# ALLEE EFFECTS AND THE PERSISTENCE OF SMALL POPULATIONS

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# Abstract

The intent of this thesis was two-fold. Firstly, to examine the role of the Allee effect in the establishment success of insect pest populations during the early phases of invasion. Secondly, to examine how spatial management at the point of introduction could render populations more vulnerable to the Allee effect and facilitate their eradication. Both aims are important, as despite strong theoretical findings that a demographic Allee effect can prevent small founder population establishment, empirical evidence is limited. Additionally, social pressure is demanding alternative 'greener' tools to achieve eradication of new incursions.

The Allee effect is defined as a positive relationship between population size and fitness and is an important factor that underpins the widespread effect of propagule pressure on establishment success. By using a weed biological control agent, *Neolema ogloblini*, as a model insect pest species, I investigated the impact of propagule size on establishment success and found evidence that cautiously supports the existence of a strong demographic Allee effect governing the establishment of this species. Further studies suggested that the demographic Allee effect is driven by at least one potential component Allee effect; that is, mate-finding failure. Heavy predation on the immature stages by generalist predators was found during predator exclusion trials, but further studies are needed to demonstrate whether it constitutes a predator-driven component Allee effect. Increased aggregation of individuals allows necessary interactions (mating, predator dilution, etc.) and minimizes the negative impacts of the Allee effect. My study indicated that adults of *N. ogloblini* potentially utilize feeding-induced plant volatiles as a cue to find their host, thereby increasing dispersal success among host patches and aggregation on host plant patches.

As the Allee effect plays an important role in the dynamics of newly established and low-density populations by driving small populations to extinction, it is critical for influencing outcomes of eradication efforts. The Allee effect, together with other processes occurring at low population sizes (e.g., demographic stochasticity), eliminate the need for removal of all individuals in a population during management actions. Results of my study indicated that limited resources at the point of introduction motivated dispersal to adjacent host patches. A higher number of adults successfully located and settled on host patches that were closer to the point of introduction (higher connectivity level) than sites where adjacent patches were further away (medium connectivity or low connectivity). Subsequent host removal of patches at the point of introduction induced additional dispersal at high connectivity treatment sites only, significantly reducing meta-population size. Meta-population size correlated significantly positively with probability of survival and per capita population growth rate. Therefore, management actions that reduces landscape connectivity (limiting and isolating host patches), and consequently population size, could subject remaining populations to the Allee effect and achieve eradication.

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# Chapter 1 - General Introduction

## Biological Invasions

The movement and establishment of species outside their native ranges are occurring in ever increasing numbers around the world, sometimes through intentional introductions, but mostly as accidental by-products of international trade and travel (Seebens et al., 2017). Insects are among the most prevalent of non-native species across the world; with Kenis et al. (2009) reporting over 300 species in Switzerland, 2000 species in the USA, and 2500 species in Hawaii. Roques et al. (2008) reported 87% of the approximate 2,500 non-native terrestrial invertebrates in Europe are insects. In New Zealand there are over 2000 non-native invertebrate species established (Brockerhoff, et al., 2010; Edney-Browne et al., 2018).

Non-native insects are best known for their economic or health impact (pests of agriculture, horticulture, stored products and forestry; vectors of human and animal diseases) than for their ecological impact (Goldson et al., 2015; Roques et al., 2008; Ward, 2014). However, the evidence for their direct and indirect impacts on natural ecosystems is growing (Kenis et al., 2009; Ward, 2014). Non-native insects can affect natural ecosystems through direct interactions (e.g., hybridisation with native related species (Jensen et al., 2004)), feeding on native plants, and preying or parasitizing native species (Snyder & Evans, 2006). For example, in North America numerous non-native forest insects, including gypsy moth (*Lymantria dispar*), emerald ash borer (*Agrilus planipennis*) and several weevils damage indigenous plants and alter forest ecosystems (Lovett et al., 2016). Similarly, several exotic social wasps (*Vespula germanica* and *V. vulgaris*) impact invertebrates, avifauna and ecosystems services in New Zealand and several countries around the world (Beggs et al., 2011; Goldson et al., 2015).

Non-native insects can also affect native species and ecosystems indirectly, through cascading effects, or through various mechanisms (e.g., by competing for food or space, carrying diseases, or sharing natural enemies with native species (Kenis et al., 2009)). Until recently the perception has been held that non-native insects invading forests and other native ecosystems, have had relatively low impact in New Zealand (Brockerhoff et al., 2010; Ridley et al., 2000). Specialist non-native species are constrained by the high level of endemism in New Zealand's flora, providing some protection to these indigenous species (Brockerhoff et al., 2010). Non-native insects with broad host or prey ranges on the other hand are not constrained and are represented among some of the most successful invaders of natural ecosystems in New Zealand (Brockerhoff et al., 2010). For example, invasive social wasps (*V. germanica* and *V. vulgaris*) are rated as the most damaging, widespread invertebrate pests in New Zealand (Lester et al., 2013), while the critically endangered Cook’s scurvy grass (*Lepidium oleraceum*) is threatened by introduced species such as the cabbage white butterfly (*Pieris rapae*) and other species of armyworms and aphids (Goldson et al., 2015; Hasenbank et al., 2011). However, due to the shortage of studies on invader impacts on native species and ecosystems, the true impact of non-native insect species is currently unknown (Brockerhoff et al., 2010; Goldson et al., 2015; Ward, 2014).

With intensifying international trade, climate change and rising human population densities, it is expected that non-native insect species will continue to arrive in new areas and some fraction will establish and become invasive (Brasier, 2008; Levine & D’Antonio, 2003; Perrings et al., 2000).

## Biosecurity and Invasion Pathways

Biosecurity, the protection of a country from impacts of biological invaders, is increasingly important for preventing the impacts of new biological invasions (Perrings et al., 2005; Poland & Rassati, 2019). Around the world, biosecurity strategies are often employed to identify, prevent, or control new invasive species. Common strategies include: compiling risk assessment databases of harmful or potentially harmful organisms (Brasier, 2008; Kenis et al., 2007), quarantine measures (e.g. commodity treatments such as fumigation, or total bans) based on risk assessments (Hulme, 2014; Kenis et al., 2007; Liebhold et al., 2016), visual inspection of imported goods (Brasier, 2008; Liebhold et al., 2016), and surveillance and eradication of nascent populations (including public-awareness campaigns and community participation) (Bradshaw et al., 2016; Meyerson & Reaser, 2006; Poland & Rassati, 2019).

The biological invasion process can be broken down into five steps: transport, arrival, establishment, spread, and impact (Lockwood et al., 2013). Transport and arrival is simply the introduction, either natural or human-assisted, of an organism to an unoccupied area (Tobin et al., 2011). Establishment occurs when population reproduces and extinction of a nascent population becomes unlikely, (i.e. its population growth rate is sufficient for the persistance of the species) (Colautti et al., 2006; Kang & Armbruster, 2011). Spread involves an increase in the number of locations or area occupied by a species during the processes of arrival and establishment are repeated across space and time (O'Reilly-Nugent et al., 2016).

When arrival cannot be prevented, the best alternative is eradication (Blackwood et al. 2012). Eradication is defined as the total elimination of a species from a given area (Blackwood et al. 2012, Tobin et al. 2014, Liebhold et al. 2016). Feasibility of eradication is increased by early detection when the density and geographical extent of newly established populations are still low, which is facilitated by effective post-border surveillance (Brockerhoff et al., 2010; Liebhold & Tobin, 2008). A strong positive relationship exists between size of the affected geographical area and the cost of eradication (Brockerhoff et al., 2010; Kriticos et al., 2005) and similarly, the probabillity of eradication success declines with invaded area (Tobin et al., 2014).

However, given the perceived difficulty and the perception (by some) that all individuals of a population need to be eliminated to achieve eradication, the practicality and feasibility of eradication have often been questioned (Myers et al., 1998; Myers et al., 2000; Simberloff, 2003; Whitten & Mahon, 2005). Furthermore, eradication can be socially controversial as programmes are often conducted in residential areas, where insecticide use, arial applications, removal of host plants and other treatments may evoke negative response among residents (Liebhold et al., 2016). Successful eradication also requires extensive knowledge of the targeted pest species, early detection, and substantial monetary, political and time commitment (Suckling et al. 2014).

There is thus a clear need to understand the basic population processes that operate during the invasion process and how this information can be applied to develop effective strategies for mitigating invasions. In this study, I will focus on key factors influencing the early establishment phase of invading insect species populations and how these can facilitate eradication efforts.

## Key factors affecting the establishment of newly arrived populations

Despite the frequency and importance of contemporary colonisation events (through intentional and accidental species introductions), our understanding of the factors that affect establishment success, persistence and fitness of colonising populations is still incomplete (Bajeux et al., 2019; Colautti et al., 2006; Melbourne et al., 2017; Tobin et al., 2011).

Records collected during intentional introductions (e.g., for purposes of conservation and biological control) can provide insight into factors affecting establishment success that can ultimately be applied to understanding accidental introductions. However, even with extensive research and effort during intentional introductions, the establishment rate in re-introduction for conservation programs is reported to be 26% (Fischer & Lindenmayer, 2000), 33% in insect biological control agents (Cock et al., 2016), and 71% for weed biocontrol agents (Schwarzländer et al., 2018). Yet, there is strong variation between the establishment rates of these introduction events, and therefore identifying a minimum set of consistent variables that would be highly predictive of establishment and invasion success remains an important research goal (Colautti et al., 2006; Hayes & Barry, 2008; Romanuk et al., 2009).

Several key factors can contribute to the extinction propensity of newly arrived populations. These include: environmental and demographic stochasticity (Liebhold & Bascompte, 2003), genetic mechanisms (Hufbauer et al., 2013; Melbourne et al., 2017; Vahsen et al., 2018), the Allee effect (Liebhold & Bascompte, 2003; Tobin et al., 2009; Yamanaka & Liebhold, 2009a), propagule pressure (Colautti et al., 2006), natural enemies (Cock et al., 2000; Paynter et al., 2012), dispersal (Jongejans et al., 2007; Jonsen et al., 2007), and habitat availability and connectivity (Jonsen et al., 2001; Jonsen et al., 2007; Taylor et al., 2006).

Most of these factors do not work in isolation but are interconnected. For example, genetic variability is related to propagule size; more individuals may increase the probability that at least some genotypes are adapted to the new habitat, and provide sufficient genetic variation for adaptation to local conditions and decrease inbreeding (Hufbauer et al., 2013). Another example is stochasticity and the Allee effect; in natural populations extinction rate at low density is simultaneously influenced by these processes and it can be difficult to separate or disentangle (Fauvergue et al., 2012; Grevstad, 1999b). When considered independently of other processes, a strong Allee effect results in a critical threshold, below which the population will never establish (Fauvergue et al., 2012; Grevstad, 1999b). But in nature, even if a population is below the Allee threshold, stochastic effects can increase population growth rate by chance such that establishment does occur (Fauvergue et al., 2012; Grevstad, 1999b). Inversely, for a population above the Allee threshold, stochastic effects can decrease population size down to a level where it is highly vulnerable to Allee effects (Fauvergue et al., 2012; Grevstad, 1999b; Liebhold & Bascompte, 2003). An important consequence of the latter effect is that even in cases where populations establish successfully from very few individuals, Allee effects cannot be ruled out entirely (Fauvergue et al., 2012). Another example of interaction between factors influencing extinction propensity is between dispersal loss, habitat patch and Allee effect. Using a theoretical modelling approach, Lewis and Kareiva (1993) found in the presence of strong Allee effects, a minimum habitat patch size should exist below which establishment of invading populations is nearly impossible.

Although all the above-mentioned factors can play an important role in establishment success and persistence of invasive species, my study focussed specifically on i) Allee effects, ii) propagule pressure, iii) dispersal, and iv) habitat fragmentation and their interactions.

### i) Allee effects

The term “Allee effect” is in acknowledgement to the animal ecologist, Warder Clyde Allee, who is considered one of the first to recognise that, at low densities, survival and reproduction may often be limited by the lack of conspecifics and that this can lead to population decline (Courchamp et al., 1999). The Allee effect is formally defined as *a decrease in individual fitness caused by a decrease in population density* (Stephens & Sutherland, 1999). Allee effects typically are important at low densities and they have been identified as playing a critical role in causing extinction of low-density populations. In particular, in the presence of a “strong Allee effect” population growth becomes negative at low densities; this creates a population threshold, below which populations could potentially be driven to extinction (Fig. 1).

One of the most prevalent reasons for the Allee effect is mate finding failure (Berec et al., 2018; Berec et al., 2017; Boukal & Berec, 2009; Fauvergue, 2013; Gascoigne et al., 2009; Shaw & Kokko, 2014). Apart from simply not detecting a potential mate, mate finding failure can arise from reproductive attempts that do not yield viable offspring (e.g. available mates could be of inferior quality, or not enough cohorts to ensure survival of offspring), or the number of reproductive opportunities per individual can be limited (e.g., not enough suitable mates available). Müller and Müller (2016) found reduced reproductive success in the mustard leaf beetle (*Phaedon cochleariae*) when mating occurred between siblings, indicating the consequences of inbreeding. Increased fitness was positively associated with the number of reproductive opportunities for the leaf beetle *Ophraella communa*, and its multiple-mating behaviour is maintained through the aggregative behaviour of field populations (Zhou et al., 2015).

Allee effects may also arise from too few individuals in a population to saturate natural enemies. In newly arrived populations, this can result in establishment failure or ‘habitat pinning’ (when range expansion at the periphery of a population is constrained due to the population producing too few dispersers to overcome the Allee threshold in the new area) (Boughton & Pemberton, 2008; Paynter et al., 2012). For example, Kramer and Drake (2010) report that predatory midge larvae of the genus *Chaoborus* can induce a demographic Allee effect in a water flea *Daphnia magna* populations via a predator-driven Allee effect, thereby potentially speeding smaller prey populations to premature extinction. Hunt-Joshi et al. (2005) studied the impact of predation by a mirid bug *Plagiognathus politis*, on the leaf beetle *Galerucella calmariensis*, a biocontrol agent against *Lythrum salicaria* in North America, and found evidence that suggests there may be a threshold in beetle populations below which mirid predation potentially limits establishment.

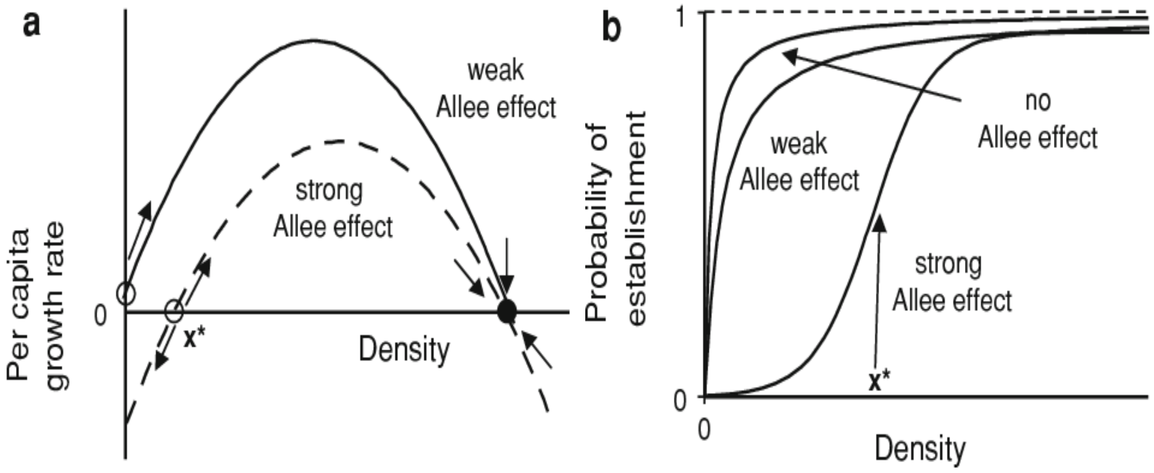

**Figure 1:** Definition of the demographic Allee effect.

a – Per capita growth rate increases with population density. For a 'weak' Allee effect, per capita growth rate is always higher than zero, while for a 'strong' Allee effect per capita growth rate is negative below a threshold density, x*. This threshold density is an unstable equilibrium.

b – Probability of establishment increases with population density. Here the threshold density of a strong Allee effect, x*, creates an inflection point in the probability of establishment.

(Graph adapted from Kramer et al. (2009).)

Stephens et al. (1999) distinguish between 'component' Allee effects (a decrease in one or more fitness components at the individual level as a result of a decrease in population density) and 'demographic' Allee effects (when component Allee effects lead to a decline in per capita population growth rate as population density decreases). Component Allee effects may not necessarily result in a demographic Allee effect, for example reduced intraspecific competition could compensate sufficiently for reduction in a component of individual fitness (Courchamp et al., 2008). For example, Angulo et al. (2007) found that reduced competition in small populations of the island fox (*Urocyon littoralis*) favoured larger litters and higher juvenile survival which compensated for reduced adult survival and reproduction.

Demographic Allee effects can also be classified as weak or strong (Courchamp et al., 2008; Taylor & Hastings, 2005). When considered independently of other processes (such as stochasticity), a weak Allee effect slows population growth rate, but does not affect population establishment. In contrast, a strong Allee effect results in a critical initial population size, below which per capita growth rate is negative, and the population does not establish (Fig. 1) (Taylor & Hastings, 2005).

Allee thresholds may have profound implications for eradication programmes of invasive species. When a strong Allee effect exists, it may be possible to achieve eradication without direct removal of all individuals (Liebhold et al., 2016; Tobin et al., 2011). Instead, populations can be suppressed below the Allee threshold and residual populations should subsequently decline towards extinction. An inherent challenge of any eradication project is determining when eradication has been achieved (Brockerhoff et al., 2010; Liebhold et al., 2016; Ward et al., 2016). Because populations at very low density can be difficult to detect, the process can be costly and time-consuming, and there is a significant risk that the last individuals will not be detected (Venette et al., 2001; Ward et al., 2016). Incorrectly or prematurely declaring an eradication project as successful is embarrassing and costly, and undermines future confidence in eradication programmes (Simberloff, 2009b; Suckling et al., 2012).

Employing the Allee threshold involves two strategies: i) population reduction to a density below the Allee threshold, and ii) increasing the Allee threshold to a level that exceeds the population density (Liebhold & Tobin, 2008). Management strategies to reduce the population includes culling (pesticide application, mass trapping, host removal) and predator augmentation (biocontrol), while an increase in the Allee threshold is achieved through management actions designed to interfere with mating (mating disruption, mass-trapping, sterile insect release, habitat modification), or aggregation to overcome host defences (chemically or genetically boosting plant defence compounds) (Tobin et al., 2011).

The existence and strength of Allee effects as well as mechanisms creating them vary considerably among taxa, suggesting corresponding differences in approaches to exploit Allee effects in the management of biological invaders (Liebhold et al., 2016; Liebhold & Tobin, 2008; Suckling et al., 2012). Therefore, some species will be more amenable to certain eradication techniques than others. Non-native organisms that can establish provide ecologists with a set of biological traits and characteristics beneficial to overcoming stochastic conditions and Allee thresholds (assuming one exists in the first place). With this information, ecologists and biosecurity managers have created databases highlighting species and groups of organisms that are likely to be transported and successfully invade a new environment (Brockerhoff et al., 2014; Drake & Lodge, 2006; Ducatez & Shine, 2019; Zenni & Nuñez, 2013).

However, empirical studies have mainly focussed on component Allee effects, while compelling evidence for demographic Allee effects is still sparse (Fauvergue, 2013; Gascoigne et al., 2009; Gregory & Courchamp, 2010; Hutchings, 2015; Kramer et al., 2009; Kuparinen, 2018). Some authors also speculate whether demographic Allee effects are actually as widespread in nature (Matter & Roland, 2013). Lack of empirical evidence is due to difficulties in censusing small populations or a failure to identify underlying mechanisms, but also because of fitness trade-offs, population spatial structure, and because the strength of component Allee effects may vary in time and space (Deredec & Courchamp, 2007; Fauvergue, 2013; Gascoigne et al., 2009). Given the current limited evidence for demographic Allee effects and the increasing number of species that are of invasion concern, it is important to determine the role a component Allee effect can play in the overall population dynamics of an invasive species and whether it translates into a demographic Allee effect.

### ii) Propagule Pressure

Invasive species usually start out as small founding populations that have been unintentionally introduced to new areas (Liebhold & Tobin, 2008). However, only some of these introductions lead to establishments and become persistent populations (Colautti et al., 2006; Tobin et al., 2011). Establishment occurs when enough individuals (propagules) arrive in a suitable habitat and extinction becomes unlikely (i.e., population growth rate is above the Allee threshold) (Berggren, 2001; Colautti et al., 2006; Kang & Armbruster, 2011). The magnitude of propagule pressure is one of the most important determinants of establishment success, consequently, the arrival of a large founding population is more likely to lead to establishment than arrival of small founding populations (Drake & Lodge, 2006; Lockwood et al., 2005; Simberloff, 2009a; Taylor & Hastings, 2005). For instance, higher rates of establishment success occur with releases of larger numbers of biological control agents (De Clerck-Floate & Bourchier, 2000; De Clerck-Floate & Wikeem, 2009; Grevstad, 1999; Grevstad et al., 2011; Memmott et al., 1998; Paynter et al., 2016; Pratt et al., 2013; Yeates et al., 2012). Similarly, during reintroduction of endangered species, larger release sizes are associated with greater establishment success (Armstrong & Wittmer, 2011; Ducatez & Shine, 2019; Wolf et al., 1998).

Even though propagule pressure has proven to be a consistent determinant of establishment success (Cassey et al., 2018), there has been cases reported of biological control introductions of very small populations (<5 individuals and single gravid females) resulting in establishment (Cameron et al., 1993; Grevstad, 1999; Memmott et al., 2005; Memmott et al., 1998). It is therefore important to first dismiss potential confounding effects of propagule biases, before other processes (such as the Allee effect) are implicated (Colautti et al., 2006).

### iii) Dispersal

Dispersal is an integral part of population dynamics and, while risky, can have selective advantages when the fitness benefits of moving to a new patch (e.g. escaping or avoiding intra- and interspecific competition, inbreeding and temporal variation in reproductive success) exceed the costs (e.g. crossing unsuitable habitats, mortality due to predation or fitness loss) (Bonte et al., 2012; Bowler & Benton, 2005). Dispersal influences the location of each individual in a population in relation to each other and therefore plays a key role in their establishment success in the presence of Allee effects (Drury et al., 2007; Garnier et al., 2012; Kanarek et al., 2013). Increased aggregation, either intentional (e.g. attraction pheromones, etc) or by chance, can affect individual fitness and subsequently impact population growth and establishment success (Kanarek et al., 2013).

