straightforward. These habitat proximity indices describe presence/absence of patches inhabited by the focal species, using distance between patches within a connected habitat (reviewed Sjögren-Gulve & Hanski 2000). Nearest Neighbour (NN) uses the distance from a patch to the nearest habitat (NH) and/or to the nearest source (patch occupied by the same species) (NS) to predict occupancy, without incorporating any other factors, such as patch size or shape. While NH is considered one of the less reliable/poorer predictors (reviewed Moilanen & Nieminen 2002; Winfree *et al*. 2005; Prugh 2009), although a simple approach, NS has been shown to perform consistently reliably in predicting occupancy

(Bastin & Thomas 1999; Winfree *et al*. 2005; Prugh 2009). The various pros, cons, applications, biological considerations, implications, comparisons, etc. of different occupancy modelling techniques have been widely evaluated (e.g. ter Braak *et al*. 1998; Sjögren-Gulve & Hanski 2000; Moilanen & Nieminen 2002; Winfree *et al*. 2005; Prugh 2009; Bini *et al*. 2009).

In addition to gardens, predominantly linear features, such as railways, waterways, etc. can function as habitat corridors, serving as direct links between ecological communities that might have historically been separate, thus further improving connectivity for species whose habitat requirements are duly met (e.g. Rudd *et al*. 2002; Angold *et al*. 2006; Hulme 2009; Shi *et al*. 2018; reviewed Beier & Noss 1998). Furthermore, as anthropogenic features, increased human use of roads, both as vehicle-users and as pedestrians, is influential in the dispersal of plant seeds/propagule matter by means of attachment (Clifford 1959; Scott & Davidson 1985; Schmidt 1989; Lonsdale & Lane 1994; Hodkinson & Thompson 1997; Zwaenepoel *et al*. 2006; Hulme 2009; Auffret & Cousins 2013), and by means of increased airflow produced by vehicular airflow (von der Lippe *et al*. 2013). Thus, as a consequence of human-mediated plant dispersal, it is likely that host-plants will be present in locations other than domestic gardens/formally planted areas, such as on wasteland and road verges. Similarly, it is likely that the dispersal of invertebrate species, particularly those that make use of passive dispersal mechanisms, will be subject to the same influence; for example, eriophyid gall-mites are known to rely on passive dispersal by wind (Washburn & Washburn 1984; Michalska *et al*. 2010; Kiedrowicz *et al*. 2017). In accordance with a heavier traffic presence, it is presumed that these effects will most likely be of importance in the presence of principal roads rather than in quieter, residential streets.

3.2.3 Potential variation in habitat suitability – distance from sea, elevation, habitat type

In addition to the presence of a metapopulation structure based on patch occupancy, with roads as potential dispersal aids, abiotic factors such as microclimate will likely affect the likelihood of patch occupancy, with microclimate effects expected to correlate with distance from sea and/or patch elevation. Similarly, differences in habitat type, notably whether a habitat is managed or unmanaged, are likely to also be influential in patch occupancy.

It is presumed that patch exposure to both salt (via, e.g. sea-spray, precipitation, soil content) and strong, coastal winds – abiotic factors that are recognised as inducing stress in plants (e.g. Vernieri *et al*. 2010) – will be greater the nearer a patch is to the sea. Salinity tolerance in plants varies between species (e.g. Rozema *et al*. 1985; Sykes & Wilson 1989; Vernieri *et al*. 2010; reviewed Parvaiz & Satyawati 2008), with effects of salt stress ranging from mild osmotic effects, through biochemical/nutritional imbalances, to eventual chlorosis and necrosis of the leaf tissues (e.g. Cheplick & Demetri 1999; Munns 2002; Sánchez-Blanco *et al*. 2004; Munns & Tester 2008; Parvaiz & Satyawati 2008). It can be surmised that salt-induced osmotic changes, plant nutritional imbalance, and changes in biochemistry will have a negative, indirect effect on a plant's invertebrate associates. In addition to requiring an adequate level of plant tissue water content, phytophagous invertebrates show a preference for plant tissue with a high nitrogen content (Mattson 1980), and as both water and nitrogen content decreases as salinity increases (Mittal *et al*. 2012; Deinlein *et al*. 2014; Ashraf 2018), it might be expected that invertebrates would choose to not feed on a salt-stressed plant. Accordingly, feeding/oviposition cues might be altered or absent (Renault *et al*. 2016 and references therein). In contrast, there is also the potential for positive effects associated with closer proximity to coast. As a consequence of differences between the heat capacity of water and that of solid, land materials, in coastal areas, the sea helps to maintain warmer temperatures by taking longer to cool down (Adams *et al*. 2013). Accordingly, as well as longer plant growing periods, the likelihood of frosts is reduced, meaning that plants are less prone to associated damage, and in turn, overwintering invertebrates have the advantage of remaining safely *in situ*.

Effects of elevation are typically evident in mountainous/high altitude environments or in environments containing a combination of elevation extremes, i.e. lows and highs, whereby types of plants that are able to grow can be limited as a consequence of altered availability of soil nutrients, strength/duration of sunlight and water absorption (e.g. Gale 2004; Dierig *et al*. 2006), which can lead to adaptations, such as those seen in alpine plants to successfully inhabit high altitudinous environments (e.g. small size, protective growth-forms (rosettes, tussocks, low stature) (Körner 2007)). Similarly, evidence suggests that atmospheric temperature decreases approximately 1°C for every elevation increase of 100m (Adams *et al*. 2013), meaning that as elevation increases, horticultural growing seasons would be shorter in duration, while the number/diversity of plants able to survive would reduce accordingly.

While the presence of such pronounced effects are principally applicable to mountainous/high altitude environments, it is possible that some effects might still be observed in environments which exhibit only small-scale differences, or which provide opportunities for the presence of microclimate effects, such as frost-prone valleys, or drier, exposed hill-tops.

Within an urban/suburban environment, in addition to formal and domestic gardens, suitable habitat for phytophagous invertebrates exists in several other key forms, notably as plants on unmanaged land, e.g., small areas of woodland, wasteland, footpaths, uncultivated roadside verges, etc., or in small-scale amenity planting, e.g. small flowerbeds, hanging baskets, planters, cultivated roadside verges, etc. Habitat types can be broadly grouped into two categories: managed or unmanaged. As such, the likely utilisation of invertebrate control mechanisms, such as chemical insecticides and/or biological control agents, is potentially greater in managed habitats, whereas unmanaged habitats are more likely to remain relatively undisturbed (exceptions to this potentially being the use of chemical weed-killers on wasteland in some public areas). Furthermore, as previously posited, the potential influence of principal roads on dispersal of seeds/plant matter means that it is very likely that host-plants will be present in unmanaged locations as well as gardens, etc. Similarly, movement of plant material from one location to another, garden escapes, removal/transfer of plant waste and/or compost, and transfer via birds, mammals, etc. are all means of introducing seeds/plant matter into new environments, either intentionally or unintentionally (Mack & Lonsdale 2001). It might therefore be expected that unmanaged habitats, such as footpaths, wasteland and roadside verges support a substantial number of patches, and that differences in patch occupancy rates will exist between managed and unmanaged habitats, with rates being greater in unmanaged habitats.

3.2.4 Study model/hypotheses

Here, I use presence/absence of 7 monophagous/narrowly oligophagous non-native invertebrate species present within a 2 x 2 km coastal, suburban area of Penzance, Cornwall, UK to test Nearest Neighbour (NN) measures and proximity to principal road as predictors of invertebrate presence (patch occupancy). In addition, the predictive capability of habitat suitability is tested using distance from sea, elevation and habitat type. In the absence of prior experimental investigation, it is not possible to state definitively that these study systems are truly representative of metapopulations in the true sense of the given definition (e.g. it is not known to what extent factors such as the introduction of populations as a consequence of human action are facilitating the species' persistence); however, given that populations of the selected species are spatially isolated within the study area, and also that connectivity between these populations is presumed to be serving to facilitate the species' persistence, here, the presence of each species within the study area is considered a metapopulation. Importantly, by studying multiple independent species in the same geographical area, it is anticipated that both overall and species-specific patterns in patch occupancy will be discernible, helping to inform as to whether such patterns apply generally or whether they are ultimately applicable at species level only.

Testing occupancy based on NN and roads as potential aids to dispersal: It is expected that as distance between patches decreases, occupancy rate increases, and that the more isolated the patch, i.e., as the distance between patches increases, occupancy rate is reduced (e.g. MacArthur & Wilson 1967; Prugh *et al*. 2008; reviewed Prugh 2009). Similarly, it is expected that availability of suitable habitats (patches) will increase as distance from a principal road decreases, and that there will be an increase in occupancy rate as distance from nearest road decreases. Based on the premise that it is proximity to nearest population that determines colonisation rather than the availability of habitat or means of dispersal (Moilanen & Nieminen 2002; Winfree *et al*. 2005; Prugh 2009), it is hypothesised that NH and distance from road will be weaker predictors than NS of occupancy.

Testing occupancy based on variation in habitat suitability: In coastal areas, despite the potential for elevation to be closely correlated with distance from sea, as well as a potentially low elevational range, it is expected that due to the potential persistence of microclimate effects granted by small variation in elevation between patches, both distance from sea and elevation will have an effect on patch occupancy. The direction of the effect of distance from sea will likely depend on the host-plant and/or invertebrate's salt stress tolerance, and/or the effect of reduced frost/warmer temperatures. Similarly, due to an increased likelihood of frost due to lower temperatures, increased exposure, etc., as elevation increases, it is expected that occupancy of habitat patches will be reduced, and that this effect will be stronger in host-plant species with native ranges that experience a warmer climate than the study location, in this case, those from Japan and/or South America. As a third habitat variable, due to the potential for reduced/no use of invertebrate control, it is expected that there will be a higher patch occupancy rate in unmanaged habitat types than in managed habitat types.

In summary, it is expected that NS will be the most reliable predictor of patch occupancy, and that one or more habitat variables will strengthen any significant effect of NS, NH and/or distance from road.

3.3 METHODS

3.3.1 Overview and study location

During August and September 2018, a 2 x 2km sq. area (tetrad), incorporating the following four 1km squares: SW4629, SW4630, SW4739, SW4730, of suburban/urban Penzance, Cornwall (Fig. 3.1) was surveyed for presence/absence of 7 monophagous/narrowly oligophagous non-native invertebrate species on all observable occurrences of their respective host-plant (Table 3.1). All publicly-accessible land was visited on foot (e.g. main roads, residential roads/areas, footpaths, parks, public gardens, playgrounds, commercial areas, car parks, etc.) with plants present in private gardens/on private land recorded if they could be seen/examined without the need to trespass, i.e. if the gardens/lands/plants bordered public areas, such as pavements, footpaths, etc. or invertebrate presence could be assessed from a distance. As the plants surveyed were fairly substantial in size, and signs of invertebrate presence overt (e.g. galling, or presence of tell-tale soot moulds/waxy secretions indicative of presence), it was possible to detect occurrences with relative ease, from an maximum initial comfortable distance of c.10m (further if binoculars were utilised). Most private front/side gardens could be assessed easily but rear gardens were sometimes less accessible; however, for ease of detection reasons described above, areas that could not be surveyed at all were very minimal, and most private gardens were able to be adequately surveyed. In total, the area surveyed constitutes 72.25% land and 27.75% water (source: https://www.brc.ac.uk/vcgrid) (Fig. 3.1).

SW4630 100% land 0% water	**SW4730** 82.9% land 17.1% water
SW4629 85.4% land 14.6% water	**SW4729** 20.7% land 79.3% water

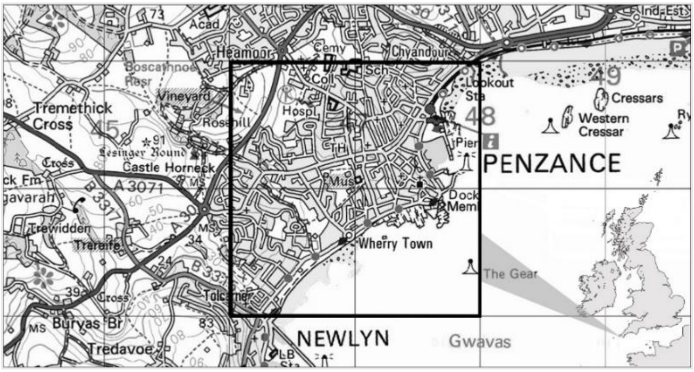


Fig. 3.1. Layout, percentage land/water cover and location of the four 1 km squares which form the tetrad in suburban/urban Penzance, Cornwall, surveyed for presence/absence of 7 non-native invertebrate species on all observable occurrences of their respective host-plant. Source: https://www.brc.ac.uk/vcgrid; https://digimap.edina.ac.uk(a)

3.3.2 Data collection

All observable separate occurrences (i.e. patches) of the following plants were recorded: *Elaeagnus x submacrophylla*, *Fuchsia* spp., *Laurus nobilis*, *Phormium tenax*, *Pittosporum* spp., and large-leaved bamboos (e.g. *Arundinaria* spp., *Bambusa* spp., *Phyllostachys* spp., *Pseudosasa japonica*, *Sasa* spp.). Patches were considered separate if they were separated by a physical barrier, such as a fence, wall, road or path or if they were more than 10m apart. Patch size was not noted; however, no patch was greater in size than 10m x 10m. For each patch, presence/absence of specific associated invertebrates was noted: *Cacopsylla fulguralis*, *Aculops fuchsiae*, *Lauritrioza alacris*, *Balanococcus diminutus*, *Powellia vitreoradiata*/unknown Pittosporum scale, and *Takecallis arundicolens* respectively (details, Table 3.1). Presence/absence was recorded as either: 1 = occupied, or 0 = not occupied. In most cases, the presence of the invertebrate was easily discernible, due to the presence of galls, soot moulds, plant deformation, etc.; however, efforts were made to check particularly thoroughly for less conspicuous/more mobile species, notably *C. fulguralis* and *T. arundicolens*, to ensure occurrences were not overlooked. For each metapopulation respectively (A to G), patches were considered occupied based on positive presence of the following (Fig. 3.2):

- A *Aculops fuchsiae* on *Fuchsia* spp.– distinctive disfiguration (galling) of flowers and vegetative matter
- B *Balanococcus diminutus* on *Phormium tenax* – individual adults, nymphs or eggs, white (epicuticular) wax at base of plant/in leaf axils
- C *Cacopsylla fulguralis* on *Elaeagnus x submacrophylla* – individual adults, nymphs or eggs, mostly on undersides of foliage
- D *Lauritrioza alacris* on *Laurus nobilis* – individual adults, nymphs or eggs, distinctive galling of foliage
- E *Powellia vitreoradiata* on *Pittosporum* spp. – individual adults, nymphs or eggs, distinctive galling of foliage
- F *Takecallis arundicolens* on large-leaved bamboos – individual adults, nymphs or eggs, usually on undersides of foliage
- G unknown Pittosporum scale on *Pittosporum* spp. – individual adults, nymphs or ovisacs on trunk/branches

Invertebrate species were selected due to their known prevalence in the survey area, their ease of detection, and their presence on host-plants that are of horticultural importance to the area, being widely planted in private gardens and as municipal floral/vegetative displays. *Lauritrioza alacris*, *P. vitreoradiata*, *T. arundicolens* and *A. fuchsiae* are recognised as having a negative economic impact, as serious horticultural ‘pests’ (Roy *et al*. 2012; Salisbury *et al*. 2014), while *B. diminutus* and *C. fulguralis* are acknowledged as horticulturally detrimental but as having less severe an impact (www.rhs.org.uk a,b), and not enough is known about the unid. Pittosporum scale for any assessment of its impact to have been made (C. Malumphy, pers. comm.). Furthermore, the selected invertebrate species are not highly mobile, all having limited dispersal capabilities, thus allowing for data to be collected by means of single location visits, with only minimal likelihood of under-detection.

During the course of the survey, locations were marked on a large-scale 1:500 Ordnance Survey (OS) map, and subsequently converted to a 10m OS grid reference.

Table 3.1. Details of focal phytophagous invertebrate species A-G, recorded as present/absent within a tetrad in suburban/urban Penzance, Cornwall, their native range, feeding type: monophagous (M), oligophagous (O), known associated host-plant(s), and for interest, their earliest known GB and Cornwall records.

	Invertebrate				**Host-plant**	**Earliest records of invertebrate**	
	Name	**Classification**	**Native range**	**Type**	**Name(s)**	**GB**	**Cornwall**
A	*Aculops fuchsiae* Keifer	Arachnida: Trombidiformes, Eriophyidae	South America	M	Gen. *Fuchsia*	Portchester, Hants, 2007	2008
B	*Balanococcus diminutus* (Leonardi, 1918)	Insecta: Hemiptera, Pseudococcidae	New Zealand	M	*Phormium tenax*	unk, unk	Penzance, 2013
C	*Cacopsylla fulguralis* (Kuwayama, 1908)	Insecta: Hemiptera, Psyllidae	China, Eastern Asia	M	Gen. *Elaeagnus*	Leigh-on-Sea, Essex 2002	Paul, 2011
D	*Lauritrioza alacris* (Flor, 1861)	Insecta: Hemiptera, Triozidae	Europe	O	Fam. Lauraceae (Gen. Laurus, Persea)	unk, 1937	St. Austell, 1982
E	*Powellia vitreoradiata* Maskell, 1879	Insecta: Hemiptera, Triozidae	New Zealand	M	Gen. *Pittosporum*	St. Mawes, Cornwall, 1993	1993
F	*Takecallis arundicolens* (Clarke, 1903)	Insecta: Hemiptera, Aphididae	China, Eastern Asia	O	Fam. Poaceae (Gen. *Arundinaria, Bambusa, Phyllostachys, Phragmites, Pseudoasa, Sasa*)	unk, 1920	Penzance, 2012
G	unid. Pittosporum scale	Insecta: Hemiptera, Diaspididae	unk	M*	Gen. *Pittosporum*	unk, unk	Penzance, 2014

* Unknown, presumed monophagous, species – awaiting ID confirmation via Fera Science Ltd.

A Invertebrate: *Aculops fuchsiae* Keifer (Arachnida: Trombidiformes, Eriophyidae); Host-plant: *Fuchsia* L.

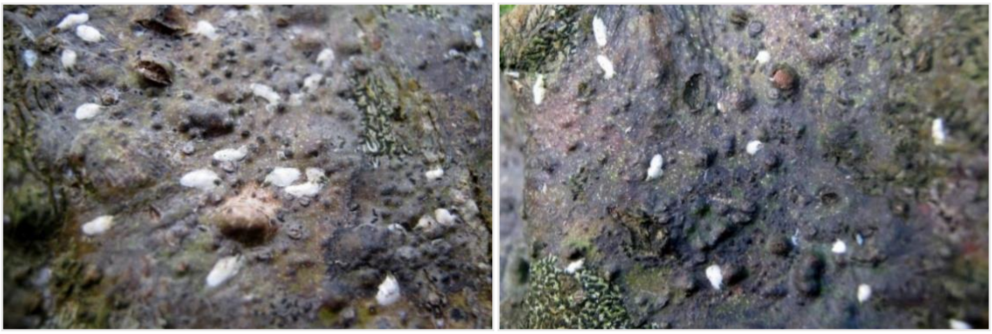
B Invertebrate: *Balanococcus diminutus* (Leonardi, 1918) (Insecta: Hemiptera, Pseudococcidae); Host-plant: *Phormium tenax* J.R.Forst. & G.Forst.

C Invertebrate: *Cacopsylla fulguralis* (Kuwayama, 1908) (Insecta: Hemiptera, Psyllidae); Host-plant: *Elaeagnus* × *submacrophylla* Servett.(syn. *E. x ebbingei*)

D Invertebrate: *Lauritrioza alacris* (Flor, 1861) (Insecta: Hemiptera, Triozidae); Host-plant: *Laurus nobilis* L.

E Invertebrate: *Powellia vitreoradiata* Maskell, 1879 (Insecta: Hemiptera, Triozidae); Host-plant: *Pittosporum* Banks ex Sol.

F Invertebrate: *Takecallis arundicolens* (Clarke, 1903) (Insecta: Hemiptera, Aphididae); Host-plant: large-leaved bamboos (e.g. *Arundinaria* Michx., *Bambusa* (L.) Voss, *Phyllostachys* Siebold & Zucc., *Pseudosasa japonica* (Siebold & Zucc. ex Steud.) Makino ex Nakai, *Sasa* Makino & Shibata)



G Invertebrate: an unknown Pittosporum scale (Insecta: Hemiptera, Diaspididae); Host-plant: *Pittosporum* Banks ex Sol.

Fig. 3.2. Invertebrates A-G and their associated survey host-plant(s). Photo credits: E (photo 2) *P. vitreoradiata* nymph Adam Poledníček, F (photo 2) *B. diminutus* on *Phormium tenax*, David Fenwick: http://www.aphotofauna.com

3.3.3 Additional data

Distance from NH/NS. For each metapopulation, UK Grid Reference Finder Batch Convert Tool (https://gridreferencefinder.com) was used first to convert OS grid references to lat./long. coordinates, and then to convert these lat./long. patch coordinates to a distance matrix: d_{ij} = distance between focal patch i and patch j where i = focal patch, j = any other patch in the defined area. A matrix was produced for NH and NS patches respectively. For each focal patch within a metapopulation, least distances from the nearest habitat (NH) and the nearest occupied patch (NS) were extracted.

Distance from sea/distance from road. Using Digimap measuring tools (https://digimap.edina.ac.uk(a)), shortest distance from each patch to the sea was manually measured. For consistency, the OS mean high water (MHW) annotation was used to represent the boundary between land and sea, and thus used to determine the nearest point from which measurements were taken. Similarly, shortest distance from each patch to the nearest principal road was manually measured, using the middle of the road as the point from which measurements were taken. Principal roads were taken to be those denoted as main/secondary roads (primary/secondary ‘A’ roads and ‘B’ roads). (Fig. 3.3)

Fig. 3.3. Principal roads: primary/secondary ‘A’ roads (green) and ‘B’ roads (orange/yellow) within the 2 km survey area of Penzance, Cornwall – to determine ‘distance from road’, the shortest distance from each patch to the nearest principal road was measured. Map details: OS VectorMap™ District/OS Terrain® 50, November 2017, accessed via Digimap (https://digimap.edina.ac.uk(a)).

Elevation. Using the GPS Visualizer DEM (digital elevation model) lookup facility (https://www.gpsvisualizer.com/elevation), elevation data from NASA's SRTM1 database was acquired for each patch, based on the patch lat./long. coordinates.

Habitat type. Each patch was categorised as either managed or unmanaged, based on observed/assumed management type/intensity. Managed – routine maintenance and/or attention from gardener(s), groundsperson(s), or similar, involving, e.g. the removal/addition of plants, alteration of planted displays, irrigation, mowing, pruning, weeding, etc. While chemical control is not believed to be used in public gardens, its use in private gardens is unknown. Patches categorised as 'managed' are as follows: public/small-scale, amenity planting; domestic/privately managed garden; public parks, formally planted/managed gardens, churchyards, etc. Unmanaged – no routine maintenance/intervention, with the exception of some occasional cutting-back along footpaths. Patches categorised as 'unmanaged' are as follows: waste ground, small wooded areas, footpaths, etc.

3.2.4 Data analysis

All statistical analyses and descriptive statistics were performed using R (v 3.6.1) (R Core Team 2019). For plotting interaction effects, the package interplot was used (Solt & Hu 2019).

With both distance from sea and elevation being useful proxies for microclimate but likely to be significantly correlated, to test for the possibility of confounding variables, these two spatial measures were checked for correlation. As a significant correlation was found, in order to examine elevation as independent from distance from sea, model residuals (the distance between the actual elevation and the value predicted by the line equation) were used to represent elevation relative to the surrounding landscape.

For each metapopulation A-G, logistic regression, by means of a binomial occupancy Generalised Linear Model (GLM) with a logit link, was used to test for the significance of the effects of independent dispersal variables: NH, NS and distance from road in predicting patch occupancy. Similarly, logistic regression was used to test for significance of the effects of independent habitat variables: distance from sea, elevation and habitat type in predicting patch occupancy. For each metapopulation model in which a dispersal-based effect was significant, the effect of the addition of each of the habitat-based variables as an interaction effect was tested for significance. At each stage, stepwise selection of GLMs was used to achieve a Minimum Adequate Model (MAM). For all tests, significance of effects and model differences were evaluated using ANOVA Chi-squared (χ^2) test, with further assessment made using model AIC values and the percentage variation provided by the model, calculated as: (null deviance – residual variance)/null deviance.

3.4 RESULTS

3.4.1 Descriptive statistics

A combined total of 821 separate habitat patches were recorded, representing 708 individually mapped patches – with mapped patches not limited to a single focal host-plant (619 patches featured 1 focal host-plant only, 70 featured 2 different focal host-plants, 15 featured 3, 3 featured 4 and 2 featured 5). 92% of mapped patches were on managed land (68% of mapped patches were within domestic/privately managed gardens (n=481), 13% were within public/small-scale, amenity planting (n=90), 12% were within public parks, formally planted/managed gardens, churchyards, etc. (n=84)), while 8% were on unmanaged land (waste ground, small wooded areas, footpaths, etc.) (n=54). Number of patches per focal host-plant ranged from 54 patches (F) to 284 patches (A), with occupancy rates ranging from 5% (G) to 86% (D). For each metapopulation A-G, a dot distribution map (Fig. 3.4) is provided.

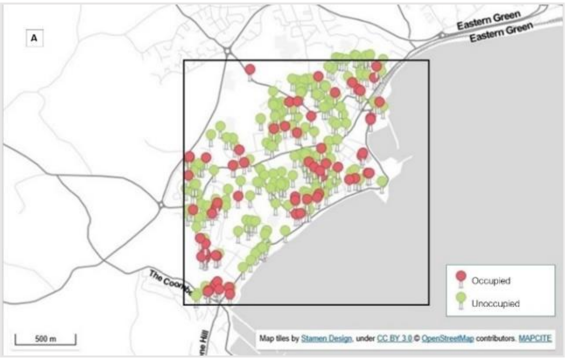


Fig. 3.4a. A. *Fuchsia*/*Aculops fuchsiae*

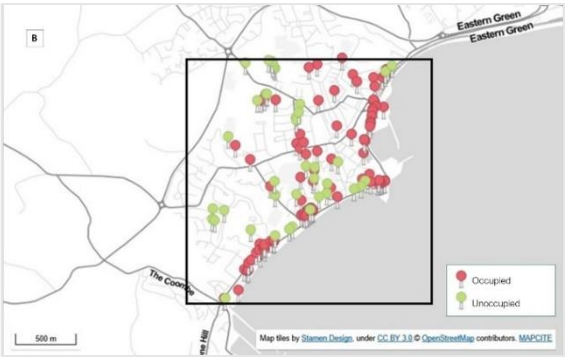


Fig. 3.4b. B. *Phormium tenax*/*Balanococcus diminutus*

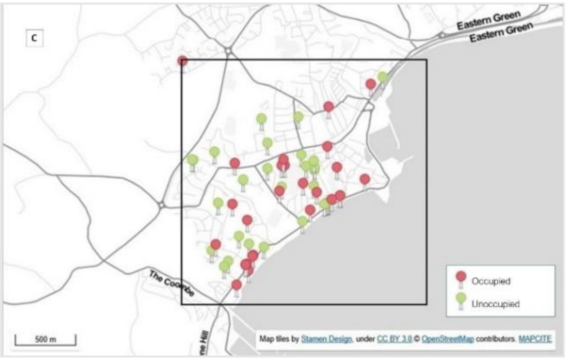


Fig. 3.4c. C. *Elaeagnus*/*Cacopsylla fulguralis*

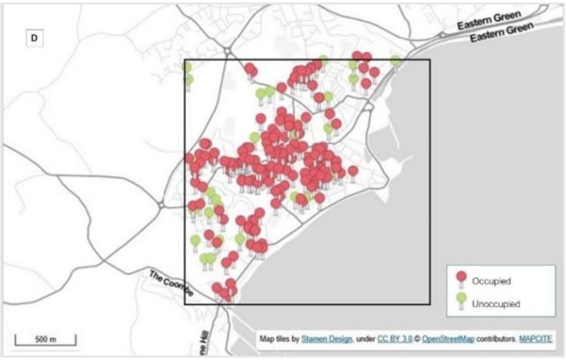


Fig. 3.4d. D. *Laurus nobilis*/*Lauritrioza alacris*

Fig. 3.4e. E. *Pittosporum*/*Powellia vitreoradiata*

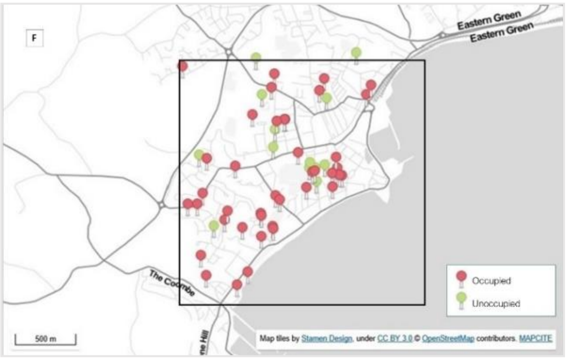


Fig. 3.4f. F. Bamboo/*Takecallis arundicolens*

Fig. 3.4g. G. *Pittosporum*/unknown Pittosporum scale

Fig. 3.4. Dot distribution maps for metapopulations: **a)** A. *Fuchsia*/*Aculops fuchsiae,* **b)** B. *Phormium tenax*/*Balanococcus diminutus,* **c)** C. *Elaeagnus*/*Cacopsylla fulguralis,* **d)** D. *Laurus nobilis*/*Lauritrioza alacris,* **e)** E. *Pittosporum*/*Powellia vitreoradiata,* **f)** F. Bamboo/*Takecallis arundicolens.* **g)** G. *Pittosporum*/unknown Pittosporum scale within the 2 km survey area of Penzance, Cornwall. Red dots represent occupied patches, green dors represent unoccupied patches. Maps produced using Microsoft Excel add-in Mapcite.

3.4.2 Statistical analyses

Due to the possibility of confounding variables, spatial measures: distance from sea and elevation were checked for correlation. A significant correlation was observed (lm: R^2 0.53 (adj. R^2 0.53); ANOVA $F_{1,707} = 797.61$ $p <.001$) (Fig. 3.5). In order to examine elevation as independent from distance from sea, model residuals (the distance between the actual elevation and the value predicted by the line equation $y=0.0394x+9.0382$) were used to represent differences in elevation relative to the surrounding landscape.

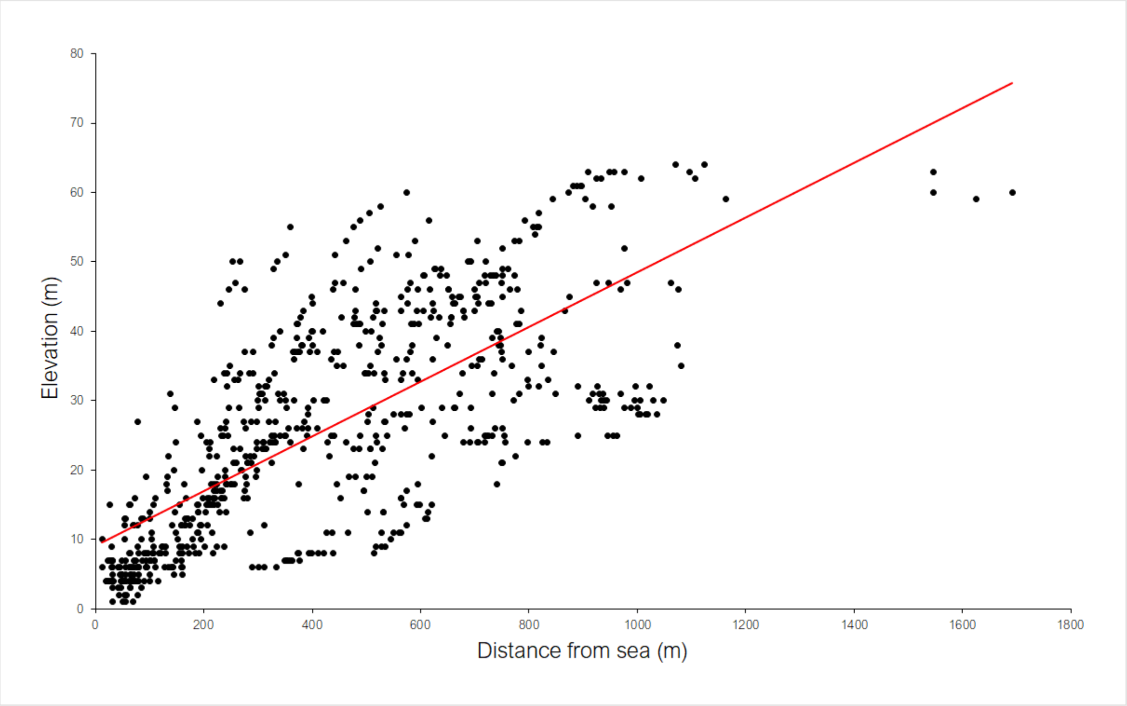


Fig. 3.5. Significant correlation (lm: R^2 0.53 (adj. R^2 0.53); ANOVA $F_{1,707} = 797.61$ $p <.001$) of distance from sea and elevation of each patch location, with fitted regression line ($y = 0.0394x + 9.0382$).