Dispersal rate also affects establishment success as high dispersal rates tend to move individuals from temporary clusters (and offspring away from parents), aggravating the demographic costs represented in component Allee effects and subjects a species to the risk of localized extinction (Kanarek et al., 2013; Kang & Armbruster, 2011; Liebhold et al., 2016; Taylor & Hastings, 2005). For example, Robinet and Liebhold (2009) contrasted the establishment success of populations of the gypsy moth with either flightless females or flight-capable females, and found that dispersal strengthened the mate-finding Allee effect in populations with flight-capable females and reduced their establishment success. Low dispersal can thus moderate the Allee effect, but can hamper movement of an invasive species beyond its initial site of establishment and slow the rate of spread (Kanarek et al., 2013; Lewis & Kareiva, 1993; Taylor & Hastings, 2005).

*Dispersal and cues:*

During dispersal the use of cues, to identify the direction and proximity of suitable habitat may reduce search time and increase dispersal success in terms of locating suitable host patches and mates. These cues could include visual (shape, size, colour) and/or olfactory signals (communication chemicals such as host-plant volatiles and pheromones) (Bowler & Benton, 2005; Fernandez & Hilker, 2007). Certain insect species utilize the chemical cues from colonised host plants to find patches of their host plant; for these species, cues released by conspecifics already colonizing the plant (pheromones), and/or plant cues induced by herbivore oviposition or feeding (herbivore-induced plant volatiles), can influence the apparency of the host patch (Fernandez & Hilker, 2007). This gives rise to a clumped distribution or aggregation of the insect species on selected host patches (Bowler & Benton, 2005). Aggregation is also thought to be an evolutionary tool to overcome demographic stochasticity and Allee effects (Gascoigne et al., 2009; Goodsman et al., 2016). The spatial structure of the population, dispersal, and Allee effects are thus strongly interconnected and knowledge on the dispersal behaviour (cues used) of an invasive species is required to predict the impacts of Allee effects on population establishment and spread (Goodsman et al., 2016; Kanarek et al., 2013).

*Dispersal and landscape connectivity:*

The landscape that a new species arrives into, and disperses from, is often heterogeneous and consists of patches of habitat of varying size, quality and isolation, all embedded in a matrix (area not occupied by suitable habitat). The term "landscape connectivity" describes the ease with which individuals can disperse and move about within this heterogeneous landscape and takes into account the behavioural response of organisms to it (Taylor et al., 1993). By affecting individual dispersal, connectivity within the introduction area is expected to shape variations in population density and ultimatley establishment success (Lustig et al., 2017; Morel-Journel et al., 2018; Musgrave et al., 2015; O'Reilly-Nugent et al., 2016; Powell et al., 2018; With, 2004).

Assessing landscape connectivity requires a species-centered approach (Taylor et al., 2006). It requires information on species' movement responses to landscape structure (e.g., movement rates through different landscape elements, dispersal range, mortality during dispersal, and boundary interactions) and how those responses differ as a function of broader-scale influences.

### iv) Habitat Modification/Host Removal

Habitat modification through habitat loss and habitat fragmentation is one of the major driving forces behind biodiversity loss (Bascompte & Sole, 1996; Debinski & Holt, 2000; Desmet, 2018; Fahrig et al., 2019; Fletcher et al., 2018). Habitat loss is defined as the removal of habitat resulting in a change in composition of the landscape structure (Hadley & Betts, 2016). Habitat fragmentation is defined as the breaking apart of habitat independent of habitat loss resulting in a change in the configuration of the landscape structure (Hadley & Betts, 2016). Habitat modification results in declining patch areas, increased isolation of patches, reduced connectivity, and increased edge effects (Fahrig, 2003; Fletcher et al., 2018)

Smaller habitat patches can lead to population decline (Bender et al., 1998), for example, because resources in smaller patches may be more limited (Zanette et al., 2000). Patch isolation can negatively affect day-to-day movements of a given species (e.g. between nesting and foraging resources for certain bird species (Luck & Daily, 2003)). Patch isolation also may negatively affect the dispersal of juveniles (e.g., ballooning dispersal of gypsy moth larvae is less successful in isolated patches) (Walter et al., 2016). The extent to which habitat modification results in patch isolation for a given species depends on the interaction between its dispersal behaviour, dispersal mode, scale of movement, habitat suitability, and how a given landscape has been modified.

Habitat modification, which is a detriment to rare and endangered species, is complementary in attempts to eliminate unwanted species from an area (Tobin et al., 2011). During management actions a population or metapopulation of an invasive species could be spatially managed through site-specific control actions so that large populations are fragmented, or that certain smaller patches across a metapopulation connected through dispersal are targeted (Blackwood et al., 2010; Tobin et al., 2011).

Host removal results in reduced habitat and increased isolation of remaining host patches with reduced connectivity and reduced population densities in each patch to levels below the Allee threshold (Keitt et al., 2001; Tobin et al., 2011). It has been found that invading species with an Allee effect must often exceed a spatial threshold, in addition to a density threshold, to persist and establish

(Desmet, 2018; Lewis & Kareiva, 1993; Vercken et al., 2011) Thus, sufficiently small and distant patches could lead to extinction of the population.

## Using a weed biocontrol agent to study invasions

Understanding the factors that explain the success or failure of introduced species is important for preventing the establishment of unwanted invasive species, but also for the preservation of threatened species and for successful establishment of biological control agents (Fowler et al., 2006; Hufbauer et al., 2013; Shea & Possingham, 2000; Yeates et al., 2012). Usually little information exists about the early stages of establishment of accidentally introduced species, as most invasion events are detected only years after their arrival and there is seldom any knowledge of the original arrival, the pathway involved, and how many individuals were introduced (Brockerhoff et al., 2014). Likewise, there is usually incomplete information about the timing of establishment or the exact size and distribution of populations that are targeted for eradication.

Introductions of species used as classical biological control agents offer unique opportunities to experimentally study the process of invasion by non-native species (Fauvergue et al., 2012; Fowler et al., 2006; Grevstad, 1999; Marsico et al., 2010; Roderick et al., 2012). In particularly, introduction of biological control agents targeting invasive plants serve as a model system for studying invasions of plant pests.

Releases of biological control agents are essentially planned biological invasions, with biogeographic, demographic, and genetic processes similar to those operating during unwanted invasions (Fagan et al., 2002; Fauvergue et al., 2012). They allow (i) observation of mechanisms at work at very small population sizes during the establishment stage, (ii) experimental manipulation of initial conditions, and (iii) conclusions that a population has indeed established or failed to establish after being introduced.

As models, biocontrol systems could provide insight into both evolutionary (e.g., genetic diversity, bottlenecks, selection, gene flow, genetic drift, and mutation) (McEvoy et al., 2012; Roderick et al., 2012), and ecological factors regulating invasion (e.g., propagule pressure, life-history traits, unsuitable climate, competition, predation, stochastic and deterministic processes, and habitat quality) (Dávalos & Blossey, 2010, 2011; Fauvergue & Hopper, 2009; Grevstad, 1999a; Grevstad & Herzig, 1997). One limitation of using weed biocontrol agents as proxy for an invasive species is the criterion of host specificity that is fundamental to biocontrol regulation and safety. Thus, weed biocontrol agents represent only this subset (specialists/monophagous/oligophagous species) of possible invaders (Marsico et al., 2010).

During this thesis experimental releases and eradications of a weed biological control agent were used as a proxy invasion system to study how propagule size, dispersal, and removal and isolation of host patches, and their interactions, influence the agent's establishment success and persistence, in the face of Allee effects. In practice, establishment or failure of a biocontrol agent population following release is typically assessed after two or three years (Grevstad et al., 2011), whereas for this study, establishment is assessed within the same season that it was released. Most new arrivals of non-native species are likely to be destroyed soon after arrival by a multitude of physical or biotic agents and do not establish (Mack et al., 2000). It is therefore necessary to study the processes acting in the first growing season after arrival, and in that sense, establishment in this study is seen as 'persistence within the first growing season'.

## Biocontrol Study System

The leaf beetle *Neolema ogloblini* (Monrós) (Coleoptera: Chrysomelidae), a biological control agent for *Tradescantia fluminensis* Vell. (Commelinaceae) in New Zealand, was used as proxy insect pest species in this study. The biological control programme was initiated against *T. fluminensis* in 2002 and the first field release of *N. ogloblini* was made in 2011 (Fowler et al., 2013). Establishment as well as a reduction in biomass have been confirmed at several sites, with widespread releases continuing (Paynter, 2018). As an invasive weed species, *T. fluminensis* is listed on the National Pest Plant Accord (NPPA), which indicates that it is an unwanted organism under the Biosecurity Act 1993 and cannot be distributed or sold in New Zealand (NPPA, n.d.). Therefore, potted specimens could not be used during field trials and another host species, the closely related *Tradescantia mundula* Kunth (Commelinaceae), a species currently not on the NPPA list, was used for this purpose. During quarantine studies by Landcare Research biocontrol workers to determine the suitability of *N. ogloblini* as a biocontrol agent for *T. fluminensis*, *T. mundula* was found to be an additional potential host species for the beetle (Fowler et al., 2013). To ensure that *T. mundula* would also be recognized and accepted as a host species under field conditions and be capable of supporting populations of *N. ogloblini*, I carried out additional host suitability tests (Appendix A). Results indicated *T. mundula* to be a suitable substitution for *T. fluminensis* as a host plant species under field conditions (Appendix A).

### *Tradescantia fluminensis*

*Tradescantia fluminensis* is native to south-east Brazil and northern Argentina, but has escaped cultivation and is now considered as one of New Zealand's worst invasive temperate forest weeds (Syrett, 2002). The weed is well established in areas of surviving lowland forests in the North Island and northern part of the South Island (Kelly & Skipworth, 1984). It is also reported as an environmental weed in a number of other countries such as Australia, Italy, Japan, New Zealand, Portugal, Russia, South Africa, and USA (Pellegrini, 2018).

In frost-free, understory habitats in New Zealand, *T. fluminensis* forms dense, monospecific mats which can have a dry bio-mass of over 1000 g/m$^2$ (Kelly & Skipworth, 1984). The primary concern is the prevention of forest regeneration and it has been shown that when the dry biomass of *T. fluminensis* infestations exceeds 200 g/m$^2$, regenerating seedlings of indigenous New Zealand tree species are out-competed and killed (Jackman et al., 2015; Standish et al., 2001). In addition, *T. fluminensis* can also alter litter decomposition and change soil nutrient availability (Standish, 2004; Standish et al., 2004; Yeates & Williams, 2001). Chemical or mechanical control of *T. fluminensis* is difficult because of the need to minimize damage to non-target plants in invaded forest remnants, and the need for repeat treatments because the plant can regenerate from small fragments (Kelly & Skipworth, 1984; Lusk et al., 2012).

### *Tradescantia mundula*

Similarly to *T. fluminensis*, *T. mundula* may also represent a potentially aggressive weed species, as it has been widely introduced through the horticultural industry and has escaped from cultivation (Pellegrini, 2018). In New Zealand *T. mundula* is currently classified as 'naturalized', but has the potential to become a future weed (Fowler et al., 2013). The species is native to Argentina, Brazil and Uruguay, where it can be found growing understorey in both moist, shaded forests or open forests (Pellegrini, 2018). In contrast to *T. fluminensis* that is considered to be self-incompatible and incapable of producing seeds (Kelly & Skipworth, 1984; Pellegrini, 2018), *T. mundula* reproduces both vegetatively and sexually, which may ultimately contribute to its aggressiveness as an invasive weed species in future.

### *Neolema ogloblini*

*Neolema ogloblini* is native to Brazil and was the first of the insect biocontrol agents to be released against *T. fluminensis* in New Zealand. The glossy metallic-black adults notch leaves from edges as they feed, while the pale greyish-brown larvae graze externally on the epidermal tissue on the underside of leaves. Adults tend to fly, fall or move to the undersides of the leaves when disturbed. As with many other Criocerinae, the larvae accumulate moulted skins and excrement which they hold as a cover over their backs, presumably to deter predators (Bacher & Luder, 2005; Bottcher et al., 2009; Morton & Vencl, 1998). Young larvae are gregarious and may be seen forming feeding fronts, while older larvae feed individually (Hayes, 2018). Pupation occurs inside a cocoon made from threads of a white oral extrusion resembling foam which solidifies (Hayes, 2018). This may mimic a fungus-infected larva, fooling prospective predators into not attacking (Hayes, 2018). Most pupae are found on the underside of leaves, or on the soil surface attached to plant detritus. The development time from egg to adult is on average 30.5 days at 24ºC (Appendix A, Fig 3).

## Research objectives and hypothesis

The aim of this thesis was to understand the role of the Allee effect during the early establishment of new insect pest populations, and how it could be used to facilitate their eradication.

By using a weed biocontrol agent as a model pest species, I investigated the following objectives:

i) The impact of **propagule size** on establishment success and population growth rate, thereby determining the presence/absence of a demographic Allee effect (Chapter 2).

ii) Potential mechanism(s) driving the **demographic Allee effect** (Chapter 3).

iii) The role of **dispersal** cues in forming populations above the Allee threshold in complex and patchy landscapes (Chapter 4).

iv) The impact of **host removal** as a management strategy to reduce populations below the Allee threshold and thereby achieving eradication (Chapter 5).

These objectives address the key factors identified from the literature as being of primary importance affecting the establishment of populations (propagule size; demographic Allee effects; dispersal; and host removal/habitat fragmentation), as introduced above.

I conclude the thesis in with a general discussion of all results reported in this thesis and how it can be applied to managing and preventing future invasions (Chapter 6).

# Chapter 2 – The impact of propagule size on establishment success and identifying a demographic Allee effect

## Introduction

New populations of non-native insect species arrive in areas outside their natural range on a continuous basis (Brockerhoff et al., 2014; Edney-Browne et al., 2018; Liebhold et al., 2018; Seebens et al., 2018). This has been reported for many areas around the world including New Zealand (Brockerhoff et al., 2014); Europe (Waage et al., 2008); the US (Aukema et al., 2010; Brockerhoff et al., 2014); and China (Lin et al., 2007). These trends are widely attributed to unprecedented growth in global trade and travel (Aukema et al., 2010; Brockerhoff, Barratt, et al., 2010; Liebhold et al., 2018; Ward, 2014). While most populations of alien insect species do not establish, some do, and it is this variability in establishment success that has motivated a sustained effort to understand the factors that influence establishment (Blackburn et al., 2015; Cassey et al., 2018; Grevstad, 1999; Grevstad & Herzig, 1997; Lockwood et al., 2005; Paynter et al., 2016; Simberloff, 2009). In addition, although most non-native species that do establish are rarely noticed, a few of these species have caused immense damage, altering ecosystem functioning and causing considerable economic impacts (Williamson & Fitter, 1996).

Establishment success of a non-native species depends on several factors. Among these are characteristics of the invaded habitat, called 'invasibility', and include habitat availability, quality and structure, and interspecific interactions such as competition, predation and mutualism (Cassey et al., 2018). Other factors are those of the invading species, such as life history features, evolutionary history, and genetic diversity (Hui et al., 2016; Szucs et al., 2014). In addition, characteristics that vary independently of species and location, such propagule pressure, also plays a role (Blackburn et al., 2015; Cassey et al., 2018; Lockwood et al., 2005).

Propagule pressure has been found to be a dominant driver of establishment success in small populations of introduced non-native species (Cassey et al., 2018; Lockwood et al., 2005). Propagule pressure refers to both propagule size (individuals per propagule), propagule numbers (the frequency of arrival), as well as the quality (Lange & Marshall, 2016) and genetic diversity (Hufbauer et al., 2013) of the arriving organisms. The arrival of a large founding population is more likely to lead to establishment than arrival of small founding populations (Colautti et al., 2006; Drake & Lodge, 2006; Hedge et al., 2012; Hufbauer et al., 2013; Lange & Marshall, 2016; Lockwood et al., 2005; Simberloff, 2009; Taylor & Hastings, 2005). Several processes may underpin the widespread influence of propagule pressure on establishment success and include demographic and environmental stochasticity (Jeppsson & Forslund, 2012; Lande, 1993); Allee effects (Courchamp et al., 2008; Liebhold & Bascompte, 2003); emigration/dispersal (Jonsen et al., 2007); inbreeding and genetic drift (Hufbauer et al., 2013; Melbourne et al., 2017); natural enemies (Cock et al., 2000; Paynter et al., 2012); and habitat quality and connectivity (Greene, 2003; Morel-Journel et al., 2016; With, 2004). The low establishment rates of small populations can be the result of any one or combinations of the above processes, making it difficult to determine which is acting in any given case.

The Allee effect is broadly defined as a decline in individual fitness with decreasing population size or density. Allee effects are typically strongest at low densities and can create critical population thresholds, below which populations can potentially be driven to extinction (Courchamp et al., 2008; Stephens et al., 1999). The Allee effect contradicts expectations that resource abundance (or carrying capacity) is the primary determinant of population growth across all population sizes or densities and that more resources result in higher per capita population growth rate. Resource limitation causes decreasing per capita population growth with increasing density, but when populations are small, Allee dynamics may result in decreasing per capita population growth rates with decreasing density.

Stephens et al. (1999) distinguish between component and demographic Allee effects. When a population experiences a component Allee effect, some component of individual fitness has a positive relationship with density (e.g., individual survival or reproduction is reduced at low density) (Stephens et al., 1999). In some cases, a component Allee effect leads to a demographic Allee effect where for a small population at low density the per capita growth rate of the population is reduced, potentially leading to negative growth and local extinction (Stephens et al., 1999). A component Allee effect does not necessarily always give rise to a demographic Allee effect as one component of fitness may be offset by an increase in other components of fitness (Angulo et al., 2007; Berec et al., 2007; Gregory & Courchamp, 2010).

Mechanisms giving rise to component Allee effects often involve social or cooperative processes among conspecifics, such that individuals do better collectively than alone (Courchamp, 2002; Courchamp et al., 2008). Well-known causes include mate-finding failure, loss of cooperative defence, loss of environmental conditioning, foraging inefficiency, and predator saturation failure (Fauvergue et al., 2012; Hunter, 2000; Kanarek & Webb, 2010; Kramer et al., 2009).

While many studies have revealed a component Allee effect, empirical support directly linking component and demographic Allee effects has been limited (Gregory et al., 2010; Kramer et al., 2009). This is often due to difficulties in censusing rare populations or a failure to identify underlying mechanisms, but also because of fitness trade-offs, population spatial structure and meta-population dynamics, and because the strength of component Allee effects may vary in time and space (Fauvergue, 2013; Gascoigne et al., 2009; Gilroy et al., 2012; Régnière et al., 2013; Walter et al., 2017). Additionally, extinction rate at low density or small population sizes is simultaneously elevated by other factors like demographic stochasticity and may mask the influence of Allee dynamics (Dennis, 2002; Liebhold & Bascompte, 2003; Roush & Hopper, 1993).

Nonetheless, evidence for demographic Allee effects has only been found for a limited number of plant and animal species, including: a plant: *Spartina alterniflora*; a copepod: *Hesperodiaptomus shoshone*; insects: the Glanville fritillary butterfly (*Melitaea cinxia*), the Eurasian Gypsy moth (*Lymantria dispar*), a parasitoid wasp *Aphelinus asychis*; and a mammal: the Californian Channel Island fox (*Urocyon littoralis*) (Angulo et al., 2007; Fauvergue & Hopper, 2009; Gascoigne et al., 2009; Johnson et al., 2006). Just how commonplace and widespread the demographic Allee effect is in natural populations is an ongoing subject of debate in the fields of biological invasion, conservation, climate change and sustainable harvesting (Armstrong & Wittmer, 2011; Berec, 2019; Fauvergue, 2013; Fauvergue et al., 2012; Gregory et al., 2010; Hutchings, 2015; Kramer et al., 2009; Kuparinen, 2018; Perälä & Kuparinen, 2017; Walter et al., 2017).

Similar to the Allee effect, demographic stochasticity plays an important role in the extinction probability of small populations. Both processes give rise to a similar, positive relationship between initial population size and probability of establishment, and it can be difficult to distinguish between the two processes (Fauvergue et al., 2012). Demographic stochasticity occurs because the birth or death of an individual in a populations is a random event, such that individuals identical in their expected reproduction or longevity still differ by chance in the number of offspring they produce or how long they will live (Lande, 1993; Melbourne, 2012). Thus, demographic stochasticity causes *variance* around the expected values of population size and per capita population growth rate. This *variance* is known as demographic variance and both within-individual and between-individual scale variation contribute to it (Melbourne, 2012). The within-individual scale contribution is the probabilistic births and deaths that occur even if all of the individuals within a population are identical. The between-individual contribution stems from variation in fecundity or survival between individuals due to genotype, body size, life stage, or age (Melbourne, 2012).

To study the role of propagule size and how it relates to the Allee effect in the early stage of establishment, the biocontrol agent *Neolema ogloblini*, together with one of its host plant species, *T. mundula*, was used as a model system. The use of a weed biocontrol system negates some of the challenges mentioned above, as it allows the initial conditions of an invasion to be manipulated and replicated in the field. By manipulating initial population size over replicated releases, I examined: i) how propagule size influences the probability of establishment, and ii) investigated the presence of the Allee effect by determining how propagule size influences the per capita population growth of established populations. As per the definition of the Allee effect, I predicted there would be a greater probability of establishment at higher populations of released propagules. Lower per capita growth rate at lower populations of released propagules would be indicative of a demographic Allee effect.

## Materials and methods

### Insects and host plants:

A starter colony of *N. ogloblini* was obtained from beetles reared for the biocontrol programme against *T. fluminensis* in New Zealand, originally imported from Brazil (Lages and Curitiba). For the purposes of this thesis, a population was maintained year-round in a glasshouse environment on caged, potted plants of *T. fluminensis* (hereafter referred to as the 'general population'). Temperatures in the glasshouse varied between 15°C - 25°C in winter and 15°C - 30°C in summer.

Both *T. fluminensis* plants used for rearing and *T. mundula* plants used for field trials were grown from cuttings in plant trays under greenhouse summer conditions, using a well-draining, compost-rich potting medium. Cuttings of both plant species were obtained from stock plants maintained at the Landcare Research facility in Lincoln, New Zealand. Authority to propagate and grow *T. fluminensis* at Landcare Research facilities was in accordance with the permission granted to Landcare Research under Sections 52 and 53 of the Biosecurity Act of 1992, signed 6 May 2014 (Landcare Research, n.d).