Independent models – occupancy based on dispersal methods: nearest habitat (NH), nearest source (NS)), and distance from road

In metapopulations C, E, F and G, no significant effects were observed for NH, NS or distance from road. A significant effect was observed for NS in metapopulations A (GLM (binom): ANOVA $\chi^2_{1,282}$ $p < .001$), B (GLM (binom): ANOVA $\chi^2_{1,135}$ $p < .001$) and D (GLM (binom): ANOVA $\chi^2_{1,211}$ $p < .001$), while in D, NH was significant also (GLM (binom): ANOVA $\chi^2_{1,212}$ $p < .001$) (Fig. 3.6). For A (NS only), 8% deviance is explained by the model, for B (NS only) 17%, and for D (NH + NS) 18%. Distance from road was not significant in any of the metapopulation models.

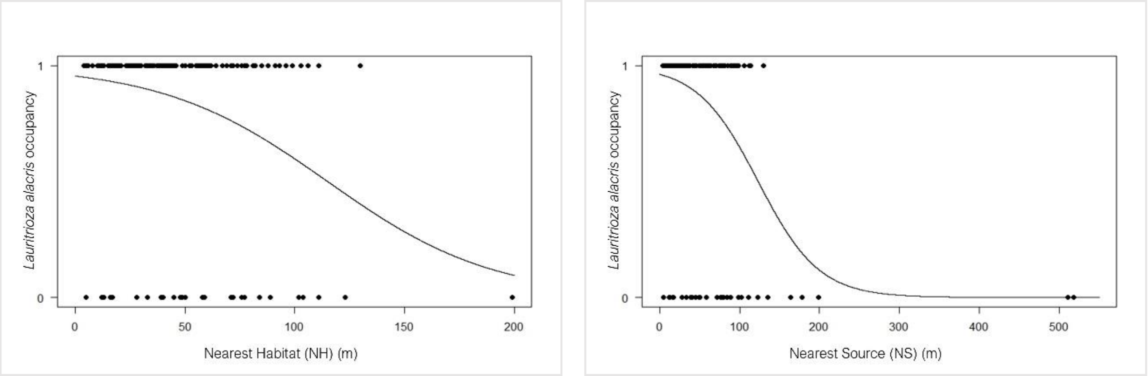


Fig. 3.6a Metapopulation D: *Lauritrioza alacris* NH (GLM (binom): ANOVA $\chi^2_{1,212}$ $p < .001$)

Fig. 3.6b Metapopulation D. *Lauritrioza alacris* NS (GLM (binom): ANOVA $\chi^2_{1,211}$ $p < .001$)

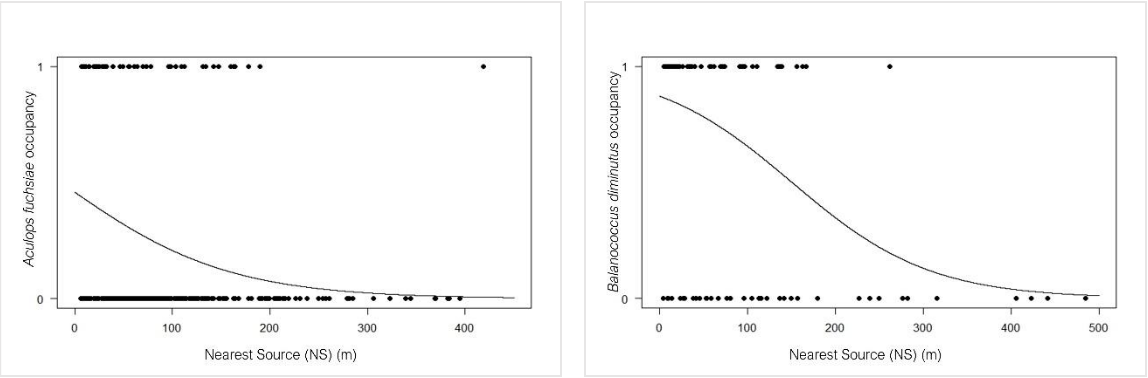


Fig. 3.6c Metapopulation A. *Aculops fuchsiae* NS (GLM (binom): ANOVA $\chi^2_{1,282}$ $p < .001$)

Fig. 3.6d Metapopulation B. *Balanococcus diminutus* NS (GLM (binom): ANOVA $\chi^2_{1,135}$ $p < .001$)

Fig. 3.6. Significant occupancy plots for tests based on dispersion: Nearest Habitat (NH), Nearest Source (NS) and distance from road (1 = occupied, 0 = not occupied) with fitted curves: **a)** D *Lauritrioza alacris* NH, **b)** D *Lauritrioza alacris* NS, **c)** A *Aculops fuchsiae* NS, **d)** B *Balanococcus diminutus* NS

Independent models – occupancy based on variation in habitat suitability: distance from sea, elevation, and habitat type

In metapopulations A, C, F and G, no significant effects were observed for distance from sea, elevation, or habitat type. In B, a significant effect was observed for distance from sea (GLM (binom): ANOVA $\chi^2_{1,136}$ $p < .001$), in D, a significant effect was observed for elevation (GLM (binom): ANOVA $\chi^2_{1,212}$ $p < .001$), while in E, a significant effect was observed for habitat type (GLM (binom): ANOVA $\chi^2_{1,75}$ $p = 0.020$) (Fig. 3.7). For B (distance from sea only), 13% deviance is explained by the model, for D (elevation only) 6%, and for E (habitat type only) 5%.

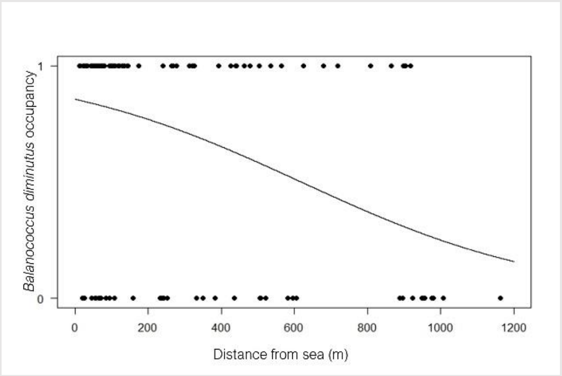


Fig. 3.7a. Distance from sea occupancy plot with fitted curve for metapopulation B: *Balanococcus diminutus* (GLM (binom): ANOVA $\chi^2_{1,136}$ $p < .001$)

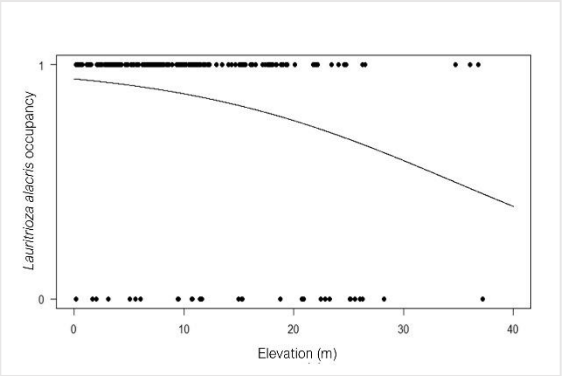


Fig. 3.7b. Elevation occupancy plot with fitted curves for metapopulation D: *Lauritrioza alacris* (GLM (binom): ANOVA $\chi^2_{1,212}$ $p < .001$)

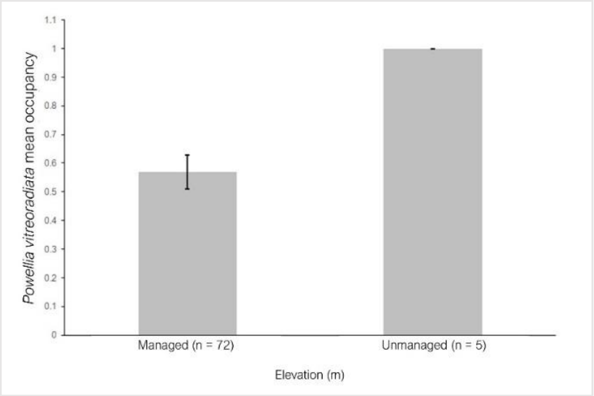


Fig. 3.7c. Mean ±SE patch occupancy according to habitat type for metapopulation E. *Powellia vitreoradiata* (GLM (binom): ANOVA $\chi^2_{1,75}$ $p = 0.020$)

Fig. 3.7. Significant effects observed for habitat variables tested independently: **a)** for metapopulation B *Balanococcus diminutus*, distance from sea, **b)** for metapopulation D *Lauritrioza alacris*, elevation, **c)** for metapopulation E *Powellia vitreoradiata*, habitat type.

Expanded models – adding habitat variables to significant NH, NS and distance from road models

All four significant dispersal-based models were improved statistically by the addition of a habitat variable, as either a significant independent covariable or a interacting covariable. As an interaction effect, the addition of distance from sea improved the metapopulation A NS only model, while as an independent effect, it improved the NS only model for B; the NH only model for D was improved by the addition of elevation as an independent variable, while as an interaction effect, habitat type improved the corresponding NS only model (Fig. 3.8); for D, NS X habitat type was a better-performing model than NH + elevation (Table 3.2).

Table 3.2. Best performing (minimum adequate) models for metapopulations A, B and D a) before and b) after the addition of the significant covariables: distance from sea (sea), elevation, habitat type (hab). To enable direct comparison, for metapopulation D, the combined model (NH + NS) plus separate models (NH only, NS only) are provided for 'before' purposes. Significant results are highlighted in bold.

	a)	Metapopulation									
		A		**B**		**D**		**D**		**D**	
	model	**NS**		**NS**		**NH + NS**		**NH**		**NS**	
		resid. dev.	***p*-value**	**resid. dev.**	***p*-value**	**resid. dev.**	***p*-value**	**resid. dev.**	***p*-value**	**resid. dev.**	***p*-value**
	NULL	312.64		163.66		177.06		177.06		177.06	
effect	NH	-	-	-	-	**158.59**	**< .001**	**158.59**	**< .001**	-	-
	NS	**287.75**	**< .001**	**136.00**	**< .001**	**146.06**	**< .001**	-	-	**146.47**	**< .001**
GLM	null deviance (df)	312.64 (283)		163.66 (136)		177.06 (213)		177.06 (213)		177.06 (213)	
	resid. deviance (df)	287.75 (282)		136.00 (135)		146.06 (211)		158.59 (212)		146.47 (212)	
	AIC	291.75		140.00		152.06		162.59		150.47	
	% deviance	8%		17%		18%		10%		15%	

	b)	**Metapopulation**							
		A		**B**		**D**		**D**	
	model	**NS X distance from sea**		**NS + distance from sea**		**NH + elevation**		**NS X habitat type**	
		resid. dev.	***p*-value**	**resid. dev.**	***p*-value**	**resid. dev.**	***p*-value**	**resid. dev.**	***p*-value**
	NULL	312.64		163.66		177.06		177.06	
effect	NH	-	-	-	-	**158.59**	**< .001**	-	-
	NS	**287.75**	**< .001**	**136.00**	**< .001**	-	-	**146.47**	**< .001**
	sea	285.89	0.172	**131.72**	**0.038**	-	-	-	-
	elevation	-	-	-	-	154.15	**0.035**	-	-
	hab	-	-	-	-	-	-	-	-
	NS X sea	**270.74**	**< .001**	-	-	-	-	-	-
	NS X hab	-	-	-	-	-	-	**140.92**	**0.019**
GLM	null deviance (df)	312.64 (283)		163.66 (136)		177.06 (213)		177.06 (213)	
	resid. deviance (df)	270.74 (280)		131.72 (135)		154.15 (211)		140.92 (210)	
	AIC	278.74		137.72		160.15		148.92	
	% deviance	13%		20%		13%		20%	

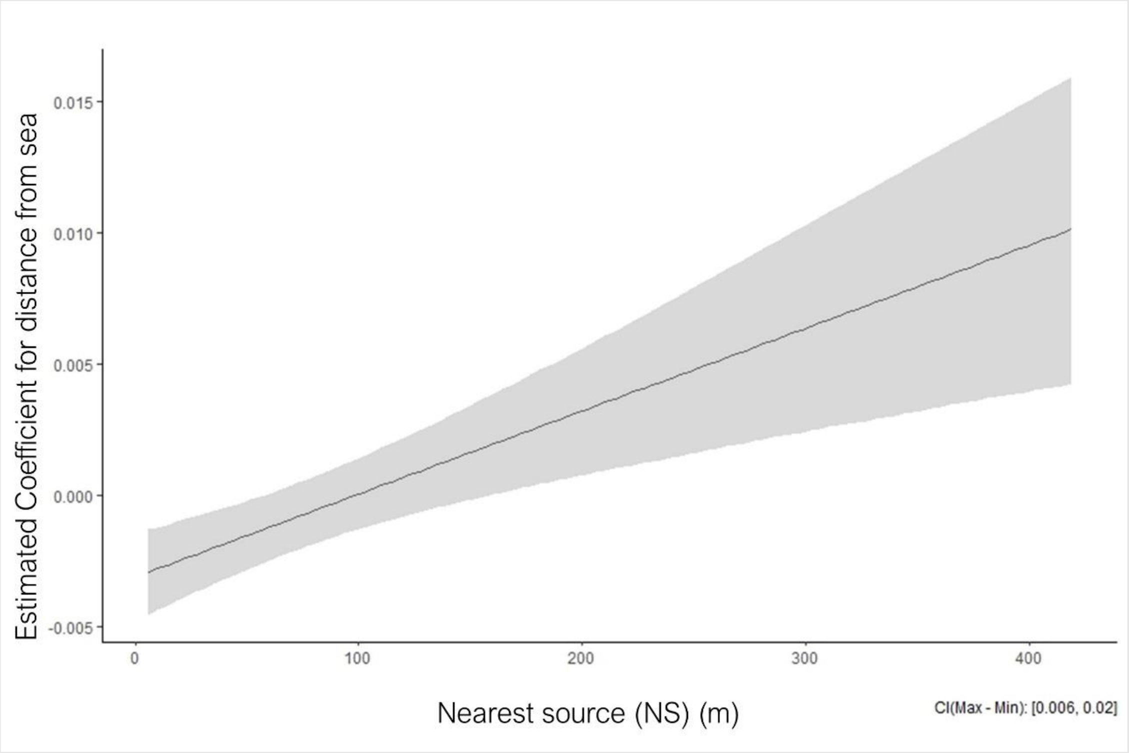


Fig. 3.8a. Interaction plot for the 2-way interaction effect of Nearest Source (NS) X distance from sea in metapopulation A model, showing that the effect of distance from sea is greater when NS is further away.

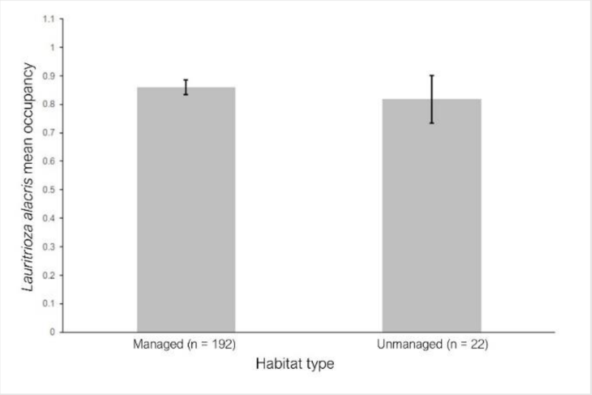


Fig. 3.8a.) Mean ±SE patch occupancy according to habitat type in metapopulation D model

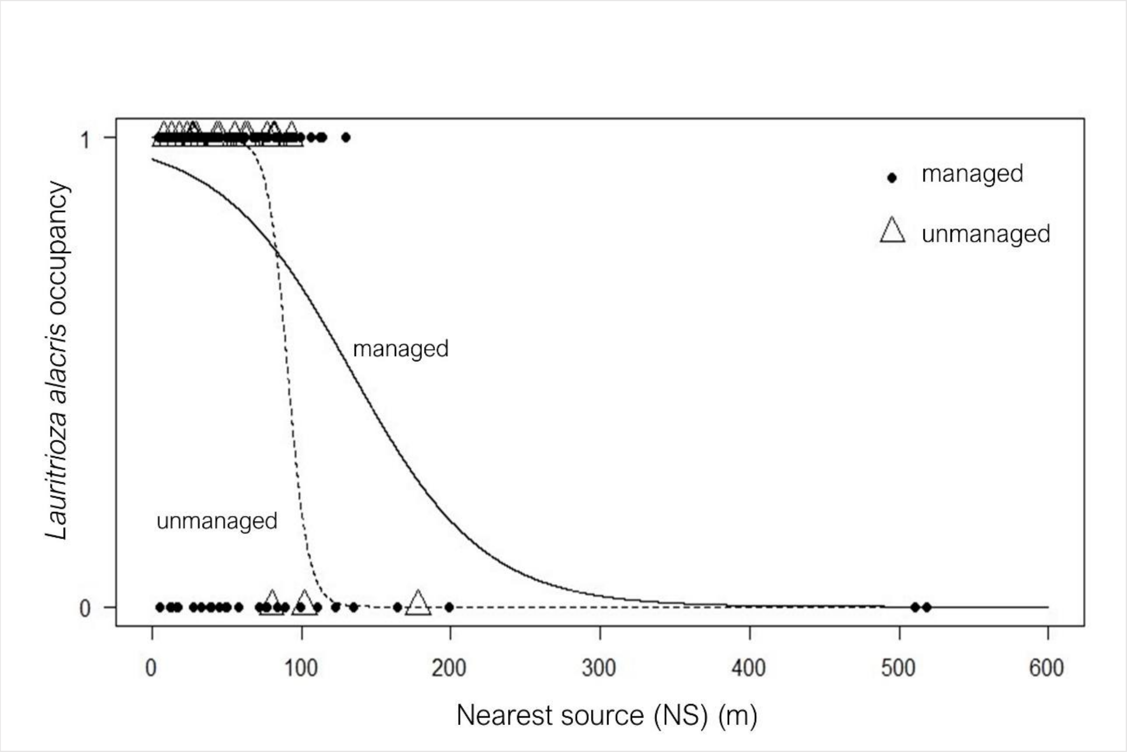


Fig. 3.8bii. The effect of habitat type on Nearest Source occupancy in metapopulation D model

Fig. 3.8. Best performing (minimum adequate) models (MAMs) for **a)** metapopulation A, and **b)** metapopulation D after the addition of the significant covariables: distance from sea (sea), elevation, habitat type (hab). For metapopulation B, best performing MAM remains as in Fig. 3.7a

3.5 DISCUSSION

It was expected that in each of the 7 metapopulations studied here, a significant effect of one or more Nearest Neighbour (NN) measures would be present, and that the effect would be strengthened by the addition of one or more habitat variables. Significant NN effects were observed for Nearest Source (NS) and/or Nearest Habitat (NH) in 3 of the 7 metapopulations. In metapopulations A (*Aculops fuchsiae*), B (*Balanococcus diminutus*) and D (*Lautitrioza alacris*), NS was significant, and in D, NH was significant also. For each significant model, the addition of a habitat variable improved the NN model, as either a significant independent covariable or a interacting covariable.

A unique strength of this analysis is that by studying multiple, independent species in the same geographical area, between-species similarities and differences in occupancy patterns can be observed. As expected, for all models in which a significant NN measure was observed, NS was found to be the better predictor. Overall, for 3 of the 7 populations, patch occupancy can be predicted by proximity of nearest occupied patch – the closer the occupied patch (NS), the more likely that patch will be occupied. These findings are consistent with metapopulation theory (Levins 1969), as well as island biogeography theory (MacArthur &Wilson 1967), supporting the premise that it is proximity to nearest population that determines colonisation rather than the availability of habitat or means of dispersal (Moilanen & Nieminen 2002; Winfree *et al*. 2005; Prugh 2009). NS distances between occupied patches in significant models are relatively similar for each metapopulation, with most distances being within the 0-c.200m range. Within the metapopulations for which the effect of NS was significant, it is the addition of habitat variables that reveals species-specific patterns.

In metapopulation A, NS was improved by the interacting effect of distance from sea, with the plot indicating that the effect of distance from sea is stronger as the greater the distance from nearest source. Distance from sea was not significant as an independent variable. There is a possibility that these results might indicate that distance from NS is correlated with microclimate suitability, with the presence of a nearby source also indicating microclimate suitability; however, any interpretation of the cause can only be speculative, and it could be due simply to the spatial structure of the metapopulations. Thus, while distance from sea is potentially confounded with NS when distance to NS is low but not when distance to NS is high, any such interaction effect of distance from sea could be seen to not add any useful explanatory power here, with the significant NS variable being the key result.

In metapopulation B, NS was improved by the addition of distance from sea as an effect, with patch occupancy shown to decrease as distance from sea increases. The metapopulation B host-plant, *Phormium tenax*, is the only host within this study in which there was an expectation of comparatively high salt tolerance (Bai *et al*. 2017), and it could be speculated that it is possible that it is has found a niche for itself in being able to tolerate conditions that other plants cannot, and that in order to exploit the plant as a food source/habitat, the mealybug *B. diminutus* has adapted accordingly to become a truly specialist phytophagous invertebrate, with its entire lifecycle being completed on the host-plant (Cox 1987; Williams & Malumphy 2012). Unless *B.*

diminutus is now dependent on coastal conditions, it would be expected to see a fairly even spread of occupied patches across the range, which is the case (Fig. 3.7a). It is possible that a bias towards coastal planting is influencing the results, with habitat patches further from the sea more widely spaced (Fig. 3.4). In all scenarios, it would be interesting to test experimentally if increased patch occupancy with closer proximity to sea is being driven to a requirement of higher salt levels on the part of *B. diminutus* (e.g. Nkem *et al*. 2006).

In metapopulation D, NS is improved by the interaction effect of habitat type, while NH is improved by the addition of elevation; however, here, the significant effects in the NH model are rendered redundant, due to NS being a stronger predictor of occupancy. Examination of the mean occupancy rates according to habitat type reveals a very slight difference between managed and unmanaged habitats, with the mean occupancy rate of managed habitats being the higher of the two, while the number of patches in managed habitats is nearly 9 times that of patches in unmanaged habitats. While the effect of habitat might be being swayed by this imbalance, the significant effect of habitat type should not be dismissed here. An unmeasured variable here is the individual size of the patch, and a possible explanation for differences according to habitat type is that in unmanaged habitats, the host-plant *Laurus nobilis* typically consist of large, mature trees, where those in managed habitats are younger, smaller plants (pers. obs.), suggesting that there might be potential differences in occupancy according to tree age/size, with the invertebrate exhibiting a preference for younger trees (e.g. Moran & Buchan 1975; Liu & Trumble 2006). An experimental approach would be required to corroborate this effect but if it is genuine, then a useful tool in mitigating the persistence of *L. alacris* populations might be in the restriction of production/trade of younger host specimens, thus over time, reducing available habitat as younger trees mature.

While no effect for any NN measure was observed for metapopulations C, E, F and G, as an independent variable, a statistically significant effect of habitat variable was observed for E (*Powellia vitreoradiata*), with mean occupancy of patches in unmanaged habitat almost twice that of patches in managed habitat; however, given the comparatively low number of habitat patches in unmanaged habitat (n=5), and as deviance explained by the model is 5% only, this result the level of ecological significance of this effect is questionable.

The lack of significance of NN measures in 4 of the metapopulations further emphasises the species-specific nature of the effects. Possible explanations for observed differences include individual species traits, such as a high dispersal level (e.g. Abbott 2011), or that the patch density is either too low or too high to provide a measurable effect, or that in species with low levels of occupancy (notably the unidentified Pittosporum scale, for which only four observations were made), there is insufficient data to provide statistical power to the results.

In all of the metapopulations, it should be acknowledged that unknown variables are potentially at play also, such as source of host-plant, length of time in location, presence/absence of invertebrate at the time of plant arrival (e.g. is invertebrate presence due to the result of spread from a nearby existing patch, or is it due to the host-plant source, e.g. garden centre, nursery, etc.?), as well as the effect of stochastic events (e.g. Haydon & Steen 1997). It is not known to what extent these factors are facilitating the species' persistence, and, in the absence of this knowledge, in order to corroborate the results provided here, an experimental approach based on the findings would be required.

It should also be recognised that further limitations exist in the form of the study's geographical scale, in that while the prescribed study area of 4 x 1km squares does incorporate most of the larger urban/suburban area in which it is located, it does not exist in isolation. It is therefore possible that important effects of other nearby patches outside the area are being overlooked, although, in the most part, it is considered that the numbers of patches are sufficiently high to allow for reliable results. What would be interesting, though, is to extend the geographic range of the study to better match the landscape variables present, e.g. to an entire, self-contained suburban/urban area, thus reducing the possibility of overlooked effects. Furthermore, in expanding the study to a meta-metapopulation scale, it is possible that some variables would be elevated in their importance. For example, it is likely that the effect of roads and other transportation means (e.g. canals, railways) as tools to dispersal will (e.g. Rudd *et al*. 2002; Angold *et al*. 2006; Hulme 2009; Shi *et al*. 2018), as would the effect of elevation (e.g. Gale 2004; Körner 2007), where the range of values would likely by larger. In contrast, it is expected that the effect of distance from sea would be of significance within a certain distance of the coast, thereafter, no effect would be expected.

In looking at the efficacy of NN measures when compared to those of more robust/sophisticated measures also based on simple occupancy models, such as those of Population viability analysis (PVA), which incorporates species-specific biological/ecological knowledge, often via the use of simulation models/computer-based packages e.g. Hanski 1994; Moilanen 1999; Lafferty & Dunne 2010; Sutherland *et al*. 2014), the observation here that NN measures were significant also without any additional variable, adds further fuel to the argument that they remain a convenient tool in their own right (Bastin & Thomas 1999; Winfree *et al*. 2005; Prugh 2009).

In conclusion, the hypothesis that patch occupancy can be predicted using NN measures is supported in 3 of the 7 metapopulations studied, and for each of these 3 metapopulations, the addition of a habitat variable provides strength to the NN effect, suggesting that the predictive power of a NN measure has the potential to be more reliable when additional variables are included also. As expected, where habitat patches are closer together the likelihood that a patch will be occupied is greater, especially if the patch is occupied; however, this effect is not universal, with species-specific effects present also, and in studying multiple independent metapopulations within the same geographical area, similarities and differences between species have been indicated, both in the efficacy of NN measures and in the added habitat variable. This study thus provides further insight into the conditions required to enable an invertebrate to establish beyond its source, and for it to persist once established. Given the potential for a non-native invertebrate to become problematic, especially as its level of presence increases, with particular regard to non-native species management, the role of metapopulation theory, including the use of simple NN measures, in predicting how host-plant presence influences a non-native species' ability to persist within an ecological community, has far-reaching, positive implications.

Chapter 4: Overlap in phytophagous invertebrate communities among native and non-native plants as a function of phylogenetic distance

4.1 ABSTRACT

An ecological community is shaped by its biotic interactions, both direct and indirect. As natural enemies of one or more host-plant species, with the exception of strictly monophagous species, phytophagous invertebrates are not confined to host-plants that align strictly with their individual native status. In a community with both native and non-native plants present, it is predicted that the more closely related a plant pair, the more likely it is that they will share one or more common enemy. Using data from comprehensive surveys of formally-planted gardens in West Cornwall, apparent competition, in the form of negative indirect interactions between native and non-native plants mediated by a shared invertebrate enemy, with the indirect interactions biased by plant relatedness, is tested. Phylogenetically ranked pairwise native/non-native plant interactions are weakly correlated with observed shared invertebrate interactions, while a significant Mantel test results indicates a significant potential for apparent competition. Findings here provide original insight into how invertebrates and plants interact in an ecological community, and how these interactions help to structure the community.

4.2 INTRODUCTION

An ecological community is shaped by its biotic interactions (e.g. Loreau *et al*. 2001; Bruder *et al*. 2019), and, in addition to the direct effect of one species on another (e.g. predation, parasitism, herbivory), the presence of indirect effects are widely recognised (e.g. Holt 1984; Wootton 1994; van Veen *et al*. 2006b; White *et al*. 2006), particularly the presence of negative indirect effects as apparent competition, whereby a species is negatively affected by a second species due to the actions of a third, mediating species (e.g. Wootton 1994; Menge 1995).

As natural enemies of one or more host-plant species, with the exception of strictly monophagous species, phytophagous invertebrates are not confined to host-plants that align strictly with their individual native status, i.e. a non-native plant might serve as a host for a native invertebrate, and a native plant might serve as a host for a non-native invertebrate (Agosta 2006). In either scenario, the involvement of a novel associate is required. In the case of a native plant serving as a host for a novel non-native invertebrate, a host shift or expansion on the part of the invertebrate has occurred. Thus, in addition to the direct effect of acquiring a novel enemy, in the sharing of a natural enemy with a non-native plant species, there exists the potential for a negative ecological interaction, i.e. 'apparent competition', in the form of a negative indirect effect between the non-native invertebrate and the native plant, mediated by the presence of a non-native plant.

4.2.1 Invertebrate-plant associations

Numerous influences and concepts have been proposed/argued as explanations as to how specific invertebrate-plant associations arise. Known influences include plant defences, biogeography, individual/population variation and host-plant phylogeny (e.g. Dethier 1941; Ehrlich & Raven 1964; Bernays & Chapman 1994; Beccera 1997; Janz & Nylin 1998; Percy *et al*. 2004; Joy & Crespi 2012), while concepts include 'bi-/tri-trophic niche hypotheses' (see Singer & Stireman 2005), ecological fitting (Janzen 1980, 1985), island biogeography (MacArthur & Wilson 1967), the 'oscillation hypothesis' (Janz & Nylin 2008), and the 'parasite paradox' (Agosta *et al*. 2010; Janz 2011). As such, it is generally accepted that invertebrate-plant associations are the consequences of dynamic combinations of various evolutionary and ecological processes, rather than solely the result of a shared, close evolutionary history, as traditionally perceived (e.g. Ehrlich & Raven 1964; Agrawal *et al*. 2006). Although recent research has focused more on the utilisation of advances in the application of molecular data (e.g. Wirta *et al*. 2014; Ouvrard *et al*. 2015; see also Von Dohlen & Moran 2000; Percy *et al*. 2004), it would seem that there is still no 'once size fits all' mechanism in action.