### Experimental design:

The initial population sizes of beetles were manipulated over replicated releases at 30 isolated sites in the Selwyn district of Canterbury, New Zealand (Fig. 1). All sites were located in an area classified as the Canterbury-Otago tussock grasslands ecoregion (Department of Conservation, 1987). Although *T. mundula* is frost sensitive and currently not widespread in the district (S. Fowler, personal communication), care was taken to ensure sites were not close to naturalized patches of *T. mundula*. This prevented beetle populations from unknown host patches in the surrounding landscape from contaminating experimental plots. As both the beetle species and its host plant prefer shady conditions, all sites were situated under trees (most sites were set up in conifer shelterbelts of rural properties), with no access by livestock and a minimum distance of 500 m between sites to prevent cross-over dispersal. A distance of 500 m was deemed as sufficient isolation between sites based on unpublished information (Chapter 4) which indicated that *N. ogloblini* are not able to disperse over substantial distances without host patches as stepping-stones. For example, when released from a distance of just 60 m to the nearest host patch, only 4.1% of beetles were able to find the patch (Chapter 4).

At each site potted plants were arranged to form a patch size with a leaf-cover of 1 $m^2$. The potted plants were placed on weed-mat to prevent rooting and minimize the likelihood of becoming established. Plants were watered on a regular basis to ensure plants stayed in a healthy growing condition. The use of patches of potted host plants grown in a shade house enabled control of confounding factors such as host quality patch size, stem density, nitrogen content, plant physiological stage, and soil type and drainage, thereby reducing the influence of aspects of environmental stochasticity on *N. ogloblini* populations.

Six population sizes were used for releases and consisted of 2, 4, 8, 16, 32, and 64 individuals released onto patches. These population size treatments were assigned randomly to the 30 sites, resulting in five replicates for each of the six propagule sizes. To obtain unmated adults of similar ages for the field releases, eggs were collected from the general population and reared on *T. fluminensis* leaves in ventilated, plastic containers (30 x 15 x 15 cm) under laboratory conditions (25:18°C temperature regime, 14L:8D photoperiod). The use of laboratory-reared adults not only aided obtaining unmated adults, but also reduced the influence of demographic variance on probability of establishment and growth rate of *N. ogloblini* populations. Under controlled rearing conditions, the high quantity and quality of resources and absence of stressors (e.g., predation, intra- and interspecific competition) tend to minimize inter-individual variance in reproductive success (Vercken et al., 2013).

On the day before the release, newly emerged adults were collected from the rearing containers. Adults of *N. ogloblini* display a pre-oviposition period of five days when no mating takes place, therefore only adults that emerged in the previous 48h were used to ensure that they were unmated. For population sizes of 32 and 64 adults, individuals were chosen at random, while equal numbers of each sex were used for populations of ≤16 adults. Morphologically it is not possible to distinguish between male and female beetles, but females tend to be larger than males (personal observation). Therefore, selection of males and females were based on size. This method worked well and was corroborated by data obtained from Experiment 1 in Chapter 3, which indicated that the sex of only four out of 530 beetles (0.75%) were assigned incorrectly. Upon selection, adults were confined overnight on cut leaves in small mesh bags to settle and feed. The leaves with adults were then gently released in a single location in the host plant patches the next morning when temperatures were cooler, in order to reduce immediate dispersal. Releases were made between 16 and 29 November 2017, and populations were left in the field to middle of April 2018.

Visits to sites depended on weather and the watering needs of the potted plants, which ranged from once a week during hot, dry weather (November to February), to every 2nd to 3rd week during cooler, rainy weather (March to April). During selected visits, each plant patch was inspected for five minutes by carefully lifting stems and turning leaves, and the presence of adults (or signs indicating the presence of adults – fresh feeding marks, newly-laid eggs and newly-emerged larvae) was noted. Such observations were done to determine whether failed establishments could be traced back to the immediate dispersal or disappearance from the site by the adults.

After 10 weeks following release (mid-summer census), plants at all sites were carefully searched for pupal cases. As development from egg to adult takes approximately 32 days (Appendix A), all populations had been in the field long enough such that at least some offspring should have reached the pupal stage. Pupal cases with exit holes were counted, recorded and then removed, while those without exit holes were counted and recorded, but left in the patch.

At the completion of the field trials (19 weeks following release), all plants were transferred to sealed plastic bags and brought to the laboratory, where all plants were carefully searched for all life stages of *N. ogloblini* and the number of each stage was recorded. Observations suggested the populations were able to produce one to two generations during this time period. To prevent double counting of pupae recorded at week 10, the number of pupal cases left in patches at that time was subtracted from the final count.

The number of pupal cases found, rather than the number of adults collected at the end of the season, was used to estimate the number of adults produced in the field during one season. Although this meant that the population would not be tracked for a whole generation, it was decided that pupal case number would provide the more reliable estimate under the unconfined, open-field situation of the experiment. The characteristic white 'foamy' pupal cases of *N. ogloblini* is very distinctive, durable and remain on or around the host plant (attached to the underside of lower leaves and the substrate surface) for months barring excessive disturbance. Previous studies using adult beetles have shown numbers collected could vary substantially as a consequence of death (old age or predation), dispersal due to patch decline/competition or intrinsically-driven dispersal after pupal eclosion (inbreeding avoidance). For example, Johnson and Horvitz (2005) found 81% of adults of the specialist chrysomelid *Cephaloleia fenestrata*, dispersed from their natal site soon after eclosion, while newly eclosed adults of *Trirhabda virgata* flew from host patches that had high conspecific densities and damage, but not from low-density patches with little defoliation (Herzig, 1995).

Under laboratory conditions, survival rate between the pupal stage and the adult stage did not vary substantially; with survival rate to the adult stage 3.5% (N=285 larvae) lower than to the pupal stage (HE Williams, unpublished data). It is acknowledged that factors such as predation or environmental conditions could additionally reduce survival from the pupal phase to the adult phase.

In the context of this study, population establishment was thus defined as successful development to the pupal stage of any offspring produced within the first growing season after introduction.

## Statistical Analysis

*Impact of propagule size on population establishment probability:*

To determine whether the probability of establishment was related to the initial propagule size released, data on the number of sites (N=30) supporting development of offspring to the pupal stage was analysed by maximum likelihood estimation using a binomial logistic regression model (a binary response, where 0 = extinction and 1 = establishment).

*Impact of propagule size on per capita population growth rate:*

To identify the presence of a demographic Allee effect, a linear regression model was used to examine the relationship between propagule size and per capita population growth rate. Per capita growth rate (r) was calculated as $r=\ln(N_1/N_0)$, with ($N_1$) the number of pupae produced during the season and ($N_0$) the propagule size released. A small non-zero number (0.001) was added to each growth rate data point prior to calculation to enable inclusion of extinct populations. Apart from measures such as using similarly-aged, laboratory reared adults and potted host plants of similar quality, the influence of demographic stochasticity was further reduced by including only sites where adults were present for an extended time in the statistical analysis. This was done with the rationalization that, the closer the actual longevities of individuals in a population are to the average, the lower the influence of demographic stochasticity, at least in terms of longevity and survival. *Neolema ogloblini* adults have been reported to live up to five months in captivity (Hayes, 2018), but under the optimum conditions experienced in the laboratory, this period is most likely at the upper limits of adult longevity. Information in the literature suggest average adult longevity of Criocerinae beetles to be between two to three months (e.g. *Plectonycha correntina* = 76 ± 40 days (Cagnotti et al., 2007), *Crioceris* sp. = 103 ± 13 days (Witt & Edwards, 2002), *Lema praeusta* = 78 ± 1 days (Das et al., 2019) and *Lilioceris cheni* = 84 ± 19 days (Manrique et al., 2017)) and personal observation suggests the same for the average longevity of *N. ogloblini* adults. Thus, only sites where adults were present for a minimum of four weeks after initiation of the experiment (about a third of the expected average longevity) were included in the statistical analysis. This resulted in the omission of four sites (one site where two adults were originally released, and three sites where four adults were originally released). Initial inspection of the data suggested nonlinearity (a hump-shaped relation); therefore, both linear and quadratic functions of propagule size were fitted to explain population growth rate. Adjusted $R^2$ and Akaike's Information Criterion corrected for small samples (AICc) were used to determine the most parsimonious model.

All analyses were conducted in R version 3.2.5 (R Core Team, 2013). Values for AICc were determined using the R package "AICcmodavg" (Mazerolle, 2019). Graphs were drawn using the R package "effects" (Fox & Hong, 2009; Fox & Weisberg, 2019).

## Results

### *Establishment probability*

In general, the number of weeks adult activity was noted at sites following initial release increased with increasing population size (Fig. 2). At only four sites (one site with initial population size of two individuals, and three sites with initial population size of four individuals) no signs of any adult activity were noted one week after release and consistently so for the duration of the experiment. At these sites, it was presumed that adults dispersed, died or were predated on within the first week after release at these sites. No eggs were recovered at these sites. Apart from these, at sites with no establishment, it is believed that establishment failure was not due to immediate dispersal of adults but rather a gradual decline in adult numbers.

Pupal case counts during the mid-summer census (10 weeks following initial release) indicated that limited numbers of pupae were produced at sites with smaller initial population sizes (two to eight adults). No pupae were produced at sites where initially two and four adults were released, and only one out of five sites where initially eight adults were released produced pupae (Fig. 3). At these sites with low populations, even though adult feeding and egg laying was observed for several weeks (Fig. 2), no pupae were produced.

At the conclusion of the experiment (19 weeks following initial release), no pupae were found at 11 out of the 30 sites. Although all initial population sizes produced pupae from at least one site (Fig. 3); all populations that went extinct were from releases of less than 16 adults.

Initial population size was positively related to the probability of establishment and the statistical significance was confirmed by a logistic regression model ($X^2$=17.122; *p*=<0.001) (Fig. 4).

*Population growth*

Per capita population growth rate ($\ln(N_1/N_0)$) was highly variable among sites, even among those with the same starting population size (Fig. 5). The statistical analysis indicated a significant quadratic relationship between population size and per capita population growth rate ($F_{2,23}=3.60$; $p=0.04$; Adj.$R^2=0.17$, AICc=133.4) (Fig. 5). Thus, per capita population growth rate initially increased as propagule size increased but decreased at higher population levels (Fig. 5). This suggests a demographic Allee effect in small populations of *N. ogloblini*. A linear relationship between population size released and per capita growth rate provided a poorer model fit to the data ($F_{1,24}=2.50$; $p=0.13$; Adj.$R^2=0.06$, AICc=135.1).

## Discussion

Results indicated that increasing initial population size increased the probability of establishment of the model organism, *N. ogloblini*. This is consistent with studies on propagule pressure as a predicator of establishment success (Cassey et al., 2018). Several studies have used releases of biocontrol agents to investigate the relationship between propagule size and establishment probability (Grevstad, 1999a; Memmott et al., 2005; Paynter et al., 2016) and population growth rate (Grevstad, 1999a). Paynter et al. (2016) analyzed the influence of biological control agent release size on weed biocontrol programmes in New Zealand and results indicated that, although agents can be established from relatively small numbers (<500), very small releases (<50) are likely to fail. Through experimental introductions of populations (2, 4, 10, 30, 90 and 270 adults) of a psyllid weed biocontrol agent *Arytainilla spartiophila*, in New Zealand, Memmott et al. (2005) found the probability of establishment was significantly and positively related to initial release size. Similarly, Grevstad (1999a) introduced two species of chrysomelid beetles, *Galerucella calmariensis* and *G. pusilla,* into stands of purple loosestrife (*Lythrum salicaria*) at four different population sizes (20, 60, 180, and 540) and monitored changes in population size over three years. For both beetle species, the probability of establishment increased with increasing initial number of propagules (Grevstad, 1999a).

In this study, although establishment occurred at all tested population sizes, smaller populations failed to establish more often. A positive relationship between initial population size and probability of establishment suggests that demographic factors (demographic stochasticity and Allee effects) whose influence depends on population size or density, played a role in determining establishment (Fauvergue et al., 2012; Lande, 1993; Shaffer, 2006; Vercken et al., 2013). In this study the relationship between initial population size and probability of establishment was strong enough not to be entirely swamped by variability in density-independent environmental factors such as micro-climate or other unknown influences.

A further objective of this experiment was to investigate the existence of a demographic Allee effect by examining the relationship between propagule size and per capita population growth rate. Technically, the experiment did not allow for estimation of the demographic Allee effect since populations could not be tracked for a full generation, however the measurement of population numbers from adults to pupae nearly consists of a full generation. In established populations in this experiment, the per capita population growth rate varied tremendously among sites for a given propagule size, potentially due to both demographic and environmental stochasticity. Since initial population sizes were low, the influence of demographic stochasticity may be so strong and thereby masking Allee dynamics. Omitting extinct sites where adults disappeared within the first four weeks from the statistical analysis, somewhat reduced the influence of demographic stochasticity and a significant positive relationship was found between per capita population growth rate and smaller propagule sizes. This result cautiously supports the presence of a demographic Allee effect in the experimental populations. As the influence of stochasticity cannot be completely separated from that of a demographic Allee effect in analysis of the data, I conclude that extinction probability in the experimental populations of *Neolema* was influenced by both a demographic Allee effect and stochasticity.

In her study to investigate the relationship between release size and per capita growth rate of experimental populations of *G. calmariensis* and *G. pusilla*, Grevstad (1999a) found per capita population growth rate increased with increasing release size, indicating the presence of an Allee effect. In contrast, experimental introductions of the psyllids provided no evidence of Allee effects (Memmott et al., 2005). Similar to my study, both Grevstad (1999a) and Memmott et al. (2005) reported strong variation in growth rate between sites, even for populations initiated with similar population sizes. In these two studies, environmental stochasticity seems to play a major role in establishment success, either because the rate of catastrophic events was high (about 30% of release sites destructed within the five years of study (Memmott et al., 2005)), or because variance in population growth rate was not explained by population size (Grevstad, 1999a).

The mechanism(s) driving the demographic Allee effect in small populations of *N. ogloblini* is unknown, but because offspring were produced at sites irrespective of initial population size (given adults were still present), it seems likely that establishment failure and lower per capita growth rates were due to the disappearance of eggs and larvae. Although not quantified, the presence of spiders and predatory mites were frequently noted and predation on eggs and smaller instars ($1^{st}$ and $2^{nd}$) were often observed. Smaller populations, though continuously producing offspring, may not have been able to produce enough offspring to saturate generalist predators and allow at least some of the larvae to develop to the adult stage. It is therefore plausible that predation could be at least one of the drivers behind the demographic Allee effect in this study system.

The most reported cause of the Allee effect in small populations is the failure of mates to locate each other at low population densities (Berec et al., 2017; Gascoigne et al., 2009; Kramer et al., 2009; Yamanaka & Liebhold, 2009). As a sexually reproducing organism, mate-finding failure could potentially be an additional component Allee effect that scales up to produce a demographic Allee effect in populations of *N. ogloblini*. Because I did not specifically measure mating success in this study, I could not attribute mate limitation to the measured differences in population growth.

These two potential mechanisms are investigated and discussed in more detail in the Chapter 3.

In addition to its consequences for establishment, Allee effects can also have consequences for the spread phase of a biological invasion (Kanarek et al., 2013; Keitt et al., 2001; Lewis & Kareiva, 1993). Newly arrived populations may fail because they arrive in a new habitat in low numbers that are subject to Allee dynamics and stochasticity (Drake & Lodge, 2006; Liebhold & Bascompte, 2003; Lockwood et al., 2005). Similarly, during the spread phase, low-density situations occur during dispersal over short and/or long distances (Tobin et al., 2011). When there is extensive short-distance dispersal, a large fraction of the population may emigrate, leaving a population that is insufficient in size or too low in density to persist (Kanarek et al., 2013; Kean & Barlow, 2000). During long distance dispersal, such as when life stages are transported anthropogenically, only a limited number of individuals may be transported to a new area (Lewis & Kareiva, 1993; Tobin et al., 2009). In these situations, Allee effects can limit the spread of populations, as well as cause pulsed invasion and range pinning of invading populations (Johnson et al., 2006; Keitt et al., 2001).

As environmental and biotic conditions vary across real-world landscapes, Allee effects may vary in time and space (Angulo et al., 2007; Tobin et al., 2007; Vercken et al., 2011; Walter et al., 2017; Walter et al., 2015). Gradients in Allee effects might occur as a species' range approaches suboptimal conditions while expanding into new territory (Walter et al., 2017). For example, lower population growth rates (and thus a stronger Allee effect) were found for populations of the gypsy moth in areas with a limited distribution of its preferred host tree species, compared to areas where host species were more abundant (Tobin et al., 2007). Kramer et al. (2011) found that temperature influenced mate-encounter rates in the copepod, *Hesperodiatomus shoshone*, with mating enhanced at higher temperatures and thus a weaker Allee effect under warmer conditions.

Because the Allee effect varies across time as well as different environmental and biotic conditions, it makes sense that Allee effects would exhibit patchiness if the mechanisms driving them (e.g. ability to find mates and satiation of predators) are influenced by habitat patchiness (Liebhold & Tobin, 2008; Walter et al., 2017). Therefore, the success rate of management actions that manipulate habitat to generate patchily distributed host plants or isolate favourable areas of habitat, can be unpredictable. For example, in silviculture practices, thinning of host trees or increasing compositional and structural diversities in the forest have been suggested as prevention measures against invasive forest insects (Klapwijk et al., 2016; Musgrave et al, 2015). In contrast, an effort to halt the spread of emerald ash borer in Ontario by establishing a 10km×30 km large ash-free zone was unsuccessful (Musgrave et al., 2015).

To increase the efficiency of habitat manipulation as a management tool, we need to explore how immigration behaviour can shape the occupancy probability of organisms in a patchy landscape (Chapter 4) and how habitat alteration in combination with an Allee effect scales up to population-level spread rate and ultimately population survival (Chapter 5).

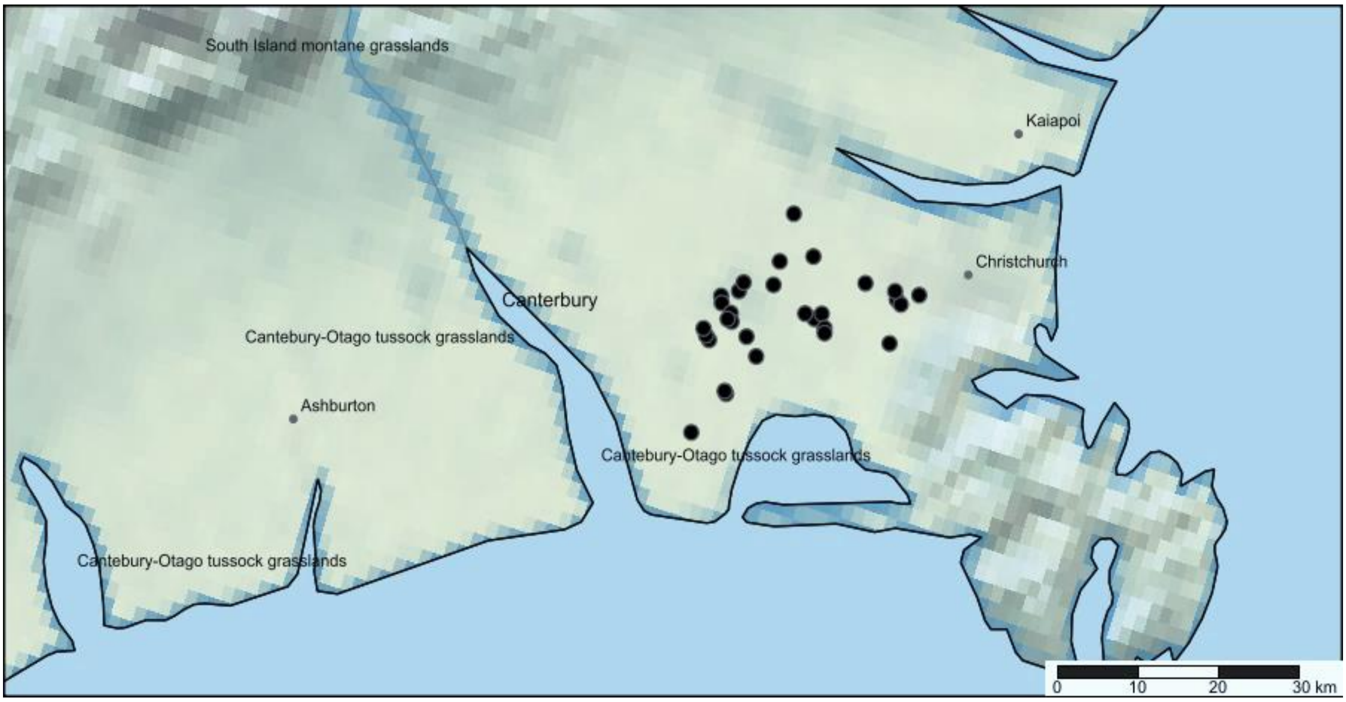

**Figure 1**: Locations of field sites (large black dots) used in this study (Selwyn district in Canterbury, New Zealand). All sites were located in areas classified as the Canterbury-Otago tussock grasslands ecoregion (Department of Conservation, 1987).

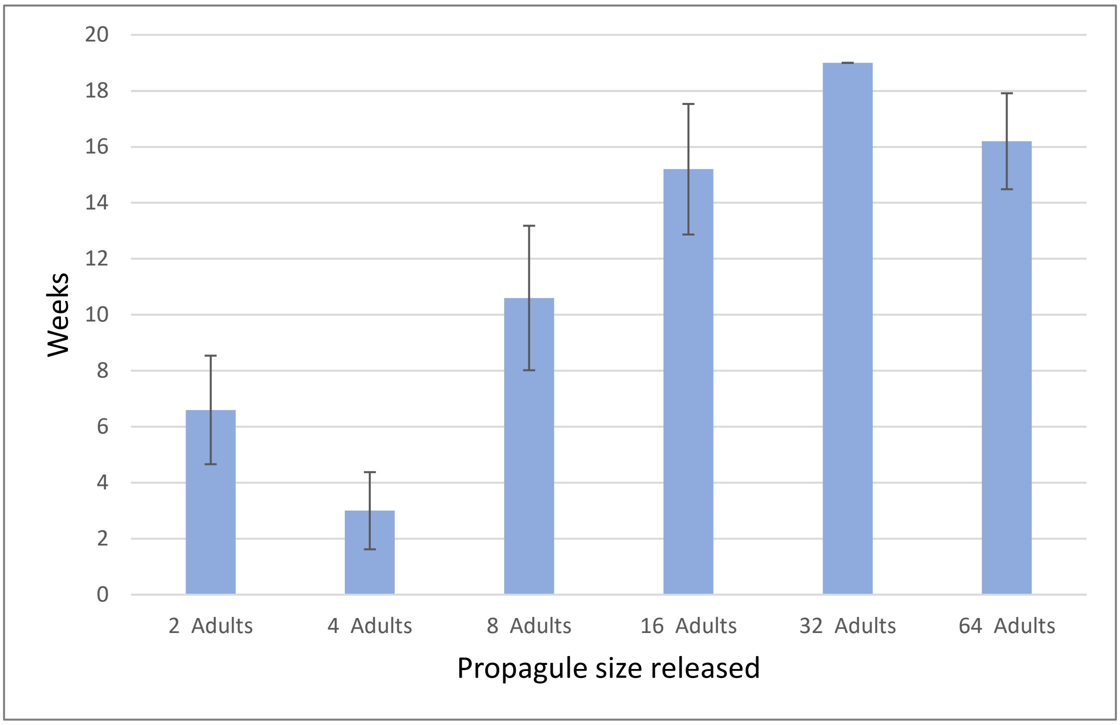

**Figure 2:** The mean number of weeks (from a maximum of 19) that adult activity was recorded at release sites for different propagule sizes. Error bars indicate standard error.