Plants possess a variety of cues/defence strategies, such as physical barriers, noxious chemicals and phenological constrictions, which serve as a deterrent/barrier to phytophagy from 'the wrong invertebrate species' by determining whether or not an invertebrate species is able to find, select or consume the particular plant (e.g. Dethier 1941; Ehrlich & Raven 1964; Becerra 1997; Renwick 2001; Chapman 2003; Agrawal

2007; McCormick *et al*. 2012). There is a proclivity for phytophagous invertebrates to have phylogenetically structured/restricted diets: specialist phytophagous invertebrates (monophagous and oligophagous species) feed on plants that are closely related (at a minimum of family level) and although considered generalists, host-plant choice in a polyphagous invertebrate species (defined here as those which feed on plants from 3 or more families) can still be fairly conservative in their host-plant choice, with highly polyphagous species being relatively few (e.g. Ødegaard *et al*. 2005; Futuyma & Agrawal 2009). The strength of a plant's cues/defence strategies are recognised as being stronger for co-evolved specialist invertebrate species than for generalist species (Keane & Crawley 2002; Tanzentzap *et al*. 2011), and thus, plant defence has traditionally been considered key in determining an invertebrate's ability to select a plant as a suitable host (e.g. War *et al*. 2018).

4.2.2 Plant phylogenetic relatedness and invertebrate host shifts/expansions

Plant phylogeny is representative of a species' evolutionary history, and is deemed a reliable proxy for plant defence traits, roughly correlating with physical, chemical, and/or phenological characteristics (e.g. Webb *et al*. 2002; Cavender-Bares *et al*. 2009; Dinnage 2013 but see e.g. Carmona *et al*. 2011; Schuldt *et al*. 2012, 2014). Thus, characteristics of closely phylogenetically related plant species are likely to be more similar than those which are phylogenetically distant. With the ability of a non-native invertebrate species to survive in a new environment being facilitated by resource and habitat suitability, the more closely phylogenetically related a potential new host-plant is to the invertebrate's co-evolved host-plant, the more likely a successful move to that novel native host-plant will be (Janz & Nylin 2008). As such, plants that are more closely phylogenetically related have a greater tendency to share phytophagous invertebrates than plants that are less closely phylogenetically related (e.g. Ness *et al*. 2011; Agrawal & Kotanen 2003; Percy *et al*. 2004; Ødegaard *et al*. 2005; Agosta 2006; Winkler & Mitter 2008; Dawson *et al*. 2009; Futuyma & Agrawal 2009; Gossner *et al*. 2009; Gilbert *et al*. 2015).

While there are a number of examples of invertebrate host shifts/expansions observed between plants which are more distantly phylogenetically related, most recognised host shifts/expansions occur between congeners and confamilials (e.g. Dethier 1954; Mitter & Farrell 1991; Janz & Nylin 1998; Winkler & Mitter 2008). As generalist species have less restricted dietary requirements, opportunities for host shifts/expansions will normally be greater than for specialist species, especially in the absence of closely-related native plant species to a specialist's co-evolved host-plant (Keane & Crawley 2002; Lau *et al*. 2008).

4.2.3 Study model/hypothesis

Thus, it is expected that in an ecological community with both native and non-native plants present, the more closely phylogenetically related native/non-native plant species there are present, the greater the opportunity for host shifts/expansions by both specialist and generalist invertebrate species, resulting in an overall greater likelihood of shared associated invertebrate species between native and non-native plants (e.g. Gilbert & Webb 2007; Dawson *et al*. 2009; Ness *et al*. 2011). Thus, the likelihood of indirect interactions in a food web increases the more closely related the community (Elias *et al*. 2013; Carvalheiro *et al*. 2014). It is therefore hypothesised that the likelihood of one or more natural enemies being shared by a native/non-native pair of plants increases, the more closely related the plants are to one another. While there are numerous examples of studies demonstrating that a greater overlap in interaction partners occurs in more closely related taxa (e.g. Bersier & Kehrli 2008; Rezende *et al*. 2009; Cagnolo *et al*. 2011; Elias *et al*. 2013; Carvalheiro *et al*. 2014), it is believed that this is the first time that anyone has specifically investigated the potential for indirect interactions between native and non-native plants mediated by a shared invertebrate enemy, that are biased by plant relatedness.

4.3 METHODS

4.3.1 Data collection

During the period June to September 2015, seven formally-planted public gardens within a 3.5 km radius of Penzance, West Cornwall, UK were surveyed (for garden details, see Chapter 2). All plants and phytophagous arthropods (insect phloem/xylem (sap)-feeders, leaf-feeders, gall-causers, leaf-miners and case-makers, and arachnid gall-causers, henceforth referred to as 'invertebrates') observed in association with the plants at the time of the survey were recorded. Recording took place via 1 to 3 visits per garden, with visits of more than 1-day duration occurring no more than 2 days apart. All visits were made in warm, sunny weather conditions.

All vascular plants – both intentionally and unintentionally planted – present within each garden at the time of the visit were recorded. Plants were identified to a minimum of genus level but to species level wherever possible. Each identified plant was subsequently allocated to a designated ‘Plant Taxonomic Unit’ (PTU), consisting of either a single species or a group of congeners of the same native (N) or non-native (NN) status and plant type (e.g. small shrub, large tree, etc.); exceptions to this are 4 PTUs where 1 or more of the former congeners has subsequently undergone a taxonomic change or where a single species has subsequently been split into several novel genera (Appendix I). Where known and where both were present, recognised cultivars/varieties were recorded as a separate PTU from the originating species – the reason being that potential differences in invertebrate-plant associations could be better accounted for.

At the same time as plant presence/area coverage was measured, an inventory of phytophagous invertebrates present on each PTU was created. Any individual exhibiting phytophagy was noted. Invertebrates were identified to species level where possible, and life-stage was noted also. Leaf-miners, case-bearers and gall-causers were identified mostly based on host-plant and mine/gall morphology, with identification of cryptic species confirmed by rearing. All visible parts of the plant were examined for invertebrate presence: foliage, stems, trunks, bark, flowers, etc.; however, for consistency and practicality, visual inspection only was used to assess invertebrate presence, i.e. no beating, digging of roots, dissection of stems or similar was performed. Where there was more than one occurrence of a PTU within a garden, a similar proportion of each occurrence was inspected. To standardise methodology, only foliage up to approx. 3m from the ground was inspected.

4.3.2 Additional data

Post-survey, additional data were sought for each Plant Taxonomic Unit (PTU) and each invertebrate, as follows:

Up-to-date plant nomenclature/taxonomic classification was determined using primarily Stace (2019) and POWO (2019) (plants), and individual sources (invertebrates), supplemented by Catalogue of Life: 2018 Annual Checklist (Roskov *et al.* 2018). Post-survey changes have subsequently been incorporated, and noted accordingly, as have disputed/ambiguous names (Appendix I, Appendix II). Taxonomic classification is presumed to be an accurate representation of plant phylogeny (see Hinchliff *et al*. 2015; Kozlov *et al*. 2016). Native/non-native status of each PTU/invertebrate was established using the Non-native Species Secretariat (NNSS) GB Non-native Species Information Portal (NNSIP) (http://www.nonnativespecies.org/) as the primary authority, supplemented by interrogation of POWO (2019) for additional detail (plants), and consultation of individual sources for data-deficient invertebrate species.

In order to remove possible error due to the presence of accidental/casual feeders/potential incidentals not previously disregarded, a flow-chart of non-subjective questions (Fig. 4.1) was used to refine observed PTU/invertebrate pairings by determining which pairings should be retained as reliable associations, and which should be removed from analyses as less reliable associations.

Garden-level data was collated to form a single dataset. For both the observed dataset and the refined dataset, details of every PTU-host/invertebrate association that occurred were extracted. Using these data subsets, lists of all native/non-native (N-NN) PTU pairings with a shared associated invertebrate (consumer overlap pairings) were used to create two matrices of pairwise associations between each native and non-native PTU, with numbers representing the total number of invertebrate species shared by a PTU pairing. Similarly, a matrix of phylogenetic relatedness between each native and non-native PTU was created using the following rank values: same Subspecies = 0, same Species = 1, same Genus = 2, same Family = 3, same Order = 4, same Superorder = 5, same Subclass = 6, same Class = 7, same Kingdom = 8.

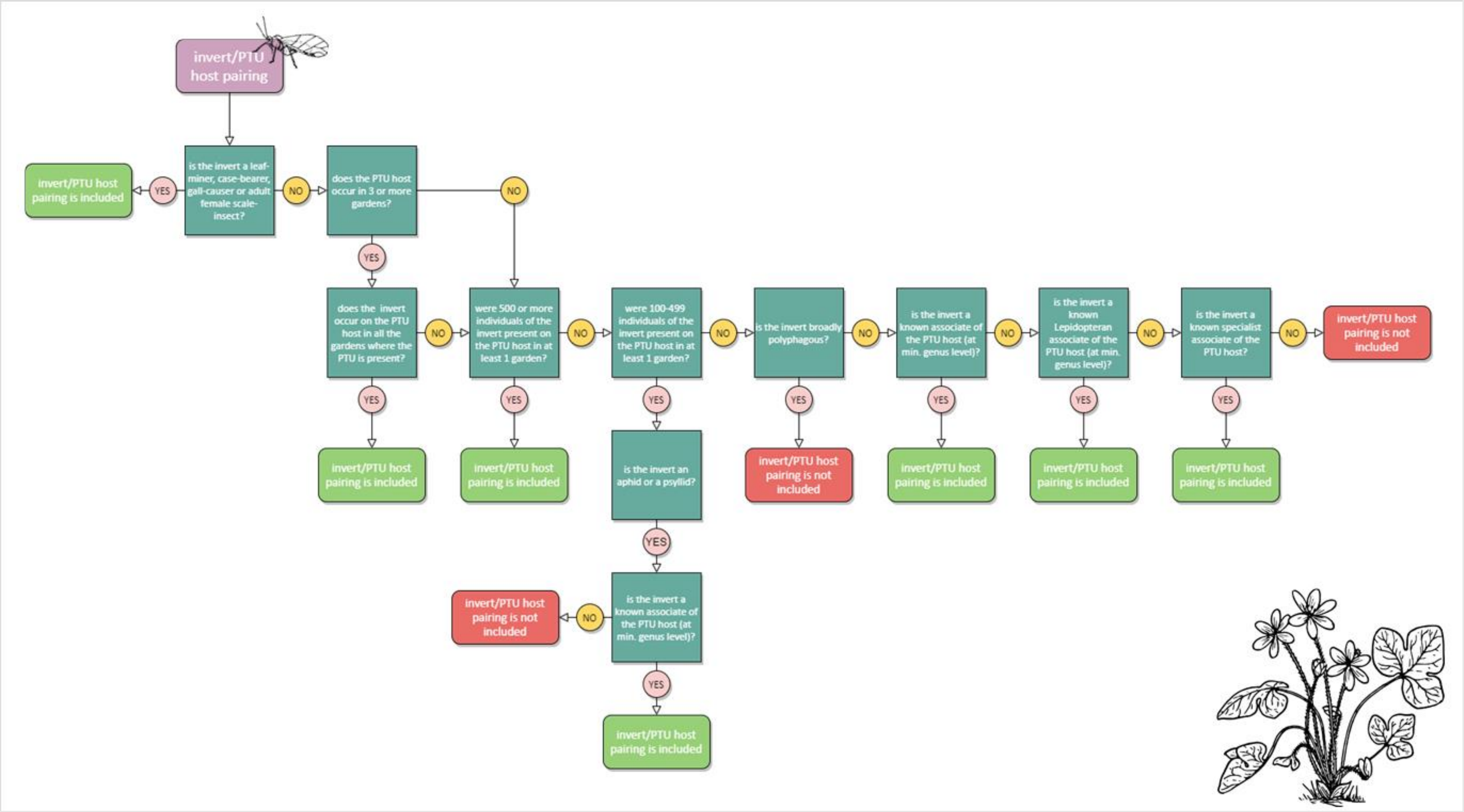


Fig. 4.1. Flow-chart of non-subjective questions used to determine which Plant Taxonomic Unit (PTU)/invertebrate pairings should be retained, and which should be removed from analyses due to possible incidental/casual feeding partnership.

4.3.3 Data analysis

All statistical analyses were performed using R (v 3.6.1) (R Core Team 2019). Visualisation of shared invertebrate species via a consumer overlap graph was produced using igraph package (Csardi & Nepusz 2006). To test for significance of association between each PTU-host/invertebrate associations matrix and the phylogenetic relatedness matrix, the Mantel test of matrix correlation was performed using vegan package (vegan 2.5.6) (Oksanen *et al*. 2019). Results for both observed data and refined data were compared. Mean phylogenetic relatedness ranking of all potential N-NN consumer overlap pairings and of all realised N-NN PTU pairings was calculated respectively for both observed data and refined data.

4.4 RESULTS

4.4.1 Descriptive statistics

124 native (N) PTUs, 266 non-native (NN) PTUs, and 20 PTUs of unknown native status were recorded, while 86 native invertebrate species, 23 non-native invertebrate species, and 7 invertebrate species of unknown native status were observed in association with one or more PTU, resulting in 212 invertebrate-PTU pairs. 85 PTUs were observed sharing an invertebrate with 1 or more other PTUs, resulting in 858 consumer overlap pairings, involving 23 invertebrate species. N-NN pairings (344) represented 40.1% of all (858) refined pairings, and involved 19 native PTUs and 34 non-native PTUs. Following application of the data refining process for each invertebrate-PTU pair (Fig. 4.1), 48 invertebrate-PTU pairs were disregarded; additionally, 8 invertebrate-PTU pairs involving the 7 invertebrate species of unknown native status were disregarded due to deficient data. Consequently, 688 consumer overlap pairings were disregarded, leaving 57 PTUs sharing an invertebrate with 1 or more other PTUs, resulting in 170 pairings, involving 21 invertebrate species. N-NN pairings (70) represented 41.2% of all (170) refined pairings, and involved 14 native PTUs and 32 non-native PTUs. Maximum possible distinct N-NN pairings (124 x 266) = 32984, with realised observed pairings (344) representing 1.0%, and realised refined pairings (69) representing <1%. (Table 4.1).

Table 4.1. Comparative summary of observed and refined data: a) Plant Taxonomic Unit (PTU) and invertebrate presence, b) All (ALL) and native-non-native (N-NN) consumer overlap pairings, and c) realised consumer overlap pairings as a percentage of maximum possible pairings.

Table 4.1a. A summary of PTU richness, invertebrate species richness, invertebrate-PTU associations, and consumer overlap pairings.

	Observed		**Refined**	
PTU richness	**no.(%) total=410**		**no.(%) total=410**	
native (N)	124 (30%)		124 (30%)	
non-native (NN)	266 (65%)		266 (65%)	
unknown status	20 (5%)		20 (5%)	
Invertebrate species richness	**no.(%) total=116**		**no.(%) total=105**	
native (N)	86 (74%)		82 (78%)	
non-native (NN)	23 (20%)		23 (22%)	
unknown status	7 (6%)		-	
Invertebrate-PTU associations	**no.(%) total=212**		**no.(%) total=156**	
native invert/native PTU	75 (35%)		64 (41%)	
native invert/non-native PTU	76 (36%)		41 (26%)	
non-native invert/native PTU	8 (4%)		8 (5%)	
non-native invert/non-native PTU	45 (21%)		43 (28%)	
unknown invert/native PTU	1 (0%)		-	
unknown invert/non-native PTU	7 (3%)		-	
PTUs in a consumer overlap pairing	**no.(%) total=85**	**21% all PTU richness**	**no.(%) total=57**	**14% all PTU richness**
native	23 (27%)	19% all native PTU richness	16 (28%)	13% all native PTU richness
non-native	62 (73%)	23% all non-native PTU richness	41 (72%)	15% all non-native PTU richness

Table 4.1b. Consumer overlap pairings – ALL pairings and N-NN pairings.

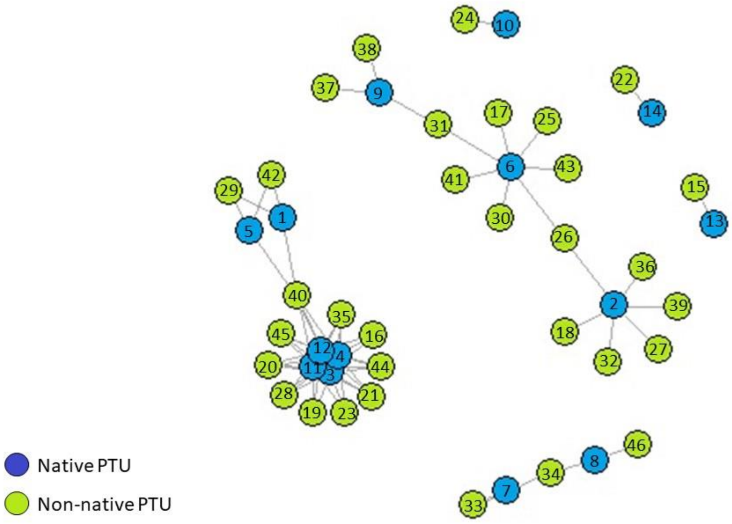
PTU pairing	consumer overlap pairings (distinct PTU pairs) – ALL invertebrates		consumer overlap pairings (distinct PTU pairs) – native invertebrates		consumer overlap pairings (distinct PTU pairs) – non-native invertebrates	
	Observed	**Refined**	**Observed**	**Refined**	**Observed**	**Refined**
ALL	858 (852)	170 (169)	785 (785)	102 (102)	73 (73)	68 (68)
N-NN	344 (344)	70 (69)	320 (320)	46 (46)	24 (24)	24 (24)

Table 4.1c. Realised consumer overlap pairings as a percentage of maximum possible pairings.

PTU pairing	no. of PTU (ALL)	no. of PTU (N)	no. of PTU (NN)	max. poss. pairings	observed pairings	%age max. pairings	refined pairings	%age max. pairings
ALL	390			151700	852	0.6%	169	<1%
N-NN		124	266	32984	344	1.0%	69	<1%

4.4.2 Consumer overlap graph and invertebrates shared

Using refined data only, a consumer overlap graph was produced for all native/non-native PTU pairs that shared 1 or more invertebrate species (Fig. 4.2). The force-directed Fruchterman-Reingold layout algorithm, whereby nodes are positioned to enable as few crossing edges (lines) as possible, allows for clearer visualisation of potential patterns in invertebrate-sharing by PTUs.



Key

1	*Hedera helix, H. hibernica*
2	*Ilex aquifolium*
3	*Jacobaea vulgaris, Senecio vulgaris*
4	*Lapsana communis*
5	*Leucanthemum vulgare*
6	*Lonicera periclymenum*
7	*Malva arborea*
8	*Papaver rhoeas*
9	*Quercus robur*
10	*Raphanus raphanistrum subsp. maritimus*
11	*Sonchus asper, S. oleraceus*
12	*Taraxacum officinale agg.*
13	*Tilia cordata, T. platyphyllos, T. × europaea*
14	*Tripleurospermum maritimum*
15	*Acer pseudoplatanus*
16	*Armoracia rusticana*
17	*Buddleja davidii*
18	*Camellia japonica, Camellia*
19	*Centaurea cyanus*
20	*Cymbalaria muralis*
21	*Cynara cardunculus*
22	*Echinops bannaticus*
23	*Erigeron glaucus*
24	*Erysimum cheiri*
25	*Escallonia rubra var. macrantha*
26	*Euonymus*
27	*Euonymus japonicus*
28	*Helminthotheca echioides*
29	*Hydrangea*
30	*Leycesteria formosa*
31	*Ligustrum ovalifolium*
32	*Luma apiculata*
33	*Malva sylvestris*
34	*Olearia macrodonta, O. paniculata, O. traversiorum, Olearia*
35	*Papaver somniferum*
36	*Pittosporum crassifolium, P. tenuifolium*
37	*Quercus ilex*
38	*Quercus pubescens*
39	*Rhododendron*
40	*Roldana petasitis*
41	*Sedum kimnachii, S. spectabile*
42	*Sorbus*
43	*Symphyotrichum*
44	*Tanacetum parthenium*
45	*Valeriana rubra*
46	*Viburnum*

Fig. 4.2. Consumer overlap graph for all native/non-native PTU pairs sharing 1 or more invertebrate species, produced using the force-directed Fruchterman-Reingold layout algorithm. Nodes represent PTUs and lines represent consumer overlap pairings.

12 invertebrate species were shared by native/non-native PTU pairs: 6 native and 6 non-native. Of the 6 native species, 2 were aphids: *Aphis (Aphis) fabae*, *Brachycaudus (Prunaphis) cardui*, (Order: Hemiptera), 1 was a leafhopper: *Eupteryx melissae* (Order: Hemiptera), and 3 were leaf-mining flies: *Aulagromyza cornigera*, *Chromatomyia 'atricornis'*, *Scaptomyza flava* (Order: Diptera). Of the

6 non-native species, 3 were aphids: *Macrosiphum (Macrosiphum) euphorbiae*, *Myzocallis (Myzocallis) boerneri*, *Myzus (Nectarosiphon) persicae* (Order: Hemiptera), 2 were scales: *Pulvinaria floccifera*, *Pulvinaria regalis* (Order: Hemiptera), and 1 was a moth (larval form): *Epiphyas postvittana* (Order: Lepidoptera).

4.4.3 Mantel test of matrix correlation

For both observed data and refined data, results of the Mantel test are statistically significant; however, the correlation between the two is weak, as indicated by the low R coefficient (observed data: Mantel statistic based on Pearson's correlation coefficient R: 0.0473, $p = 0.004$; refined data: Mantel statistic based on Pearson's correlation coefficient R: 0.05806, $p < .001$). For each test, 9999 permutations were specified. As a means of illustrating this result, a comparison of mean ±SE phylogenetic relatedness ranking of maximum possible N-NN pairings, observed realised N-NN pairings and refined realised N-NN pairings is shown (Fig. 4.3). N-NN consumer overlap pairings mean mean phylogenetic relatedness ranking of maximum possible N-NN consumer overlap pairings (n=32984) is 6.78 ±SE 0.01. For observed data, mean phylogenetic relatedness ranking of all realised N-NN PTU pairings (n=344) is 6.17 ±SE 0.08. For refined data, mean phylogenetic relatedness ranking of all realised N-NN PTU pairings (n=69) is 4.61 ±SE 0.21.

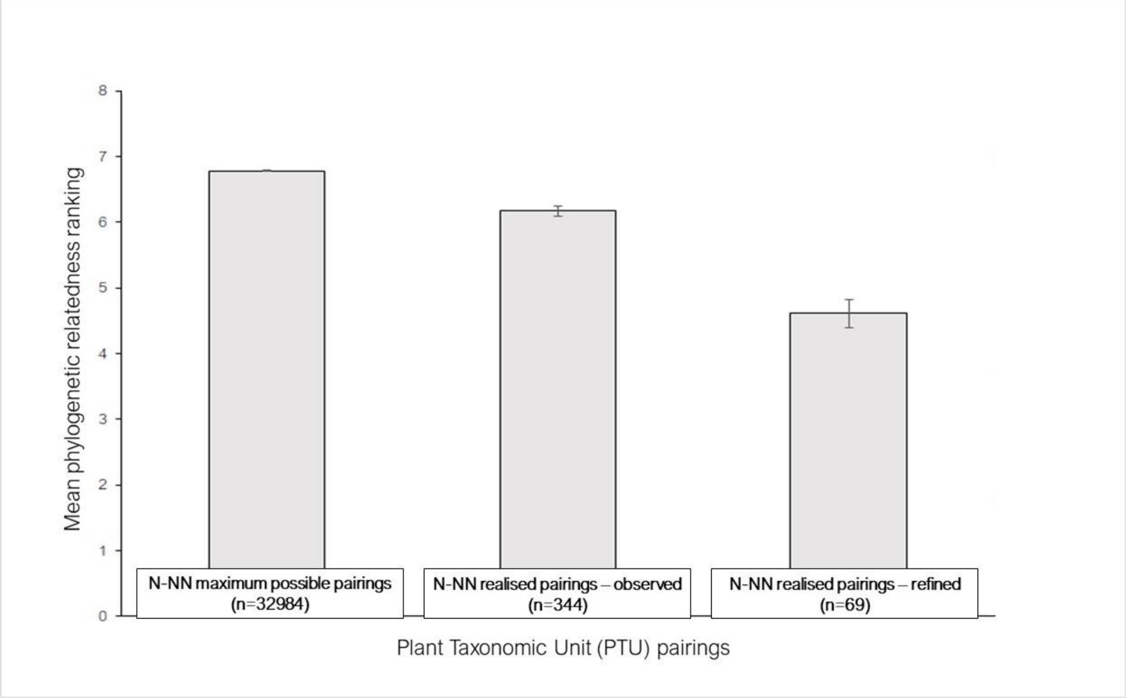


Fig. 4.3. Comparison of mean ±SE phylogenetic relatedness ranking of all maximum possible N-NN consumer overlap pairings, all observed realised N-NN consumer overlap pairings, and all refined realised N-NN consumer overlap pairings.

4.5 Discussion

It was hypothesised that the likelihood of one or more natural enemies being shared by a native/non-native pair of plants increases, the more closely related the plants are to one another, and as such, it was expected that a statistically significant relationship between native and non-native plant pair relatedness and the presence/absence of a shared invertebrate would be seen. While a significant Mantel test result was observed, a weak correlative effect was indicated. This suggests that, importantly, while the mean predictive power of relatedness is limited, there does exist a significant potential for the presence of apparent competition between native and non-native plants, in the form of an (invertebrate) enemy-mediated negative indirect effect.

Little is known regarding the influence of plant phylogenetic relatedness as an agent of bias in indirect interactions, and in order to verify the existence of such apparent competition here, a within-network experimental approach (e.g. Henneman & Memmott 2001; Morris *et al*. 2004) would be required, such as one in which plant pairs are artificially manipulated to test for correlative effects of plant phylogenetic relatedness on host switching/expansion in native/non-native invertebrates. Comparing these results with those of others who have investigated phylogenetic relatedness of a plant pair as an indirect effect, in their meta-analysis of 750 plant-pollinator networks, Carvalheiro *et al*. (2014) observed that the probability of a pair of plant species sharing a pollinator was lower the more distantly related the pair, although they found no effect of plant origin (native or non-native), while in a multi-trophic local network, Elias *et al*. (2013) found a positive correlation between plant species relatedness and aphid consumer overlap; however, in contrast with these results, in neither study was a distinction in the results given according to the native status of each plant within a pair.

The single-visit method of data collection used here means that there is a possibility that invertebrates observed on plants were not actually feeding, leading to the question of how much error would there be in retaining all the data. After testing both observed data and a carefully refined dataset, the results were very similar, suggesting that the level of potential error is low. For both observed and refined data, the Mantel test statistic was significant but correlation coefficient R values were low, indicating a weak correlation. The R value for refined data is slightly higher than for observed data, and the corresponding mean PTU phylogenetic ranking value is lower for refined data than for observed data. In both cases, PTU phylogenetic ranking values are lower than that pertaining to the maximum possible number of pairings. Further examination of the mean phylogenetic ranking values reveals that, although there are between-group differences in the means, the ranking values are indicative of relatively low taxonomic relatedness, with the mean value for refined data (4.61) representing mean relatedness at the Order-Superorder level. With most recognised host shifts/expansions reported as occurring between congeners and confamilials (e.g. Dethier 1954; Mitter & Farrell 1991; Janz & Nylin 1998; Winkler & Mitter 2008), a lower mean phylogenetic ranking value might have been expected, and a possible explanation for the results seen here, is that at least some of the invertebrates involved here are extreme generalist species, and that this is what is driving the result.

Using the refined dataset, looking more closely at the mean phylogenetic ranking values according to PTU pairs sharing a single invertebrate species, mean and/or mode phylogenetic ranking values of the corresponding plant pairs for 6 of the 12 invertebrate species are 3 or below, representing at least a confamilial relationship between the PTU pairs, while for the remaining invertebrate species, means and/or modes are above 3, representing a relationship at or above Order level. For most invertebrates recognised as specialists, corresponding PTU pairs have mean/mode values 3 or below; however, the exception to this is the aphid *Myzus persicae*, for which the mean value is 4.5 (mode n/a). The species, for which the corresponding PTU pairs have the highest mean/mode values (both 7) is the native generalist aphid *Aphis fabae*, representing two Class-level pairings. Furthermore, despite the same ratio of generalist and specialist invertebrates per native/non-native grouping, overall, PTU pairs sharing a native invertebrate have lower mean/mode values than those sharing a non-native invertebrate. For one non-native invertebrate species only (the specialist aphid *Myzocallis boerneri*), the mean/mode of the corresponding PTU pairs is 3 or below. This suggests that, although here, it is a native species that is associated with the highest mean/mode values, this is an exception, and it is non-native invertebrates that are exhibiting a more extreme generalist tendency than native species, and in the absence of directly comparable findings, it would be interesting to see if this pattern is replicated in future studies.

The Fruchterman-Reingold visualisation of how invertebrates are being shared by N-NN PTU pairs, as provided by the consumer overlap figure (Fig. 4.3), is a helpful tool in further attempting to make sense of why the R value provided by the Mantel test is low, and in suggesting further lines of enquiry (see Traud *et al*. 2009). Clear clusters/connected groups of PTUs are shown, mostly depicting radial groups of non-native PTUs connecting to a comparatively low number of native PTUs. Close examination of the source data reveals that in all but two of the clusters/connected groups, it is a single invertebrate species being shared, the exceptions being #6 *Lonicera periclymenum*, which shares 1 invertebrate with 1 non-native species and a second with 5 non-native species, and #2 *Malva arborea*, which shares 1 invertebrate with 1 non-native species and 1 with another. In all cases, the number of non-native PTUs involved in the sharing of a single invertebrate species is equal to or greater than the number of equivalent native PTUs involved, with the ratio of non-native to native being generally greater for shared non-native invertebrates than for native invertebrates. For native invertebrates, 4 of the 6 species are each shared by a single N-NN PTU pair, 1 is shared by 1 N/2 NN PTUs, and 1 is shared by 4 N/10 NN PTUs. In contrast, for non-native invertebrates, 2 of the 6 species are each shared by a single N-NN PTU pair, 1 is shared by 1N/2NN PTUs, 1 by 1N/3NN PTUs, 1 by 1N/5NN PTUs and 1 by 1N/5NN PTUs.

If PTU pairs sharing a native invertebrate are more closely phylogenetically related than those sharing a non-native invertebrate, extrapolating further from these observations, it can be reasoned that if more non-native invertebrates than native invertebrates exhibit extreme generalist behaviour, and if more non-native than native PTUs are involved in N-NN PTU pairs, that not only will this lead to an imbalance in the level of phylogenetic relatedness in the paired PTU data, with fewer native PTUs sharing fewer (extreme) generalist species) but that this imbalance will impact on mean/mode values also, thus negatively affecting any potential correlative effect. What this suggests is that the predictive power of phylogenetic relatedness might be stronger when a native invertebrate rather than non-native invertebrate is being shared, and it would be interesting to address these potential differences in future studies.

It is worth re-emphasising that this study is an examination of the potential for apparent competition in the form of a negative indirect effect mediated by a shared invertebrate, and that while the percentage of realised N-NN pairings here is 1% or lower, meaning that the probability of any given random N-NN PTU pair being engaged in apparent competition is comparatively low, importantly, because the number of maximum possible PTU pairings is itself high, the potential likelihood of apparent competition between N-NN PTU pairs occurring here is also high. Furthermore, this study uses data from a single, whole community, enabling examination of the potential for invertebrate-sharing between co-occurring plants. A similar study with a wider geographical scale would likely reveal native plants that are more closely-related to the non-native plants present, and as such, a greater chance of one or more invertebrates being shared might thus be provisioned; however, as the point of interest here is the potential for indirect population interactions in an ecological community, rather than an examination e.g. of the risk of vectoring invasive invertebrates at a national scale (e.g. Brancatelli & Zalba 2018), for which a phylogenetic signal would also be expected (e.g. Chown *et al*. 2015; Roe *et al*. 2018), this study is deemed to be at the appropriate scale.

Additionally, it is acknowledged that with taxonomic relatedness being used as a crude representation of phylogenetic relatedness, it could be argued that a more reliable alternative would be the use of genetic divergence as a measure; however, as taxonomy is considered a both a reliable proxy and more easily-accessible, ‘user-friendly’ measure (see Hinchliff *et al*. 2015), with ranked relatedness calculated incorporating any recent changes (e.g. Stace 2019), there is no reason to expect different results, and the use of a less crude method is considered unlikely to enhance the result’s R value(s).

In conclusion, while the weak correlation coefficient(s) in the statistical analyses suggest that the mean predictive power of relatedness is limited, the Mantel test result(s) indicate that there is a significant potential for the presence of apparent competition. Results from this study provide fuel for further investigations, including exploring patterns in resource overlap between native and non-native invertebrates, repeating the tests using observational data from comparable ecological communities to observe if statistical results and patterns shown here are replicated elsewhere, and, importantly, experimental manipulations of within-network interactions to verify the presence of apparent competition. Furthermore, implications of these findings in their potential to better predict host-switching/expansion, particularly in non-native invertebrates, is far-reaching, contributing to an improved ability to reliably assess a plant’s susceptibility to herbivory, or to mitigate an invertebrate’s presence via removal or introduction of a plant, based on its relatedness to other plants present. Of particular note, is that, while it is widely acknowledged that a greater overlap in interaction partners occurs in more closely related taxa (e.g. Bersier & Kehrli 2008; Rezende *et al*. 2009; Cagnolo *et al*. 2011; Elias *et al*. 2013; Carvalheiro *et al*. 2014), the potential for indirect interactions between a native and a non-native plant mediated by a shared invertebrate enemy, that are biased by plant relatedness seems not to have been previously studied. This means that the findings here provide original insight into how invertebrates and plants interact in an ecological community, and how these interactions help to structure the community.

Chapter 5: Seeking evidence for indirect ecological effects in a gall wasp community

5.1 ABSTRACT

While the direct effect of a non-native species on a native species has been widely studied, indirect effects are less often considered. Indirect effects can be negative or positive. The presence of apparent competition in a gall wasp community is tested, in the form of the negative indirect effect of a non-native plant on a native plant, mediated by a non-native gall wasp, and in the form of the negative indirect effect of a non-native gall wasp on a native gall-wasp, potentially mediated by the modifying presence of one or more shared parasitoids. No evidence is found to support the overall hypothesis of the presence of apparent competition; however, potential evidence for the unexpected occurrence of apparent mutualism is provided. How these findings contribute to a better understanding of interactions within a gall wasp community, and the broader implications is discussed.

5.2 INTRODUCTION

An ecosystem persists by means of the dynamic effect of a multitude of biotic and abiotic interactions. Interspecific biotic interactions are either direct, e.g. a plant-pollinator relationship or a predator-prey relationship, or indirect – whereby the presence of one species affects the presence of another species but only when mediated by a third species.

While the direct effect of a non-native species on a native species has been widely studied, indirect effects are less often considered (reviewed White *et al*. 2006). For example, the presence of a non-native species within an ecological community might give rise to ‘apparent competition’ by causing an increase in the native species’ natural enemies, or by negatively altering the native species’ habitat requirements (e.g. Wootton 1994; Chaneton & Bonsall 2000; Dangremond *et al*. 2010). In phytophagous invertebrate communities, an increase in a species’ susceptibility to parasitoid attack might be caused by the arrival of a second host, with the latter increasing overall availability of resources for the parasitoid, which, in turn, leads to an increase in the parasitoid's numbers, subsequently leading to an increase in parasitoid attack of both hosts (e.g. Holt 1977, 1984; Settle & Wilson 1990; Wootton 1994; Denno *et al*. 1995; reviewed Bonsall & Hassell 1999; Chaneton & Bonsall 2000; van Veen *et al*. 2006a, 2006b; Kaser & Ode 2016). While indirect effects such as those mediated by a shared enemy, are often reciprocally negative (apparent competition), effects can alternatively be positive (apparent mutualism) or neutral (amensalism), or a combination thereof (Kaser & Ode 2016 and references therein). Thus, indirect interactions play a fundamental role in ecosystem structure, and, as well as leading to the exclusion of the less dominant species, can, alternatively, beget coexistence between species (e.g. Sanders & van Veen 2012).

5.2.1 Gall wasps

Gall wasps (Hymenoptera: Cynipidae, Tribe Cynipini) are a large group of gall causers (c. 1000 species worldwide (Abe *et al*. 2007)), members of which induce gall growth in plants from the Fagaceae family, with most species being associated with one or more species of oak (*Quercus* spp.). Gall wasps exhibit heterogony, in that, for the most part, two distinct generations of each species are recognised: sexual (sx.) and agamic/asexual (ag.) (see Pujade-Villar *et al*. 2001)). The galls of each generation are morphologically distinct, and in some species (Gen. *Andricus* Hartig 1840 and *Callirhytis* Förster 1869 only), heteroecy (host alternation) occurs, whereby different *Quercus* spp. are utilised by the sexual and agamic generations respectively (Pujade-Villar *et al*. 2001; Williams 2010). In Britain, galls of both sexual and agamic generations of native gall wasps are induced on native oaks *Q. robur/petraea* only, while for non-native species, a non-native oak (*Q. cerris* or *Q. ilex*) is utilised by at least one generation. Distributions of gall wasps are tied to those of their associated oak host(s), with the arrival of most non-native species inextricably linked to the human-mediated range expansion of *Q. cerris* throughout the past four centuries (Schönrogge *et al*. 1998; Stone *et al*. 2002, 2007; Nicholls *et al*. 2010). As such, 49 separate gall wasps species are currently recognised as present on oak in Britain (Williams 2010; Redfern & Shirley 2011; Forshage *et al*. 2017; Leach, *in press*), 16 of which are considered non-native (Appendix III).

5.2.2 Indirect interactions and apparent competition

Heteroecy in oak gall wasps provides the ideal model to test for the presence of apparent competition in an ecological assemblage. Firstly, there is a potential for an enemy-mediated indirect interaction between *Q. cerris* and *Q. robur/petraea*, whereby the non-native *Q. cerris* is the source of non-native gall wasps, which, in order to complete their lifecycle, exploit the native *Q. robur/petraea* also. The greater the presence of *Q. cerris*, the greater the opportunity for host penetration by the non-native gall wasp, thus, the greater the expected density of non-native gall wasps present on *Q. robur/petraea* also. Secondly, there is a potential for an enemy-mediated indirect interaction between non-native and native gall wasps, via the modifying presence of shared parasitoids. Non-native species arrive in a novel environment either with or without a natural enemy, and three (non-exclusive) scenarios exist to explain the mechanism by which a parasitoid is either retained or acquired: The Host Pursuit Hypothesis (the non-native gall wasp will be pursued by its natural enemies from the same range), the Host Shift Hypothesis (parasitoid recruitment is made over time from local parasitoid populations), and the Introduction Hypothesis (a natural enemy arrives with the gall wasp, potentially via trade in galls) (Nicholls *et al*. 2010 and references therein, Schönrogge *et al*. 2012). Knowledge of parasitoid retention/acquisition in non-native gall wasps remains fairly limited (e.g. Schönrogge *et al*. 1996, 2012). There exists only two known examples of Host Pursuit: *Megastigmus stigmatizans* (Fabricius, 1798) with *Andricus kollari* (Nicholls *et al*. 2010), and *Pediobius rotundatus* (Fonscolombe, 1832) with *Plagiotrochus quercusilicis* (McCormack 2017), and thus it is presumed that in other non-native species present, parasitoids are, or have been, recruited via Host Shift (Cornell & Hawkins 1993; Stone *et al*. 1995; Schönrogge *et al*. 1996, 1998, 2000, 2012). Known recruitment time is variable, with examples of a single generation-only lag (Schönrogge *et al*. 2000) contrasting with lags of 20+ years (Collins *et al*. 1983; Hails *et al*. 1990). In all cases, it is expected that the diversity of a enemies pertaining to a non-native species will increase over time (e.g. Cornell & Hawkins 1993).

With non-native gall wasps (mostly) arriving without their natural enemies, populations can be expected to establish/grow relatively uninhibited (Keane &

Crawley 2002; Torchin & Mitchell 2004; Verhoeven *et al*. 2009; Dostál *et al*. 2013). Thus, in addition, the greater the density of non-native gall wasps present on *Q. robur/petraea*, the greater the potential for a negative effect on native gall wasps to be observed via one or more forms of resource competition, such as a reduction in the availability of suitable oviposition sites, or the interaction of multiple species triggering the induction of biochemical tree defences, e.g. herbivore-induced plant volatiles (HIPVs) (Paré & Tumlinson 1999; Dicke & Baldwin 2010) and/or phenolic compounds (notably tannin, quercetin and kaempferol) (Salminen & Karonen 2011; Kant *et al*. 2015 but see Taper & Case 1987; Tooker *et al*. 2008). It is expected that such effects will be especially prominent in native/non-native pairs that share the same host niche, i.e. bud-gallers, leaf-gallers, acorn-gallers, etc. If parasitoid recruitment increases over time (Collins *et al*. 1983; Cornell & Hawkins 1993; Schönrogge *et al*. 2000), then it is expected that in more established non-native species, parasitoids will be playing a larger role in limiting populations, and that negative effects will therefore be greater the more recent the arrival of the non-native gall wasp.

Not all non-native gall wasps exhibit heteroecy; e.g. both sexual and agamic forms of *Plagiotrochus* spp. use *Q. ilex* (and potentially other closely-related species) for the completion of their lifecycles, while *Pseudoneuroterus saliens* uses *Q. cerris* only. While, in these examples, resource competition of oviposition sites is not relevant, apparent competition could still be present as negative indirect effects mediated by shared parasitoids, again, with negative effects of the presence of these non-native gall wasps on native gall wasps being greater the greater the non-native presence and the more recent its arrival.

5.2.3 Study model/hypotheses

Drawing on the expectations posited above, with gall density as a proxy for gall wasp presence, utilising data acquired from repeated surveys of 40 *Quercus* spp. transects in Cornwall, UK, it is hypothesised that:

i) the density of *Q. cerris* will have a corresponding positive effect on the density of non-native gall wasps on *Q. robur/petraea*, and that therefore a significant relationship between *Q. cerris* density and each non-native gall-wasp density is expected.

ii) the density of individual non-native gall wasp species will negatively affect the density of individual native gall wasp species on *Q. robur/petraea*, and that therefore a significant relationship between each non-native density and each native gall-wasp density is expected.

5.3 METHODS

5.3.1 Data collection

From May to September 2018, gall wasp-induced galls on *Quercus* spp. in Cornwall (VC1), UK were systematically counted. Potentially suitable sites for data collection were identified using personal knowledge and via consultation of the local biological records database: ERICA (http://www.cornishbiodiversitynetwork.org), based on presence of native and non-native *Quercus* spp., ease of access and wide geographical spread of the sites. Sites were selected from four geographically separate areas (Zones): Camborne, Helston, Penryn, Penzance (Fig. 5.1). Selected sites were visited to assess suitability, noting factors such as species and number of trees present, and ease of access to both trees and their foliage.

Fig. 5.1. Location of four geographic ‘zones’ in Cornwall, UK. Within each zone, 10 transects were surveyed for presence of gall wasp-induced galls on *Quercus* spp. Surveying took place from May to September 2018.

Linear transects of 50m were measured, ideally following an established path, with minimal requirements per transect considered to be at least 6 individual oak trees or a minimum 2000mm total circumference of all trunks measured at 1m above ground. Where necessary, permissions to collect data were sought and obtained (Cornwall Wildlife Trust, National Trust/Natural England, Cornwall Council).

Within each area, 10 transects were determined from a minimum of 2 and maximum of 5 separate sites, providing a total of 40 transects, as follows:

Camborne

Red River Valley Local Nature Reserve (LNR) (3 transects) - a former industrialised mining valley, now partially wooded valley with heathland, lakes and ponds; a mix of Quercus spp., dominated by native species, including mature trees. Duchy College Rosewarne (2 transects) – a former experimental horticultural station set in 65 ha. of horticultural/semi-natural habitat; a mix of *Quercus* spp., with field borders dominated by medium-sized *Q. ilex*. Tehidy Country Park (5 transects) – a former family estate, now Cornwall Council owned country park, consisting of 100 ha. of mature woodland, lakes and rides; a mix of *Quercus* spp., including mature trees.

Helston

Degibna Wood (5 transects) – mature woodland bordering Loe Pool on the eastern side of the National Trust Penrose Estate, a 620 ha. estate featuring farmland, woodland, willow carr, a large freshwater pool, beach and mining heritage; a mix of *Quercus* spp., dominated by mature *Q. robur/petraea* and *Q. cerris*. Penrose Estate (5 transects) – the western side of Penrose Estate, bordering a SSSI-designated oak woodland; mostly *Q. robur/petraea* with a mix of young and large, mature trees adjoining a wide, public path.

Penryn

Devichoys Wood (5 transects) – a Cornwall Wildlife Trust reserve, consisting of 18 ha. of ancient, semi-natural woodland, dominated by mature *Q. petraea*, with smaller *Q. cerris* and *Q. ilex* trees; the site is undergoing restoration by Working Woodlands Cornwall CIC, by means of a revival of traditional woodland management techniques, including coppicing, charcoal burning and horse logging. Penryn Campus (5 transects) – the former historic estate of Tremough House, now a campus shared by University of Exeter and Falmouth University; an important horticultural site, featuring a variety of habitats; a mix of *Quercus* spp. present, including mature *Q. robur/petraea* and *Q. cerris*, and *Q. ilex* hedging.

Penzance

King's Road (1 transect) – a residential street with mature *Q. ilex* mature trees and hedging. Long Rock Industrial Estate (1 transect) – a small industrial estate on the edge of Penzance, featuring amenity planting, including a row of established *Q. ilex*. Mound Wood (Newlyn Carne)/Mount Misery (2 transects) – a small, steep-sided mature woodland, with mostly *Q. robur/petraea*, and a nearby small, scrubby copse adjoining a main road, with a mix of *Quercus* spp. present, including large *Q. cerris* trees. Paul (3 transects) – a semi-natural area on the outskirts of a rural village, with existing woody patches and willow carr, supplemented with newer plantings; *Quercus* spp. present include young *Q. robur/petraea* and more established *Q. ilex*. Tesco (3 transects) – amenity plantings bordering a supermarket car park and adjoining a small stream; stretches of *Q. ilex* trees and hedging present.

For each transect, location and start coordinates were noted. All oak trees present within 5m either side of the transect line were recorded by means of noting their native or non-native status, and their species (non-native only). As a proxy for both individual tree age and overall tree coverage (density), a measurement of each tree's trunk circumference at 1m above ground was taken. Where trees were less than 1m in height, the maximum circumference was used.

Over a continual period of 18 weeks separated into 3 blocks of 6 weeks, each transect was visited a total of 3 times, once per 6-week block. On each occasion, trees were searched manually for galls using visual inspection to locate gall presence. To standardise data collection, only galls within human reach were counted, and mechanical means of collection (e.g. tree shaking, use of saws to remove higher branches) were not employed. Anecdotal evidence (J. Bowdery, R. Maidstone, pers. comm.) suggests that preference for the tree canopy is exhibited by some species, notably *Andricus quercusramuli* and *A.*

quercusradicis (the latter is usually considered a root galler but has occasionally been found in tree canopies, especially in continental Europe), while results of previous studies looking at gall distribution – albeit within a tree height range range of 0 to c.2m only (Askew 1962, Ejlersen 1978, K. Schönrogge, pers. comm.) – suggests that vertical stratification of galls is likely, and it is therefore possible that one or more species of gall-wasp present were undetected as a consequence of the limitations of the methodology; however, the standardisation of data collection means that the data collected is considered consistent between transect, and the possible omission of potentially overlooked data is not considered detrimental to the study. Galls were counted for 30 minutes per transect or until no more galls were found. For each transect, the number of individual galls per species/generation counted from *Quercus petraea/robur*, *Q. cerris* and *Q. ilex* respectively were recorded.

5.3.2 Data analysis

All statistical analyses and descriptive statistics were performed using R (v 3.6.1) (R Core Team 2019).

For all gall wasps, density per transect was determined by means of gall presence, calculated as total galls per mm circumference host tree (at 1m), where tree circumference is a proxy for tree density. For all *Quercus* spp., proxy measures of tree density (total tree circumference at 1m) and tree age (mean tree circumference at 1m) were checked for association. A significant association was observed for all (*Q. cerris*: GLM ANOVA $F_{1,38} = 88.821$ $p < .001$; *Q. ilex*: GLM ANOVA $F_{1,38} = 7.5522$ $p = 0.009$; *Q. robur/petraea*: GLM ANOVA $F_{1,38} = 17.748$ $p < .001$), thus tree density only was used to represent tree presence).

Sequential stepwise selections of Generalised Linear Models (GLMs) were performed to produce Minimum Adequate Models (MAMs) addressing the above hypotheses, as follows:

i) Using gall density as the response variable, for each non-native gall wasp, a GLM was used to test for the significance of the tree density (total circumference at 1m per transect) of the non-native hosts (*Q. cerris*, *Q. ilex*) and native hosts

(*Q. robur/petraea*) respectively, with the expectation that *Q. cerris* only would be significant.

ii) Using gall density as the response variable, for each native gall wasp, a GLM was used to test for a significant relationship with the density of non-native gall wasps respectively. In order to test for density dependence of the native host, *Q. robur/petraea* was included in the model.

For each model, the additive effect of geographic location (zone) was tested also. Use of a mixed effects model is not appropriate here due to there being 4 zones only, which is fewer than the 5 levels of random variables required to achieve robust estimates of variance (Harrison 2015; Harrison *et al*. 2018). Significance of effects/relationships and model differences were evaluated using ANOVA Type II test, using the car package in R (Fox & Weisberg 2019), and further assessed using AIC values and percentage deviance provided by the model, the latter calculated as: (null deviance – residual variance)/null deviance.

5.4 RESULTS

5.4.1 Descriptive statistics

Galls of 16 gall wasp species were observed (8 native, 8 non-native), a single generation of 13 species, and both agamic and sexual generations of 3 species (Fig. 5.2a-b). Galls were found on *Q. robur/petraea* and *Q. ilex* but not on *Q. cerris*.

Fig. 5.2a. Native gall wasp species/forms (l-r): Row 1 *Andricus curvator* (Hartig 1840) sx., *Andricus curvator* (Hartig 1840) sx. (twig form), *Andricus foecundatrix* (Hartig 1840) ag.; Row 2 *Andricus seminationis* (Giraud 1859) ag., *Cynips quercusfolii* Linnaeus 1758 ag. (tuberculate form) [*Neuroterus numismalis* also present], *Cynips quercusfolii* Linnaeus 1758 ag. (smooth form); Row 3 *Neuroerus albipes* (Schenck 1863) ag., *Neuroterus anthracinus* (Curtis 1838) ag., *Neuroterus anthracinus* (Curtis 1838) (gall flaps) ag.; Row 4 *Neuroterus numismalis* (Fourcroy 1785) ag., *Neuroterus numismalis* (Fourcroy 1785) sx., *Neuroterus politus* Hartig 1840 sx.; Row 5 *Neuroterus quercusbaccarum* (Linnaeus 1758) ag., *Neuroterus quercusbaccarum* (Linnawus 1758) sx., *Neuroterus quercusbaccarum* (Linnaeus 1758) sx.

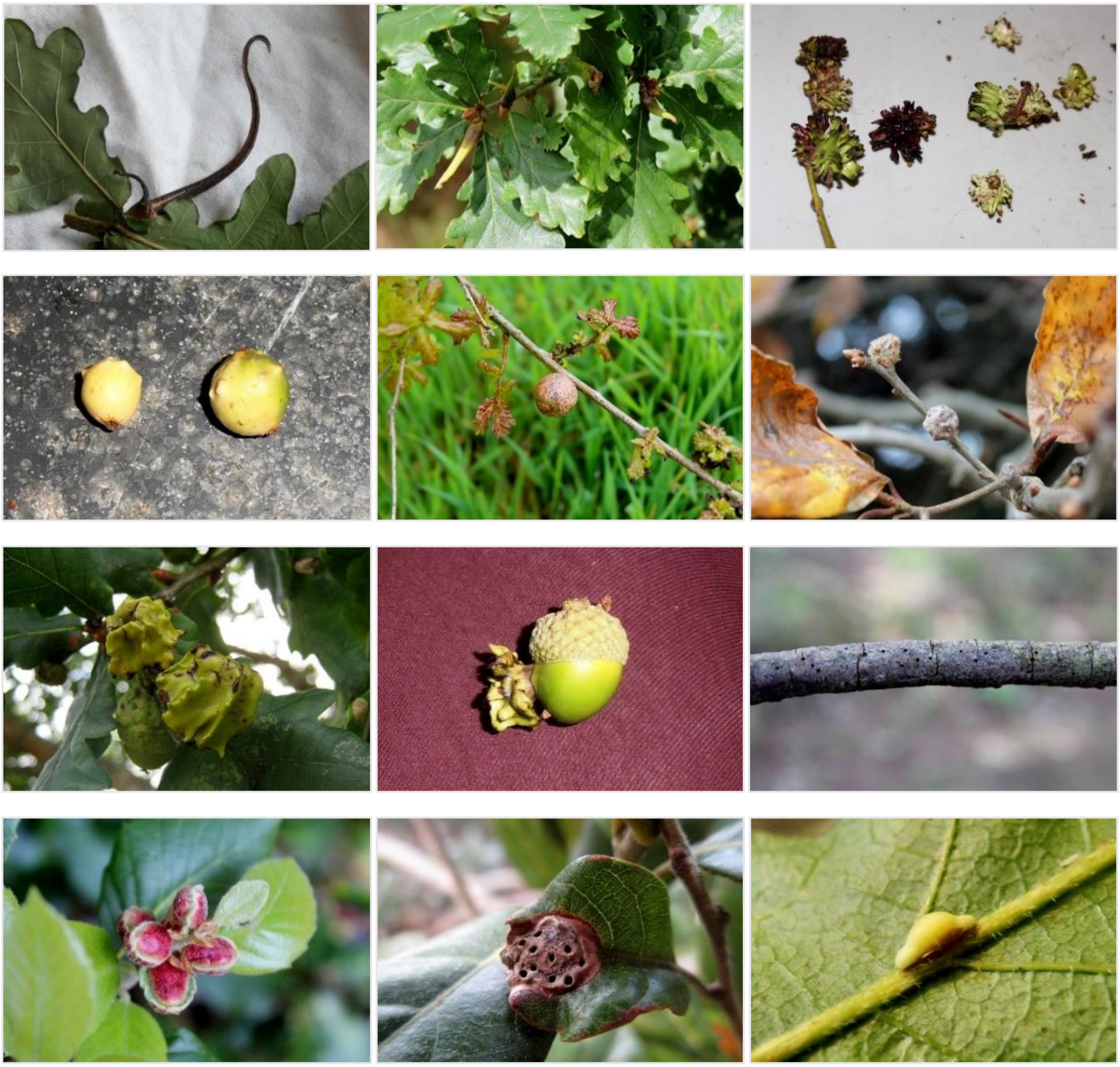


Fig. 5.2b. Non-native gall wasp species/forms (l-r): Row 1 *Andricus aries* (Giraud 1859) ag., *Andricus aries* (Giraud 1859) ag., *Andricus grossulariae* Giraud 1859 ag.; Row 2 *Andricus infectorius* (Hartig 1843) ag., *Andricus kollari* (Hartig 1843) ag., *Andricus lignicola* (Hartig 1840) ag.; Row 3 *Andricus quercuscalicis* (Burgsdorf 1783) ag., *Andricus quercuscalicis* (Burgsdorf 1783) ag., *Plagiotrochus quercusilicis* (Fabricius 1798) ɤ; Row 4 *Plagiotrochus quercusilicis* (Fabricius 1798) ♀♂, *Plagiotrochus quercusilicis* (Fabricius 1798) sx., *Pseudoneuroterus saliens* (Kollar 1857) ag.

Fig. 5.2. Gall wasp species/forms (ag. = agamic, sx. = sexual) observed by means of gall presence on *Quercus* spp: a) native species/forms, b) non-native species/forms.

Where gall wasps were present in fewer than 10% (i.e. <4) all transects, data was disregarded as numbers were considered too low to allow for meaningful analysis. Thus, 5 gall wasps were removed due to low occurrence: *Andricus grossulariae* ag., *A. infectorius* ag., *Neuroterus numismalis* sx., *N. politus* sx. and *Pseudoneuroterus saliens* ag. Similarly, *Plagiotrochus quercusilicis* ag. was disregarded, as exit holes in twigs/branches, indicating presence only, were observed, rather than any galls. Remaining gall wasps used for analyses are as follows: native: *Andricus curvator* sx., *A. foecundatrix* ag., *Cynips quercusfolii* ag., *Neuroterus albipes* ag., *N. anthracinus* ag., *N. numismalis* ag., *N. quercusbaccarum* ag., *N. quercusbaccarum* sx.; non-native: *Andricus aries* ag., *A. kollari* ag., *A. lignicola* ag., *A. quercuscalicis* ag., *P. quercusilicis* sx. Mean ±SE density of each gall per mm host trunk circumference at 1m is shown (Fig. 5.3), calculated as total galls per mm circumference host tree (at 1m), where tree circumference is a proxy for tree density. No accounting is made for relative size of individual gall nor for the number of gall wasp occupants per gall.

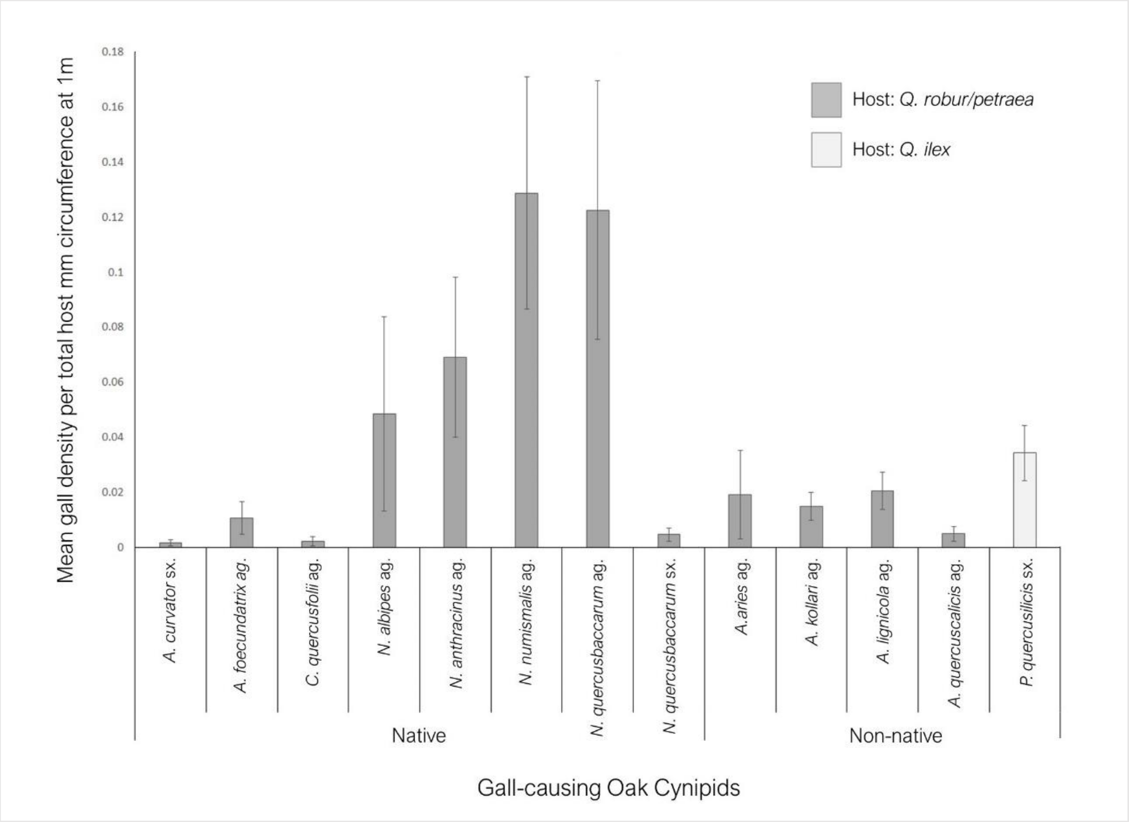


Fig. 5.3. Mean ±SE density of native/non-native gall wasps per mm host trunk circumference at 1m, calculated as total galls per mm circumference host tree, where tree circumference is a proxy for tree density.

5.3.2 Statistical analyses

i. Effect of non-native host density on non-native gall density

No significant results were observed for the effect of *Q. cerris* density on non-native gall density on native hosts; however, a negative significant relationship between *Q. ilex* and *A. lignicola* ag. density was observed (GLM ANOVA $\chi^2 = 10.23$ $p = 0.001$), with zone significant also (GLM ANOVA $\chi^2 = 26.42$ $p < .001$). The relationship between *Q. ilex* density and *A. lignicola* ag. with the additive significant effect of zone is shown in a scatterplot with regression lines (Fig. 5.4). A negative significant relationship between *Q. robur/petraea* and A. *kollari* ag. density was observed (GLM ANOVA $\chi^2 = 6.15$ $p = 0.013$). No significant results were observed in models with the response variables: *A. aries* ag. or *P. quercusilicis* sx., while in the *A. quercuscalicis* ag. model, zone only was significant (GLM ANOVA $\chi^2 = 7.82$ $p = 0.05$). Percentage deviance provided by each of the significant models is as follows: *A. kollari* ag. 16%, *A. lignicola* ag. 49%, *A. quercuscalicis* ag. 21%.

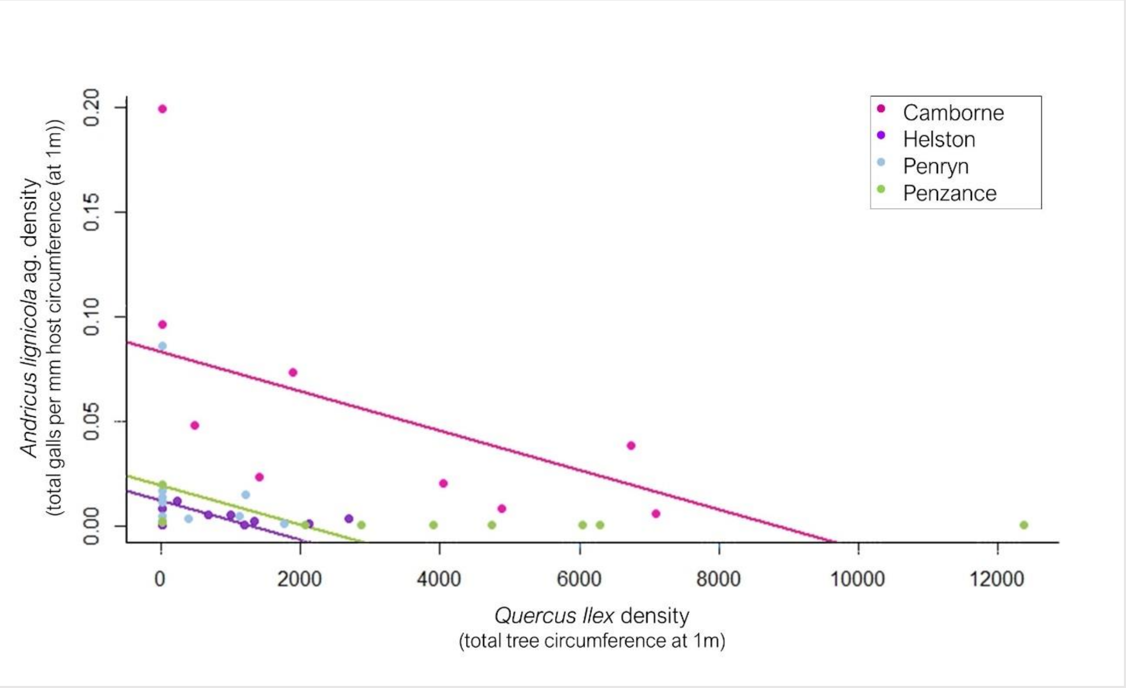


Fig. 5.4. The significant relationship between *Q. ilex* density and *Andricus lignicola* ag. (GLM ANOVA $\chi^2 = 10.23$ $p = 0.001$) with the additive significant effect of zone (GLM ANOVA $\chi^2 = 26.42$ $p < .001$). N.B. the Penryn regression line is obscured by the Penzance regression line.

ii. Effect of non-native gall density on native gall density

The effect of the gall density of each of the five non-native gall wasps: *A. aries* ag., *A. kollari* ag., *A. lignicola* ag., *A. quercuscalicis* ag. and *P. quercusilicis* sx., as well as zone and native *Q. robur/petraea* tree host density on the gall density of each of the eight native gall wasps: *A. curvator* sx., *A. foecundatrix* ag., *C. quercusfolii* ag., *N. albipes* ag., *N. anthracinus* ag., *N. numismalis* ag., *N. quercusbaccarum* ag., *N. quercusbaccarum* sx. was tested.