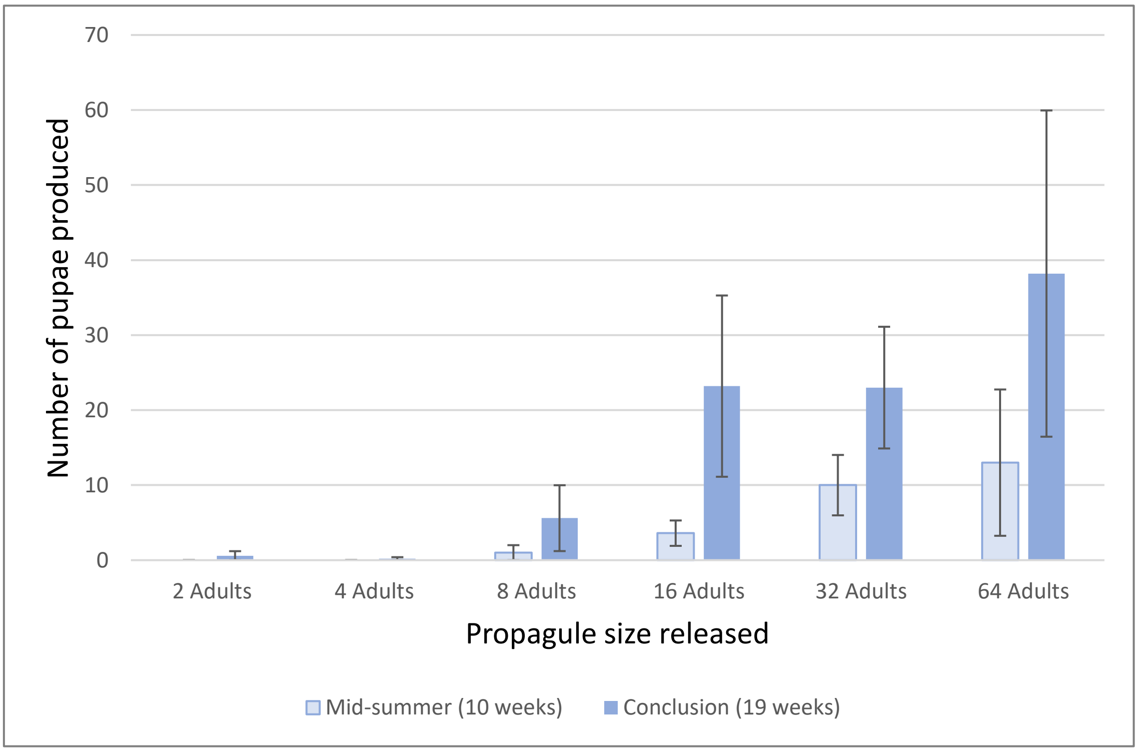

**Figure 3:** The mean number of pupae produced from Nov 2016 - April 2017, but separated for mid-summer (light blue) and conclusion of experiment (dark blue). Error bars indicate standard error.

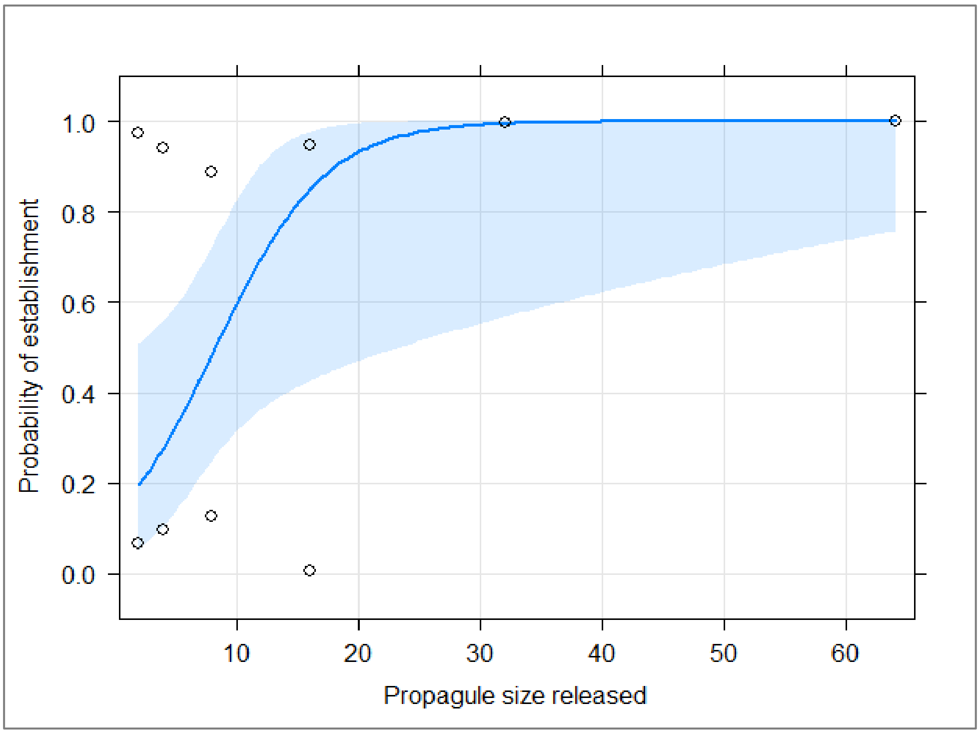

**Figure 4:** The relationship between propagule size released and the probability of establishment of *Neolema ogloblini*. The solid blue line represents values predicted from a logistic regression model. The shaded area is a pointwise confidence band for the fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. The circles are partial residuals points.

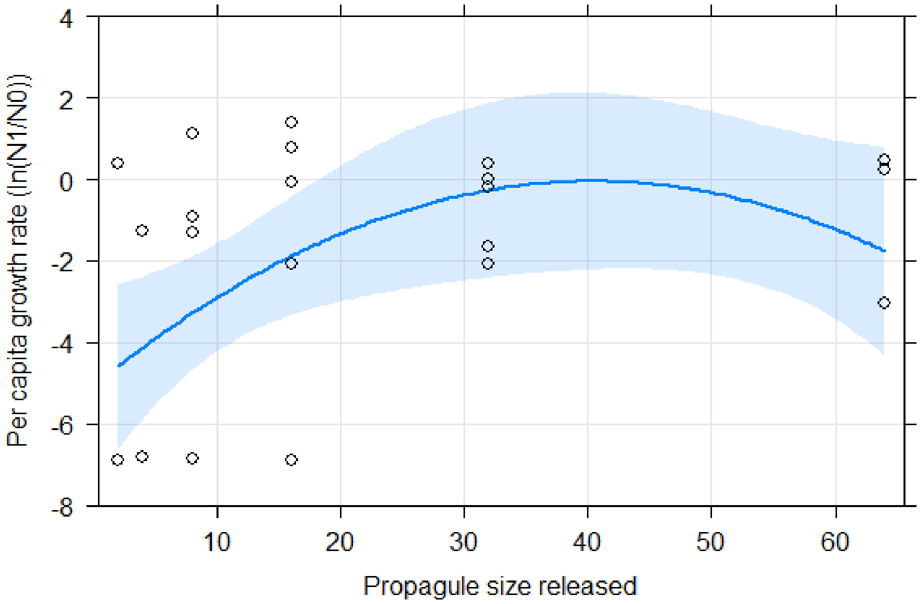

**Figure 5:** The relationship between propagule size released and per capita growth rate ($\ln(N_1/N_0)$) of *Neolema ogloblini*. To take into consideration the influence of demographic stochasticity, only sites where adults (or their activities) were noted for more than four weeks after the initiation of the experiment, were included in the analysis. The shaded area is a pointwise confidence band for the fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. The circles are partial residuals points.

# Chapter 3 – Mechanisms governing the demographic Allee effect in small populations of *Neolema ogloblini*

## Introduction

When arriving in a novel region, small populations of non-native species face various challenges that can influence their survival, reproduction and ultimately their establishment. One of these challenges is the Allee effect which refers to positive-density dependence, that is, individual fitness decreasing as population size decreases (Stephens et al., 1999).

Mate-finding failure is one of the most reported causes of a component Allee effect (Fauvergue, 2013; Gascoigne et al., 2009; Kramer et al., 2009; Shaw et al., 2018; Yamanaka & Liebhold, 2009a). The inability to find a suitable mate can arise for a variety of reasons. Temporal mismatch between the emergence pattern of males or females (protandry or protogyny) can result in mating failure. For example, Rhainds (2013) found that males of the bagworm *Thyridopteryx ephemeraeformis* emerged earlier than females in the season and caused a lower ratio of males per female late in the season. The ensuing decline in female mating probability later in the season due to protandry provided indirect evidence for a component Allee effect resulting in local extinction of populations (Rhainds, 2013). Another factor influencing the ability to find mates is spatial mismatches in reproductive activity between males and females. Walter et al. (2015) found that spatial heterogeneity in temperature resulted in heterogeneity in developmental time and the resulting reproductive asynchrony reduced population growth of invading gypsy moth (*Lymantria dispar*) populations. In small or low density populations, mating failure may result simply due to the low probability of random encounters between males and females (Fauvergue, 2013; Gascoigne et al., 2009). For example, Régnière et al. (2013) found a component mate-finding Allee effect in the eastern spruce budworm (*Choristoneura fumiferana*) with decreasing mating success correlated with decreasing population density. The existence of a mate-encounter component Allee effect that translates into a demographic Allee effect has thus far only been demonstrated for *L. dispar*, even though such mechanisms may be important in other species (Contarini et al., 2009; Tobin et al., 2013).

When defining the Allee effect, much emphasis has been placed on reproduction in general and on mate-finding in particular (Boukal & Berec, 2002; Wells et al., 1998), but components of fitness reducing survival in small populations may be as important (Fauvergue & Hopper, 2009; Gascoigne & Lipcius, 2004; Kramer & Drake, 2010). Predation is an alternative or additional factor that can explain the positive effect of population size on population growth rate. Gascoigne and Lipcius (2004) laid out a theoretical framework for Allee effects driven through predator-prey interactions. The authors proposed the possibility of a predation-driven Allee effect for individual survival for predators that do not respond numerically to fluctuations in prey density (functional response of type II). This is especially true for predation by generalist predators (Pavlová & Berec, 2012). Predator consumption decreases with increasing prey density as a result of predator satiation, resulting in lower survival rates at lower prey density. In these circumstances an Allee effect may emerge in the prey population; the lower the prey density, the lower the probability of each individual escaping predation (Berec et al., 2007; Gascoigne & Lipcius, 2004; Gregory & Courchamp, 2010).

Since predation is a fundamental ecological mechanism and a type II functional response in predators is the most frequent type of functional responses observed in nature (Pavlová & Berec, 2012), a predator-driven Allee effect can potentially impact the establishment of many newly arrived, small populations of non-native species, irrespective of life history (Gascoigne & Lipcius, 2004; Kramer & Drake, 2010). However, there is been limited evidence for a predator-driven demographic Allee effect in invertebrates when compared to vertebrates, and Kramer et al. (2009) speculated this was either the result of study bias or a real difference between taxonomic groups, thus identifying a gap for further research. Nonetheless, predation by larvae of two predacious midge species in the genus *Chaoborus*, can cause extinction of small populations of a water flea *Daphnia magna* via a predator-driven demographic Allee effect (Kramer & Drake, 2010). The gypsy moth has been a prominent exemplar for studies on the Allee effect, and although a generalist predator *Peromyscus* spp., a deer mouse, is regarded as one of most important predators of low-density gypsy moth populations (Larsen et al., 2018; Tobin et al., 2009), the role of natural enemies in causing or contributing to the demographic Allee effect is still unclear (Tobin et al., 2009; Walter et al., 2015).

Releases of weed biological control agents could potentially provide indirect evidence of predator-driven Allee effects causing declining population growth and establishment failure. It has been reported that native natural enemies may interfere with the initial establishment of weed biocontrol agents or their subsequent population build-up, spread and impact (Crider, 2011; Ding & Blossey, 2005; Downey et al., 2007; Ghosheh, 2005; Sebolt & Landis, 2004). However, evidence for the importance of predation in limiting biocontrol agent populations is largely anecdotal (Dávalos & Blossey 2010), but since predators have to be ‘caught in the act’, predation is likely under-reported (Paynter et al., 2018). In their study on the impact of predation by a mirid bug *Plagiognathus politis* on the leaf beetle *Galerucella calmariensis*, a biocontrol agent against *Lythrum salicaria* in North America, Hunt-Joshi et al. (2005) found evidence that suggest there may be a population threshold above which the beetle may escape the limiting influence of mirid predation. Predation by *P. politis,* along with that by ladybird beetles, ground beetles, and ground-dwelling spiders on immatures of the beetles has been found to vary in space and time (Dávalos & Blossey, 2010). Predation was low in areas of central New York (Dávalos & Blossey, 2010), while Wiebe and Obrycki (2004) reported it to be severe and widespread in Iowa. In New Zealand, predation is considered to significantly reduce the impact of at least four agents on their target weeds, with the potential of more unsuccessful agents being added to the list in future surveys investigating predation levels (Paynter et al., 2018).

Unless the impact of predation has been quantified in relation to population density or size, the incidence of predation in low populations is not always indicative of predator-driven Allee effects. This was clearly demonstrated in the case of the bone-seed leaf roller (*Tortrix* s.l. sp. ‘*chyrsanthemoides’*) released against the invasive plant *Chrysanthemoides monilifera* ssp. *monilifera* in New Zealand. In the presence of a predator-driven Allee effect, it is expected that frequency of establishment would be positively related to population size. However, Paynter et al. (2012) found establishment of the bone-seed leaf roller was significantly lower in the presence of predatory ant species. But, contrary to expectation that establishment success should increase with increasing release size, over half of the establishment failures were associated with the highest (>500 moths) release sizes (Paynter et al., 2012). It seems that although predation contributed to establishment failure, a predator-driven Allee effect did not appear to play a role. One possible explanation for such a deviation is a type III predator response. The ants were attracted to honey-dew producing scale insects that occupied the same habitat as the bone-seed leaf roller. Paynter et al. (2012) found that the presence of ants was positively correlated with the proportion of plants with scale insects and with the abundance of scale insects. The behaviour of the ants suggests a Type III functional response where they have multiple prey (for protein vs carbohydrate resources) and can switch between prey. According to Gascoigne and Lipcius (2004) a type III response can arise from 'prey switching' and can keep prey (bone seed leaf roller) at a low stable equilibrium, sometimes called a 'predator pit'. This functional response does not have the potential to create an Allee effect, and could potentially counteract an Allee effect in some other component of fitness (Gascoigne & Lipcius, 2004).

To further improve our understanding of the Allee effect and the mechanisms potentially driving the demographic Allee effect in *N. ogloblini* populations, in this thesis I focussed on two processes: mate-finding failure and generalist predation of immature life-stages.

Since *N. ogloblini* is a sexually producing organism, there is a possibility that mate-finding failure may drive a component Allee effect. In order to evaluate such an effect, population sizes of newly eclosed, unmated adults in host patches were manipulated and the impact of male density on the mating status of females was evaluated after three weeks in the field early in their adult lifespan.

A high larval disappearance rate was observed during field experiments to test the influence of population size on establishment success (Chapter 2). In order to evaluate the effect of generalist predation on establishment success, population sizes of immatures were manipulated and tested the impact of predator exclusion on immature survival to the pupal stage at different population densities.

It was expected that: i) in the presence of a mate-finding Allee effect, more unmated females will be found in smaller populations; and ii) in the presence of a predator-driven Allee effect, survival of larvae would be higher in larger populations.

## Materials and Methods

### *Experiment 1: Impact of male density on the mating status of females*

This experiment was conducted at sites in the Selwyn district of Canterbury, New Zealand (Fig. 1), in the summer of 2017/2018 and again in late summer 2019. Site selection and patch setup were similar to the methods used in Chapter 2.

The experiment was run for a period of three weeks. Under laboratory conditions adults of *N. ogloblini* commence mating after completing a pre-oviposition period of approximately six days. It was therefore reasonable to assume that a three-week period would be long enough to give an indication of the potential for a mate-finding Allee effect in small populations of the beetle.

In 2017/2018, the influence of population size on female mating success in populations where 2, 8, and 16 individuals were initially released, and in 2019, in populations where 8, 16, 32, and 64 individuals were initially released, was tested. There were six replicates for each propagule size in each year. The replicates in 2017/2018 were staggered over the period from November 2017 to March 2018, and the replicates in 2019 staggered from March 2019 to April 2019.

To obtain unmated adults of similar ages for the field releases, the same general methods as described in Chapter 2 were used. The day before release, the appropriate number of newly emerged, unmated adults were collected and confined in small mesh bags on cut leaves of *T. mundula* to settle and feed.

For population sizes of 32 and 64 adults, individuals were chosen at random, while equal numbers of each sex were used for populations of ≤16 adults. The leaves with adults were then gently released in a single location in the host plant patches the next morning when temperatures were cooler, in order to reduce immediate dispersal. After three weeks the plants were bagged in sealed plastic bags and brought back to the laboratory, carefully searched and the presence of each life stage noted. Adults were collected and placed individually into small containers with *T. mundula* foliage. Each container was monitored for up to 14 days to determine: i) the gender of the adult – containers with eggs were assumed to be female, while those without eggs assumed to be male (females laid eggs irrespective of being mated, though at a lower rate); and ii) the mating status of the females – by determining if any eggs laid were fertilized and hatched into larvae. Foliage were replaced as needed. Any females that did not lay fertilized eggs were then exposed to two males from the general population (from the rearing facility) and any resulting eggs monitored to ensure that she was capable of mating and laying fertilized eggs. Females that laid fertilized eggs only after being exposed to males from the general population indicated that they were unmated when collected from the field and signify mate-finding failure.

Data on the mean maximum daily temperatures during the time periods the experiments were run was obtained from a weather station near Landcare Research grounds in Lincoln (Lincoln Broadfield Electronic Weather Station, Longitude: 172.4704; Latitude: -43.6262) (data available at http://cliflo.niwa.co.nz/).

*Experiment 2: Impact of generalist predation on the survival of immature stages*

Predator exclusion experiments to investigate the influence of generalist predation on the survival of *N. ogloblini* immatures at different population densities were conducted in the summer of 2018 (March-April) and again in 2019 (Jan-Feb). The trials were carried out in the grounds of the Lincoln Landcare Research facilities. In 2018, larval survival in populations initiated with 20 or 50 eggs, and with or without predator access, were compared. However, low survival observed in both these population sizes prompted additional trials with larger population sizes in 2019, using populations initiated with 50, 100, and 200 eggs.

Potted plants of *T. mundula*, equal in size and age, were used for the experiments. Following a factorial design, each plant was randomly assigned to one of two levels of predation (exposed or not exposed), and three levels of egg density (50, 100, or 200 eggs) (only two levels in 2018, 20 or 50 eggs). To obtain desired initial egg densities, adults were released onto individual potted plants and allowed to oviposit for two days. After removing adults, excess eggs were removed according to each density treatment. The plants were then randomly placed under trees with a minimum distance of at least 4m between the plants. To exclude predators, selected plants were enclosed by fine white mesh bags tied closed at the top and which could be opened to inspect the plant inside. Plants allocated to allow predator access were not enclosed. The plants were left in the field for approximately four weeks to allow development to the pupal stage. At the end of this period, plants were carefully searched, and the number of pupae recorded. There were three replicates for each density level in 2018 and nine for each density level in 2019.

## Statistical Analysis

*Experiment 1: Impact of male density on the mating status of females*

Mating status of females

To determine whether female mating success was related to male population density, data on the mating status of each recovered individual female (n=270 – females pooled from all propagule sizes and across years) was analysed by maximum likelihood estimation using generalized linear models. Two explanatory variables and their interaction were included: 1) the number of live males recovered, and 2) the mean daily maximum temperature during the time period the replicates were in the field (as the replicates were run at different times of the season). The number of 'live males recovered' rather than 'males released' were used in an effort to reduce variation caused by immediate dispersal and mortality factors. Several models were fitted; including a logistic model with binomial error structure, a logistic binomial model using Firth's biased reduced penalized-likelihood logit for rare events data, and a generalized linear mixed model which included the propagule size released in each patch as a fixed factor. The most appropriate model was selected by comparing Akaike information criterion (AIC) values.

Dispersal propensity of adults

To determine whether adults stayed in their host patches within the three week time period, or disappeared (due to dispersal, predation or natural death), the relationship between initial population size and the proportion of adults recovered were examined using a generalized linear quazi-binomial model (to compensate for overdispersion). The explanatory variables included propagule size and mean daily maximum temperature, and their interactions.

*Experiment 2: Impact of generalist predation on the survival of immature stages*

Experiments for each year were analyzed separately because the design changed slightly. To determine how generalist predation impacts the survival of larvae under field conditions, data on the proportion of immatures that successfully developed from eggs to pupae was analysed by maximum likelihood estimation using a generalized linear model with binomial errors. The explanatory variables included access by generalist predators (or not), population size, and their interactions.

## Results

*Experiment 1: Impact of male density on the mating status of females*

Mating status of females

Across all years and populations, 530 (61%) out of the 876 adults released were recovered. Of these, 270 were female, of which 17 (6.3%) were unmated. The best fitting model (logistic regression model with binomial error structure – Table 1) indicated that the probability of females being mated was significantly associated with both the total number of males recovered, as well as the interaction between the mean daily maximum temperature and the total number of males recovered (Table 2). In general, the probability of being mated increased as both the number of males recovered and mean daily maximum temperature increased (Fig. 2). The increase was the sharpest over a range of low male densities and at higher temperatures (temperature = 23-25°C) (Fig. 2). In contrast, at the lowest temperature (temperature = 20°C), the probability of females being mated was equal across all male densities (Fig. 2). This was possibly due to the beetles being less active and staying together in the host patch. With higher temperatures, higher levels of activity could be expected and at sites with lower male density the few males that were available either dispersed or were predated on by the also more-active predators. Overall, the effect of male density on mating success, although significant, was not strong. At a median of 22 °C mean daily maximum temperature, the model predicted a probability of 0.81 in mating success in the presence of no males, with an increase in female mating success of 18.5% between the minimum observed density (zero males) and maximum observed density (25 males).