Significant relationships between non-native and native gall density were observed in models with the response variables: *N. albipes* ag., *N. anthracinus* ag., *N. quercusbaccarum* ag. and *N. quercusbaccarum* sx. No significant results were observed in models with the response variables: *A. curvator* sx., *A. foecundatrix* ag., *C. quercusfolii* and *N. numismalis* ag. For *N. albipes* ag., *N. anthracinus* ag., *N. quercusbaccarum* ag. and *N. quercusbaccarum* sx., positive significant relationship with *A. aries* ag. was observed. In the model with *N. albipes* ag. as the response variable, also observed was a significant positive relationship with *A. quercuscalicis* ag. (GLM ANOVA $\chi^2 = 14.20$ $p < .001$), and a negative significant relationship with *A. kollari* ag. (GLM ANOVA $\chi^2 = 16.01$ $p < .001$); however, when tested as single variables in independent models, *A. quercuscalicis* ag. was not significant (GLM ANOVA $\chi^2 = 0.04$ $p = 0.847$), and a positive relationship rather than negative relationship was observed with *A. kollari* ag. (GLM ANOVA $\chi^2 = 2.48$ $p = 0.040$). This suggests the presence of multicollinearity in the combined model, potentially caused by correlation between two or more explanatory variables. As it is the relationship of the predictors to the outcome, rather than the relationship between predictors, that is of interest here, results from the separate models are reported. No significant results were observed for the effect of non-native gall wasp species *A. lignicola* ag. or *P. quercusilicis* sx. on any native gall wasp species. Neither *Q. robur/petraea* nor Zone was significant in any of the models. Details of the MAM for each model in which significant results were observed are provided (Table 5.1), and displayed as scatterplots with regression lines (Fig. 5.5).

Table 5.1. Details of the best performing (minimum adequate) model for the effect of non-native gall density on native gall density for each model in which significant results were observed, with Type II ANOVA χ^2 and *p*-values. Due to the effects of multicollinearity, for *Neuroterus albipes* ag., significant explanatory values (*Andricus aries* ag. and *A. kollari* ag.) were tested individually in separate models.

Response variable	Explanatory variable	GLM				
		chi	***p*-value (direction of effect)**	**null deviance (df)**	**resid. deviance (df)**	**% deviance**
***N. albipes* ag.**	*A. aries* ag.	119.95	< .001(+)	1.39695 (33)	0.05002 (32)	96
***N. albipes* ag.**	*A. kollari* ag.	4.57	0.033(+)	1.39695 (33)	1.22240 (32)	12
***N. anthracinus* ag.**	*A. aries* ag.	708.98	< .001(+)	0.95313 (33)	0.04121 (32)	96
***N. q'baccarum* ag.**	*A. aries* ag.	119.95	< .001(+)	2.47434 (33)	0.52109 (32)	79
***N. q'baccarum* sx.**	*A. aries* ag.	19.25	< .001(+)	0.00620 (33)	0.00387 (32)	38

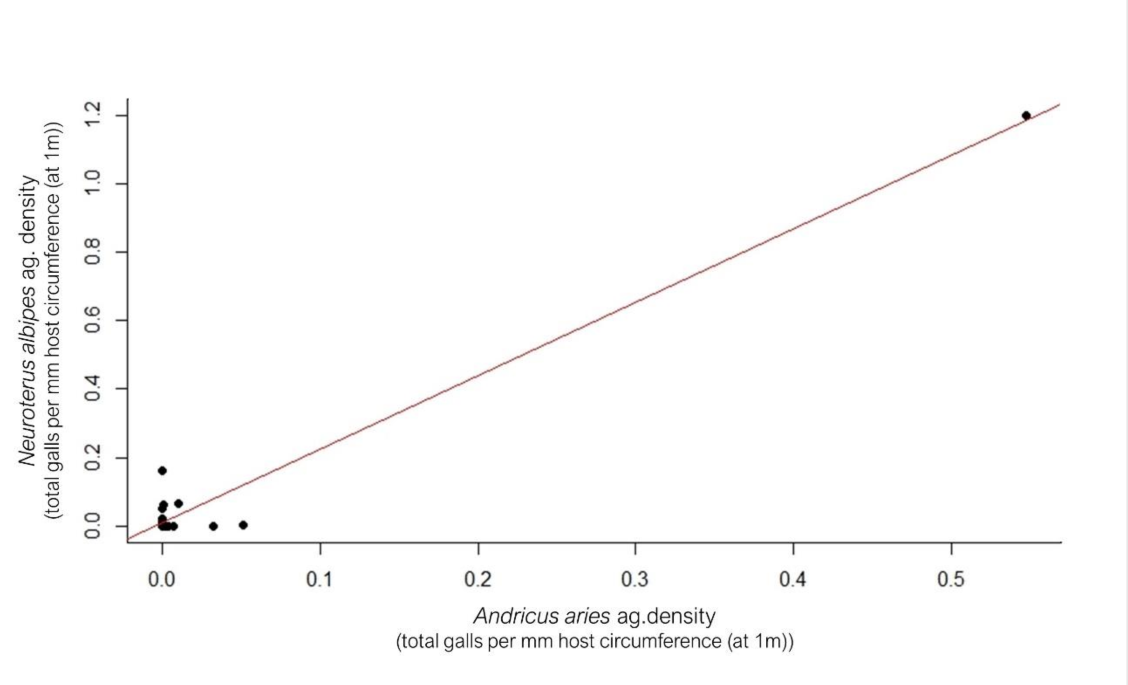


Fig. 5.5a. The significant relationship between *Andricus aries* ag. density and *Neuroterus albipes* ag. density (GLM ANOVA χ^2 = 119.95 $p < .001$)

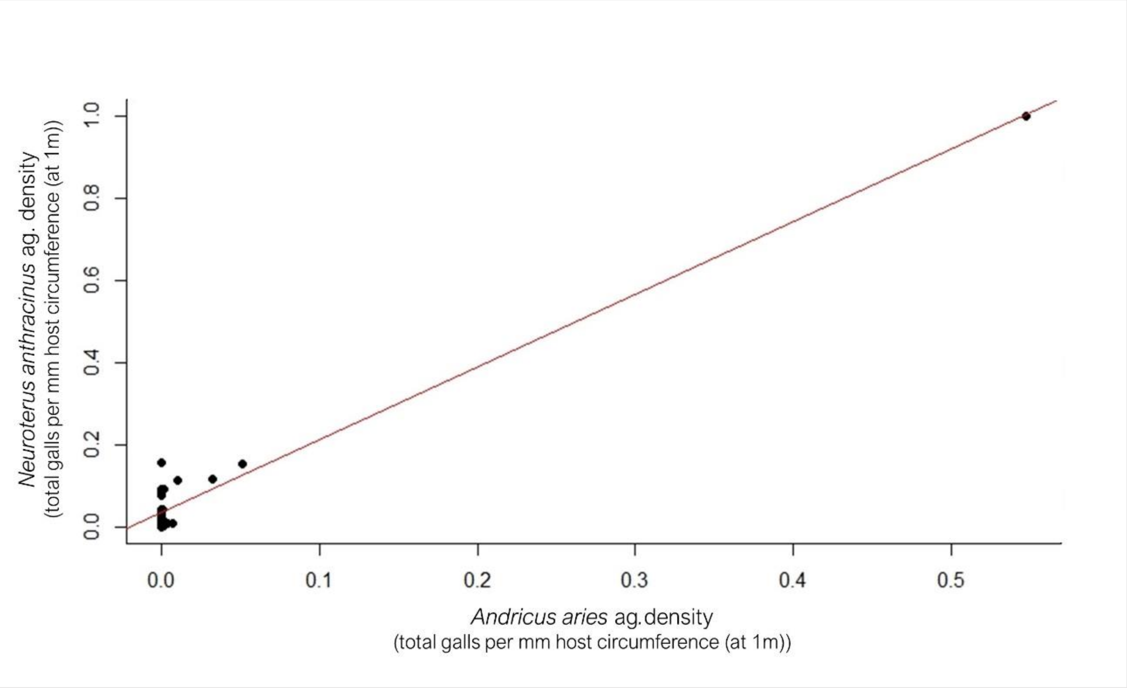


Fig. 5.5b. The significant relationship between *Andricus aries* ag. density and *Neuroterus anthracinus* ag. density (GLM ANOVA χ^2 = 708.98 *p* < .001).

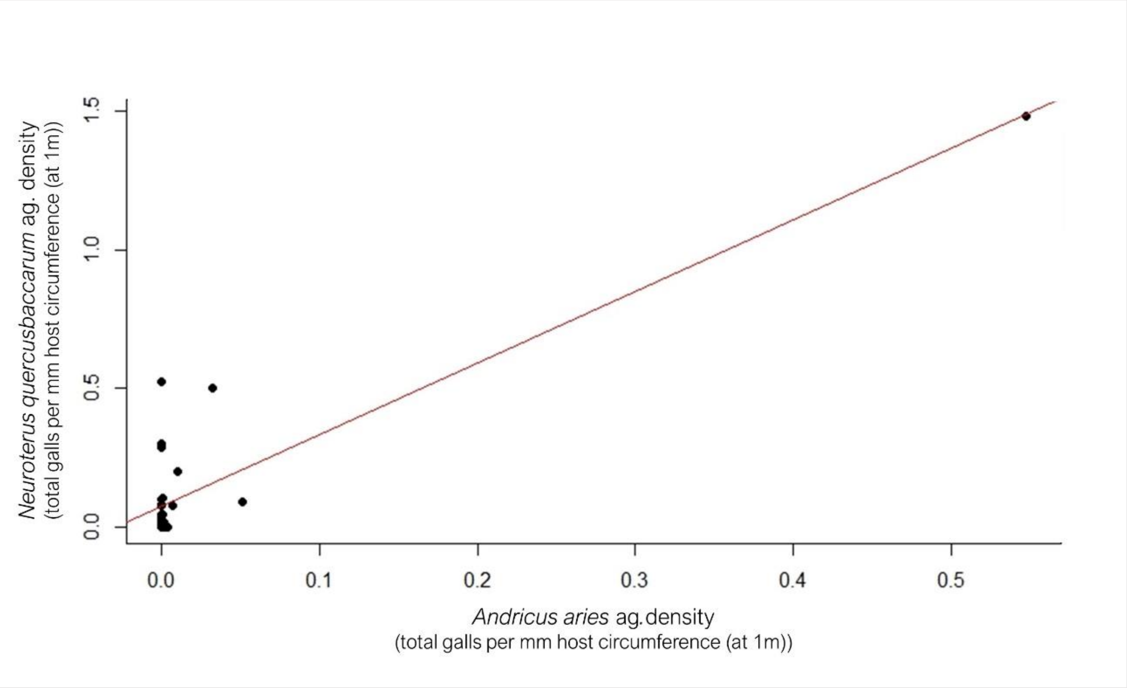


Fig. 5.5c. The significant relationship between *Andricus aries* ag. density and *Neuroterus quercusbaccarum* ag. density (GLM ANOVA χ^2 = 119.95 *p* < .001).

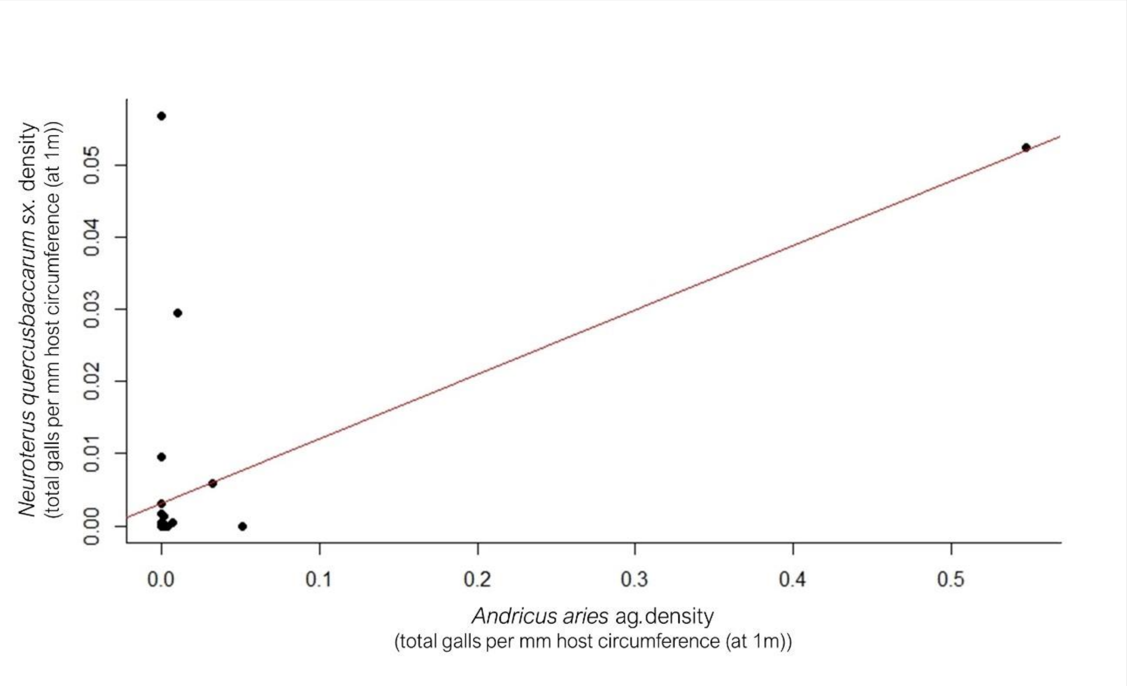


Fig. 5.5d. The significant relationship between *Andricus aries* ag. density and *Neuroterus quercusbaccarum* sx. density (GLM ANOVA $\chi^2 = 19.25$ $p < .001$).

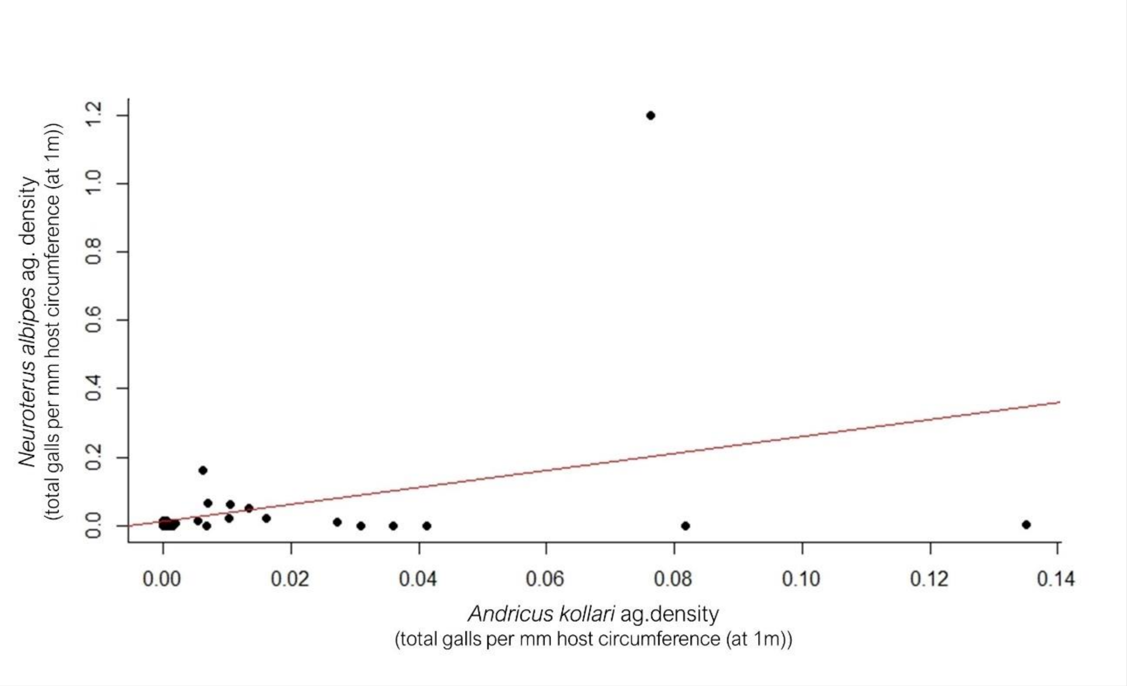


Fig. 5.5e. The significant relationship between *Andricus kollari* ag. density and *Neuroterus albipes* ag. density (GLM ANOVA $\chi^2 = 4.57$ $p = 0.033$).

Fig. 5.5. Significant positive relationships between of non-native gall wasp density and native gall wasp density.

Although data values were deemed to be correct, with no reason to suspect errors, due to the presence of an extreme value for *A. aries* ag. gall density, models were rerun with the corresponding datapoint removed from the dataset. *A. aries* ag. remained significant in the *N. anthracinus* ag. model only, while in the *N. albipes* ag. model, *A. quercuscalicis* ag. only was significant (Table 5.2, Fig. 5.6). No other significant relationships were observed.

Table 5.2. Details of the best performing (minimum adequate) model for the effect of non-native gall density on native gall density for each model in which significant results were observed, following removal of the extreme *Andricus aries* ag. datapoint, with Type II ANOVA χ^2 and p-values.

Response variable	Explanatory variable	GLM				
		chi	***p*-value (direction of effect)**	**null deviance (df)**	**resid. deviance (df)**	**% deviance**
***N. albipes* ag.**	*A. q'scalicis* ag.	1.16	< .001(+)	0.03127 (32)	0.01998 (31)	36
***N. a'racinus* ag.**	*A. aries* ag.	16.31	< .001(+)	0.06040 (32)	0.03958 (31)	34

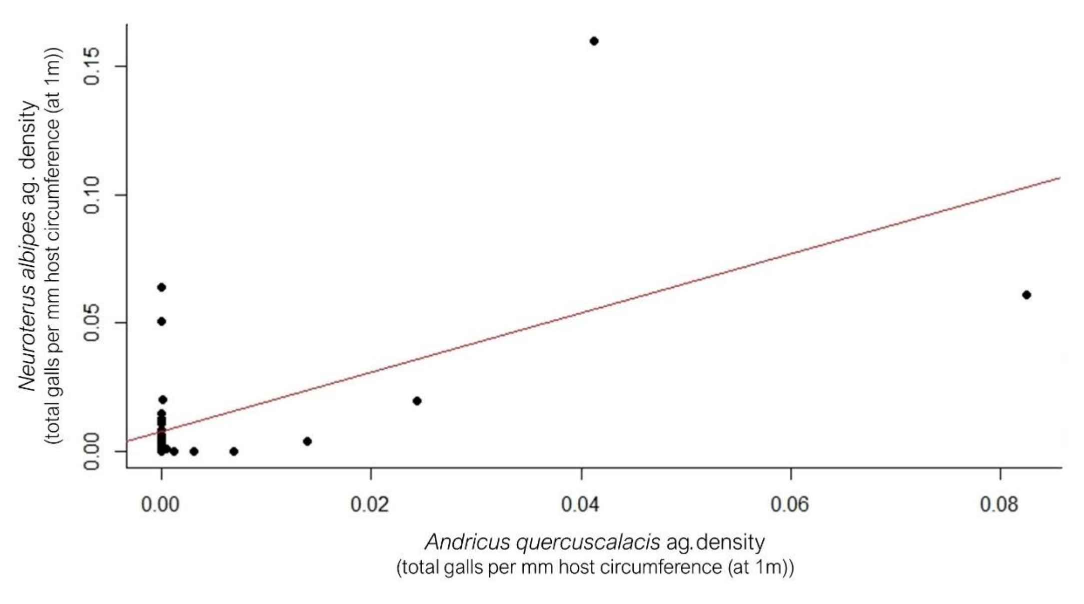


Fig. 5.6a. The significant relationship between *Andricus quercuscalicis* ag. density and *Neuroterus albipes* ag. density (GLM ANOVA χ^2 = 16.31 p < .001).

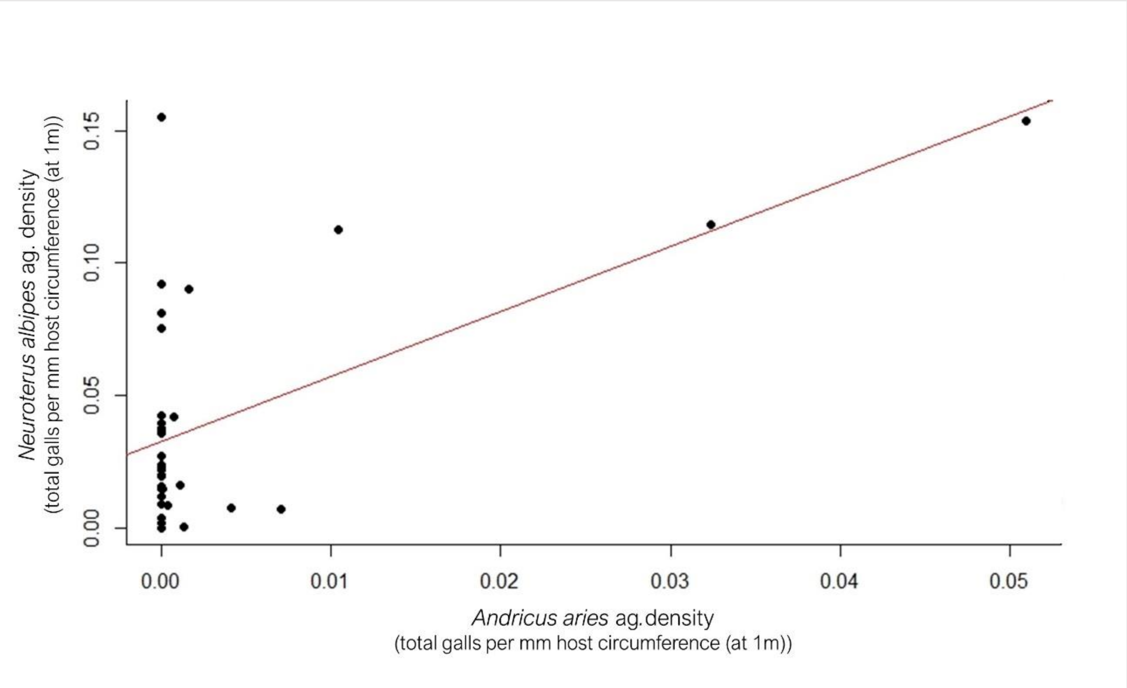


Fig. 5.6b. The significant relationship between *Andricus aries* ag. density and *Neuroterus albipes* ag. density (GLM ANOVA χ^2 = 1.16 *p* < .001).

Fig. 5.6. Significant positive relationships between non-native gall wasp density and native gall wasp density, using data with the extreme *A. aries* ag. datapoint removed.

5.5 DISCUSSION

Expected results were a positive relationship between *Q. cerris* density and non-native gall density on *Q. robur/petraea*, and a negative relationship between non-native gall density and native gall density, consistent with a positive effect of a non-native host on a non-native gall-wasp on a native host, and a negative effect of a non-native gall-wasp on a native gall-wasp, respectively. Neither of these relationships were observed, with patterns in the effect of non-native gall density opposite to the above expectation. Thus, the results provide no evidence to support the overall hypothesis of the presence of apparent competition in the form of the negative indirect effect of a non-native plant on a native plant, mediated by a non-native gall wasp, or in the form of the negative indirect effect of a non-native gall-wasp on a native gall-wasp, mediated by the modifying presence of one or more shared parasitoids, nor do they provide evidence of resource competition for oviposition sites.

In the *A. lignicola* ag. model, while no significant relationships with *Q. cerris* were observed, a significant negative relationship with *Q. ilex* was observed, with zone being significant also. The effect of zone could indicate an underlying microclimate effect or other unmeasured environmental variable influencing gall production; however, what is of particular interest here, is the significant relationship between *Q. ilex* and *A. lignicola* ag. itself. Potential explanations include something as straightforward as reduced *A. lignicola* host density as a direct consequence of greater *Q. ilex* density; however, if this were having an effect, then results would be expected in other non-native gall wasps. An alternative explanation is that an indirect effect of the *Q. ilex* gall wasp *P. quercusilicis* on *A. lignicola*, mediated by a shared parasitoid is occurring. While there are numerous examples of parasitoid species documented as associated with both of the gall wasp species here (Williams 2010; McCormack 2017, Noyes 2019), in the absence of parasitoid data, here, the level of parasitoid attack and distribution of parasitoids between host species cannot be tested, and robust field data combined with an experimental approach would be required to determine parasitoid-sharing and/or the presence of indirect effects (Schönrogge & Crawley 2000; Naniagua *et al*. 2009) or to test for the effect of other potential contributory variables.

Significant positive relationships between *A. aries* ag. density and native gall density were observed in 4 of the 8 native gall wasps, with an additional weaker relationship between *A. kollari* ag. and native gall density observed in one of the models only. In models re-run after the removal of the corresponding datapoint for an extreme value in the *A. aries* ag. data, a significant positive relationship *A. aries* ag. and native gall density continued to be significant in one model only, whereas where the relationship between *A. kollari* ag. and native gall density was previously significant, the relationship between *A. quercuscalicis* ag. and native gall density was now significant, with all effects still positive.

There are several possible explanations for the presence of positive relationships rather than the expected negative relationships. Firstly, it is important to note that results here represent correlational relationship from observed field data rather than from experimental data. Despite standardised data collection, for reasons not obvious from the data available, there were clear differences in gall presence between transects, with the presence of an extreme value effectively producing two-point regressions. As such, a positive correlation is not always representative of a cause and effect relationship, and, it is unwise to interpret these relationships as ecologically significant, as any apparent effect is contingent on a single outlier. That aside, it remains possible that a positive correlation is caused by both the non-native and native gall wasp responding equally to one or more favourable external variables, such as the presence of quality habitat, which could potentially be obscuring any negative interaction also occurring; however, this raises further questions, such as why the same result is not observed for all native/non-native gall wasp pairings. Another possible explanation is the spatial scale of the study, in that results might be seen to differ if the spatial approach were altered, e.g. by examining effects at tree level in one direction, or examining effects at a wider landscape level in the other direction (Heads & Lawton 1983; Wiens 1989; Levin 1992; Tack *et al*. 2011), or by increasing the sample size. Similarly, altering the temporal scale of the study to better incorporate all lifecycle stages of the interacting species and/or the effects of population cycling might produce different results (e.g. Abrams *et al*. 1998; van Veen *et al*. 2006a). Of particular relevance here is the potential effect of the absence of data pertaining to the early spring generation galls, missed by the timing of the study (Stone *et al*. 2002; Williams 2010).

A further, more interesting explanation is that the results are representative of a real effect, that of apparent mutualism (Holt & Lawton 1994), whereby, rather than in apparent competition, where the indirect effect of one species on another via a mediating species is negative, here the indirect effect is positive, i.e. of benefit to the recipient. Despite substantial evidence for apparent competition within food web structures, apparent mutualism is less frequently reported, especially with regard to gall causer-host dynamics. Indirect effects within food web structures are most often studied via host-parasitoid interactions, with a distinct difference between the two systems being that the presence of a gall causer does not kill its host, the latter a big driver in host-parasitoid interactions (e.g. Hawkins 1994; Quicke 2015). Thus, caution should be heeded when making direct comparisons between the two systems; however, in the absence of evidence pertaining to gall causer-host interactions, information garnered from host-parasitoid systems can still be useful.

In host-parasitoid interactions, for apparent mutualism to be present, a given requirement is for the shared enemy (the parasitoid) to be satiated or to switch to more abundant prey (the host) (Holt 1977). In an attempt to translate this mechanism to a host-gall wasp study system, this would suggest that, as the gall wasps are tied to the same host-plant, in order for the non-native gall wasp to be 'satiated', it would have needed to have attained the optimum level of oviposition sites, thus making available at least an equally sufficient level of oviposition sites for the native gall wasp. What this also requires is for the shared gall wasps to be utilising the same parts of the host-plant for oviposition. While oviposition behaviour have been widely theorised (e.g. Larsson *et al*. 1995; van Loon 1996; Bonebrake *et al.* 2015), information pertaining to Cynipids remains limited (Kato & Hijii 1993; Atkinson *et al*. 2002; Panzavolta *et al*. 2012), and thus, very little is known about the existence of optimum oviposition levels in gall wasps. Furthermore, looking here at the non-native/native gall wasp pairs for which significant results were observed, in all cases, contrasting oviposition sites are used: non-native gall wasps *A. aries* ag. and *A. kollari* ag. are bud-gallers, and *A. quercuscalicis* ag. an acorn-galler, while native gall wasp *N. albipes* ag., *N. anthracinus* ag., *N. quercusbaccarum* ag. and *N. quercusbaccarum* sx. are all leaf-gallers, with the latter being a catkin-galler also. Thus, a more likely scenario would be that the non-native gall wasp is being limited by an unmeasured effect, such as reduced availability of oviposition sites, or a disproportionately high level of parasitoid attack (Holt & Lawton 1994). For example, Stone *et al*. (2002) observed that population sizes and galling rates of *A. quercuscalicis* ag. are driven by oak masting (acorn crop levels) cycles, indicating that reduced availability of oviposition sites can be limiting, thus potentially conferring a competitive advantage to the native gall wasp; however, it is not known if similar patterns apply in other gall wasp species (K. Schonrogge, *pers. comm.*). For all scenarios, a manipulative experimental approach would be required to verify the genuine presence of such effects (e.g. Morris *et al*. 2004; Tack *et al*. 2011; Frost *et al*. 2016).

While the findings here are in contrast to the majority of similar/related studies, which tend to focus on and provide support for the important role of apparent competition in structuring ecological communities (e.g. Memmott *et al*. 1994; van Veen *et al*. 2008; Müller *et al*. 1999; Morris *et al*. 2004), empirical evidence of apparent mutualism is provided by a handful of more recent studies (e.g. Tack *et al*. 2011; Long *et al*. 2012; Van Maanen *et al*. 2012), with additional indications of its presence coming from observational studies also (e.g. Teder & Tammaru 2003; Hambäck *et al*. 2006); however, despite suggestions that its prevalence is being overlooked (Tack *et al*. 2011; Frost *et al*. 2016), this evidence remains in relative short supply.

Additional study limitations to those already discussed include the unknown effect of missing data, notably, as a consequence of out-of-reach galls, or galls that are difficult to detect due to their size and/or location. Ideally, all parts of trees would have been surveyed; however, this was impractical here. Furthermore, as referred to above, extending the temporal range of the study to better incorporate the spring gall season would hopefully allow for the detection of sexual generation non-native galls on *Q. cerris*, which, in addition to improving the reliability of the results by means of a more complete dataset, would enable testing for correlative effects of host and gall density, thus helping to verify that *Q. cerris* density is a reliable proxy for gall wasp density levels.

In conclusion, while the study hypotheses are not supported here, the results have provided interesting food for thought, in that they provide potential evidence for the occurrence of apparent mutualism rather than apparent competition; however, as the results are based on observational data, in order to test for the genuine existence of apparent mutualism, it is necessary for all findings and predictions to be corroborated by means of a manipulative experimental approach. Overall, this study contributes to a better understanding of how the presence of one non-native gall wasp might affect a non-native gall wasp via indirect interactions. What the findings especially indicate is that indirect effects mediated by non-native gall wasps have the potential to be positive as well as negative, and that a blanket approach based on the stance that the impact of a non-native species within an ecological community will either be negative or neutral, is ill-advised. In terms of practical applications, e.g. in biological control, landscape planning or site management, these findings could help in enhancing the ability to successfully mitigate any predicted negative effect of a potentially invasive species, or in contrast, to effectively utilise any positive effect that has been indicated.

5.6 ACKNOWLEDGEMENTS

With grateful thanks to Cornwall Council (Tehidy Country Park), National Trust/Natural England (Penrose Estate), and Cornwall Wildlife Trust (Devichoys Wood) for permissions to collect data.

Chapter 6: General Discussion

6.1 Synopsis of the results

With invasive species widely acknowledged as one of the key drivers of biodiversity loss, and among the greatest threats to ecosystem stability (Mack *et al*. 2000; Sala *et al*. 2000; Duraiappah *et al.* 2005), and given that the probability of ecological invasions will likely increase as consequence of the projected impacts of climate change and the current accelerated declines in biodiversity (Diez *et al*. 2012; Bellard *et al*. 2013; Hulme 2017), having the means to predict and ultimately manage how non-native species integrate in native food webs is now especially important. Such knowledge is key to being able to both predict and/or mitigate any potential negative impact of their presence. Non-native species arrive via numerous pathways, and for non-native terrestrial invertebrates, the ‘ornamental plant contaminant’ pathway is recognised as the principal means of introduction (NNSS 2019). For a non-native phytophagous species, a particular non-native ornamental plant could thus be its initial route of entry into a novel ecosystem, while the continued presence of the plant and/or the presence of other suitable host-plants within an ecological community is fundamental to how the invertebrate interacts within that community, and whether or not it will become established.

Here, using observational field data, and utilising a number of statistical methods, I sought to examine the role of non-native plants in how non-invertebrates integrate in native food webs, both facilitating the establishment and persistence of non-native phytophagous invertebrates and as mediators in indirect interactions, hypothesising that:

- in formally-planted gardens, non-native plant richness and/or other garden/landscape variables would predict non-native invert presence (Chapter 2)
- in a non-native invertebrate metapopulation, a Nearest Neighbour measure would predict patch occupancy, and that this would be strengthened by an additional habitat variable (Chapter 3)

- in a local community, phylogenetic relatedness of a native/non-native plant pair would predict the likelihood that the pair will share a natural enemy, thus indicating potential for apparent competition (Chapter 4)
- in a gall wasp community, there would be evidence of apparent competition in the form of the negative indirect effect of a non-native plant on a native plant, mediated by a non-native gall wasp, and in the form of the indirect effect of a non-native gall-wasp on a native gall-wasp, mediated by the modifying presence of one or more shared parasitoids (Chapter 5)

Overall, hypotheses were at least partially supported, with the key exception being Chapter 5, in which the results provided no evidence for the presence of apparent competition.

In Chapter 2, significant results were observed for the garden level effect of plant species richness, with, as predicted, a greater non-native PTU richness observed to be associated with a greater non-native invertebrate species richness (e.g. Moeed & Meads 1985, 1992; Crisp *et al*. 1998; Unsicker *et al*. 2006), This demonstrates that a high non-native plant species richness likely corresponds to a high non-native invertebrate species richness, and importantly, while the probability of any one non-native invertebrate species becoming problematic may be considered relatively low (e.g. Roy *et al.* 2014), a higher richness of non-native invertebrate species in a community means that the likelihood of the presence of a problem species being among them is greater also. At species level, a greater presence of non-native invertebrates was observed on woody plants than on non-woody plants, irrespective of the plant's native status, with invertebrate presence on woody plants (and all plants), being greater for generalist than for specialist species – despite a greater number of individual specialist species (15) than generalist species (8). Additionally, the presence of one or more non-native invertebrates on a woody PTU increased as the number of gardens in which the host-plant is present increased, and while this effect might be due to more frequent importation of the plant, increasing the likelihood of its direct introduction (Levine & D'Antonio 2003; Brockerhoff *et al.* 2006; Jones & Baker 2007; Kenis *et al.* 2007; Smith *et al.* 2005, 2007; Brasier 2008; Hulme *et al.* 2008; Roy *et al.* 2012, 2014; Bergey *et al.* 2014; Turbelin *et al*. 2016; NNSS 2019), it might also be due to an overall greater presence of the host-plant within the survey area contributing to a larger and/or more stable metapopulation of the invertebrate, as a consequence of more closely-linked habitat patches (Levins 1969; reviewed Hanski 1999). As any similar effect in non-woody plants is negligible, this pattern suggests that proximity of woody plants is potentially key to maintaining an effective non-native invertebrate metapopulation structure, while non-native invertebrates on non-woody plants persist in more isolated patches.

The findings here link fittingly with the notion that distribution/number of habitat patches within an area play a crucial role in enabling the persistence of a species within a community (e.g. MacArthur & Wilson 1967; Prugh *et al*. 2008; reviewed Prugh 2009), thus enabling it to potentially increase in size to become problematic, and in Chapter 3, metapopulation theory was used to test if the ability of a non-native invertebrate to persist within a community can be predicted by proximity of habitat patch, especially if that patch is already occupied by the focal invertebrate species. For 3 out of 7 metapopulations, significant Nearest Neighbour effects were observed with Nearest Source being better than Nearest Habitat at predicting patch occupancy, findings that are consistent with both metapopulation theory (Levins 1969) and island biogeography theory (MacArthur & Wilson 1967), in that it is reasoned that it is proximity to nearest population that determines colonisation rather than the availability of habitat or means of dispersal (Moilanen & Nieminen 2002; Winfree *et al*. 2005; Prugh 2009). For each of the 3 metapopulations, the strength of the effect was improved by the addition of a different habitat variable: an interaction effect of distance from sea, an additive effect of distance from sea, and habitat type. A particular strength of this analysis is that by studying multiple, independent species in the same geographical area, between-species similarities and differences in occupancy patterns can be observed. These differences, as well as the lack of significant Nearest Neighbour measures in 4 of the 7 metapopulations, serve to reinforce the species-specific of the effect of both Nearest Neighbour measures and other habitat variables.

In Chapters 4 and 5, the role of non-native plants in how the presence of indirect effects within an ecological community, particularly in apparent competition, could be used to make predictions regarding the potential impact of a non-native invertebrate was examined.

In Chapter 4, using a comprehensive dataset of garden survey data, ranked relatedness of 32,984 possible pairwise native/non-native plant interactions was correlated with all observed invertebrate interactions (344), by means of a Mantel test, thus testing for the potential for apparent competition, in the form of a negative indirect interaction between the native and non-native plant, mediated by a shared invertebrate enemy, with the indirect interactions biased by plant relatedness. To examine the effect of possible error caused by including observations where host-feeding could not be confirmed, the test was repeated with a carefully refined set of invertebrate interactions (69). It was predicted that the more closely related a plant pair, the more likely it would be that they shared one or more common invertebrate enemies (e.g. Gilbert & Webb 2007; Dawson *et al*. 2009; Ness *et al*. 2011). A significant Mantel rest result was observed for both observed and refined data, thus indicating potential for the presence of apparent competition; however, a weak correlative effect, as indicated by a low Pearson's R value, suggests that here, the mean predictive power of relatedness is limited. Findings here provide a springboard for further studies, importantly, experimental manipulations of within-network interactions to further test for the presence of apparent competition. Additionally, while evidence from comparable resource overlap studies suggests that phylogenetic relatedness in consumers is not significant (e.g. Elias *et al.* 2013), patterns in level of sharing according to the native/non-native status of the invertebrate here seem present, and it would be interesting to add to the finds here by further examining resource overlap between native and non-native invertebrates. Furthermore, there appears a lack of similar studies examining the potential for interactions between a native and a non-native plant mediated by a shared invertebrate enemy, being biased by plant relatedness. Thus, importantly, the findings here provide original insight into how invertebrates and plants interact in an ecological community, and how these interactions help to structure the community.

While Chapter 4 addressed the potential for the presence of apparent competition, Chapter 5 sought evidence of its existence by examining how indirect interactions can help to shape an oak gall-wasp community. It was expected that in a community where both native and native gall-wasps are present, and in which the non-native gall-wasps exhibit heteroecy, that non-native host presence would have a positive effect on non-native gall density on a native host, and also that non-native gall density would have a negative effect on native gall density (e.g. Collins *et al.* 1983; Cornell & Hawkins 1993; Schönrogge & Crawley 2000; Schönrogge *et al.* 2000; Keane & Crawley 2002; Torchin & Mitchell 2004; Naniagua *et al.* 2009; Verhoeven *et al.* 2009; Dostál *et al.* 2013). Although none of the expected effects were observed, in direct contrast to the expected results, findings suggest the possible presence of apparent mutualism (Holt & Lawton 1994), rather than apparent competition. With apparent mutualism being either less well-studied or genuinely less common in ecological communities (e.g. Tack *et al.* 2011), the possibility of its presence here is especially interesting, and warrants further investigation.

6.2 Synthesis

What is clearly shown here is that it is possible to make predictions about a non-native invertebrate's presence and how it interacts with other species within an ecological community, using measures of non-native plant presence. Non-native plant richness, type and level of presence facilitates the establishment of a non-native invertebrate, while the distribution of a non-native plant within a community can have a predictable effect on a non-native invertebrate's ability to persist and potentially increase in population size to become problematic. Furthermore, a greater taxonomic diversity of plants present within a community could reduce the likelihood of host-switching or host-expansion by a non-native invertebrate, thus negatively impacting the invertebrate's ability to establish and persist. Also demonstrated is evidence for the potential predictive ability of indirect effects, and that these are not always in the direction expected. Importantly, while there are discernible patterns in how non-native invertebrates respond to non-native plant presence, such as non-native plant species richness driving non-native invertebrate species richness, or an invertebrate preference for woody plants, it is clear that responses to effects can also be species-specific, indicating that in some cases, an individual investigative approach might be of benefit.

There are clear benefits in maintaining a local focus, such as producing reliable findings that can make a scientifically-informed contribution to the development of local management approaches to invasive species management. Additionally, findings here are potentially globally transferable, notably as predictions in similar ecological communities elsewhere, such as those particularly prone to the effects of climate change (Parmesan & Yohe 2003; Hickling *et al*. 2006; Parmesan 2006; Chen *et al*. 2011; Cook *et al*. 2013; Kosanic *et al*. 2018). Here, the overall local focus of this study is an important factor in the interpretation of its findings. In particular, the comprehensive sampling intensity of the study means that confidence in the results are high. Furthermore, while the geographical breadth of the studies here is small, any potential weaknesses that this might confer are balanced by avoiding the presence of potentially problematic confounding effects of additional variables, such as flora/fauna differences, climate effects, geographic variation, etc.

6.3 Further research

In all studies, observational field data was used to test hypotheses, and thus, the use of manipulative experimental studies to corroborate the findings is clearly important. For example, studies such as those that test the negative effect on invertebrate occupancy levels in a metapopulation via removal of habitat patches, or those that aim to demonstrate the limiting effect of the reduction of woody plant presence in a community, or how an increase in plant taxonomic diversity limits the level of host-switching/expansion by a non-native invertebrate. Furthermore, such experimental approaches would enable more robust disentanglement of the indirect interactions indicated by the results. In particular, verification of the presence of apparent mutualism rather than apparent competition in gall wasp interactions could pave the way for the discovery of such findings in similar study systems.

While the benefits of locally-focused studies such as this one have been justified, it would be interesting to repeat these studies at a wider geographical scale and/or to extend the area in which local-scale studies are carried out, as well as more closely considering the temporal aspects of such studies. This would enable a direct comparison of results, and to seek explanations for similarities and differences indicated, thus serving to establish what might be driving these differences, and how that relates to the overall bigger picture.

6.4 Implications and the bigger picture

The implications of these findings are far-reaching, from new knowledge that will enable the prediction of how non-native plant presence influences non-native invertebrate presence, to further insight into how species interact in ecological communities, in particular, how indirect effects help to shape those interactions. In addition to informing further research, practical applications of these findings are many, including having the ability to mitigate the presence of a potentially problematic non-native invertebrate species via planting decisions, such as reducing the number of non-native plant species present, particularly the number of and area coverage of non-native woody plants, and minimising the introduction of non-native plants that are closely-related to native plants present. Importantly, given that species-specific responses to effects are indicated, assessment of the individual impact of a species' presence is always favourable, especially considering that the presence of a non-native species is not always negative or cause for concern (e.g. Manchester & Bullock 2000; Davis *et al*. 2011; Salisbury *et al*. 2015a), and, ultimately, the key goal is the persistence of a healthy, functioning ecological community. While the ecological impacts of a non-native invertebrate are emphasised here, the employment of any targeted management effort should have an economic knock-on effect also, with a perceived reduction in costly intervention needs, such as those involved in the control or removal of a problematic invertebrate.

Overall, results of this study provide fresh insight into the role of non-native plants in how non-native invertebrates interact in native food webs, addressing questions such as: What makes one ecological community more likely to have a non-native invertebrate presence than another, and what factors serve to influence that presence by increasing species numbers or enabling their persistence and population growth? How does the presence of indirect interactions involving a non-native invertebrate species help shape an ecological community? And fundamentally, why is the knowledge important?

The principal issue here is that globally, invasive species are widely acknowledged as one of the key drivers of biodiversity loss, and among the greatest threats to ecosystem stability. Therefore, having the scientific knowledge granted by increased understanding of the factors that determine and influence how a non-native species interacts within a food web, in order to better predict and consequently prevent invasiveness or to mitigate its effects, is crucial. Findings here clearly show that non-native invertebrate species are already prevalent in ecological communities, and while not all non-native invertebrates are recognised as invasive, all species have the potential to become a problem, e.g. if population levels reach a certain size, or if host-switching/expansion to an important native plant occurs. Importantly, as the extent of the impact of every non-native invertebrate species cannot be fully known, especially when it comes to recent arrivals, a better awareness of factors contributing to an increased level of the overall presence of non-native invertebrates is clearly advantageous in mitigating the impact of problem species, and in informing relevant decision-makers. Furthermore, given that the probability of ecological invasions will likely increase as a consequence of climate change and the current accelerated declines in biodiversity, the importance of insights gained from studies such as this one are vital.

Appendix I: Garden survey – detailed combined inventory of PTUs present (Chapters 2 and 4).

Abbreviations:

Status: N = native; NN = non-native; Unk = Unknown.

Plant type: F = fern/horsetail; H(f) = herb (forb); H(g) = herb (graminoid); W = tree/shrub

Species	Notes	Common Name	Genus	Family	Order	Class	Status	Plant type
Acacia Mill.		Unid. *Acacia* sp(p).	*Acacia*	Fabaceae	Fabales	Magnoliopsida	NN	.
Acanthus mollis L.		Bear's Breech	*Acanthus*	Acanthaceae	Lamiales	Magnoliopsida	NN	H(f)
Acca sellowiana (O. Berg) Burret		Feijoa	*Acca*	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Acer negundo L.		Ash-leaved Maple	*Acer*	Sapindaceae	Sapindales	Magnoliopsida	NN	W
Acer pseudoplatanus L.		Sycamore	*Acer*	Sapindaceae	Sapindales	Magnoliopsida	NN	W
Achillea millefolium L.		Yarrow	*Achillea*	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Actinidia chinensis var. *deliciosa* (A.Chev.) A.Chev.		Chinese Gooseberry	*Actinidia*	Actinidiaceae	Ericales	Magnoliopsida	NN	W
Aegopodium podagraria L.		Ground-elder	*Aegopodium*	Apiaceae	Apiales	Magnoliopsida	NN	H(f)
Aeonium Webb & Berthel.		Unid. *Aeonium* sp(p).	*Aeonium*	Crassulaceae	Saxifragales	Magnoliopsida	NN	W
Aesculus hippocastanum L.		Horse-chestnut	*Aesculus*	Sapindaceae	Sapindales	Magnoliopsida	NN	W
Aethusa cynapium L.		Fool's Parsley	*Aethusa*	Apiaceae	Apiales	Magnoliopsida	N	H(f)
Agapanthus praecox Willd.		African Lily	*Agapanthus*	Amaryllidaceae	Asparagales	Liliopsida	NN	H(f)
Agave americana L.		Century Plant	*Agave*	Asparagaceae	Asparagales	Liliopsida	NN	W
Agrostemma githago L.		Common Corncockle	*Agrostemma*	Caryophyllaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Agrostis stolonifera L.		Creeping Bent	*Agrostis*	Poaceae	Poales	Liliopsida	N	H(g)
Ailanthus altissima (Mill.) Swingle		Tree-of-Heaven	*Ailanthus*	Simaroubaceae	Sapindales	Magnoliopsida	NN	W
Alchemilla mollis (Buser) Rothm.		Lady's-mantle	*Alchemilla*	Rosaceae	Rosales	Magnoliopsida	NN	H(f)
Allium moly L.		Yellow Garlic	*Allium*	Amaryllidaceae	Asparagales	Liliopsida	NN	H(f)
Allium triquetrum L.		Three-cornered Garlic	*Allium*	Amaryllidaceae	Asparagales	Liliopsida	NN	H(f)
Alnus cordata (Loisel.) Duby		Italian Alder	*Alnus*	Betulaceae	Fagales	Magnoliopsida	NN	W
Aloiampelos striatula (Haw.) Klopper & Gideon F.Sm, *Aloidendron* (A.Berger) Klopper & Gideon F.Sm., *Kumara* Medik., *Aloiampelos* Klopper & Gideon F.Sm., *Aloe* L., *Aristaloe* Boatwr. & J.C.Manning, *Gonialoe* (Baker) Boatwr. & J.C.Manning	Form. *Aloe*	Hardy Aloe, unid. aloe(s)	*Aloe, Aloiampelos, Aloidendron, Aristaloe, Kumara, Gonialoe*	Asphodelaceae	Asparagales	Liliopsida	NN	W
Amicia zygomeris DC.		Yoke-leaved Amicia	*Amicia*	Fabaceae	Fabales	Magnoliopsida	NN	H(f)
Anigozanthos Labill.		Kangaroo Paw	*Anigozanthos*	Haemodoraceae	Commelinales	Liliopsida	NN	H(f)
Anthriscus sylvestris (L.)		Cow Parsley	*Anthriscus*	Apiaceae	Apiales	Magnoliopsida	N	H(f)

Species	Notes	Common Name	Genus	Family	Order	Class	Status	Plant type
Anthyllis vulneraria L.		Kidney Vetch	*Anthyllis*	Fabaceae	Fabales	Magnoliopsida	N	H(f)
Aquilegia L.		Unid. *Aquilegia* sp(p). (NN)	*Aquilegia*	Ranunculaceae	Ranunculales	Magnoliopsida	NN	H(f)
Aralia elata (Miq.) Seem.		Chinese Angelica-tree	*Aralia*	Araliaceae	Apiales	Magnoliopsida	NN	W
Araucaria araucana (Molina) K. Koch		Monkey Puzzle	*Araucaria*	Araucariaceae	Pinales	Pinopsida	NN	W
Arctium minus (Hill) Bernh.		Lesser Burdock	*Arctium*	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Argyranthemum frutescens (L.) Sch.Bip.		Marguerite	*Argyranthemum*	Asteraceae	Asterales	Magnoliopsida	NN	W
Armeria maritima (Mill.) Willd.		Thrift	*Armeria*	Plumbaginaceae	Caryophyllales	Magnoliopsida	N	H(f)
Armoracia rusticana P. Gaertn., B. Mey. & Scherb.		Horseradish	*Armoracia*	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Arrhenatherum elatius (L.) P.Beauv. ex J.Presl & C.Presl.		False Oat-grass	*Arrhenatherum*	Poaceae	Poales	Liliopsida	N	H(g)
Arum italicum subsp. *neglectum* (F.Towns.) Prime		Italian Lords-and-Ladies	*Arum*	Araceae	Alismatales	Liliopsida	N	H(f)
Arum maculatum L.		Lords-and-Ladies	*Arum*	Araceae	Alismatales	Liliopsida	N	H(f)
Asplenium adiantum-nigrum L.		Black Spleenwort	*Asplenium*	Aspleniaceae	Polypodiales	Polypodiopsida	N	F
Asplenium scolopendrium L.		Hart's-tongue Fern	*Asplenium*	Aspleniaceae	Polypodiales	Polypodiopsida	N	F
Asplenium trichomanes L.		Maidenhair Spleenwort	*Asplenium*	Aspleniaceae	Polypodiales	Polypodiopsida	N	F
Astelia chathamica (Skottsb.) L.B.Moore		Silver Spear	*Astelia*	Asteliaceae	Asparagales	Liliopsida	NN	W
Aucuba japonica Thunb.		Spotted Laurel	*Aucuba*	Garryaceae	Garryales	Magnoliopsida	NN	W
Banksia L.f.		Unid. *Banksia* sp(p).	Banksia	Proteaceae	Proteales	Magnoliopsida	NN	W
Begonia cucullata var. *hookeri* (A.DC.) L.B.Sm. & B.G.Schub.		A begonia	Begonia	Begoniaceae	Cucurbitales	Magnoliopsida	NN	H(f)
Bellis perennis L.		Common Daisy	Bellis	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Berberis aquifolium Pursh	Syn. *Mahonia aquifolium*	Oregon Grape	Berberis	Berberidaceae	Ranunculales	Magnoliopsida	NN	W
Berberis darwinii Hook., *Berberis* L.		Darwin's Barberry, Unid. *Berberis* sp(p).	Berberis	Berberidaceae	Ranunculales	Magnoliopsida	NN	W
Berberis thunbergii DC.		Japanese Barberry	Berberis	Berberidaceae	Ranunculales	Magnoliopsida	NN	W
Bergenia crassifolia (L.) Fritsch		Elephant-ears	Bergenia	Saxifragaceae	Saxifragales	Magnoliopsida	NN	H(f)
Beschorneria yuccoides K.Koch		Yucca-leaved Beschorneria	Beschorneria	Asparagaceae	Asparagales	Liliopsida	NN	H(f)
Betonica officinalis L.	Syn. *Stachys officinalis*	Betony	Betonica	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Betula L.		Unid. *Betula* sp(p.) (NN)	Betula	Betulaceae	Fagales	Magnoliopsida	NN	W
Betula pendula Roth, *Betula pubescens* Ehrh.		Silver Birch, Downy Birch	Betula	Betulaceae	Fagales	Magnoliopsida	N	W
Brachyglottis × *jubar* P.D.Sell		Shrub Ragwort	Brachyglottis	Asteraceae	Asterales	Magnoliopsida	NN	W
Brassica napus L.	*Brassica napus* subsp. *napus*	Oilseed Rape	Brassica	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Buddleja Houst. ex L.		Unid. *Buddleja* sp(p).	Buddleja	Scrophulariae	Lamiales	Magnoliopsida	NN	W
Buddleja davidii Franch.		Butterfly-bush	Buddleja	Scrophulariae	Lamiales	Magnoliopsida	NN	W
Buddleja globosa Hope		Orange-ball Tree	Buddleja	Scrophulariae	Lamiales	Magnoliopsida	NN	W
Buxus sempervirens L.		Common Box	Buxus	Buxaceae	Buxales	Magnoliopsida	N	W

Species	**Notes**	**Common Name**	**Genus**	**Family**	**Order**	**Class**	**Status**	**Plant type**
Calendula officinalis L.		Pot Marigold	Calendula	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Callianthe megapotamica (A.Spreng.) Dorr	Syn. *Abutilon megapotamicum*	Trailing Abutilon	*Callianthe*	Malvaceae	Malvales	Magnoliopsida	NN	W
Calluna vulgaris (L.) Hull		Ling (cultivars)	Calluna	Ericaceae	Ericales	Magnoliopsida	N	W
Calystegia sepium (L.) R.Br.		Hedge Bindweed	Calystegia	Convolvulaceae	Solanales	Magnoliopsida	N	H(f)
Camellia japonica L., *Camellia* L.		Camellia, unid. *Camellia* sp(p).	Camellia	Theaceae	Ericales	Magnoliopsida	NN	W
Campanula portenschlagiana Schult., *Campanula poscharskyana* Degen		Adria Bellflower, Trailing Bellflower	Campanula	Campanulaceae	Asterales	Magnoliopsida	NN	H(f)
Canna indica L.		Canna	Canna	Cannaceae	Zingiberales	Liliopsida	NN	H(f)
Capsella bursa-pastoris (L.) Medik.		Shepherd's-purse	Capsella	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Cardamine flexuosa With., *Cardamine hirsuta* L.		Wavy Bittercress, Hairy Bittercress	Cardamine	Brassicaceae	Brassicales	Magnoliopsida	N	H(f)
Carex L.		Unid. *Carex* sp. (NN)	Carex	Cyperaceae	Poales	Liliopsida	NN	H(g)
Carex pendula Huds.		Pendulous Sedge	Carex	Cyperaceae	Poales	Liliopsida	N	H(g)
Carpobrotus edulis (L.) N.E.Br.		Hottentot-fig	Carpobrotus	Aizoaceae	Caryophyllales	Magnoliopsida	NN	W
Castanea sativa Mill.		Sweet Chestnut	Castanea	Fagaceae	Fagales	Magnoliopsida	NN	W
Catalpa × *erubescens* Carrière		Indian Bean Tree	Catalpa	Bignoniaceae	Lamiales	Magnoliopsida	NN	W
Cedrus atlantica (Endl.) Manetti ex Carrière		Atlantic Blue Cedar	Cedrus	Pinaceae	Pinales	Pinopsida	NN	W
Centaurea cyanus L.		Cornflower	Centaurea	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Centaurea nigra L.		Common Knapweed	Centaurea	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Cerastium fontanum Baumg.		Common Mouse-ear	Cerastium	Caryophyllaceae	Caryophyllales	Magnoliopsida	N	H(f)
Cerastium tomentosum L.		Snow-in-Summer	Cerastium	Caryophyllaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Ceratostigma Bunge		Unid. *Ceratostigma* sp.	Ceratostigma	Plumbaginaceae	Caryophyllales	Magnoliopsida	NN	W
Cestrum parqui (Lam.) L'Hér.		Chilean Jessamine	Cestrum	Solanaceae	Solanales	Magnoliopsida	NN	W
Chaenomeles japonica (Thunb.) Lindl. ex Spach		Maule's Quince	Chaenomeles	Rosaceae	Rosales	Magnoliopsida	NN	W
Chamaecyparis Spach		Unid. *Chamaecyparis* sp(p).	Chamaecyparis	Cupressaceae	Pinales	Pinopsida	NN	W
Chamaenerion angustifolium L.		Rosebay Willowherb	Chamaenerion	Onagraceae	Myrtales	Magnoliopsida	N	H(f)
Chamaerops humilis L.		Mediterranean Dwarf Palm	Chamaerops	Arecaceae	Arecales	Liliopsida	NN	W
Chasmanthe bicolor (Gasp.) N.E.Br.		Chasmanthe	Chasmanthe	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Chenopodium album L.		Fat-hen	Chenopodium	Amaranthaceae	Caryophyllales	Magnoliopsida	N	H(f)
Circaea lutetiana L.		Enchanter's-nightshade	Circaea	Onagraceae	Myrtales	Magnoliopsida	N	H(f)
Cirsium vulgare (Savi) Ten.		Spear Thistle	Cirsium	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Cistus L.		Unid. *Cistus* sp(p).	Cistus	Cistaceae	Malvales	Magnoliopsida	NN	W
Clematis vitalba L.		Travellers-joy	Clematis	Ranunculaceae	Ranunculales	Magnoliopsida	N	W
Cordyline australis (G.Forst.) Endl.		Cabbage-palm	Cordyline	Asparagaceae	Asparagales	Liliopsida	NN	W
Cornus kousa Bürger ex Hance, *Cornus mas* L., *Cornus* L.		Cornelian Cherry, Chinese Dogwood, Unid. *Cornus* sp(p). (NN)	Cornus	Cornaceae	Cornales	Magnoliopsida	NN	W
Correa backhouseana Hook.		Tasmanian-fuchsia	Correa	Rutaceae	Sapindales	Magnoliopsida	NN	W
Cortaderia selloana (Schult. & Schult.f.) Asch. & Graebn.		Pampas Grass	Cortaderia	Poaceae	Poales	Liliopsida	NN	H(g)

Species	Notes	Common Name	Genus	Family	Order	Class	Status	Plant type
Corylus avellana L., *Corylus avellana* var. *avellana* (Bean) Rehder.		Hazel, Contorted Hazel	Corylus	Betulaceae	Fagales	Magnoliopsida	N	W
Cotinus coggygria Scop.		European Smoketree	Cotinus	Anacardiaceae	Sapindales	Magnoliopsida	NN	W
Cotoneaster Medik.		Unid. *Cotoneaster* sp(p). (NN)	Cotoneaster	Rosaceae	Rosales	Magnoliopsida	NN	W
Crassula multicava Lem.		Fairy Crassula	Crassula	Crassulaceae	Saxifragales	Magnoliopsida	NN	W
Crataegus L.		Unid. *Crataegus* sp. (NN)	Crataegus	Rosaceae	Rosales	Magnoliopsida	NN	W
Crataegus crus-galli L.		Cockspurthorn	Crataegus	Rosaceae	Rosales	Magnoliopsida	NN	W
Crataegus monogyna Jacq.		Hawthorn	Crataegus	Rosaceae	Rosales	Magnoliopsida	N	W
Crepis capillaris (L.) Wallr.		Smooth Hawksbeard	Crepis	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Crocosmia × *crocosmiiflora* (Lemoine) N.E.Br.		Montbretia	Crocosmia	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Cryptomeria japonica (Thunb. ex L. f.) D. Don		Japanese Cedar	Cryptomeria	Cupressaceae	Pinales	Pinopsida	NN	W
Cymbalaria muralis G.Gaertn., B.Mey. & Schreb.		Ivy-leaved Toadflax	Cymbalaria	Plantaginaceae	Lamiales	Magnoliopsida	NN	H(f)
Cynara cardunculus L.		Cardoon	Cynara	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Cyperus longi-involucratus Lye		Umbrella Sedge	Cyperus	Cyperaceae	Poales	Liliopsida	NN	H(g)
Cytisus × *praecox* Bean		Warminster Broom	Cytisus	Fabaceae	Fabales	Magnoliopsida	NN	W
Dactylis glomerata L.		Cock's-foot	Dactylis	Poaceae	Poales	Liliopsida	N	H(g)
Dahlia Cav.		Unid. *Dahlia* sp(p).	Dahlia	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Datisca cannabina L.		Cretan Hemp	Datisca	Datiscaceae	Cucurbitales	Magnoliopsida	NN	H(f)
Davidia involucrata Baill.		Dove-tree	Davidia	Nyssaceae	Cornales	Magnoliopsida	NN	W
Delairea odorata Lem.		Cape Ivy	Delairea	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Dianella caerulea Sims		Blue Flax-lily	Dianella	Asphodelaceae	Asparagales	Liliopsida	NN	H(f)
Dianthus barbatus L., *Dianthus caryophyllus* L.		Sweet William, Carnation	Dianthus	Caryophyllaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Dicksonia antarctica Labill.		Tree-fern	Dicksonia	Dicksoniaceae	Cyatheales	Polypodiopsida	NN	W
Digitalis purpurea L.		Foxglove	Digitalis	Plantaginaceae	Lamiales	Magnoliopsida	N	H(f)
Diplotaxis muralis (L.) DC.		Annual Wall-rocket	Diplotaxis	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Dimorphotheca ecklonis DC., *Dimorphotheca jucunda* E.Phillips	Syn. *Osteospermum*	Cape Marguerite, African Daisy	Dimorphotheca	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Dipsacus fullonum L.		Wild Teasel	Dipsacus	Caprifoliaceae	Dipsacales	Magnoliopsida	N	H(f)
Dodonaea viscosa Jacq.		Purple Hop Bush	Dodonaea	Sapindaceae	Sapindales	Magnoliopsida	NN	W
Dryopteris dilatata (Hoffm.) A. Gray, *Dryopteris filix-mas* (L.) Schott		Broad buckler-fern, Male-fern	Dryopteris	Dryopteridaceae	Polypodiales	Polypodiopsida	N	F
Echinops bannaticus Rochel ex Schrad.		Blue Globe-thistle	Echinops	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Echium candicans L.f.		Pride of Madeira	Echium	Boraginaceae	Boraginales	Magnoliopsida	NN	H(f)
Echium pininana Webb & Berthel.		Giant Viper's-bugloss	Echium	Boraginaceae	Boraginales	Magnoliopsida	NN	H(f)
Elaeagnus × *submacrophylla* Servett.	Syn. *E. x ebbingei*	Elaeagnus × submacrophylla	Elaeagnus	Elaeagnaceae	Rosales	Magnoliopsida	NN	W
Elegia L.		Unid. *Elegia* sp(p).	Elegia	Restionaceae	Poales	Liliopsida	NN	H(g)
Embothrium coccineum J.R. Forster & G. Forster		Chilean Firebush	Embothrium	Proteaceae	Proteales	Magnoliopsida	NN	W