Dispersal propensity of adults

Out of the total of 876 adults released in different propagule sizes, 346 beetles (39%) were not recovered during the three week monitoring period. The proportion of adults recovered at end of trials depended significantly on both mean daily maximum temperature; and the propagule size released (Table 3). There was no interaction effect ($F_{(1)}$=1.688; p=0.195). As mean daily maximum temperature increased, the proportion of adults recovered decreased (Table 3, Fig. 3). This is possibly due to reduced activity levels of both beetles and predators at lower temperatures resulting in lower levels of dispersal and predation and thus higher recovery rate. As population size increased, the proportion of adults recovered decreased (Table 3, Fig. 4). At higher population levels, limited patch size potentially caused intraspecific competition in the population and increased dispersal propensity of adults.

### *Experiment 2: Impact of generalist predation on the survival of immature stages*

Predation by generalist predators had a profound influence on the survival of immatures to the pupal stage. Throughout the experiment, predation by several spider species, lacewing larvae, and predatory mites were frequently and directly observed, especially on younger instars. At the conclusion of the experiment, remains of larvae (dried husks typically left by predacious mites and/or remains tangled in spider web threads) were often found on leaves near larval feeding marks.

In 2018, predator exclusion, but not population size significantly influenced immature survival to the pupal stage (Table 4). There was no significant interaction between population size and predator exclusion ($F_{(1)}$=0.769; p=0.406). Larval survival was very low on plants where predators could access, with only 1.0% of immatures across all population sizes able to survive to the pupal stage (Fig. 5). On plants protected from predator access survival was 51.4% across all population sizes (Fig. 5).

In 2019, in an additional attempt to find a population size where the number of larvae present would satiate predation, larger initial populations of eggs were used. Once again, predator exclusion, but not population size significantly influenced immature survival to the pupal stage (Table 4). There was no significant interaction between population size and predator exclusion ($F_{(2)}$=1.134; p=0.331). Larval survival was very low on plants where predators could access, with only 0.9% of immatures across all population sizes able to survive to the pupal stage (Fig. 6). On plants protected from predator access survival was 74.6% across all population sizes (Fig. 6).

## Discussion

Results from the experiments above confirm the presence of at least one component Allee effect in small populations of *N. ogloblin*i, that is, mate-finding failure. Massive predation by generalist predators was found on the immature stages of *N. ogloblini*, but a positive relationship between larval survival and population size could not be confirmed.

During the first three weeks of their adult lifespan, the probability of females being mated increased with male population density, indicating the presence of a component mate-finding failure Allee effect in this period. It is expected that this component Allee effect would be relatively weak and may not be the main driving force behind a demographic Allee effect, due to several reasons. Firstly, the increase in mating success from lowest to highest male densities was 18.5%, with the largest changes in mating success happening when male density was very low (e.g., between 0 to 5 males the probability of being mated increased by 11.4%, while between 6 and the maximum of 25 males the probability increased by only 7.06%). Secondly, adults of *N. ogloblini* can live up to five months in captivity (personal observation) and have been noted to partake in multiple mating events. Yamanaka and Liebhold (2009b) predicted that for insect species with long-lived adults and capable of multiple mating events, Allee effects arising from mate-finding failure should be relatively weak. It is thus likely that the mating-failure component Allee effect present in the first three weeks of adulthood of small populations of *N. ogloblini* would be offset over time (by multiple mating and being long-lived), provided adults are not lost through dispersal or predation before mating could take place. Thirdly, results from the mating experiment indicated a negative relationship between the proportion of adults recovered and initial population size. The higher rate of dispersal from larger populations suggests that this behaviour may be selected as a mechanism to avoid intraspecific competition while it may have adverse consequences for predator avoidance or the search for potential mates. In the absence of intraspecific competition, adults of *N. ogloblini* showed little tendency to disperse thereby reducing the potential for a mate-finding Allee effect. Dispersal away from the point of introduction prior to mating may intensify mate-location difficulties and can intensify the probability of mating failure in small populations (Kanarek et al., 2013; Robinet et al., 2008). When intraspecific competition remains low, a female has little to lose by remaining in a patch with other females present. While dispersal away from a host patch may provide an opportunity to avoid competition, it carries a risk of mating failure in patches of low population densities and/or when populations are highly isolated. Therefore, it may be adaptive for females to remain in a patch with conspecifics and thereby reducing the potential for mate-finding failure (Shaw & Kokko, 2015).

Recent studies have reported on the spatial-temporal variance in the strength of Allee effects (Bancroft et al., 2009; Rhainds, 2013; Robinet et al., 2008; Walter et al., 2017). Environmental conditions can influence component Allee effects, for instance altering predator densities or how rates of mate-finding scale with population density (Kramer et al., 2011; Rhainds, 2013; Walter et al., 2015). Kramer et al. (2011) found higher temperatures increased the swimming speed and mate-encounter rates of a copepod *Hesperodiatomus shoshone*, thereby influencing the critical density threshold for establishment. Similarly, Rhainds (2013) suggested that reduced level of activity of males of the bagworm *Thyridopteryx ephemeraeformis* at temperatures below 18 °C, may account in part for the low mating probability of females. Experimental results with adults of *N. ogloblini* indicated female mating success in general increased with increasing temperatures, but at the lowest temperature (temperature = 20 °C), the probability of females being mated was virtually equal across all male densities (Fig. 2). This was possibly due to the beetles being less active and remaining together in the host patch thereby increasing probability of mating. With higher temperatures, higher levels of activity could be expected and at sites with lower male density the few males that were available either dispersed or were predated on by the also more-active predators.

In this study I investigated generalist predation as a second potential component Allee effect driving the demographic Allee effect in small populations of *N. ogloblini*. Larvae of *N. ogloblini* display well-known anti-predator behaviours, for example, food-regurgitation, and retaining faeces and skin moults as a shield over their bodies (Bacher & Luder, 2005), but, they are also slow-moving and relatively sessile and therefore potentially susceptible to predation (Eubanks & Denno, 2000). Since its introduction as a biocontrol agent in 2011 in New Zealand, no parasitoids have been found attacking *N. ogloblini* populations in the field (Q. Paynter, personal communication, June 2019). This is in agreement with the prediction made by Fowler et al. (2013) that parasitism of *N. ogloblini* should be low in New Zealand due to the low diversity of taxonomically related native Chrysomelidae (and therefore lack of chrysomelid-specialist natural enemies). This follows from the inference by Paynter et al. (2010) that higher numbers of parasitoids are more likely to be recruited onto weed biocontrol species that have native 'ecological analogues' (i.e., a native New Zealand insect that is taxonomically related to the agent and has a similar lifestyle niche and feeds on the target weed) that can act as source of potential parasitoids. Allocation of predation to individual predator species is difficult as predators generally must be 'caught in the act' or their prey items detected using molecular techniques (e.g., Ward & Ramón-Laca, 2013). The native analogue approach is less useful for predicting predation, especially when the predators are generalists (Paynter et al., 2018). Personal observations and reports from biocontrol workers on generalist predators have included spiders, predatory mites, lacewing larvae, skinks and wasps, feeding on larvae and adults of *N. ogloblini* (Q. Paynter, personal communication, June 2019).

Direct evidence for a predator-driven component Allee effect can only be demonstrated if the per capita mortality rate caused by generalist predators is higher at low immature density. Results from the predator exclusion trials indicated that in the presence of generalist predation, immature survival was virtually zero at, and independent of all the tested larval population densities. A controlled experiment where both predator and immature levels are manipulated, would be needed to confirm whether the high level of predation constitutes to a predator-driven Allee effect in populations of *N. ogloblini*.

Generalist predation, irrespective of it causing a component Allee effect or not, could still influence establishment probability of small populations. As an ubiquitous ecological interaction, generalist predation could reduce population densities and interact with other component Allee effects (e.g., mate-finding, reduced foraging efficiency, reduced environmental conditioning or inbreeding) and enhance the extinction risk of small populations.

Any process that reduces pest population size or density (e.g, generalist predation, dispersal, etc.) to levels below the Allee threshold should benefit management actions intend on harnessing the Allee effect to achieve eradication. Eradication can thus potentially be accomplished by reducing population sizes to below the Allee threshold or to levels where the interacting process can drive populations to below the Allee threshold. In systems where generalist predation contributes to the demographic Allee effect, variation in predator pressure could be of particular concern in management efforts to eradicate a newly arrived pest species. Variability not only arises with regards to the pest species, but also with the potential predator. Population densities of generalist predators can be variable in space and time (Bellone et al., 2017; Birkhofer et al., 2008; Larsen et al,. 2018). Cycling predator populations can fluctuate up to an order of magnitude or greater, while weather and temperature can influence encounter rates between predator and prey (Walter, Grayson, et al., 2017). Therefore the contribution of generalist predation to the demographic Allee effect can vary as well, and needs to be taken into consideration with pest management actions (Berec et al., 2007; Liebhold et al., 2016) .

**Table 1:** Various regression models fitted to examine the effect of male density and mean daily maximum temperature on *Neolema ogloblini* mating success.

| Models fitted | AIC |
|---|---|
| **Binomial logistic regression #** | **120.62** |
| Firth's biased reduced penalized-likelihood logit model | 120.86 |
| Logistic regression mixed model – with propagule size as fixed factor | 126.57 |

# best model

**Table 2:** Estimates of a binomial logistic regression model examining the effect of male density and mean daily maximum temperature on *Neolema ogloblini* mating success.

| Variable | Log-odd (β) | SE | Odds ratio ($e^{\beta}$) | Confidence interval | | z | P value |
|---|---|---|---|---|---|---|---|
| | | | | 2.5% | 97.5% | | |
| Intercept | 9.798 | 4.966 | | | | 1.973 | 0.049 |
| Male Density | -2.014 | 0.960 | 0.133 | 0.015 | 0.730 | -2.100 | 0.036 |
| Mean Daily Maximum Temperature | -0.378 | 0.224 | 0.685 | 0.442 | 1.078 | -1.691 | 0.091 |
| Male Density: Mean Daily Maximum Temperature | 0.101 | 0.047 | 1.106 | 1.020 | 1.229 | 2.171 | 0.030 |

**Table 3:** Estimates of a generalized linear model (quasi-binomial error structure) to examine the effect of propagule size released and mean daily maximum temperature on the proportion *Neolema ogloblini* adults recovered after three weeks in the field.

| Variable | Log-odd (β) | SE | Odds ratio ($e^{\beta}$) | Confidence interval |  | t | p value |
|---|---|---|---|---|---|---|---|
|  |  |  |  | 2.5% | 97.5% |  |  |
| Intercept | 8.864 | 0.725 |  |  |  | 12.234 | <0.0001 |
| Mean Daily Maximum Temperature | -0.350 | 0.032 | 0.705 | 0.662 | 0.750 | -10.900 | <0.0001 |
| Propagule Size | -0.014 | 0.002 | 0.986 | 0.982 | 0.990 | -7.752 | <0.0001 |

**Table 4:** Estimates of generalized linear models (quasi-binomial error structure) to examine the effects of population size and generalist predator access on the proportion *Neolema ogloblini* larvae surviving to the pupal stage during experiments completed in 2018 and 2019.

| Variable | Log-odd (β) | SE | Odds ratio ($e^{\beta}$) | Confidence interval |  | t | p value |
|---|---|---|---|---|---|---|---|
|  |  |  |  | 2.5% | 97.5% |  |  |
| **2018** |  |  |  |  |  |  |  |
| Intercept | 0.042 | 0.227 |  |  |  | 0.187 | 0.856 |
| Population Size (Low) | 0.051 | 0.420 | 1.053 | 0.461 | 2.410 | 0.123 | 0.905 |
| Predator Access (Open) | -4.702 | 1.013 | 0.009 | 0.001 | 0.043 | -4.644 | 0.001 |
| **2019** |  |  |  |  |  |  |  |
| Intercept | 0.917 | 0.108 |  |  |  | 8.481 | <0.0001 |
| Population Size (Low) | 0.556 | 0.279 | 1.743 | 1.026 | 3.077 | 1.991 | 0.052 |
| Population Size (Medium) | 0.008 | 0.186 | 1.008 | 0.702 | 1.456 | 0.043 | 0.966 |
| Predator Access (Open) | -5.848 | 0.429 | 0.003 | 0.001 | 0.006 | -13.619 | <0.0001 |

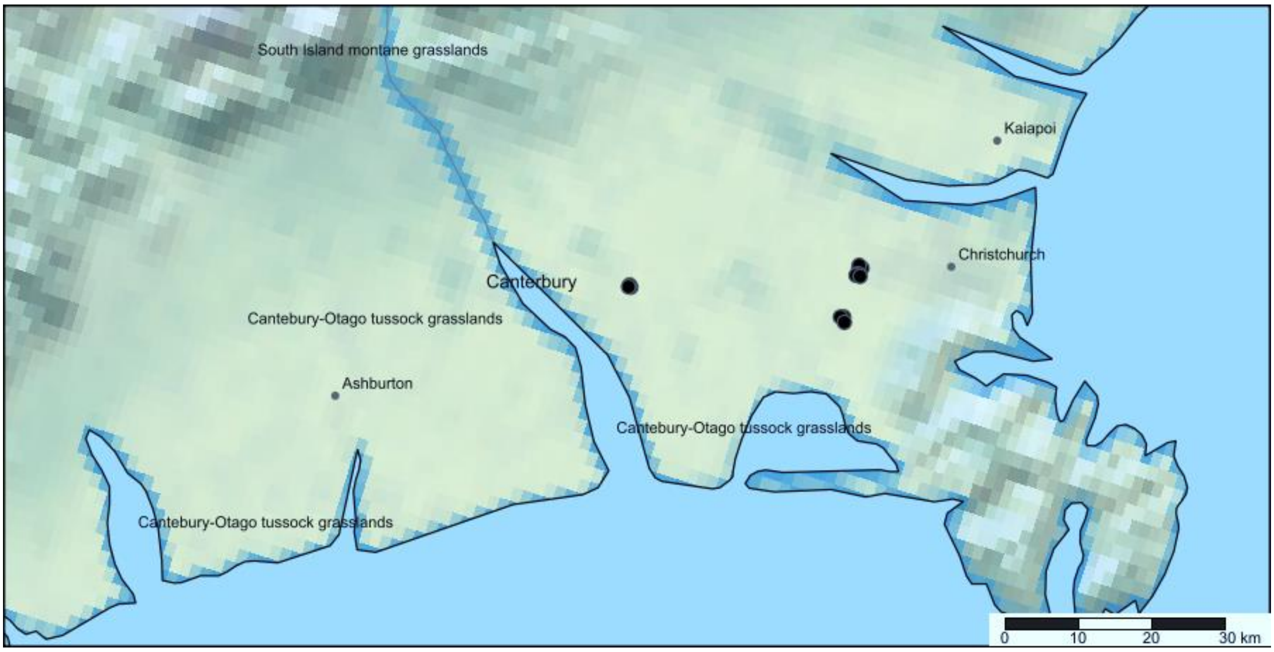

**Figure 1:** Locations of field sites (large black dots) used for mating experiments (Selwyn district in Canterbury, New Zealand). All sites were located in areas classified as the Canterbury-Otago tussock grasslands ecoregion (Department of Conservation, 1987).

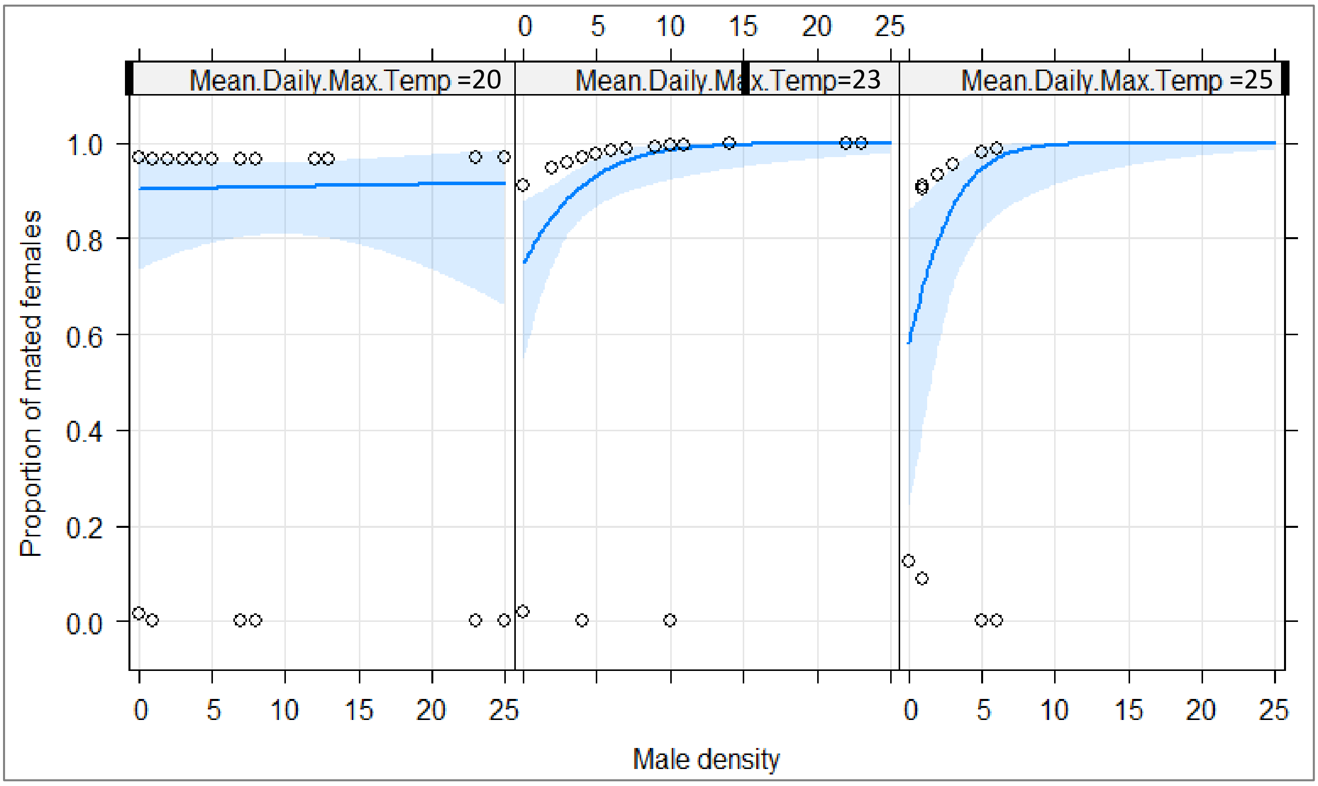

**Figure 2:** Relationship between male density and mean daily maximum temperature (20-25°C) on *Neolema ogloblini* mating success. The solid blue lines are predicted values from binomial logistic regression model. The shaded area is a pointwise confidence band for the fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. The circles are partial residuals points. Temperature increases from left to right.

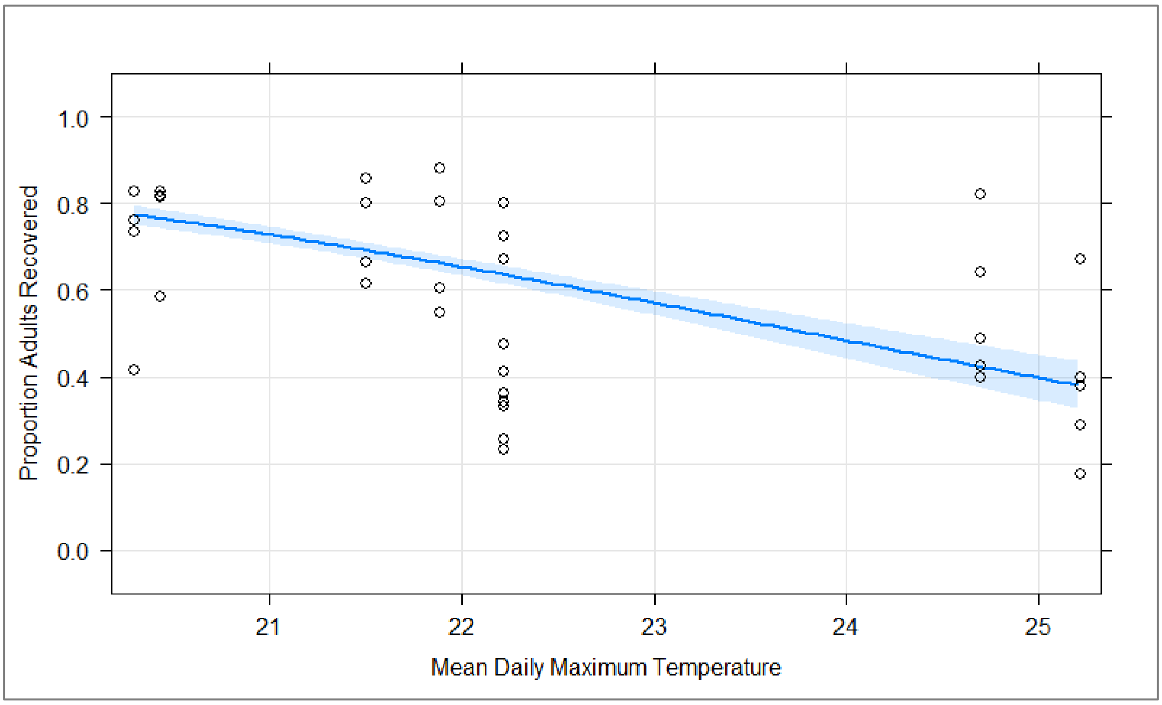

**Figure 3:** Relationship between the mean daily maximum temperature and the proportion of *Neolema ogloblini* adults recovered after three weeks in the field. The solid blue line represents values predicted from a generalized linear regression model (quasi-binomial). The shaded area is a pointwise confidence band for the fitted values, based on standard errors. The circles are partial residuals points.