Species	**Notes**	**Common Name**	**Genus**	**Family**	**Order**	**Class**	**Status**	**Plant type**
Eomecon chionantha Hance		Snow-poppy	Eomecon	Papaveraceae	Ranunculales	Magnoliopsida	NN	H(f)
Epilobium hirsutum L.		Great Willowherb	Epilobium	Onagraceae	Myrtales	Magnoliopsida	N	H(f)
Epilobium montanum L., *Epilobium parviflorum* Schreb.		Broad-leaved Willowherb, Hoary Willowherb	Epilobium	Onagraceae	Myrtales	Magnoliopsida	N	H(f)
Equisetum L.		Unid. *Equisetum* sp.	Equisetum	Equisetaceae	Equistales	Equisetopsida	N	F
Erica arborea L.		Tree Heath	Erica	Ericaceae	Ericales	Magnoliopsida	NN	W
Erigeron L.	Form. *Conyza*	Unid. *Erigeron* sp(p). (NN)	Erigeron	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Erigeron glaucus Ker-Gawl.		Beach Aster	Erigeron	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Erigeron karvinskianus DC.		Mexican Fleabane	Erigeron	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Eriobotrya japonica (Thunb.) Lindl.		Loquat	Eriobotrya	Rosaceae	Rosales	Magnoliopsida	NN	W
Eriocapitella × hybrida (L.H.Bailey) Christenh. & Byng [artificial hybrid], *Anemone* L., *Eriocapitella* Nakai	Form. *Anemone*	Japanese Anemone, unid. *Anemone* sp(p)., unid. *Eriocapitella* sp(p).	Eriocapitella	Ranunculaceae	Ranunculales	Magnoliopsida	NN	H(f)
Erodium cicutarium (L.) L'Hér.		Common Storksbill	Erodium	Geraniaceae	Geraniales	Magnoliopsida	N	H(f)
Erysimum cheiri (L.) Crantz		Wallflower	Erysimum	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Escallonia rubra var. macrantha (Hook. & Arn.) Reiche	Syn. *Escallonia rubra*	Chilean Gum-box	Escallonia	Escalloniaceae	Escalloniales	Magnoliopsida	NN	W
Eschscholzia californica Cham.		California Poppy	Eschscholzia	Papaveraceae	Ranunculales	Magnoliopsida	NN	H(f)
Eucalyptus L'Hér.		Unid. *Eucalyptus* sp(p).	Eucalyptus	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Eucalyptus cinerea F.Muell. ex Benth.		Grey Eucalyptus	Eucalyptus	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Euonymus L.		Unid. *Euonymus* sp(p). (NN)	Euonymus	Celastraceae	Celastrales	Magnoliopsida	NN	W
Euonymus japonicus Thunb.		Evergreen Spindle	Euonymus	Celastraceae	Celastrales	Magnoliopsida	NN	W
Euphorbia characias subsp. *wulfenii* (Hoppe ex W.D.J.Koch) Radcl.-Sm.		Mediterranean Spurge	Euphorbia	Euphorbiaceae	Malpighiales	Magnoliopsida	NN	H(f)
Euphorbia mellifera Aiton		Honey Spurge	Euphorbia	Euphorbiaceae	Malpighiales	Magnoliopsida	NN	H(f)
Euphorbia peplus L.		Petty Spurge	Euphorbia	Euphorbiaceae	Malpighiales	Magnoliopsida	N	H(f)
Euryops chrysanthemoides (DC.) B.Nord.		African Bush-daisy	Euryops	Asteraceae	Asterales	Magnoliopsida	NN	W
Fagus sylvatica L.		European Beech	Fagus	Fagaceae	Fagales	Magnoliopsida	N	W
Fascicularia bicolor (Ruiz & Pav.) Mez		Fascicularia	Fascicularia	Bromeliaceae	Poales	Liliopsida	NN	W
Fatsia japonica (Thunb.) Decne. & Planch.		Japanese Aralia	Fatsia	Araliaceae	Apiales	Magnoliopsida	NN	W
Festuca Tourn. ex L.		Unid. *Festuca* sp.	Festuca	Poaceae	Poales	Liliopsida	N	H(g)
Ficus carica L.		Fig	Ficus	Moraceae	Rosales	Magnoliopsida	NN	W
Foeniculum vulgare Mill.		Fennel	Foeniculum	Apiaceae	Apiales	Magnoliopsida	NN	H(f)
Fragaria vesca L.		Wild Strawberry	Fragaria	Rosaceae	Rosales	Magnoliopsida	N	H(f)
Francoa appendiculata Cav.	Syn. *Francoa sonchifolia*	Bridalwreath	Francoa	Francoaceae	Geraniales	Magnoliopsida	NN	H(f)
Fraxinus excelsior L.		Ash	Fraxinus	Oleaceae	Lamiales	Magnoliopsida	N	W
Fremontodendron 'California Glory' (F. californicum (Torr.) Coult. x *F. mexicanum* (Davidson))		Flannel Bush	Fremontodendron	Malvaceae	Malvales	Magnoliopsida	NN	W
Fuchsia magellanica Lam.		Fuchsia	Fuchsia	Onagraceae	Myrtales	Magnoliopsida	NN	W
Fuchsia splendens Zucc.		A fuchsia	Fuchsia	Onagraceae	Myrtales	Magnoliopsida	NN	W

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Fumaria Tourn. ex L.		Unid. *Fumaria* sp(p).	Fumaria	Papaveraceae	Ranunculales	Magnoliopsida	N	H(f)
Galinsoga quadriradiata Ruiz & Pav.		Shaggy Soldier	Galinsoga	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Galium aparine L.		Cleavers	Galium	Rubiaceae	Gentianales	Magnoliopsida	N	H(f)
Gaultheria Kalm ex L.		Unid. *Gaultheria* sp.	Gaultheria	Ericaceae	Ericales	Magnoliopsida	NN	W
Gazania rigens (L.) Gaertn.		Treasure Flower	Gazania	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Geranium Tourn. ex L.		Unid. *Geranium* sp(p). (NN)	Geranium	Geraniaceae	Geraniales	Magnoliopsida	NN	H(f)
Geranium dissectum L., *Geranium molle* L., *Geranium robertianum* L.		Cut-leaved Cranesbill, Dove's-foot Cranesbill, Herb-robert	Geranium	Geraniaceae	Geraniales	Magnoliopsida	N	H(f)
Geum urbanum L.		Wood Avens	Geum	Rosaceae	Rosales	Magnoliopsida	N	H(f)
Ginkgo biloba L.		Ginkgo	Ginkgo	Ginkgoaceae	Ginkgoales	Ginkgoopsida	NN	W
Gladiolus Tourn. ex L.		Unid. *Gladiolus* sp(p).	Gladiolus	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Glechoma hederacea L.		Ground Ivy	Glechoma	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Grevillea R.Br. ex Knight		Unid. *Grevillea* sp(p).	Grevillea	Proteaceae	Proteales	Magnoliopsida	NN	W
Griselinia littoralis (Raoul) Raoul		Kapuka	Griselinia	Griseliniaceae	Apiales	Magnoliopsida	NN	W
Gunnera manicata Linden ex André		Giant Rhubarb	Gunnera	Gunneraceae	Gunnerales	Magnoliopsida	NN	H(f)
Hedera helix L., *Hedera hibernica* Poit.		Common Ivy, Atlantic Ivy	Hedera	Araliaceae	Apiales	Magnoliopsida	N	W
Hedychium J.Koenig		Unid. *Hedychium* sp(p).	Hedychium	Zingiberaceae	Zingiberales	Liliopsida	NN	H(f)
Helichrysum italicum (Roth) G.Don		Curry Plant	Helichrysum	Asteraceae	Asterales	Magnoliopsida	NN	W
Helleborus foetidus L.		Stinking Hellebore	Helleborus	Ranunculaceae	Ranunculales	Magnoliopsida	N	H(f)
Helminthotheca echioides (L) Holub	Syn. *Picris echioides*	Bristly Ox-tongue	Helminthotheca	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Hemerocallis fulva (L.) L.		Orange Day-lily	Hemerocallis	Asphodelaceae	Asparagales	Liliopsida	NN	H(f)
Heracleum sphondylium L.		Hogweed	Heracleum	Apiaceae	Apiales	Magnoliopsida	N	H(f)
Hippophae rhamnoides L.		Sea Buckthorn	Hippophae	Elaeagnaceae	Rosales	Magnoliopsida	N	W
Holcus lanatus L.		Yorkshire Fog	Holcus	Poaceae	Poales	Liliopsida	N	H(g)
Houttuynia cordata Thunb.		Fish Mint	Houttuynia	Saururaceae	Piperales	Magnoliopsida	NN	H(f)
Hydrangea Gronov. ex L.		Unid. *Hydrangea* sp(p).	Hydrangea	Hydrangeaceae	Cornales	Magnoliopsida	NN	W
Hypericum androsaemum L.		Tutsan	Hypericum	Hypericaceae	Malpighiales	Magnoliopsida	N	W
Hypericum calycinum L.		Rose-of-Sharon	Hypericum	Hypericaceae	Malpighiales	Magnoliopsida	NN	W
Hypericum calycinum L. 'Hidcote'		Hypericum Hidcote	Hypericum	Hypericaceae	Malpighiales	Magnoliopsida	NN	W
Hypericum perforatum L.		Perforate St John's-wort	Hypericum	Hypericaceae	Malpighiales	Magnoliopsida	N	H(f)
Hypochaeris radicata L.		Catsear	Hypochaeris	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Ilex aquifolium L.		Holly	Ilex	Aquifoliaceae	Aquifoliales	Magnoliopsida	N	W
Impatiens Riv. ex L.		Unid. *Impatiens* sp(p).	Impatiens	Balsaminaceae	Ericales	Magnoliopsida	NN	H(f)
Iris Tourn. ex L.		Unid. *Iris* sp(p). (NN)	Iris	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Iris foetidissima L.		Stinking Iris	Iris	Iridaceae	Asparagales	Liliopsida	N	H(f)
Jacobaea vulgaris L., *Senecio vulgaris* L.	Form. *Senecio*	Common Ragwort, Groundsel	Jacobaea, Senecio	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Jasminum L.		Unid. *Jasminum* sp(p).	Jasminum	Oleaceae	Lamiales	Magnoliopsida	NN	W
Juncus effusus L.		Soft-rush	Juncus	Juncaceae	Poales	Liliopsida	N	H(g)
Juniperus L.		Unid. *Juniperus* sp(p). (NN)	Juniperus	Cupressaceae	Pinales	Pinopsida	NN	W
Kniphofia Moench		Unid. *Kniphofia* sp(p).	Kniphofia	Asphodelaceae	Asparagales	Liliopsida	NN	H(f)

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Kunzea ambigua (Sm.) Druce		White Kunzea	Kunzea	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Laburnum anagyroides Medik.		Laburnum	Laburnum	Fabaceae	Fabales	Magnoliopsida	NN	W
Lamium purpureum L.		Red Deadnettle	Lamium	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Lampranthus roseus (Willd.) Schwantes		Rosy Dewplant	Lampranthus	Aizoaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Lapsana communis L.		Nipplewort	Lapsana	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Larix decidua Mill.		European Larch	Larix	Pinaceae	Pinales	Pinopsida	NN	W
Laurus nobilis L.		Bay	Laurus	Lauraceae	Laurales	Magnoliopsida	NN	W
Lavandula angustifolia Mill.		Lavender	Lavandula	Lamiaceae	Lamiales	Magnoliopsida	NN	W
Lechea Kalm ex L.	Form. Gaura	Unid. *Lechea* sp(p).	Lechea	Onagraceae	Myrtales	Magnoliopsida	NN	H(f)
Lepidium didymum L.		Lesser Swinecress	Lepidium	Brassicaceae	Brassicales	Magnoliopsida	NN	H(f)
Leptospermum scoparium J.R.Forst. & G.Forst., *Leptospermum* J.R.Forst. & G.Forst.		Manuka, unid. *Leptospermum* sp(p).	Leptospermum	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Leucadendron R.Br.		Unid. *Leucadendron* sp(p).	Leucadendron	Proteaceae	Proteales	Magnoliopsida	NN	W
Leucanthemum vulgare Lam.		Oxeye Daisy	Leucanthemum	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Leucothoe axillaris (Lam.) D. Don 'Curly Red'		A leucothoe	Leucothoe	Ericaceae	Ericales	Magnoliopsida	NN	W
Leycesteria formosa Wall.		Himalayan Honeysuckle	Leycesteria	Caprifoliaceae	Dipsacales	Magnoliopsida	NN	W
Libertia Spreng.		Unid. *Libertia* sp(p).	Libertia	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Ligustrum ovalifolium Hassk.		Garden Privet	Ligustrum	Oleaceae	Lamiales	Magnoliopsida	NN	W
Linaria purpurea (L.) Mill.		Purple Toadflax	Linaria	Plantaginaceae	Lamiales	Magnoliopsida	NN	H(f)
Linaria vulgaris Mill.		Common Toadflax	Linaria	Plantaginaceae	Lamiales	Magnoliopsida	N	H(f)
Liquidambar styraciflua L.		American Sweetgum	Liquidambar	Altingiaceae	Saxifragales	Magnoliopsida	NN	W
Liriodendron tulipifera L.		Tulip-tree	Liriodendron	Magnoliaceae	Magnoliales	Magnoliopsida	NN	W
Lobelia erinus L.		Garden Lobelia	Lobelia	Campanulaceae	Asterales	Magnoliopsida	NN	H(f)
Lolium perenne L.		Perennial Rye-grass	Lolium	Poaceae	Poales	Liliopsida	N	H(g)
Lonicera periclymenum L.		Honeysuckle	Lonicera	Caprifoliaceae	Dipsacales	Magnoliopsida	N	W
Lotus corniculatus L.		Common Bird's-foot Trefoil	Lotus	Fabaceae	Fabales	Magnoliopsida	N	H(f)
Luma apiculata (DC.) Burret		Chilean Myrtle	Luma	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Lupinus polyphyllus Lindl.		Garden Lupin	Lupinus	Fabaceae	Fabales	Magnoliopsida	NN	H(f)
Luzula DC.		Unid. *Luzula* sp.	Luzula	Poaceae	Poales	Liliopsida	N	H(g)
Lysimachia arvensis (L.) U.Manns & Anderb.	Syn. *Anagallis arvensis*	Scarlet Pimpernel	Lysimachia	Primulaceae	Ericales	Magnoliopsida	N	H(f)
Magnolia grandiflora L., *Magnolia* Plum. ex L.		Southern Magnolia, unid. *Magnolia* sp(p).	Magnolia	Magnoliaceae	Magnoliales	Magnoliopsida	NN	W
Malus domestica (Suckow) Borkh.	Syn. *Malus pumila*	Apple	Malus	Rosaceae	Rosales	Magnoliopsida	NN	W
Malus sylvestris (L.) Mill.		Crab Apple	Malus	Rosaceae	Rosales	Magnoliopsida	N	W
Malva arborea (L.) Webb & Berth.	Syn. *Lavatera arborea*	Tree Mallow	Malva (form. Lavatera)	Malvaceae	Malvales	Magnoliopsida	N	H(f)
Malva sylvestris L.		Common Mallow	Malva	Malvaceae	Malvales	Magnoliopsida	NN	H(f)
Matricaria discoidea DC.		Pineappleweed	Matricaria	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Medicago arabica (L.) Huds.		Spotted Medick	Medicago	Fabaceae	Fabales	Magnoliopsida	N	H(f)

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Melaleuca L.	Form. *Callistemon*	Unid. *Melaleuca* sp(p).	*Melaleuca*	Myrtaceae	Myrtales	Magnoliopsida	NN	W
Melissa officinalis L.		Lemon Balm	Melissa	Lamiaceae	Lamiales	Magnoliopsida	NN	H(f)
Mentha spicata L.		Spearmint	Mentha	Lamiaceae	Lamiales	Magnoliopsida	NN	H(f)
Miscanthus sinensis Andersson		Zebra Grass	Miscanthus	Poaceae	Poales	Liliopsida	NN	H(g)
Musa basjoo Siebold & Zucc. ex Iinuma		Hardy Banana	Musa	Musaceae	Zingiberales	Magnoliopsida	NN	H(f)
Myosotis sylvatica Ehrh. ex Hoffm.		Wood Forget-me-not	Myosotis	Boraginaceae	Boraginales	Magnoliopsida	N	H(f)
Nassella trichotoma (Nees) Hack. & Arechav.		Serrated Tussock Grass	Nassella	Poaceae	Poales	Liliopsida	NN	H(g)
Neopanax laetus (Kirk) Allan		A neopanax	Neopanax	Araliaceae	Apiales	Magnoliopsida	NN	W
Nothofagus obliqua (Mirb.) Oerst.		Roble Beech	Nothofagus	Nothofagaceae	Fagales	Magnoliopsida	NN	W
Nymphaea L.		Unid. *Nymphaea* sp(p). (NN)	Nymphaea	Nymphaceae	Nymphaeales	Magnoliopsida	NN	H(f)
Oemleria cerasiformis (Torr. & A.Gray ex Hook. & Arn.)		Oso Berry	Oemleria	Rosaceae	Rosales	Magnoliopsida	NN	W
Oenothera L.		Unid. *Oenothera* sp(p).	Oenothera	Onagraceae	Myrtales	Magnoliopsida	NN	H(f)
Olea europaea L.		Olive	Olea	Oleaceae	Lamiales	Magnoliopsida	NN	W
Olearia macrodonta Baker, *Olearia paniculata* Druce, *Olearia traversiorum* (F.Muell.) Hook.f., *Olearia* Moench		New Zealand Holly, Akiraho, Chatham Island Akeake, unid. *Olearia* sp(p).	Olearia	Asteraceae	Asterales	Magnoliopsida	NN	W
Olearia semidentata Decne. ex Hook.		Daisy Bush	Olearia	Asteraceae	Asterales	Magnoliopsida	NN	W
Olearia solandri Hook.f.		Coastal Daisy-bush	Olearia	Asteraceae	Asterales	Magnoliopsida	NN	W
Ophiopogon planiscapus Nakai		Black Mondo Grass	Ophiopogon	Asparagaceae	Asparagales	Liliopsida	NN	H(f)
Oxalis acetosella L.		Wood-sorrel	Oxalis	Oxalidaceae	Oxalidales	Magnoliopsida	N	H(f)
Oxalis L.		Unid. *Oxalis* sp(p). (NN)	Oxalis	Oxalidaceae	Oxalidales	Magnoliopsida	NN	H(f)
Ozothamnus R.Br.		Unid. *Ozothamnus* sp(p).	Ozothamnus	Asteraceae	Asterales	Magnoliopsida	NN	W
Paeonia delavayi Franch.	Syn. *Paeonia lutea*	Tree Peony	Paeonia	Paeoniaceae	Saxifragales	Magnoliopsida	NN	W
Paeonia L.		Unid. *Paeonia* sp(p).	Paeonia	Paeoniaceae	Saxifragales	Magnoliopsida	NN	W
Papaver rhoeas L.		Common Poppy	Papaver	Papaveraceae	Ranunculales	Magnoliopsida	N	H(f)
Papaver somniferum L.		Opium Poppy	Papaver	Papaveraceae	Ranunculales	Magnoliopsida	NN	H(f)
Parietaria judaica L.		Pellitory-of-the-Wall	Parietaria	Urticaceae	Rosales	Magnoliopsida	N	H(f)
Parthenocissus heptaphylla (Planch.) Britton		Sevenleaf Creeper	Parthenocissus	Vitaceae	Vitales	Magnoliopsida	NN	W
Passiflora caerulea L.		Common Passion-flower	Passiflora	Passifloraceae	Malpighiales	Magnoliopsida	NN	W
Pelargonium L'Hér. ex Aiton		*Pelargonium* sp(p).	Pelargonium	Geraniaceae	Geraniales	Magnoliopsida	NN	H(f)
Penstemon Schmidel		Unid. *Penstemon* sp(p).	Penstemon	Plantaginaceae	Lamiales	Magnoliopsida	NN	H(f)
Pentaglottis sempervirens (L.) Tausch ex L.H.Bailey		Green Alkanet	Pentaglottis	Boraginaceae	Boraginales	Magnoliopsida	NN	H(f)
Persicaria Mill.		Unid. *Persicaria* sp. (NN)	Persicaria	Polygonaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Petasites pyrenaicus (Loefl.) G.López	Syn. *Petasites fragrans*	Winter Heliotrope	Petasites	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Phalaris canariensis L.		Canary Grass	Phalaris	Poaceae	Poales	Liliopsida	NN	H(g)
Philadelphus L.		Unid. *Philadelphus* sp.	Philadelphus	Hydrangeaceae	Cornales	Magnoliopsida	NN	W
Philadelphus coronarius L.		Sweet Mock-orange	Philadelphus	Hydrangeaceae	Cornales	Magnoliopsida	NN	W

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Phlomis fruticosa L.		Jerusalem Sage	Phlomis	Lamiaceae	Lamiales	Magnoliopsida	NN	H(f)
Phoenix canariensis H.Wildpret.		Canary Island Date Palm	Phoenix	Arecaceae	Arecales	Liliopsida	NN	W
Phormium tenax J.R.Forst. & G.Forst.		New Zealand Flax	Phormium	Asphodelaceae	Asparagales	Liliopsida	NN	W
Photinia Lindl.		Unid. *Photinia* sp.	Photinia	Rosaceae	Rosales	Magnoliopsida	NN	W
Picea A.Dietr.		Unid. *Picea* sp.	Picea	Pinaceae	Pinales	Pinopsida	NN	W
Pinus L.		Unid. *Pinus* sp(p). (NN)	Pinus	Pinaceae	Pinales	Pinopsida	NN	W
Pittosporum crassifolium Banks & Sol. ex A.Cunn., *Pittosporum tenuifolium* Gaertn.		Karo, Kōhūhū	Pittosporum	Pittosporaceae	Apiales	Magnoliopsida	NN	W
Pittosporum tobira (Thunb.) W.T.Aiton		Japanese Pittosporum	Pittosporum	Pittosporaceae	Apiales	Magnoliopsida	NN	W
Plantago coronopus L., *Plantago lanceolata* L., *Plantago major* L.		Buck's-horn Plantain, Ribwort Plantain, Greater Plantain	Plantago	Plantaginaceae	Lamiales	Magnoliopsida	N	H(f)
Platanus L.		*Platanus* sp.	Platanus	Platanaceae	Proteales	Magnoliopsida	NN	W
Poa annua L.		Annual Meadow-grass	Poa	Poaceae	Poales	Liliopsida	N	H(g)
Podocarpus L'Hér. ex Pers.		Unid. *Podocarpus* sp(p).	Podocarpus	Podocarpaceae	Pinales	Pinopsida	NN	W
Podocarpus salignus D. Don		Willow-leaf Podocarp	Podocarpus	Podocarpaceae	Pinales	Pinopsida	NN	W
Polygonum aviculare L.		Common Knotgrass	Polygonum	Polygonaceae	Caryophyllales	Magnoliopsida	N	H(f)
Polypodium interjectum Shivas, *Polypodium vulgare* L.		Intermediate Polypody, Common Polypody	Polypodium	Polypodiaceae	Polypodiales	Polypodiopsida	N	F
Populus L.		Unid. *Populus* sp.	Populus	Salicaceae	Malpighiales	Magnoliopsida	N	W
Potentilla reptans L., *Potentilla sterilis* (L.) Garcke		Creeping Cinquefoil, Barren Strawberry	Potentilla	Rosaceae	Rosales	Magnoliopsida	N	H(f)
Primula vulgaris Huds.		Primrose	Primula	Primulaceae	Ericales	Magnoliopsida	N	H(f)
Prostanthera Labill.		Unid. *Prostanthera* sp.	Prostanthera	Lamiaceae	Lamiales	Magnoliopsida	NN	W
Prunella vulgaris L.		Self-heal	Prunella	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Prunus L.		Unid. *Prunus* sp(p). (NN)	Prunus	Rosaceae	Rosales	Magnoliopsida	NN	W
Prunus laurocerasus L.		Cherry Laurel	Prunus	Rosaceae	Rosales	Magnoliopsida	NN	W
Prunus persica (L.) Batsch		Peach	Prunus	Rosaceae	Rosales	Magnoliopsida	NN	W
Prunus spinosa L.		Blackthorn	Prunus	Rosaceae	Rosales	Magnoliopsida	N	W
Pseudopanax K.Koch		Unid. *Pseudopanax* sp(p).	Pseudopanax	Araliaceae	Apiales	Magnoliopsida	NN	W
Pseudosasa japonica (Siebold & Zucc. ex Steud.) Makino ex Nakai		Arrow bamboo	Pseudosasa	Poaceae	Poales	Liliopsida	NN	W
Pteridium aquilinum (L.) Kuhn		Bracken	Pteridium	Dennstaedtiaceae	Polypodiales	Polypodiopsida	N	F
Pulicaria dysenterica (L.) Bernh.		Common Fleabane	Pulicaria	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Puya alpestris (Poepp.) Gay		A puya	Puya	Bromeliaceae	Poales	Liliopsida	NN	H(f)
Quercus cerris L.		Turkey Oak	Quercus	Fagaceae	Fagales	Magnoliopsida	NN	W
Quercus ilex L.		Holm Oak	Quercus	Fagaceae	Fagales	Magnoliopsida	NN	W
Quercus pubescens Willd.		Downy Oak	Quercus	Fagaceae	Fagales	Magnoliopsida	NN	W
Quercus robur L.		Pedunculate Oak	Quercus	Fagaceae	Fagales	Magnoliopsida	N	W
Ranunculus repens L.		Creeping Buttercup	Ranunculus	Ranunculaceae	Ranunculales	Magnoliopsida	N	H(f)
Raphanus raphanistrum subsp. *maritimus* (Sm.) Thell.		Sea Radish	Raphanus	Brassicaceae	Brassicales	Magnoliopsida	N	H(f)
Restio Rottb.		Unid. *Restio* sp(p).	Restio	Restionaceae	Poales	Liliopsida	NN	H(g)

Species	**Notes**	**Common Name**	**Genus**	**Family**	**Order**	**Class**	**Status**	**Plant type**
Reynoutria japonica Houtt.	Syn. *Fallopia japonica*	Japanese Knotweed	Reynoutria	Polygonaceae	Caryophyllales	Magnoliopsida	NN	W
Rhododendron L.		Unid. *Rhododendron* sp(p).	Rhododendron	Ericaceae	Ericales	Magnoliopsida	NN	W
Rhododendron L. [Azalea]		Unid. *Rhododendro*n sp(p). (Azalea)	Rhododendron	Ericaceae	Ericales	Magnoliopsida	NN	W
Rhus typhina L.		Staghorn Sumac	Rhus	Anacardiaceae	Sapindales	Magnoliopsida	NN	W
Ricinus communis L.		Castor-oil Plant	Ricinus	Euphorbiaceae	Malpighiales	Magnoliopsida	NN	H(f)
Rodgersia podophylla A. Gray		Rodgers' Bronze-leaf	Rodgersia	Saxifragaceae	Saxifragales	Magnoliopsida	NN	H(f)
Roldana petasitis (Sims) H. Rob. & Brettell		Velvet Groundsel	Roldana	Asteraceae	Asterales	Magnoliopsida	NN	W
Rosa L.		Unid. *Rosa* sp(p). (NN)	Rosa	Rosaceae	Rosales	Magnoliopsida	NN	W
Rosa rugosa Thunb.		Japanese Rose	Rosa	Rosaceae	Rosales	Magnoliopsida	NN	W
Rubus fruticosus agg.		Bramble	Rubus	Rosaceae	Rosales	Magnoliopsida	N	W
Rumex acetosa L., *Rumex acetosella* L., *Rumex crispus* L., *Rumex obtusifolius* L., *Rumex pulcher* L., *Rumex sanguineus* L.		Common Sorrel, Sheep's Sorrel, Curled Dock, Broad-leaved Dock, Fiddle Dock, Wood Dock	Rumex	Polygonaceae	Caryophyllales	Magnoliopsida	N	H(f)
Ruscus aculeatus L.		Butcher's-broom	Ruscus	Asparagaceae	Asparagales	Liliopsida	N	W
Sagina apetala Ard., *Sagina procumbens* L.		Annual Pearlwort, Probumbent Pearlwort	Sagina	Caryophyllaceae	Caryophyllales	Magnoliopsida	N	H(f)
Salix L.		Unid. *Salix* sp(p). (NN)	Salix	Salicaceae	Malpighiales	Magnoliopsida	NN	W
Salix caprea L., *Salix cinerea* L.		Goat Willow, Grey Willow	Salix	Salicaceae	Malpighiales	Magnoliopsida	N	W
Salvia elegans Vahl		Pineapple Sage	Salvia	Lamiaceae	Lamiales	Magnoliopsida	NN	H(f)
Salvia rosmarinus Spenn.	Syn. *Rosmarinus officinalis*	Rosemary	Salvia	Lamiaceae	Lamiales	Magnoliopsida	NN	W
Sambucus nigra L.		Elder	Sambucus	Adoxaceae	Dipsacales	Magnoliopsida	N	W
Saxifraga × urbium D.A.Webb		London Pride	Saxifraga	Saxifragaceae	Saxifragales	Magnoliopsida	NN	H(f)
Schefflera J.R.Forst. & G.Forst.		Unid. *Schefflera* sp.	Schefflera	Araliaceae	Apiales	Magnoliopsida	NN	W
Scrophularia auriculata L.		Water Figwort	Scrophularia	Scrophulariae	Lamiales	Magnoliopsida	N	H(f)
Scrophularia nodosa L.		Common Figwort	Scrophularia	Scrophulariae	Lamiales	Magnoliopsida	N	H(f)
Sedum album L.		White Stonecrop	Sedum	Crassulaceae	Saxifragales	Magnoliopsida	N	H(f)
Sedum anglicum Hudson		English Stonecrop	Sedum	Crassulaceae	Saxifragales	Magnoliopsida	N	H(f)
Sedum kimnachii V.V.Byalt*, Sedum spectabile* Boreau	*S. kimnachii = S. confusum*	Lesser Mexican-stonecrop, Butterfly Stonecrop	Sedum	Crassulaceae	Saxifragales	Magnoliopsida	NN	H(f)
Senegalia Raf., *Vachellia* Wight & Arn.	Form. *Acacia*	*Senegalia* or *Vachellia* sp.	Senegalia or Vachellia	Fabaceae	Fabales	Magnoliopsida	NN	W
Sidalcea A.Gray ex Benth.		Unid. *Sidalcea* sp(p).	*Sidalcea*	Malvaceae	Malvales	Magnoliopsida	NN	H(f)
Silene coronaria (L.) Clairv.		Rose Campion	*Silene*	Caryophyllaceae	Caryophyllales	Magnoliopsida	NN	H(f)
Silene dioica (L.) Clairv.		Red Campion	*Silene*	Caryophyllaceae	Caryophyllales	Magnoliopsida	N	H(f)
Sisyrinchium striatum Sm.		Pale yellow-eyed-grass	*Sisyrinchium*	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Skimmia Thunb.		Unid. *Skimmia* sp(p).	*Skimmia*	Rutaceae	Sapindales	Magnoliopsida	NN	W
Solanum L.		Unid. *Solanum* sp(p). (NN)	*Solanum*	Solanaceae	Solanales	Magnoliopsida	NN	H(f)
Solanum nigrum L.		Black Nightshade	*Solanum*	Solanaceae	Solanales	Magnoliopsida	N	H(f)