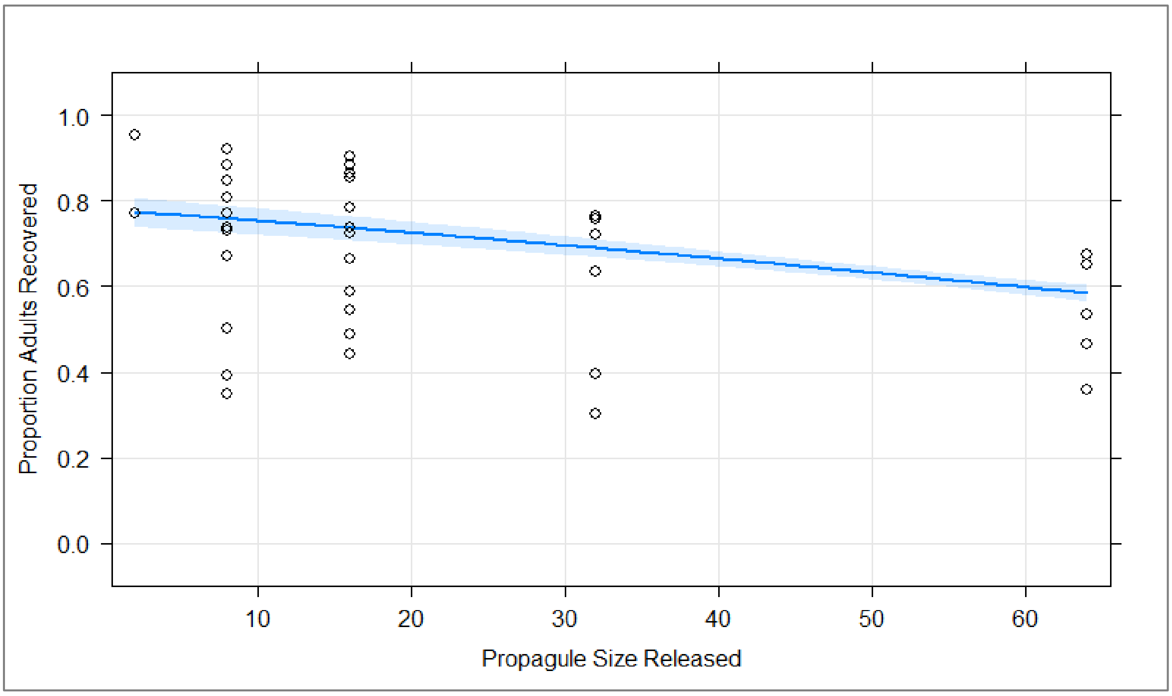

**Figure 4:** Relationship between initial population size and the proportion of *Neolema ogloblini* adults recovered after three weeks in the field. The solid blue line represents values predicted from a generalized linear regression model (quasi-binomial). The shaded area is a pointwise confidence band for the fitted values, based on standard errors. The circles are partial residuals points.

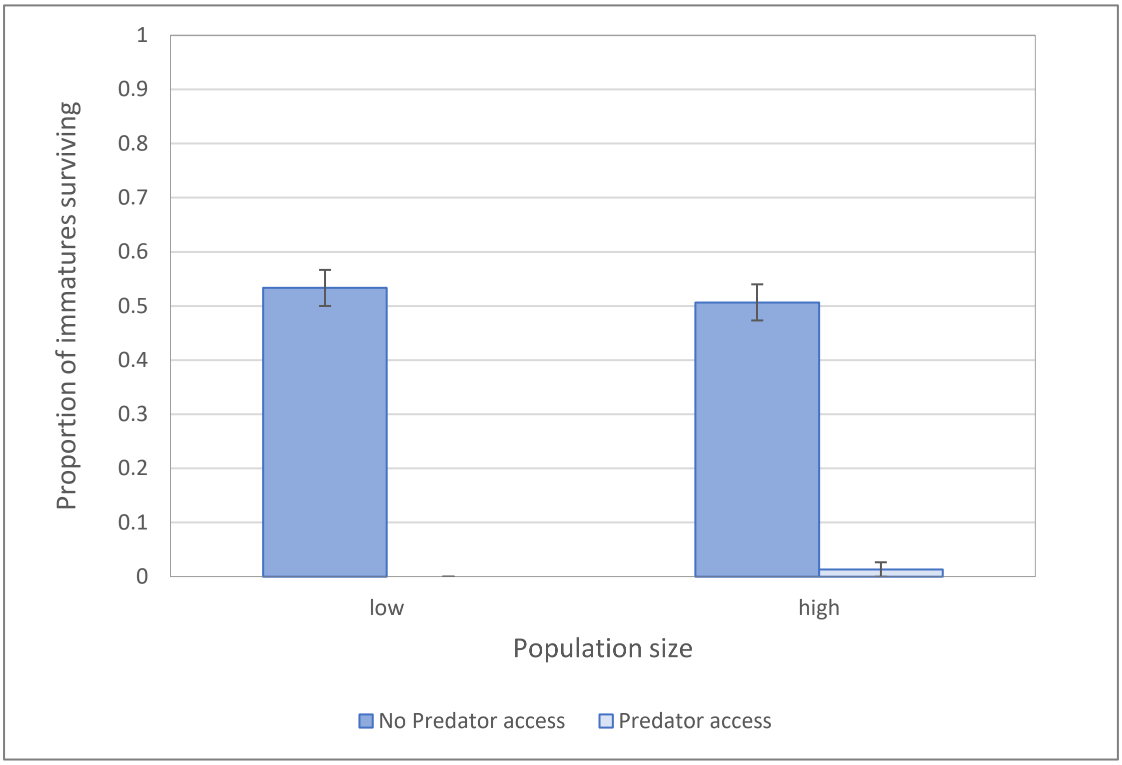

**Figure 5:** The effect of predator exclusion treatment and population size on *Neolema ogloblini* immature survival to the pupal stage in 2018. Population sizes are: Low = 20, High = 50 eggs. Error bars represent SE.

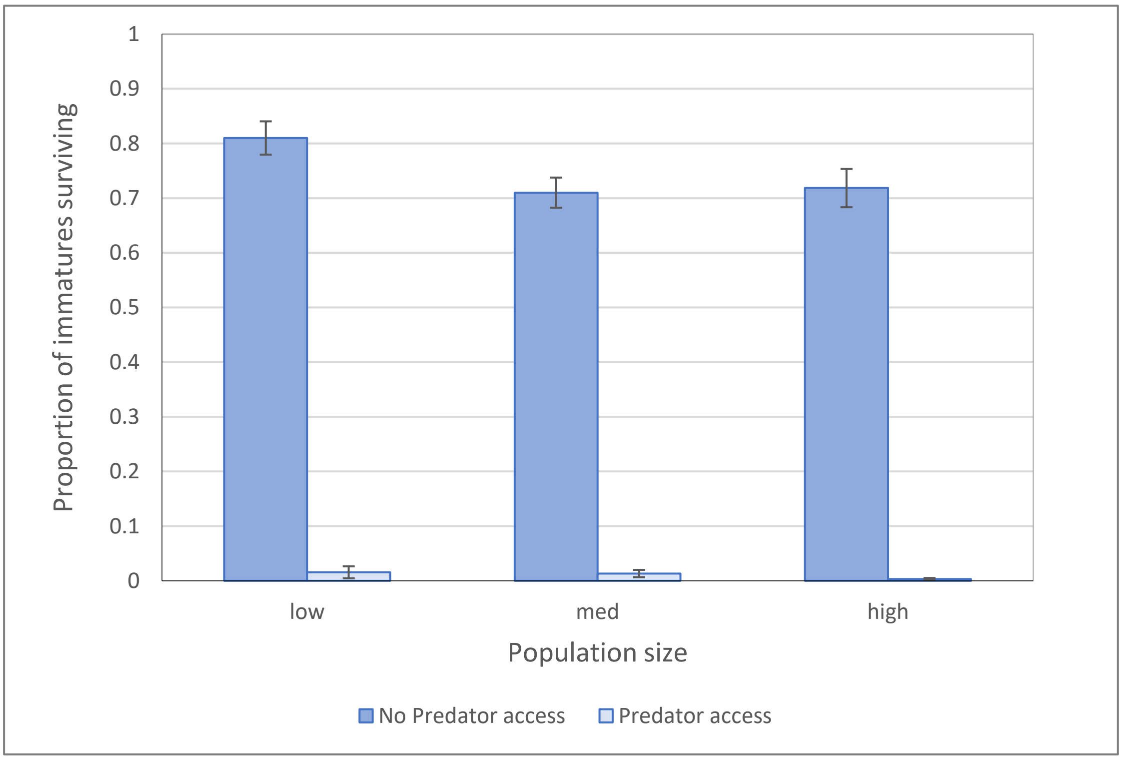

**Figure 6:** The effect of predator exclusion treatment and population size on *Neolema ogloblini* immature survival to the pupal stage in 2019. Population sizes are: Low = 50, Medium = 100, High = 200 eggs. Error bars represent SE.

# Chapter 4 – Role of dispersal cues in host-finding and aggregation in patchy landscapes

## Introduction

Dispersal is an integral part of population dynamics, where the movement of each individual has consequences not only for its own fitness, but also for the persistence and distribution of the population as a whole (Bowler & Benton, 2005). Newly arrived populations of potentially invasive species are usually small, and dispersal behaviour could play an important role in their establishment success. Species with a high dispersal rate could spread too fast, resulting in few individuals in the immediate environment, potentially leading to the inability to find suitable mates, the loss of a predator dilution effect, or to actively defend against predators (Kanarek et al., 2013). These and/or other component Allee effects could scale up to a demographic Allee effect and ultimately lead to the demise local extinction of the population (Stephens & Sutherland, 1999).

The landscape newly arrived species encounter is often a complex and heterogeneous mixture of habitats, which influence dispersal outcomes (Baguette et al., 2013; Goodwin & Fahrig, 2002b). The degree to which the landscape enables or hinders movement among resource patches has been defined as "landscape connectivity" (Taylor et al., 1993) and is both landscape-specific and species-specific (Tischendorf & Fahrig, 2000). For dispersing individuals, landscape connectivity can be influenced by properties of their habitat patches, for example, the quality, size, location of, and distance between patches (Baguette et al., 2013; Goodwin & Fahrig, 2002b). For instance, Sezen et al. (2017) found that adults of the thistle head weevil (*Rhinocyllus conicus*) were more likely to disperse into large patches, while dispersal rate was highest out of small patches.

Landscape connectivity is also influenced by the suitability and permeability of the matrix surrounding host patches (Ewers & Didham, 2006). Jonsen et al. (2001) demonstrated that the probability of immigration for the flea beetle *Aphthona nigriscutis* was much higher when moving through a grass-dominated matrix than a shrub-dominated matrix. Similarly, *Prokelisia crocea*, a planthopper, prefers to disperse through patches of the exotic grass smooth brome (*Bromus inermis*) and avoids dispersal across mudflats (Haynes & Cronin, 2003).

Both dispersal and the Allee effect have the potential to reduce population persistence. Dispersal may reduce population persistence through inherent mortality and deferred costs (Bonte et al., 2012), and the Allee effect through reduced individual fitness (Courchamp et al., 2008). Organisms have therefore evolved a variety of behaviours to assist in host recognition during dispersal, and/or to mitigate or avoid low density situations (Courchamp et al., 2008).

Herbivorous insects use multiple cues to locate suitable habitat, recognize host and non-host plants, assess host quality, aggregate and find mates (Reinecke & Hilker, 2014; Visser, 1986; Wadhams et al., 2006). These could include olfactory cues such as plant volatiles (Reinecke & Hilker, 2014), sex pheromones (Reddy & Guerrero, 2004; Xu & Turlings, 2018), aggregation pheromones (Dickens, 2006; Fernandez & Hilker, 2007), feeding-induced plant volatiles (Poelman & Dicke, 2014; Xu & Turlings, 2018), conspecific faeces (Wan & Harris, 1996), larval secretions (Rostás & Hilker, 2002), and visual cues such as colour, size, morphology and texture (Bruce et al., 2005; Reeves, 2011; Smith & Hough-Goldstein, 2013) and combinations thereof. Perception of these cues may prompt herbivores to cross through unsuitable habitat, effectively increasing matrix permeability.

Understanding how host location, habitat patch choice and dispersal ability drive population distribution in a specific landscape setting is vital for population management and predicting population response to changes in the environment. This is particularly important in conservation and the re-introduction of endangered species, but also the biological control and management of alien species (Catton et al., 2014; Grilli & Fachinetti, 2018; Hudgens et al., 2012).

In this chapter I focussed on the biological control agent, *Neolema ogloblini*, as a model representing a newly arrived species to study how dispersal cues guide host finding and patch choice in a variable landscape. *Neolema ogloblini* is a mobile species and clumped distributions of beetle populations have been observed on its host plant after release.

The study consisted of two separate experiments. The first experiment was undertaken to investigate whether certain factors can influence the aggregative response of *N. ogloblini* on its host, *Tradescantia mundula*. Specifically, I sought to determine whether the dispersal and resultant density were affected by conspecifics already present on the plants (alone or coupled with beetle-feeding damage), and if the sex of the conspecifics already present on the plants affected this density.

In the second experiment, I investigated how the aggregative response may prompt beetles to cross through unsuitable habitat, effectively increasing matrix permeability. Specifically, I examined the effects of patch characteristics (presence vs. absence of conspecifics) and release location (matrix type and distance to target patch) on colonization of *T. mundula.*

## Materials and Methods

### *Experiment 1: Cues affecting the aggregative response*

An open-field experiment was performed (4 to 7 March 2019) to determine how dispersal to host plants, and resultant density on host plants, were influenced when adults were given a choice between the following five different host plant and conspecifics combinations (cue treatments):

i) a plant with non-feeding adults of both sexes together (the inference being that attraction is based on pheromone released by males or females without feeding);

ii) a plant with feeding adults of both sexes together (attraction based on a synergistic relationship between pheromone released (by males or females) and feeding-induced plant volatiles);

iii) a plant with feeding males only (attraction based on a synergistic relationship between male aggregation pheromone and feeding-induced plant volatiles);

iv) a plant with feeding females only (attraction based on a synergistic relationship between female sex pheromone and feeding-induced plant volatiles); and

v) a plant without beetles acting as control (attraction based on undamaged plant volatiles).

In all five cue treatments a single host plant, 30 cm in diameter, was used. To create the host plant/conspecifics combinations (cue treatments), groups of either three adult pairs or six beetles of the appropriate sex, were collected from the general population 12h prior to the start of the experiment. For each plant with feeding adults (treatments ii – iv), the groups of adults were placed in mesh bags that were tied over a branch of the appropriate host plant, allowing the beetles to feed and produce feeding-induced plant volatiles. For these treatments the beetles were allowed to feed throughout the duration of the experiment. For each plant with non-feeding adults (treatment i), the mesh bags were placed in-between branches of the host plants and the adults therefore not able to feed. An empty bag was tied to the control plants.

The five treatment plants were arranged in a circle, 5 m from a central point (plants were *ca*. 2 m apart) in the grounds of the Lincoln Landcare Research facility. A total of 100 beetles of mixed sexes were randomly collected from the general population and placed into containers (200 ml) with a few *T. mundula* leaves. The containers were chilled for approximately 5 min at 5 °C. The beetles were then released in the middle of the circle of plants by leaving the containers open on the ground. Beetles were recaptured on each plant at 24 h and 48 h after release, and the number counted and sexed. It was assumed that the density of beetles on plants after 24 h and 48 h related to the relative attractiveness of that plant. Ten replicates of each treatment were completed.

### *Experiment 2: Dispersal cues and permeability of matrix*

An open-field mark-release-recapture experiment was performed to determine how rates of colonization of host patches by *N. ogloblini* adults are influenced by:

i) the distance of the target patch from the point of release,

ii) the presence of conspecifics in the target patch, and

iii) the matrix through which the dispersers will have to navigate to reach the target patch.

As *T. mundula* is a forest edge colonizer (Pellegrini, 2018), matrix types consisting of forest, open grass, and forest edge were chosen. These matrix types represent the most common and contrasting habitats *N. ogloblini* beetles will have to navigate to find potential host patches.

A target-centred release and recapture method (Grevstad & Herzig, 1997) was used to study the movement of *N. ogloblini* through the different matrix types. In this method, the beetles were released at various distances from a single central target patch, from which they were recovered a week later. This contrasts with the more common release-centred approach where organisms are released at one location and recovered at sampling points or traps at various distances from that location (Dávalos & Blossey, 2011; Grevstad & Herzig, 1997; Hough-Goldstein et al., 2013). The target-centred method avoids the influence or dilution by traps or collection points on beetles as they disperse along the way. Overall, this method is appropriate for studying interpatch dispersal (as opposed to dispersal along more continuous habitat) and for determining the probabilities of reaching a particular patch from given distances (Grevstad & Herzig, 1997).

The layout of the experiment comprised two sites for each replicate (Illustration 1). Each site had a single, central target host patch which was created from potted *T. mundula* plants (leaf-cover area was 1.0 m$^2$). One site had conspecifics present, where 30 beetles of mixed sexes were enclosed in a mesh bag tied over a branch in the target host patch and thus able to feed. The other site had no conspecifics present and only an empty bag was tied to a branch. The sites were separated by approximately eight kilometres. To expose dispersing beetles to different matrix types, each site consisted of a forested area (mixture of deciduous and coniferous tree species) adjacent to an open grass area. During spring and prior to the experiments, the grass areas was kept short with mowing. During the experiment (13 February to 4 April 2019) no mowing took place as growth of grass was slowed by drier summer weather. The target host patch was placed just inside the edge of the forested area. Release points were marked at two distances (30 m and 60 m) along six transect lines radiating from the target patch; two lines into the forest, two along the forest margin, and two into the grass area. There were twelve release points at each site.

The day before release, beetles were randomly collected from the general population. To differentiate between beetles from the different release points, adults were marked with six different coloured florescent powders (represented by the coloured dots in Illustration 1). The marked beetles were placed in containers with ample leaf material to allow them to settle, groom and feed. On the morning of the release, the beetles were aspirated into small 200ml containers (50 beetles to a container) with fresh *T. mundula* leaves and kept chilled (10 °C) until field release. Between 10 and 12 am, 50 beetles were released at each of the marked release points, by leaving the containers open on the ground. Keeping the beetles chilled until release and the presence of fed-on *T. mundula* leaves prevented the initial dispersal frenzy. After five days, the potted plants from each target patch of the two sites were bagged in sealed plastic bags and brought back to the laboratory. They were carefully searched, and the number of beetles counted, collected and their sex and colour markings verified. Four replicates were completed sequentially by using the same sites. A period of seven days was allowed between replicates to avoid interference between replicates.

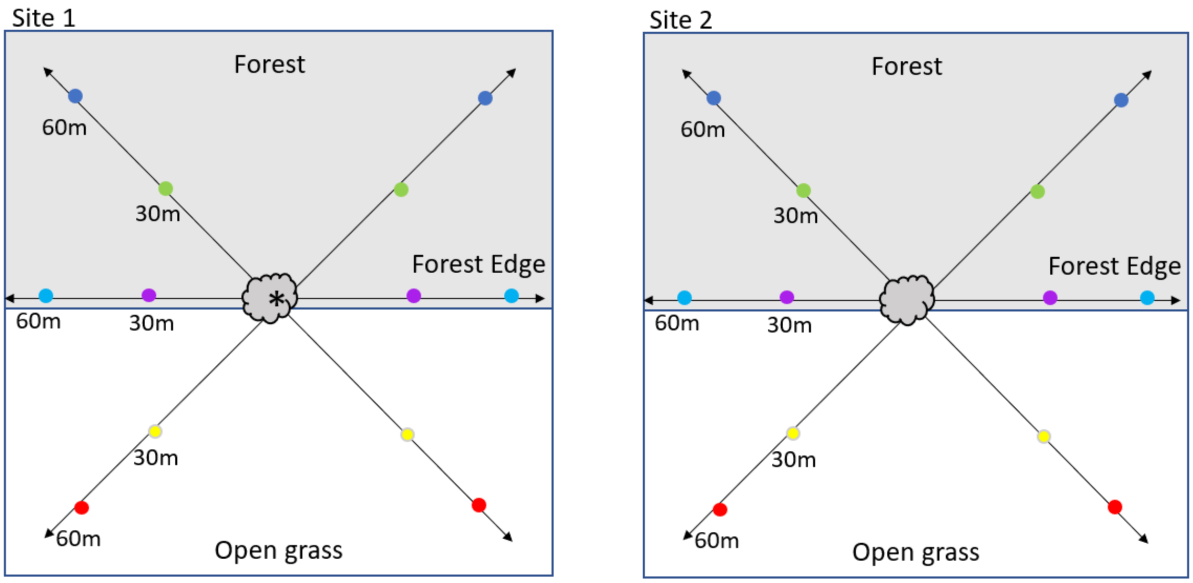

**Illustration 1:** Schematic representation of the layout of the target-centred, mark-release-recapture experiment. Two sites were used per replicate: site 1 consisted of a target host patch with conspecifics present on the host plants (marked with *), and site 2 consisted of a target host patch where conspecifics were absent.

## Statistical Analysis

*Experiment 1: Cues affecting the aggregative response*

Recapture data were analyzed using a generalized linear model (GLM) with quasi-binomial error distribution to compensate for overdispersion in the data. The proportion of adults recaptured was included as the response variable, while the sex of the recaptured adults and cue treatment (feeding females, feeding males, feeding adult pair, non-feeding adult pair, and control), as well as their interactions were included as predictor variables. The maximal model was simplified to the minimal adequate model by removing non-significant interactions until no further improvement in fit (measured using Likelihood Ratios) was observed. The R package “multcomp” was used to perform post-hoc analysis on the statistical differences between the proportions recaptured from different cue plant types (Hothorn et al., 2008). Graphs were drawn using the R package “effects” (Fox & Hong, 2009; Fox & Weisberg, 2019).

*Experiment 2: Dispersal cues and permeability of matrix*

Recapture data were analyzed using a generalized linear mixed effects model (GLMM) with binomial error distribution with proportion recaptured as the response variable. Matrix type (forest, forest edge or open grass), conspecific adult presence (present or not), distance released from target (30 m or 60 m - treated as categorical variable), gender (male or female), and their interactions were included as fixed predictors. As the experiment layout had a split-plot design with separate sites for target patches with either conspecifics present or not, site was included as a random effect. The model was fitted by maximum likelihood using the Laplace approximation in the R package “lme4” (Bates et al., 2015). The optimizer BOBYQA and a maximum of 100,000 function evaluations was used to aid in model convergence (Bates et al., 2015). No overdispersion was detected in the model. The maximal model was simplified to the minimal adequate model by removing non-significant interactions until no further improvement in fit (measured using Likelihood Ratios and lowest AIC) was observed. The R package “DHARMa” was used to evaluate model fit (Hartig, 2018). The R package “multcomp” was used to perform post-hoc analysis on the statistical differences between the proportions recaptured from different matrix types (Hothorn et al., 2008). Graphs were drawn using the R package “effects” (Fox & Hong, 2009; Fox & Weisberg, 2019).

## Results

*Experiment 1: Cues affecting the aggregative response*

The proportion of adults recovered at end of the experiments depended significantly on cue treatment ($F_{(4, 95)}$=12.677; p=<0.001). A higher proportion of adults were recovered on plants where conspecifics were present and able to feed (plants with cue treatments: feeding females, feeding males and feeding pairs), than on plants with no adults (control) or on plants where the adults were not able to feed (Table 1, Fig. 1). Post-hoc comparisons indicated that adults did not differentiate between plants with feeding males, feeding females, or feeding pairs, as there was no significant difference between the proportions of adults recovered from these plants (Table 2, Fig. 1). Proportions of adults found on the less preferred plants (control and non-feeding pair treatment) did not significantly differ (Table 2, Fig. 1).

Including sex of the recovered beetles as an additional explanatory variable did not improve model fit ($F_{(1)}$=0.757; p=0.387), indicating the proportions of males to females recovered on plants of the different treatments did not differ significantly. Thus, males and females responded similarly to the cues from the different treatment plants. There was no significant interaction between cue treatment and sex of recovered beetles ($F_{(4)}$=0.170; p=0.953).

*Experiment 2: Dispersal cues and permeability of matrix*

The number of beetles recaptured was low; only 278 beetles (5.79%) were recovered on the target patches out of the 4,800 released over the whole of the experiment. Recapture totals did not substantially vary among the four replicates (1.06-1.92%). Habitat matrix type, distance from target patch, the presence of conspecifics and gender all significantly influenced the proportions of adults recruited onto the target patch (Table 3). There were no significant interactions between the fixed predictor variables. Post-hoc pairwise analysis indicated that dispersal was more successful through an open grass matrix, than along a forest edge, or through a forest matrix (Fig. 2, Table 4). Dispersal rates along the forest edge was the lowest (Fig. 2, Table 4). The proportion of adults recovered decreased as distance from the release point increased (Fig. 3, Table 3). A higher proportion of adults was recovered on target patches when conspecifics were present than when they were absent (Fig. 4, Table 3). More males than females were recovered on the target patch (Fig. 5, Table 3).

## Discussion

*Cues affecting the aggregative response*

Results of the first experiment indicated that adults of *N. ogloblini* were strongly attracted to plants that were occupied by actively-feeding conspecific beetles, with significantly more attraction than to unoccupied plants or to adults that were not feeding. Three potential scenarios explain these results: an aggregation (or sex) pheromone is present but is only released while feeding, or the aggregation (or sex) pheromone is only active synergistically with feeding-induced plant volatiles, or there is no pheromone involved and the attraction medium is feeding-induced plant volatiles only.

Aggregation pheromones have been identified and described for several chrysomelid subfamilies (e.g., Alticinae, Chrysomelinae, Criocerinae, and Galerucinae), however, in most cases these compounds only become powerful attractants in the presence of feeding-induced plant volatiles (Bartelt et al., 2006; Cossé et al., 2005; Dickens, 2006; Rao et al., 2003; Soroka et al., 2005). In these studies, the aggregation pheromones are all male-produced compounds and result in aggregations of both males and females on patches of their host plant. For example, both males and females of *Oulema melanopus*, a leaf beetle in the same subfamily as *N. ogloblini*, are strongly attracted to a male-secreted aggregation pheromone resulting in temporary aggregations on their host plant (Rao et al., 2003).

In the case of *N. ogloblini*, adults were equally attracted to plants with either feeding pairs, feeding females or feeding males, therefore, the probability of the aggregation medium being a male-produced aggregation pheromone is low. If an aggregation pheromone is involved, both sexes are producing it. A literature survey could find no known species in the Chrysomelidae where females and males both produce an aggregation pheromone.

Sex pheromones for long-distance communication have been identified and described for only a few species of Chrysomelidae, all belonging to the genus *Diabrotica* (Guss et al., 1983; Krysan, McDonald, & Tumlinson, 1989). Some evidence suggests that females of *Longitarsus jacobaeae* emit a sex pheromone, but the chemical compound has not been identified (Zhang & McEvoy, 1994). These pheromones are emitted by female beetles and attracts only males (Guss et al., 1983). Since females and males of *N. ogloblini* did not differ in their reaction to the different plant cue types, and the proportions recovered from plants with feeding males and feeding females did not differ significantly, the probability of the aggregation medium being a female-produced sex pheromone is low. It could be argued that as soon as a male reached any of the plants, it would feed and could start emitting an aggregation pheromone, and consequently attraction to any of the other cue plant types as well. In this case it would still be expected that the feeding-male plants would attract the highest proportion of adults as this plant would initially be the most conspicuous of the plant cue types.

Finally, the results suggest that no pheromone is produced, and the aggregation medium is mainly feeding-induced plant volatiles. To confirm this conclusion, additional research in the electrophysiological response of *N. ogloblini* adults to compounds and volatiles emitted in the different host plant and conspecific feeding combinations is needed. Nonetheless, feeding-induced plant volatiles would be an important dispersal cue used by *N. ogloblini* to find patches of its host plant, to facilitate aggregation of individuals on host patches and thereby contributing to establishment success and spread of the beetle.

The potential reasons for aggregation by *N. ogloblini* adults are multiple. Firstly, the beetles may use cues from conspecifics in order to help them find their host plants and/or habitat patches of proven quality (Grevstad & Herzig, 1997; Stamps, 2001). For example, Miller et al. (2013) found that females of *Narnia femorata*, a cactus-feeding coreid, laid a higher number of eggs on a higher quality resource than a lower quality resource in the absence of conspecifics. In the presence of conspecifics though, an equal amount of eggs was laid on both high and low quality resources (Miller et al., 2013).

Secondly, the beetles may aggregate to find mates. Indeed, aggregation is thought to be an adaptation to mitigate or avoid a mate-finding Allee effect (Gascoigne et al., 2009). Adults of *N. ogloblini* mate repeatedly throughout their adult lifetime and multiple mating could potentially increase female fecundity. Laboratory studies found the fecundity of *N. ogloblini* females in the presence of males was 63% greater than females that were exposed to males for only the first 10 days of a 74-day period (HE Williams, unpublished results). The same trend was found for *G. calmariensis* where fecundity of multiply-mated females in a laboratory setting was 57% greater than that of females mated only once (Grevstad & Herzig, 1997). Aggregation thus ensures not only initial mate-finding after eclosion, but also opportunities to maintain fertility levels of females.

Thirdly, aggregation of beetles may enhance survival through predator dilution (the reduced predation risk to individual group members due to the presence of alternative targets), thereby ameliorating the contribution of generalist predation to the Allee effect (Courchamp et al., 2008).

### *Dispersal cues and permeability of matrix*

Results of the second experiment supported the findings in experiment one of the importance of conspecific feeding-induced plant volatiles as dispersal cue for *N. ogloblini* adults. It was easier for dispersing adults to recognize the target patches when feeding conspecifics were present on them; with a higher proportion of adults recovered than in the absence of conspecifics.

Results clearly indicate that matrix type had as strong effect on the colonization of *T. mundula* patches by *N. ogloblini*. The proportion of *N. ogloblini* adults reaching the target patch was the highest when dispersing over open grass areas, with dispersal more successful through open grass than either through forest or along the forest edge. In terms of providing additional resources, all three matrix types are of low quality for *N. ogloblini*, since the beetle is highly specific to host plant species in the genus *Tradescantia* (Fowler et al., 2013). Therefore, the variance in dispersal success through the different matrix types is likely related to the structural complexity in the matrix type (Bowler & Benton, 2005). In this study, the open grass areas were the simplest in terms of structural complexity, followed by forest floors that supported only sparse populations of low-growing plants, and finally, forest edges that were structurally the most complex. Along the forest edge, the combination of longer grass, the presence of a variety of pioneer-type plant species that were common, and low-hanging overhead branches of larger trees, all contributed to the complexity that dispersing adult beetles had to navigate. Increased permeability of habitats with reduced structural complexity has been reported for several herbivorous insect species (Dávalos & Blossey, 2011; Jonsen et al., 2001; Ricketts, 2001). Goodwin and Fahrig (2002a) found that adults of the goldenrod beetle (*Trirhabda borealis*) moved slower in a structurally complex-low quality matrix which limited the beetle's overall movement through unsuitable habitat.

Hough-Goldstein et al. (2013) found *Rhinoncomimus latipes*, a weevil species, preferentially colonized edge habitat during field trials. Their research suggested the weevil may have evolved a host-plant search strategy concentrated on edge habitats, as its host *Persicaria perfoliate* occurs primarily in riparian areas and along the edges of forests. Since *Tradescantia* is similarly a forest edge colonizer in forest remnants, one would expect *N. ogloblini* to likewise be adept in dispersing along forest edges. In my experiment though, dispersal rates were the lowest along the forest edge. This finding might be explained by the fact that in its native area, *Tradescantia* patches are often small (≤0.25 m$^2$) and ephemeral and has been found to virtually disappear from sites where it had been abundant in previous years (Fowler et al., 2013). The beetle might therefore have evolved a host-plant search strategy very much dependent on patchy distribution of its host rather than along a continuous axis such as riparian areas and forest edges.

As expected, the proportion of adults recovered decreased as distance from the release point increased, due to higher mortality associated with longer distances the beetles had to travel to the target patch (Bowler & Benton, 2005). More males than females were recovered on the target patch. Although the sex-ratio of the general population was not known at the time the experiment was taken, the sex-ratio of adults from a study on larval development indicated a population with 57% females (N=429). If this was the case with the population used for experiment two, the higher recovery rate of males 61% (N=278) was significantly different from a 50:50 sex ratio ($p<0.001$), suggesting that males are potentially more sensitive towards cues.

The results of the second experiment suggest that in the absence of feeding-induced plant volatiles, volatiles or visual cues from undamaged host plants could potentially play a role as host-finding cue, but in the presence of feeding-induced plant volatiles, these cues take on a lower rank. Alternatively, dispersal by adults could initially be random until some individuals in the population encounter a suitable host patch and their feeding subsequently induce aggregation by others.

In conclusion, the establishment success and spread of a newly arrived potentially invasive species will critically depend on the ability of individuals to find suitable patches of its host while dispersing through unsuitable habitat. In the case of *N. ogloblini*, dispersal of the beetle will be more successful onto host patches imbedded in structurally simple landscapes than more complex landscapes. Additionally, feeding-induced plant volatiles increase the apparency of host patches and facilitates the aggregation of the beetles on their host plant. Aggregation ensures amelioration of the Allee effect, by providing opportunities for mating, reducing individual's risk to predation and satisfying predator pressure.

**Table 1:** Generalized linear model (GLM) (quasibinomial error distribution) examining the effect of cue treatment (plants with either: feeding females, feeding males , feeding adult pairs, non-feeding adult pairs, and control plant) on the proportion of *Neolema ogloblini* adults recruited onto potted plants of its host, *Tradescantia mundula* **.**

| **Cue Treatment** | **Log-odd (β)** | **SE** | **Odds ratio $e^{(\beta)}$** | **Confidence interval** | | **t** | **p value** |
|---|---|---|---|---|---|---|---|
| | | | | 2.5% | 97.5% | | |
| (Intercept) Control | -3.623 | 0.373 | 0.027 | 0.013 | 0.055 | -9.715 | <0.001 |
| Non-feeding pairs | -0.195 | 0.554 | 0.823 | 0.279 | 2.432 | -0.352 | 0.725 |
| Feeding Females | 1.783 | 0.411 | 5.947 | 2.661 | 13.290 | 4.338 | <0.001 |
| Feeding Males | 1.682 | 0.414 | 5.376 | 2.393 | 12.080 | 4.065 | <0.001 |
| Feeding pairs | 1.074 | 0.438 | 2.950 | 1.254 | 6.940 | 2.455 | 0.015 |

**Table 2:** Post-hoc pairwise analysis (Tukey) on *Neolema ogloblini* adult attraction to plants with different cue treatments.

| **Cue treatment comparisons** | **Log-odd (β)** | **SE** | **Confidence interval** | | **z** | **p value** |
|---|---|---|---|---|---|---|
| | | | **2.5%** | **97.5%** | | |
| Feeding Females - Control | 1.783 | 0.411 | 0.674 | 2.892 | 4.338 | <0.001 |
| Feeding Males - Control | 1.682 | 0.414 | 0.565 | 2.799 | 4.065 | <0.001 |
| Feeding pairs - Control | 1.074 | 0.438 | -0.107 | 2.255 | 2.455 | 0.094 |
| Non-feeding pairs - Control | -0.195 | 0.554 | -1.689 | 1.299 | -0.352 | 0.997 |
| Feeding Males - Feeding Females | -0.101 | 0.249 | -0.772 | 0.570 | -0.406 | 0.994 |
| Feeding pairs - Feeding Females | -0.709 | 0.287 | -1.482 | 0.065 | -2.472 | 0.090 |
| Non-feeding pairs - Feeding Females | -1.978 | 0.444 | -3.176 | -0.779 | -4.453 | <0.001 |
| Feeding pairs - Feeding Males | -0.608 | 0.291 | -1.392 | 0.177 | -2.090 | 0.212 |
| Non-feeding pairs - Feeding Males | -1.877 | 0.447 | -3.082 | -0.671 | -4.201 | <0.001 |
| Non-feeding pairs - Feeding pairs | -1.269 | 0.469 | -2.534 | -0.004 | -2.707 | 0.049 |

**Table 3:** Generalized linear mixed effects model (GLMM) (Binomial error distribution) examining the effect of matrix (forest vs open grassland vs forest edge), distance released from target patch, the presence of conspecific (present vs absent) on the target patch, and gender on the proportion adults of *Neolema ogloblini* recruited onto patches of its host plant, *Tradescantia mundula*.

| **Variable** | **Log-odd ($\beta$)** | **SE** | **Odds ratio $e^{(\beta)}$** | **z** | **p value** |
|---|---|---|---|---|---|
| (Intercept) | -7.066 | 0.264 | 0.001 | -26.765 | <0.001 |
| Matrix (Forest) | 0.625 | 0.194 | 1.868 | 3.224 | 0.001 |
| Matrix (Open Grass) | 0.990 | 0.180 | 2.691 | 5.488 | <0.001 |
| Distance (60 m) | -0.558 | 0.134 | 0.572 | -4.169 | <0.001 |
| Conspecifics (Present) | 1.258 | 0.227 | 3.517 | 5.544 | <0.001 |
| Gender (Male) | 0.422 | 0.124 | 1.524 | 3.411 | 0.001 |

**Table 4:** Post-hoc pairwise analysis (Tukey) on *Neolema ogloblini* adult dispersal rate through different matrix types.

| **Variable comparisons** | **Log-odd ($\beta$)** | **SE** | **Odds ratio $e^{(\beta)}$** | **z** | **p value** |
|---|---|---|---|---|---|
| Forest – Edge | 0.625 | 0.194 | 1.868 | 3.224 | 0.004 |
| Open grass – Edge | 0.990 | 0.180 | 2.690 | 5.488 | <0.001 |
| Open grass – Forest | 0.365 | 0.144 | 1.440 | 2.527 | 0.030 |

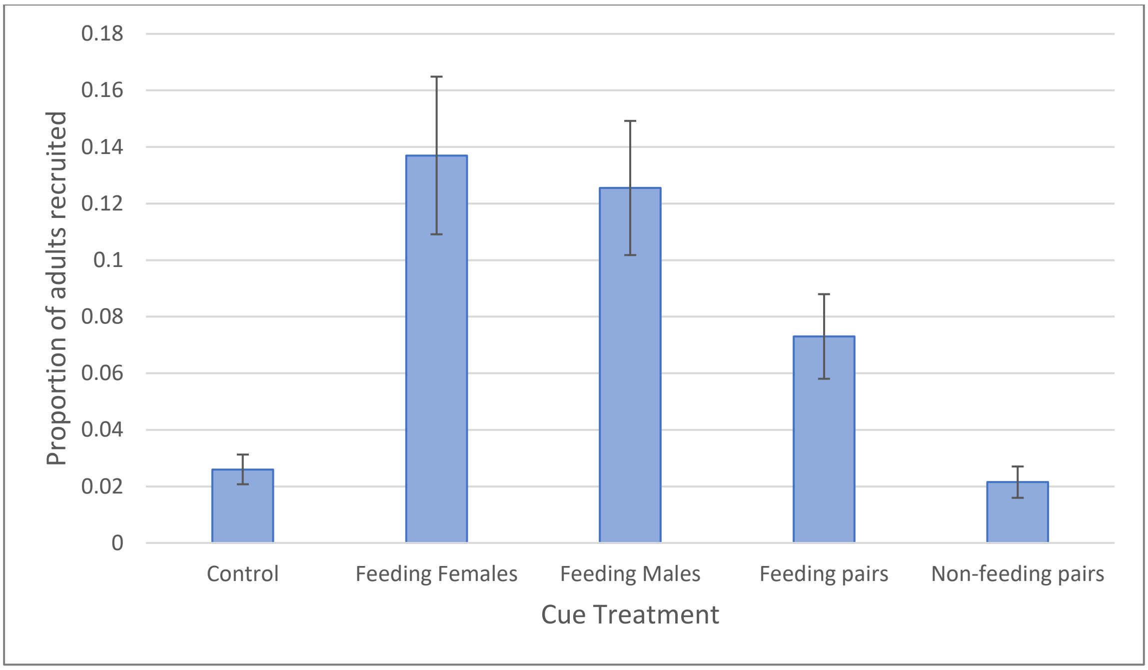

**Figure 1:** Mean proportion adults recruited onto plants of different cue treatments. The cue treatments consisted of plants with either no adults, feeding females, feeding males, feeding adult pairs or non-feeding adult pairs. The error bars indicate standard errors.

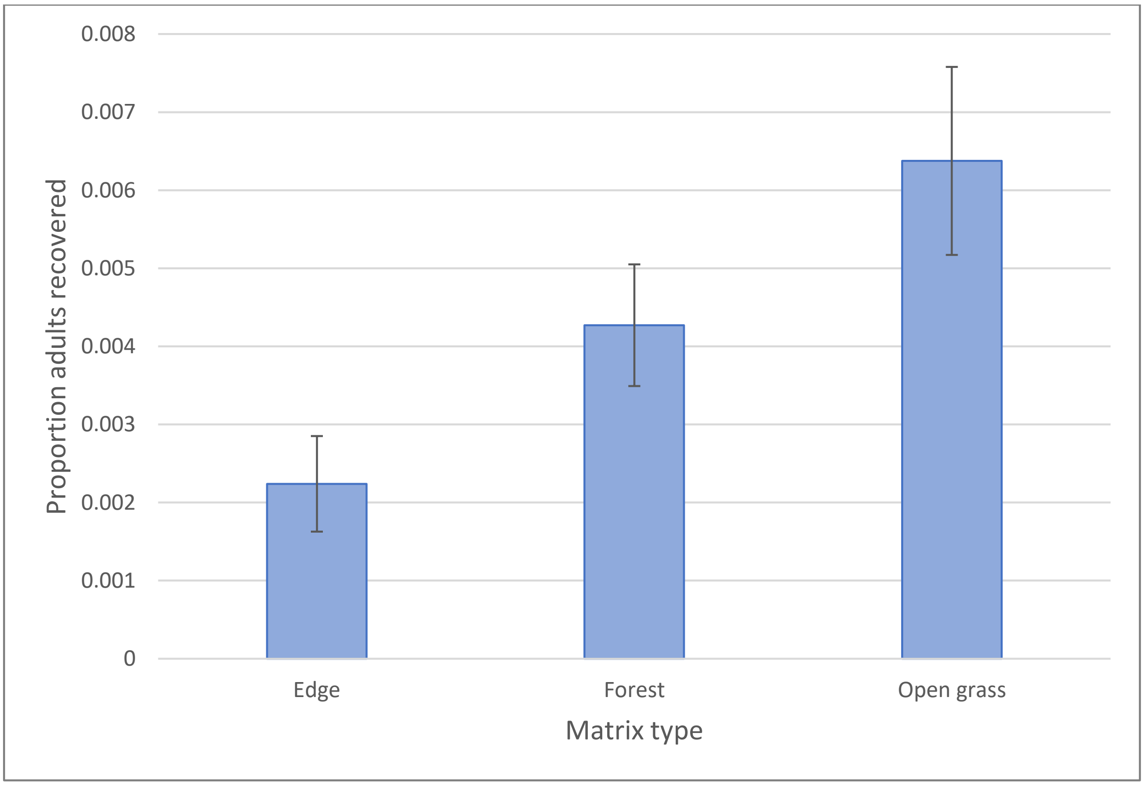

**Figure 2:** Influence of matrix type on the mean proportion of *Neolema ogloblini* adults recovered on target patches of their host plant, *Tradescantia mundula*. The error bars indicate standard errors.

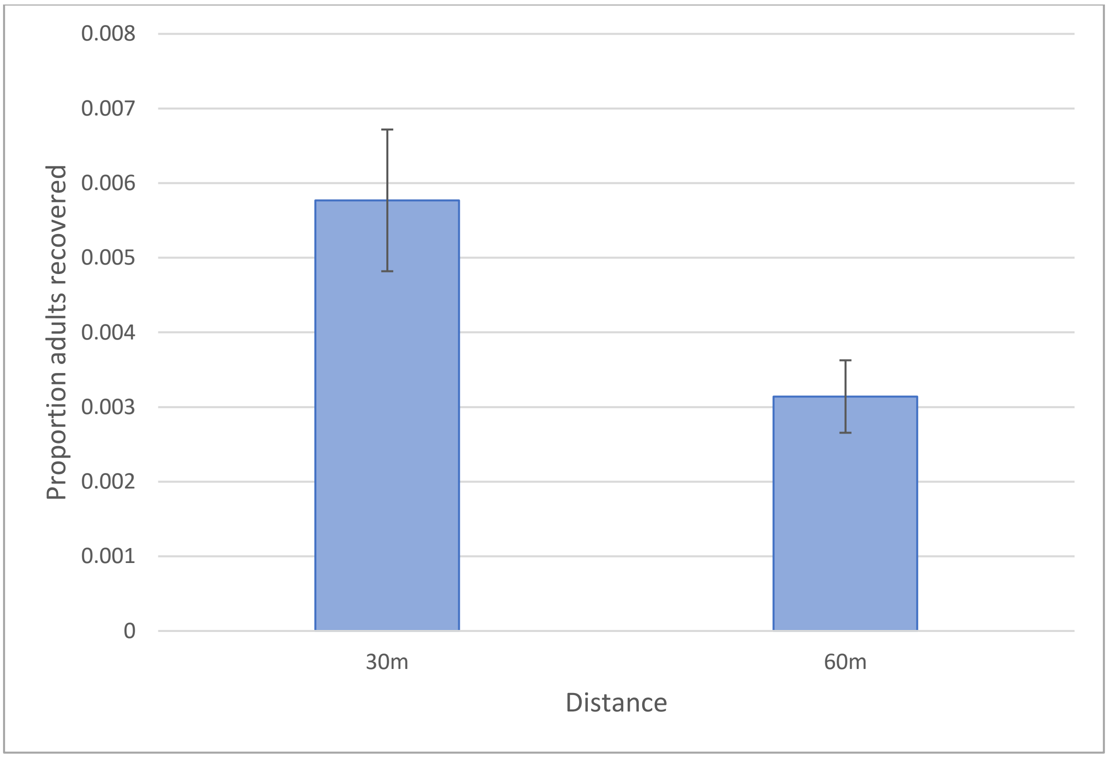

**Figure 3:** Influence of distance on the mean proportion of *Neolema ogloblini* adults recovered on target patches of their host plant, *Tradescantia mundula*. The error bars indicate standard errors.