Species	**Notes**	**Common Name**	**Genus**	**Family**	**Order**	**Class**	**Status**	**Plant type**
Soleirolia soleirolii (Req.) Dandy		Mind-your-own-business	*Soleirolia*	Urticaceae	Rosales	Magnoliopsida	NN	H(f)
Sonchus asper (L.) Hill, *Sonchus oleraceus* L.		Prickly Sow-thistle, Smooth Sow-thistle	*Sonchus*	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Sorbus L.		Unid. *Sorbus* sp. (NN)	*Sorbus*	Rosaceae	Rosales	Magnoliopsida	NN	W
Sorbus aucuparia L.		Rowan	*Sorbus*	Rosaceae	Rosales	Magnoliopsida	N	W
Stachys palustris L.		Marsh Woundwort	*Stachys*	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Stachys sylvatica L.		Hedge Woundwort	*Stachys*	Lamiaceae	Lamiales	Magnoliopsida	N	H(f)
Symphyotrichum Nees		Unid. *Symphyotrichum* sp(p).	*Symphyotrichum*	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Symphytum officinale L.		Common Comfrey	*Symphytum*	Boraginaceae	Boraginales	Magnoliopsida	N	H(f)
Syringa vulgaris L.		Lilac	*Syringa*	Oleaceae	Lamiales	Magnoliopsida	NN	W
Tamarix gallica L.		Tamarisk	*Tamarix*	Tamaricaceae	Caryophyllales	Magnoliopsida	NN	W
Tanacetum parthenium (L.) Sch. Bip.		Feverfew	*Tanacetum*	Asteraceae	Asterales	Magnoliopsida	NN	H(f)
Taraxacum officinale agg.		Dandelion	*Taraxacum*	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Taxus L.		Unid. *Taxus* sp. (NN)	*Taxus*	Taxaceae	Pinales	Pinopsida	NN	W
Taxus baccata L.		Yew	*Taxus*	Taxaceae	Pinales	Pinopsida	N	W
Tetrapanax papyrifer (Hook.) K.Koch 'Rex'		Chinese rice-paper plant 'Rex'	*Tetrapanax*	Araliaceae	Apiales	Magnoliopsida	NN	W
Teucrium hircanicum L.		Iranian Wood Sage	Teucrium	Lamiaceae	Lamiales	Magnoliopsida	NN	H(f)
Tibouchina Aubl.		Unid. *Tibouchina* sp(p).	Tibouchina	Melastomataceae	Myrtales	Magnoliopsida	NN	W
Tilia cordata Mill., *Tilia platyphyllos* Scop., *Tilia* × *europaea* L.		Small-leaved lime, Large-leaved lime, Common lime	Tilia	Malvaceae	Malvales	Magnoliopsida	N	W
Trifolium dubium Sibth., *Trifolium pratense* L., *Trifolium repens* L.		Lesser Trefoil, Red Clover, White Clover	Trifolium	Fabaceae	Fabales	Magnoliopsida	N	H(f)
Tripleurospermum maritimum (L.) W.D.J.Koch		Sea Mayweed	Tripleurospermum	Asteraceae	Asterales	Magnoliopsida	N	H(f)
Triteleia laxa Benth.		Common Triteleia	Triteleia	Asparagaceae	Asparagales	Liliopsida	NN	H(f)
Ulex europaeus L.		European Gorse	Ulex	Fabaceae	Fabales	Magnoliopsida	N	W
Ulex europaeus L. 'Flore-pleno'		Double-blossomed Gorse	Ulex	Fabaceae	Fabales	Magnoliopsida	N	W
Ulmus minor Mill.		Field Elm	Ulmus	Ulmaceae	Rosales	Magnoliopsida	N	W
Umbilicus rupestris (Salisb.) Dandy		Wall Pennywort	Umbilicus	Crassulaceae	Saxifragales	Magnoliopsida	N	H(f)
Urtica dioica L.		Common Nettle	Urtica	Urticaceae	Rosales	Magnoliopsida	N	H(f)
Valeriana rubra L.	Syn. *Centranthus ruber*	Red Valerian	Centranthus	Caprifoliaceae	Dipsacales	Magnoliopsida	NN	W
Valerianella carinata Loisel., *Valerianella locusta* (L.) Laterr.		Keel-fruited Cornsalad, Common Cornsalad	Valerianella	Caprifoliaceae	Dipsacales	Magnoliopsida	N	H(f)
Verbascum thapsus L.		Great Mullein	Verbascum	Scrophulariae	Lamiales	Magnoliopsida	N	H(f)
Verbena bonariensis L.		Argentinian Vervain	Verbena	Verbenaceae	Lamiales	Magnoliopsida	NN	H(f)
Veronica L.	form. *Hebe* sp(p).	Unid. *Veronica* sp(p). (NN)	Veronica	Plantaginaceae	Lamiales	Magnoliopsida	NN	W
Veronica catarractae G.Forst.	Syn. *Parahebe catarractae*	A parahebe	Veronica	Plantaginaceae	Lamiales	Magnoliopsida	NN	W
Veronica chamaedrys L., *Veronica serpyllifolia* L.		Germander Speedwell, Thyme-leaved Speedwell	Veronica	Plantaginaceae	Lamiales	Magnoliopsida	N	H(f)
Veronica persica Poir.		Common Field-speedwell	Veronica	Plantaginaceae	Lamiales	Magnoliopsida	NN	H(f)

Species	Notes	Common Name	Genus	Family	Order	Class	Status	Plant type
Viburnum L.		Unid. *Viburnum* sp(p). (NN)	Viburnum	Adoxaceae	Dipsacales	Magnoliopsida	NN	W
Viburnum rhytidophyllum Hemsl.		Wrinkled Viburnum	Viburnum	Adoxaceae	Dipsacales	Magnoliopsida	NN	W
Vicia hirsuta (L.) Gray		Hairy Tare	Vicia	Fabaceae	Fabales	Magnoliopsida	N	H(f)
Vicia sativa L.		Common Vetch	Vicia	Fabaceae	Fabales	Magnoliopsida	N	H(f)
Vinca major L.		Greater Periwinkle	Vinca	Apocynaceae	Gentianales	Magnoliopsida	NN	H(f)
Viola riviniana Rchb.		Common Dog-violet	Viola	Violaceae	Malpighiales	Magnoliopsida	N	H(f)
Watsonia borbonica (Pourr.) Goldblatt		Cape Bugle-lily	Watsonia	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Watsonia pillansii L.Bolus		Bugle-lily	Watsonia	Iridaceae	Asparagales	Liliopsida	NN	H(f)
Weigela Thunb.		Unid. *Weigela* sp.	Weigela	Caprifoliaceae	Dipsacales	Magnoliopsida	NN	W
Weigela florida (Bunge) A. DC.		A weigela	Weigela	Caprifoliaceae	Dipsacales	Magnoliopsida	NN	W
Wollemia nobilis W.G.Jones, K.D.Hill & J.M.Allen		Wollemi Pine	Wollemia	Araucariaceae	Pinales	Pinopsida	NN	W
Woodwardia radicans (L.) Sm.		European Chain Fern	Woodwardia	Blechnaceae	Polypodiales	Polypodiopsida	NN	F
Xanthorrhoea johnsonii A.T.Lee		Johnson's Grass Tree	Xanthorrhoea	Asphodelaceae	Asparagales	Liliopsida	NN	W
Yucca gloriosa L.		Spanish-dagger	Yucca	Asparagaceae	Asparagales	Liliopsida	NN	W
Zantedeschia aethiopica (L.) Spreng.		Arum Lily	Zantedeschia	Araceae	Alismatales	Liliopsida	NN	H(f)
Unknown species A		Unknown	Unknown	Unknown	Unknown	Unknown	Unk	Unk
Unknown species B		Unknown bamboo	Unknown	Poaceae	Poales	Liliopsida	NN	H(g)
Unknown species C		Unknown cactus	Unknown	Cactaceae	Caryophyllales	Magnoliopsida	NN	W
Unknown species D		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species E		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	Unk
Unknown species F		Unknown succulent	Unknown	Unknown	Unknown	Magnoliopsida	Unk	Unk
Unknown species G		Unknown conifer	Unknown	Unknown	Unknown	Pinopsida	Unk	W
Unknown species H		Unknown shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species I		Unknown palm	Unknown	Unknown	Unknown	Liliopsida	Unk	W
Unknown species J		Unknown shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species K		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species L		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species M		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species N		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species O		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species P		Unknown tree/shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species Q		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species R		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species S		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species T		Unknown shrub	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W
Unknown species U		Unknown	Unknown	Unknown	Unknown	Unknown	Unk	Unk
Unknown species V		Unknown tree	Unknown	Unknown	Unknown	Magnoliopsida	Unk	W

Appendix II: Garden survey – detailed combined inventory of phytophagous invertebrate species (insect phloem/xylem (sap)-feeders, leaf-feeders, gall-causers, leaf-miners and case-makers, and arachnid gall-causers) present on each PTU (Chapters 2 and 4).

Abbreviations:

Status: N = native; NN = non-native; Unk = Unknown.

Feeding method: CB = case-bearer; GC = gall-causer; LF = leaf-feeder; LM = leaf-miner; SF = phloem/xylem (sap)-feeder; PF(GC) = phloem/xylem (sap)-feeder/part gall-causer

Feeding type: M = monophagous; O = oligophagous; NO = narrowly oligophagous; P = polyphagous; BP = broadly polyphagous; NP= narrowly polyphagous; Unk = Unknown.

Species	Notes	Common name	Family	Order	Class	Status	Feeding method	Feeding type (GB&I)	Host plants (GB&I)
Aceria ilicis (Canestrini, 1890)		A gall-causing mite	Eriophyidae	Trombidiformes	Arachnida	N	GC	M	Gen. *Quercus*
Acrocercops brongniardella (Fabricius, 1798)		Brown Oak Slender	Gracillariidae	Lepidoptera	Insecta	N	LM	M	Gen. *Quercus*
Aculops fuchsiae Keifer		Fuchsia Gall Mite	Eriophyidae	Trombidiformes	Arachnida	NN	GC	M	Gen. *Fuchsia*
Acyrthosiphon (Acyrthosiphon) malvae (Mosley, 1841)		Geranium Aphid, Pelargonium Aphid	Aphididae	Hemiptera	Insecta	N	SF	O	Fam. Geraniaceae
Agromyza abiens Zetterstedt, 1848		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Boraginaceae
Agromyza demeijerei Hendel, 1920		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	M	*Laburnum anagyroides*

Species	Notes	Common name	Family	Order	Class	Status	Feeding method	Feeding type (GB&I)	Host plants (GB&I)
Agromyza nana Meigen, 1830		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Fabaceae
Amauromyza flavifrons (Meigen, 1830)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	NP	Fam. Caryophyllaceae, Chenopodiaceae
Amauromyza labiatarum (Hendel, 1920)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	NP	Fam. Lamiaceae, Verbenaceae
Amauromyza morionella (Zetterstedt, 1848)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Lamiaceae
Aphis (Aphis) fabae Scopoli, 1763		Black Bean Aphid	Aphididae	Hemiptera	Insecta	N	SF	BP	
Aphis (Aphis) farinosa J.F. Gmelin, 1790		Small Willow Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Salix*
Aphis (Aphis) gossypii Glover, 1877		Melon Aphid, Cotton Aphid	Aphididae	Hemiptera	Insecta	NN	SF	BP	
Aphis (Aphis) ilicis Kaltenbach, 1843		Holly Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	*Ilex aquifolium*
Aphis (Aphis) ruborum (Börner, 1932)		Bramble Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Rubus*
Aphis (Bursaphis) epilobii Kaltenbach, 1843		Willowherb Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Epilobium*
Aphis sp. 1		An aphid	Aphididae	Hemiptera	Insecta	Unk	SF	Unk	
Aphis sp. 2		An aphid	Aphididae	Hemiptera	Insecta	Unk	SF	Unk	
Aspidiotus nerii Bouché, 1833		Oleander Scale	Diaspididae	Hemiptera	Insecta	NN	SF	BP	
Aulacorthum (Aulacorthum) solani Kaltenbach, 1843		Glasshouse-potato Aphid, Foxglove Aphid	Aphididae	Hemiptera	Insecta	N	SF	BP	
Aulagromyza cornigera (Griffiths, 1973)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Caprifoliaceae
Aulagromyza hendeliana (Hering, 1926)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Caprifoliaceae

Species	**Notes**	**Common name**	**Family**	**Order**	**Class**	**Status**	**Feeding method**	**Feeding type (GB&I)**	**Host plants (GB&I)**
Balanococcus diminutus (Leonardi, 1918)		Phormium Mealybug	Pseudococcidae	Hemiptera	Insecta	NN	SF	M	*Phormium tenax*
Brachycaudus (Acaudus) klugkisti (Börner, 1942)		A campion aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Silene*
Brachycaudus (Prunaphis) cardui (Linnaeus, 1758)		Plum-thistle Aphid	Aphididae	Hemiptera	Insecta	N	SF	O	Fam. Asteraceae
Cacopsylla fatsiae (Jensen, 1957)/*Psylla tetrapanaxae* Yang, 1984		A psyllid	Psyllidae	Hemiptera	Insecta	NN	SF	O	Fam. Araliaceae
Cacopsylla fulguralis (Kuwayama, 1908)		Elaegnus Sucker	Psyllidae	Hemiptera	Insecta	NN	SF	M	Gen. *Elaeagnus*
Cacopsylla peregrina (Förster, 1848)		A psyllid	Psyllidae	Hemiptera	Insecta	N	SF(GC)	M	Gen. *Crataegus*
Calaphis flava Mordvilko, 1928		Yellow Dark-veined Birch Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Betula*
Cameraria ohridella Deschka & Dimic, 1986		Horse Chestnut Leaf-miner	Gracillariidae	Lepidoptera	Insecta	NN	LM	NP	Fam. Sapindaceae (Gen. Acer, Aesculus)
Capitophorus elaeagni (del Guercio, 1894)		Common Oleaster Aphid	Aphididae	Hemiptera	Insecta	N	SF	O (prim.host), O (sec. host)	Fam. Elaeagnaceae (primary host), Fam. Asteraceae (secondary host)
Cavariella (Cavariella) aegopodii (Scopoli, 1763)		Willow-carrot Aphid	Aphididae	Hemiptera	Insecta	N	SF	M (prim. host), O (sec. host)	Gen. *Salix* (primary host), Fam. Apiaceae (secondary host)
Cecidophyes rouhollahi Craemer, 1999		A gall-causing mite	Eriophyidae	Trombidiformes	Arachnida	N	GC	M	Gen. *Galium*
Chirosia histricina (Rondani, 1866)		A gall-causing fly	Anthomyiidae	Diptera	Insecta	N	LM	NP	Fam. Dennstaedtiaceae, Dryopteridaceae
Chromatomyia 'atricornis' (Meigen, 1838)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Asteraceae
Cionus scrophulariae (Linnaeus, 1758)		Figwort Weevil	Curculionidae	Coleoptera	Insecta	N	LM	NP	Fam. Buddlejaceae, Scrophulariaceae

Species	Notes	Common name	Family	Order	Class	Status	Feeding method	Feeding type (GB&I)	Host plants (GB&I)
Coccus hesperidum Linnaeus, 1758		Brown Soft-scale	Coccidae	Hemiptera	Insecta	NN	SF	BP	
Coleophora flavipennella (Duponchel, [1843])		Tipped Oak Case-bearer	Coleophoridae	Lepidoptera	Insecta	N	CB	M	Gen. *Quercus*
Cosmopterix pulchrimella Chambers, 1875		Beautiful Cosmopterix Moth	Cosmopterigidae	Lepidoptera	Insecta	NN	LM	M	*Parietaria judaica*
Craesus septentrionalis (Linnaeus, 1758)		Birch Sawfly, Hazel Sawfly	Tenthredinidae	Hymenoptera	Insecta	N	LF	BP	
Crypturaphis grassii Silvestri, 1935		Italian Alder Aphid	Aphididae	Hemiptera	Insecta	NN	SF	M	*Alnus cordata*
Cucullia verbasci (Linnaeus, 1758)		The Mullein	Noctuidae	Lepidoptera	Insecta	N	LF	NP	Fam. Buddlejaceae, Scrophulariaceae
Dasineura plicatrix (Loew, 1850)		Blackberry Leaf Midge	Cecidomyiidae	Diptera	Insecta	N	GC	M	Gen. *Rubus*
Dasineura pteridicola (Kieffer, 1901)		A gall-causing midge	Cecidomyiidae	Diptera	Insecta	N	GC	O	Fam. Polypodiaceae
Depressaria radiella (Goeze, 1783)		Parsnip Flat-Body	Oecophoridae	Lepidoptera	Insecta	N	LF	O	Fam. Apiaceae (Gen. Heracleum, Pastinaca)
Drepanosiphum platanoidis (Schrank, 1801)		Common Sycamore Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Acer*
Dynaspidiotus britanicus (Newstead, 1898)		Holly Scale	Diaspididae	Hemiptera	Insecta	N	SF	BP	
Edwardsiana sp.		A leafhopper	Cicadellidae	Hemiptera	Insecta	N	SF	Unk	
Enteucha acetosae (Stainton, 1854)		Sorrel Pigmy	Nepticulidae	Lepidoptera	Insecta	N	LM	M	Gen. *Rumex*
Epiphyas postvittana (Walker, 1863)		Light Brown Apple Moth	Tortricidae	Lepidoptera	Insecta	NN	LF	BP	
Eriophyes similis (Nalepa, 1890)		A gall-causing mite	Eriophyidae	Trombidiformes	Arachnida	N	GC	M	Gen. *Prunus*
Eucallipterus tiliae (Linnaeus, 1758)		Common Lime Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Tilia*
Euceraphis sp.		An aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Betula*

Species	**Notes**	**Common name**	**Family**	**Order**	**Class**	**Status**	**Feeding method**	**Feeding type (GB&I)**	**Host plants (GB&I)**
Euleia heraclei (Linnaeus, 1758)		Celery Fly	Tephritidae	Diptera	Insecta	N	LM	O	Fam. Apiaceae
Eupteryx melissae Curtis, 1837		Sage Leafhopper	Cicadellidae	Hemiptera	Insecta	N	SF	NP	Fam. Lamiaceae, Malvaceae
Eupteryx urticae (Fabricius, 1803)		A leafhopper	Cicadellidae	Hemiptera	Insecta	N	SF	O	Fam. Urticaceae
Gracillaria syringella (Fabricius, 1794)		Common Slender	Gracillariidae	Lepidoptera	Insecta	N	LM	NP	Fam. Caprifoliaceae, Oleaceae
Hayhurstia atriplicis (Linnaeus, 1761)		Chenopodium Aphid	Aphididae	Hemiptera	Insecta	N	SF	O	Fam. Chenopodioideae
Heterarthrus aceris (Kaltenbach, 1856)		A leaf-mining sawfly	Tenthredinidae	Hymenoptera	Insecta	N	LM	M	*Acer pseudoplatanus*
Lauritrioza alacris (Flor, 1861)	Syn. *Trioza alacris*	Bay Sucker	Triozidae	Hemiptera	Insecta	NN	SF(GC)	NO	Fam. Lauraceae (Gen. Laurus, Persea)
Liriomyza congesta (Becker, 1903)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Fabaceae
Liriomyza strigata (Meigen, 1830)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	BP	
Lygocoris (Lygocoris) pabulinus (Linnaeus, 1761)		Common Green Capsid	Miridae	Hemiptera	Insecta	N	SF	BP	
Macrosiphum (Macrosiphum) euphorbiae (Thomas, 1878)		Potato Aphid	Aphididae	Hemiptera	Insecta	NN	SF	BP	
Macrosiphum (Macrosiphum) euphorbiellum Theobald, 1925	Syn. *Macrosiphum (Macrosiphum) amygdaloides*	Euphorbia Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Euphorbia*
Macrosiphum (Macrosiphum) hellebori Theobald & Walton, 1923		Hellebore Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Helleborus*
Macrosiphum (Macrosiphum) rosae (Linnaeus, 1758)		Rose Aphid	Aphididae	Hemiptera	Insecta	N	SF	NP	Gen. *Rosa* (primary host), Fam. Dipsaceae, Valerianaceae (secondary host)
Metallus lanceolatus (C.G. Thomson, 1870)		A leaf-mining sawfly	Tenthredinidae	Hymenoptera	Insecta	N	LM	M	Gen. Geum
Microlophium carnosum (Buckton, 1876)		Common Nettle Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	*Urtica dioica*

Species	**Notes**	**Common name**	**Family**	**Order**	**Class**	**Status**	**Feeding method**	**Feeding type (GB&I)**	**Host plants (GB&I)**
Myzocallis (Myzocallis) boerneri Stroyan, 1957		Turkey Oak Aphid	Aphididae	Hemiptera	Insecta	NN	SF	M	Gen. *Quercus*
Myzocallis (Myzocallis) coryli (Goeze, 1778)		Hazel Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Corylus*
Myzocallis (Myzocallis) schreiberi Hille Ris Lambers & Stroyan, 1959		Holm Oak Aphid	Aphididae	Hemiptera	Insecta	NN	SF	M	Gen. *Quercus* (principally *Q. ilex*)
Myzus (Nectarosiphon) persicae Sulzer, 1776		Peach-potato Aphid	Aphididae	Hemiptera	Insecta	NN	SF	M (prim. host), P (sec. host)	Gen. *Prunus* (primary host)
Orchestes (Salius) fagi (Linnaeus, 1758)		Beech Leaf-miner	Curculionidae	Coleoptera	Insecta	N	LM	M	Gen. *Fagus*
Orgyia antiqua (Linnaeus, 1758)		The Vapourer	Lymantriidae	Lepidoptera	Insecta	N	LF	BP	
Orthochaetes insignis (Aubé, 1863)		A weevil	Curculionidae	Coleoptera	Insecta	N	LM	P	
Pegomya laticornis (Fallén, 1825)		A leaf-mining fly	Anthomyiidae	Diptera	Insecta	N	LM	M	Gen. *Arctium*
Pegomya solennis (Meigen, 1826)		A leaf-mining fly	Anthomyiidae	Diptera	Insecta	N	LM	M	Gen. *Rumex*
Periphyllus testudinaceus (Fernie, 1852)		Common Periphyllus Aphid	Aphididae	Hemiptera	Insecta	N	SF	NO	Fam. Sapindaceae (Gen. *Acer, Aesculus*)
Philaenus spumarius (Linnaeus, 1758)		Common Froghopper	Aphrophoridae	Auchenorrhyncha	Insecta	N	SF	BP	
Phyllaphis fagi (Linnaeus, 1767)		Beech Woolly Aphid	Aphididae	Hemiptera	Insecta	N	SF	M	Gen. *Fagus*
Phyllocolpa leucosticta (Hartig, 1837)		A sawfly	Tenthredinidae	Hymenoptera	Insecta	N	LF	M	Gen. *Salix*
Phyllocoptes goniothorax (Nalepa, 1889)		A gall-causing mite	Eriophyidae	Trombidiformes	Arachnida	N	GC	M	Gen. *Crataegus*
Phyllonorycter maestingella (Müller, 1764)		Beech Midget	Gracillariidae	Lepidoptera	Insecta	N	LM	M	Gen. *Fagus*
Phyllonorycter messaniella (Zeller, 1846)		Garden Midget	Gracillariidae	Lepidoptera	Insecta	N	LM	NP	Fam. Betulaceae, Fagaceae, Rosaceae

Species	**Notes**	**Common name**	**Family**	**Order**	**Class**	**Status**	**Feeding method**	**Feeding type (GB&I)**	**Host plants (GB&I)**
Phyllonorycter oxyacanthae (Frey, 1856)		Common Thorn Midget	Gracillariidae	Lepidoptera	Insecta	N	LM	O	Fam. Rosaceae (Gen. Crataegus, Cydonia, Sorbus)
Phyllonorycter spinicolella (Zeller, 1846)		Sloe Midget	Gracillariidae	Lepidoptera	Insecta	N	LM	M	Gen. *Prunus*
Phytomyza aquilegiae Hardy, 1849		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Ranunculaceae (Gen. Aquilegia, Thalictrum)
Phytomyza chaerophylli Kaltenbach, 1856		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Apiaceae
Phytomyza ilicis Curtis, 1846		Holly Leaf-miner	Agromyzidae	Diptera	Insecta	N	LM	M	*Ilex aquifolium*
Phytomyza minuscula Goureau, 1851		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Ranunculaceae (Gen. Aquilegia, Thalictrum)
Phytomyza plantaginis Robineau-Desvoidy, 1851		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	M	Gen. *Plantago*
Phytomyza ranunculi (Schrank, 1803)		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	M	Gen. *Ranunculus*
Phytomyza spondylii Robineau-Desvoidy, 1851		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	O	Fam. Apiaceae (Gen. *Astrantia, Heracleum, Pastinaca*)
Phytomyza vitalbae Kaltenbach, 1872		A leaf-mining fly	Agromyzidae	Diptera	Insecta	N	LM	M	Gen. *Clematis*
Plagiotrochus quercusilicis (Fabricius, 1798)		A gall-causing wasp	Cynipidae	Hymenoptera	Insecta	NN	GC	M	Gen. *Quercus (Q. coccifera, ilex)*
Pontania (Pontania) bridgmanii (Cameron, 1883)	Syn. *Euura bridgmanii*	A gall-causing sawfly	Tenthredinidae	Hymenoptera	Insecta	N	GC	M	Gen. *Salix*
Powellia vitreoradiata Maskell, 1879	Syn. *Trioza vitreoradiata*	Pittosporum Psyllid	Triozidae	Hemiptera	Insecta	NN	SF(GC)	M	Gen. *Pittosporum*
Psyllopsis fraxinicola (Förster, 1848)		A psyllid	Psyllidae	Hemiptera	Insecta	N	SF(GC)	M	Gen. *Fraxinus*
Pulvinaria floccifera (Westwood, 1870)		Cottony Camellia Scale	Coccidae	Hemiptera	Insecta	NN	SF	BP	
Pulvinaria regalis Canard, 1968		Horse Chestnut Scale	Coccidae	Hemiptera	Insecta	NN	SF	BP	
Ribautiana ulmi (Linnaeus, 1758)		A leafhopper	Cicadellidae	Hemiptera	Insecta	N	SF	BP	

Species	**Notes**	**Common name**	**Family**	**Order**	**Class**	**Status**	**Feeding method**	**Feeding type (GB&I)**	**Host plants (GB&I)**
Scaptomyza flava (Fallén, 1823)		A leaf-mining fly	Drosophilidae	Diptera	Insecta	N	LM	P	Principally Fam. Brassicaceae
Stigmella aurella (Fabricius, 1775)		Golden Pigmy	Nepticulidae	Lepidoptera	Insecta	N	LM	O	Fam. Rosaceae
Stigmella hybnerella (Hübner, 1796)		Greenish Thorn Pigmy	Nepticulidae	Lepidoptera	Insecta	N	LM	M	Gen. *Crataegus*
Stigmella plagicolella (Stainton, 1854)		Scrubland Pigmy	Nepticulidae	Lepidoptera	Insecta	N	LM	M	Gen. *Prunus*
Takecallis arundicolens (Clarke, 1903)		Black-tailed Bamboo Aphid	Aphididae	Hemiptera	Insecta	NN	SF	O	Fam. Poaceae (Gen. *Arundinaria, Bambusa, Phyllostachys, Phragmites, Pseudoasa, Sasa*)
Toxoptera aurantii (Boyer de Fonscolombe, 1841)		Camellia Aphid, Black Citrus Aphid	Aphididae	Hemiptera	Insecta	NN	SF	BP	
Trioza urticae (Linnaeus, 1758)		Nettle Psyllid	Triozidae	Hemiptera	Insecta	N	SF(GC)	M	Gen. *Urtica*
Uroleucon (Uromelan) sonchi (Linnaeus, 1767)		Large Sow-thistle Aphid	Aphididae	Hemiptera	Insecta	N	SF	O	Fam. Asteraceae (principally Gen. Sonchus)
unid. Pittosporum scale			Diaspididae	Hemiptera	Insecta	NN	SF	M	Gen. *Pittosporum*
unid. aphid (Rhododendron)			Aphididae	Hemiptera	Insecta	Unk	SF	Unk	
unid. aphid (Pittosporum)			Aphididae	Hemiptera	Insecta	Unk	SF	Unk	
unid. aphid (Fatsia/Ficus)			Aphididae	Hemiptera	Insecta	Unk	SF	Unk	
unid. flea beetle (Fuchsia)			Chrysomelidae	Coleoptera	Insecta	Unk	LF	Unk	
unid. mine (Prunus)			Unk	Unk	Insecta	Unk	LM	Unk	

Appendix III: Non-native oak Cynipid gall wasps in order of arrival.

Species	**First known record and location**	**Author**	**Sexual generation host**	**Agamic generation host**
Andricus kollari **(Hartig 1843)**	1834 Exe Valley, Devon	Smith (1854)	*Q. cerris*	*Q. robur/petraea*
Andricus quercuscalicis **(Burgsdorf 1783)**	1961 Salcey Wood, East Anglia	Claridge (1964)	*Q. cerris*	*Q. robur/petraea*
Andricus lignicola **(Hartig 1840)**	1972 Wiggonholt, West Sussex	Hutchinson (1974)	*Q. cerris*	*Q. robur/petraea*
Andricus corruptrix **(von Schlechtendal 1870)**	1972 Wiggonholt, West Sussex	Hutchinson (1974)	*Q. cerris*	*Q. robur/petraea*
Andricus lucidus **(Hartig)***	1992 Richmond, London	Stone & Sunnucks (1993)	*Q. cerris*	*Q. robur/petraea*
Andricus aries **(Giraud 1859)**	1997 Maidenhead, Berkshire	Crawley (1999)	*Q. cerris* (induced in captivity)	*Q. robur/petraea*
Aphelonyx cerricola	1999 Hampstead, London	Leach & Shirley (1999)	*not known*	*Q. cerris*
Andricus grossulariae **Giraud 1859**	2000 Windsor, Greater London	Walker (2001)	*Q. cerris*	*Q. robur/petraea*
Plagiotrochus quercusilicis	2004 Eden project, Cornwall	Hancy & Hancy (2004)	*Q. ilex*	*Q. ilex*
Pseudoneuroterus saliens **(Kollar 1857)**	2006 Hackney, London	Redfern (2006)	*Q. cerris*	*Q. cerris*
Plagiotrochus australis	2007 Glamorgan, Wales	Robbins (2007)	*Q. ilex*	*Q. ilex*
Plagiotrochus coriaceus**	2007 Glamorgan, Wales	Robbins (2007)	*Q. ilex*	*Q. ilex*
Andricus gemmeus **(Giraud 1859)**	2008	Bowdery (2009)	*Q. cerris*	*Q. robur/petraea*
Andricus singularis **Mayr 1870**	2010 Cuxton, Kent	Jennings (2014)	*Q. cerris, ilex, suber*	*not known*
Andricus infectorius	2013 Penzance, Cornwall	Leach (2020)	*Q. cerris*	*Q. robur/petraea*
Andricus ?cryptobius **Wachtl 1880*****	2015 Dunwich Heath, East Suffolk	Bowdery (2015)	*Q. cerris*	not known

* single record 1893 (Loch Lomond)

** potentially misidentified

*** presumed ID

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