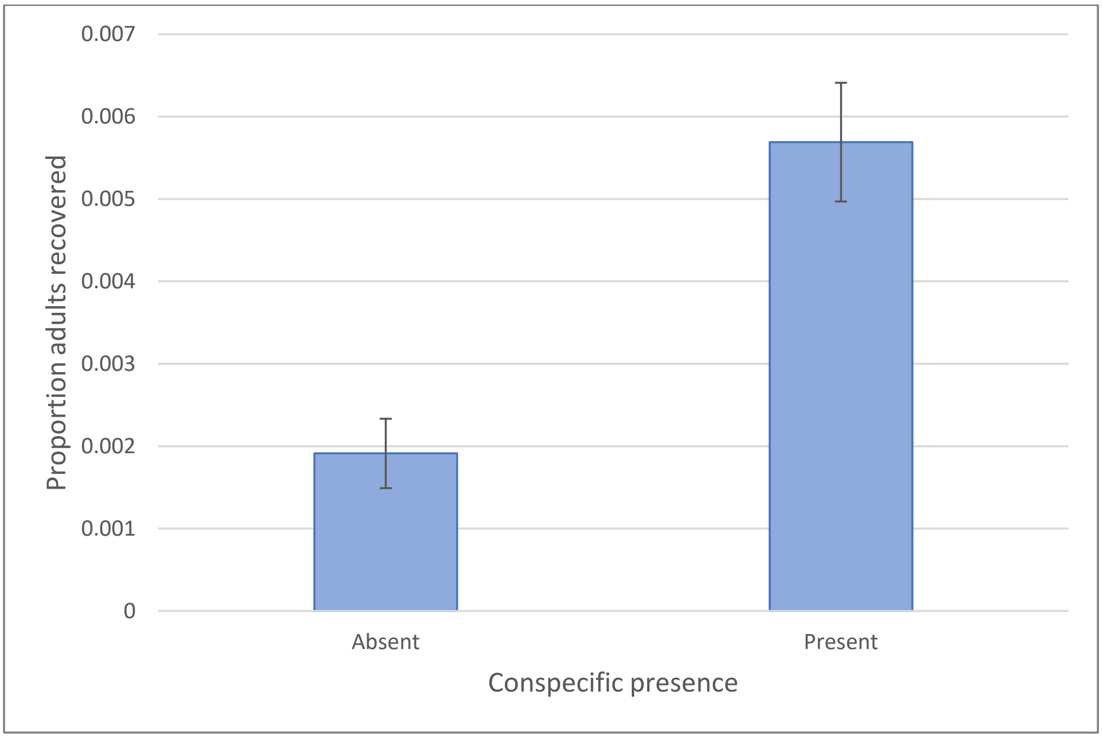

**Figure 4:** Influence of the presence of conspecifics on the target patch on the mean proportion of *Neolema ogloblini* adults recovered on target patches of their host plant, *Tradescantia mundula*. The error bars indicate standard errors.

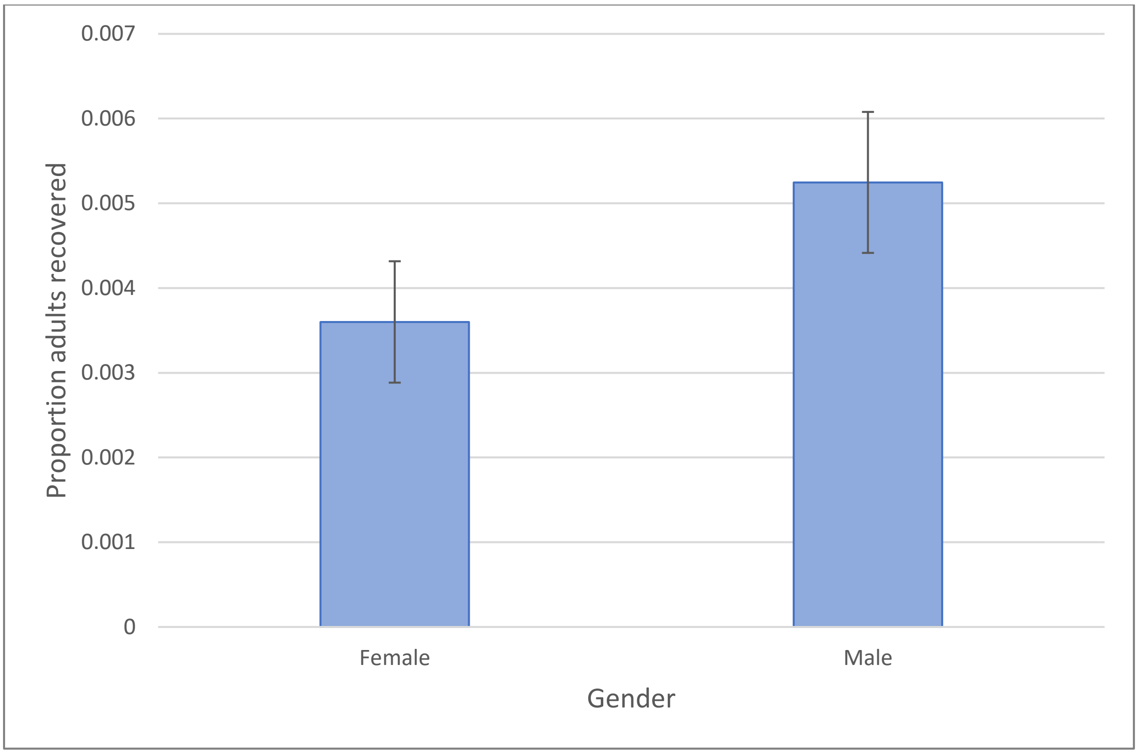

**Figure 5:** Influence of gender on the proportion of *Neolema ogloblini* adults recovered on target patches of their host plant, *Tradescantia mundula*. The error bars indicate standard errors.

# Chapter 5 – The impact of host removal on population persistence in a patchy landscape

## Introduction

With the continual arrival of non-native species in new areas across the world, eradication is an increasingly important tool for protection of biological diversity and for averting future economic impacts of invasive species (Brockerhoff et al., 2010; Genovesi, 2007; Liebhold et al., 2016; Simberloff, 2009). While preventing new invasions is generally considered the most effective way for mitigating impacts, when prevention has failed, the next level of exclusion is through detection and eradication (Brockerhoff et al., 2010; Liebhold & Kean, 2019).

The majority of invading populations initially arriving in new areas fail to establish, in part due to habitat unsuitability (e.g., lack of host plants, unsuitable climate, etc.), but also because incipient populations arriving in low numbers are subject to extinction (Liebhold & Tobin, 2008). Two of the main causes of extinction in low-density populations are stochasticity (random environmental and demographic influences) and Allee effects (Courchamp et al., 2008; Lande, 1993). The presence of a strong Allee effect has profound implications for eradication programmes because eliminating a population does not require killing every last individual. Instead, populations need only be reduced below the Allee threshold and extinction may proceed without further intervention (Liebhold et al., 2016; Tobin et al., 2011). In natural populations though, stochastic effects can increase population growth rate by chance so that populations below the threshold can escape from the demographic levels where extinction is most likely and may still survive (Fauvergue et al., 2012). Therefore, to ensure success, conservative population densities need to be targeted when implementing strategies to reduce populations below the Allee threshold (Liebhold et al., 2016; Tobin et al., 2011).

Theoretical and empirical studies have confirmed that both habitat loss and fragmentation contribute to local population extinctions of rare and endangered species (Ewers & Didham, 2006; Fahrig, 2003; Fardila et al., 2017; Swift & Hannon, 2010). By removing suitable resources, habitat loss directly affects the carrying capacity of a given area, and its ability to support large populations (Baguette et al., 2014). Fragmentation increases the distances among suitable habitat patches, which in turn decreases the settlement probability of dispersing individuals. The reduced functional connectivity between populations reduces both the probability of dispersers reaching vulnerable populations (the rescue effect), and the rate of settlement in unoccupied habitat patches (Brown & Kodric-brown, 1977; Taylor et al., 1993; Tscharntke & Brandl, 2004).

Habitat loss and fragmentation, while being detrimental to rare and endangered species, can be complementary in attempts to eliminate unwanted species from an area (Barron et al., in press; Tobin et al., 2011). Habitat loss and fragmentation can reduce population size and dispersal success between populations such that populations could then become susceptible to an Allee effect (Tobin et al., 2011).

Host removal can be used as a management action to achieve eradication and can be effective for insects that are host-specific and have not spread too far (Brockerhoff, Liebhold, et al., 2010). Host removal targets specific patches in a meta-population connected through dispersal, or aims to fragment large populations (Blackwood et al., 2010; Tobin et al., 2011). Host removal results in reduced habitat resources and increased isolation of remaining host patches with lowered functional connectivity (Taylor et al., 2006). When host patches with the highest population densities (i.e., the invasion epicentre) are targeted, an immediate reduction in the invasive species population level is achieved, potentially below the Allee threshold and which may then result in extinction (Liebhold et al., 2016). In populations with population densities still above the Allee threshold, lowered functional connectivity between remaining host patches reduces individual dispersal success, possibly resulting in eventual extinction of the population (Keitt et al., 2001; Tobin et al., 2011). It has been found that invading species with an Allee effect must often exceed a spatial threshold, in addition to a density threshold, to persist and establish (Desmet, 2018; Lewis & Kareiva, 1993; Vercken et al., 2011). Thus, management actions resulting in sufficiently small and distant patches could lead to eradication of an invasive population.

Eradication programmes have employed host plant removal as an eradication tool in the past, often in conjunction with other tactics (Brockerhoff, Liebhold, et al., 2010; Liebhold et al., 2016; Liebhold & Kean, 2019; Tobin et al., 2014). For example, the painted apple moth (*Teia anartoides*) was successfully eradicated from Auckland, New Zealand, through a combination of host removal, application of *Bacillus thuringiensis* var. *kurstaki*, a microbial insecticide, and sterile insect technique (SIT) (Suckling et al., 2007). Host plant removal was also part of successful eradication programmes targeting the Asian longhorned beetle (*Anoplophora chinensis*) (Haack et al., 2009).

Host removal though, can be unpopular with the public, particularly in urban situations (Brockerhoff, Liebhold, et al., 2010; Liebhold et al., 2016; Liebhold & Kean, 2019). To enhance the effectiveness of host removal as an eradication tool, studies to understand the underlying mechanisms and processes of how species respond to host removal and fragmentation are necessary.

In this study, I investigated the influence of host removal on survival and growth of populations of an invasive species model, *Neolema ogloblini*, in a patchy landscape.

The experiment consisted of three phases. In phase one, I introduced similar-sized populations of *N. ogloblini* at selected sites in an area where neither the host plant nor the insect occurred, each consisting of three experimental host patches at differing levels of connectivity. I allowed a period of six weeks to encourage dispersal onto all three patches to form meta-populations at each site. Population sizes in the experiment were thus *indirectly* manipulated through the initial connectivity levels between host patches and dispersal success. In phase two, I removed the epicentre (introduction patch) to simulate host removal as management action to attain eradication. In the final phase, I allowed the persisting meta-populations to feed and produce offspring for the remainder of the experiment (16 weeks) before eventually determining survival (i.e., establishment) or eradication.

Specifically, I examined:

i) the influence of initial connectivity (before host removal) on dispersal success from the introduction point, by determining meta-population size before host removal;

ii) the influence of host removal on surviving population size, by determining meta-population size after host removal;

iii) the influence of the Allee effect on population survival, by determining the per capita population growth rate of surviving meta-populations;

iv) the influence of host removal and resultant connectivity (after host removal) on the extinction/eradication of meta-populations, by determining the probability of meta-populations to produce pupae.

## Materials and Methods

### *Experimental design*

Thirty-six sites were chosen in Selwyn District of Canterbury, New Zealand, with the majority situated in shelter belts (among rows of conifer trees planted as wind breaks) and a few in gardens under trees. At each site, three host patches were created with potted plants of *T. mundula*; two outer patches were 2.0 $m^2$ each, and the middle patch smaller (0.5 $m^2$). The middle patch was smaller to ensure that intraspecific competition would rapidly force adults to disperse to adjacent patches, creating meta-populations at each site. To create different levels of connectivity, the three patches were separated by either 5 m between each patch (high connectivity), 15 m between each patch (medium connectivity) or 30 m between each patch (low connectivity). The matrices between patches of all sites were mostly trees and deemed to be structurally complex. There were six replicate and six control sites for each connectivity level.

The day before release, populations of 100 adults (sex not determined) were randomly collected from the general population (for rearing methods see Chapter 1). The adults were confined in ventilated containers (500 ml) with cut leaves of *T. mundula* and left overnight in the laboratory to settle and feed. The next morning, between 9:00 am and 12:00 am, the leaves with adults were gently released on the middle host patch of each release site. Cooler morning temperatures and the presence of fed-on *T. mundula* leaves reduced the likelihood of initial dispersal. The releases were staggered between 6 to 19 December 2018.

To encourage intraspecific competition at the middle patch and enhance dispersal numbers to adjacent patches, an additional 50 adults (sex not determined) were released in the middle patch at each site, two weeks after the initial set-out of replicates in the field.

Six weeks after the initial releases, the middle host patch of each site designated as ‘host removal treatment’ site, along with all life stages of *N. ogloblini* on it, was removed. This took place between 15 to 28 Jan 2019. At control sites no host patches were removed, and additional plants were added to augment depleted patches and maintain the level of connectivity. At the time when host removal was carried out, all patches, either removed or left in field, were searched through and the number of adults was counted to determine population sizes, both before and after host removal treatment (surviving population). All adults present at this stage were part of the initial populations released as offspring development had not yet reached the pupal stage. The host patches were left in the field over the rest of the summer season (to the end of May 2019).

During midsummer, 13 weeks after the start of each replicate (i.e., between 5 and 18 of March 2019), all host patches were searched, and the number of adults was counted to determine population sizes. At the end of summer, 22 weeks after the start of each replicate (i.e., between 14 and 27 of May 2019), all plants were transferred into cloth bags, secured to prevent the escape of any adults and returned to the laboratory. There, plants were carefully searched for pupae and adults of *N. ogloblini* and the number of each stage was recorded. In the context of this study, population establishment was defined as successful development to the pupal stage of any offspring produced within the first growing season after introduction (Chapter 2). Therefore, for this experiment, population eradication is defined as the inability of populations to produce enough offspring to ensure survival to pupal stage.

Sites where no pupal cases were found at the conclusion of the experiment, were deemed as eradicated.

## Statistical Analysis

### *i) Influence of initial connectivity level (before host removal) on dispersal success to adjacent patches from the point of introduction*

At all sites, the small middle patch on which the adults were released represented a finite resource and forced adult dispersal through intraspecific competition (similarly, in Chapter 3, higher population sizes (increased competition) resulted in higher dispersal). To determine how the level of initial connectivity between the point of introduction and nearby suitable host patches influenced dispersal success, data on the total number of adults on all three patches (meta-population size) at each site was analyzed by maximum likelihood estimation using a generalized linear model (GLM). A quasipoisson error structure was used to compensate for overdispersion in the data. Population size (before host removal) was the response variable and initial connectivity level was included as the explanatory variable.

### *ii) Influence of host removal on meta-population size*

To determine how host removal influenced the meta-population sizes at each initial connectivity level, the means of meta-population sizes before and after removal at each initial connectivity level were compared with Wilcoxon rank sum tests for all the treatment sites.

### *iii) Influence of host removal and resultant connectivity on per capita population growth rate*

To determine the presence of a demographic Allee effect, a linear regression model was used to examine the influence of initial connectivity level, treatment (host removal), meta-population size before removal, and their interactions on per capita population growth rate. Per capita growth rate (r) was calculated as $r=\ln(N_1/N_0)$, with ($N_1$) the number of pupae produced during the season and ($N_0$) the propagule size released (150 adults). A small non-zero number (0.001) was added to each growth rate data point prior to calculation to allow inclusion of extinct populations. Adjusted $R^2$ values and Akaike's Information Criterion corrected for small samples (AICc) were used to determine the most parsimonious model.

### *iv) Influence of host removal and resultant connectivity on the probability of survival of meta-populations*

In this study, population eradication was defined as the inability of populations to produce enough offspring during the duration of the experiment (22 weeks) to ensure survival to pupal stage (thus a binary response, where no pupae produced = eradication (0) and some pupae produced = survival (1)). A binomial logistic regression model was used to evaluate survival probability. The number of sites (out of n=36) supporting development of offspring to the pupal stage was the response variable, and initial connectivity level, treatment (host removal), meta-population size before removal, and their interactions were fitted as explanatory variables. McFadden's Pseudo $R^2$ values (the logistic regression equivalent of the coefficient of determination) and Akaike's Information Criterion corrected for small sample sizes (AICc) were used to determine the most parsimonious model.

All analyses were conducted in R version 3.2.5 (R Core Team, 2013). Values for McFadden's Pseudo $R^2$ were determined with the R package "pscl" (S. Jackman, 2017), and those for AICc using the R package

“AICcmodavg” (Mazerolle, 2019). Graphs were drawn using the R package “effects” (Fox & Hong, 2009; Fox & Weisberg, 2019). Where applicable, values are presented as means ± SE.

## Results

### *i) Influence of initial connectivity level on dispersal success to adjacent patches from the point of introduction (before host removal)*

Results indicated a significant relationship between initial connectivity level and the resultant meta-population size before host removal ($F_{(2)}$=19.812; p<0.001) (Fig. 1). The mean meta-population size was highest (17.3 ± 2.6 adults) at sites with high connectivity levels and decreased as the distance between host patches increased (medium connectivity = 5.3 ± 1.5 adults, low connectivity = 3.0 ± 0.7 adults) (Fig. 1). Inspection of the raw data indicated higher numbers of adults at sites designated as host removal treatment sites. Wilcoxon rank sum tests were performed to determine if differences in mean meta-population size between host removal treatment sites and control sites, before host removal was carried out, were significant. The results indicated that, for the highly-connected patches, the mean size of meta-populations at the control sites (10.5 ± 2.6 adults) were already significantly lower compared to the treatment sites (24.0 ± 2.2 adults ) (W=2, p=0.013), even before any host removal was done (Fig. 2a and 2b). It was not known which factors contributed to this higher loss of adults at the control sites.

There were no differences between the surviving meta-populations of the control versus treatment sites at either the medium connectivity sites (W = 17, p=0.935), or at the low connectivity sites (W=20, p=0.805) (Fig. 2a and 2b).

### *ii) Influence of host removal on meta-population size*

Comparison of meta-population sizes before and after host removal at treatment sites indicated that none of the populations were significantly affected by host removal (Wilcoxon rank sum tests, high connectivity: W=26.5, p=0.195; medium connectivity: W=27, p=0.157; low connectivity: W=28.5, p=0.090) (Fig. 2b). As nearly all of the initial release patches at this stage were almost depleted of plant material, most of the adults had already dispersed to find additional resources. As a result, no significant reduction in population size took place when the middle patches were removed.

The mean meta-population sizes were also determined 13 weeks following the initial release (census two). Although meta-population sizes declined at all sites, the decrease in mean population sizes from week six to week thirteen was not significant (Wilcoxon rank sum tests: Host removal treatment sites – medium: W=19, p=0.9328; low: W=19.5, p=0.8551. Control sites – high: W=27, p=0.1712; medium: W=22, p=0.5732; low: W=27.5, p=0.1402) (Fig. 2a and 2b). The only exception was at highly connected treatment sites where mean meta-population size was significantly reduced from 19.67 (± 1.80) beetles to 9.50 (± 4.06) beetles (Fig. 2b). These were sites where initial population sizes were the highest (just before host removal), and the high populations in combination with host patch removal, possibly resulted in higher levels of intraspecific competition and higher numbers of beetles lost through elevated dispersal. This loss was such that by week 13, meta-population sizes between highly connected host removal treatment sites and highly connected control sites did not significantly differ (W=18.5, p=1.0) (Fig. 2a and 2b).

### *iii) Influence of host removal and resultant connectivity on per capita population growth rate*

Per capita population growth rate was significantly related to meta-population size (as formed before host removal), but not to connectivity or host removal treatment (Table 1). Excluding these two parameters (connectivity and host removal treatment) from the model improved model fit (Table 2). There were also no significant interactions between meta-population size and treatment ($F_{(2)}$=0.854; p=0.435) or between meta-population size and connectivity ($F_{(4)}$=1.343; p=0.277) and including these interactions did not improve model fit (Table 2).

Per capita population growth rate was negative across the range of meta-population sizes but increased as meta-population size increased (Fig. 3). This suggests the presence of a strong, demographic Allee effect in the meta-populations. A demographic Allee effect is signified by a positive relationship between per capita growth rate and population size over small population sizes, while populations subjected to a strong Allee effect experience negative per capita growth rates when population size falls below a critical threshold (Taylor & Hastings, 2005).

### *iv) Influence of host removal and resultant connectivity on the probability of survival of meta-populations*

Probability of survival (and thus eradication) was significantly related to meta-population size (as formed before host removal), but not to connectivity or host removal treatment (Table 3). Excluding these two parameters (connectivity and host removal treatment) from the model improved model fit (Table 4). There were no significant interactions between meta-population size and treatment ($X^2$=4.6815; p=0.0963) or between meta-population size and connectivity ($X^2$=1.5482; p=0.818) and including these interactions did not improve model fit (Table 4). As meta-population size decreased, the probability of survival decreased (Fig. 4). This result is in agreement with findings that the Allee effect and demographic stochasticity decrease the chance of population persistence at low density (Dennis, 2002; Duncan et al., 2014; Engen et al. , 2003; Lande, 1993)

## Discussion

The aim of this study was to investigate the influence of host removal (resulting in reduced connectivity and reduced population size) on per capita propulation growth rate and probability of survival of populations introduced into a patchy landscape.

Dispersal success from the point of introduction was strongly modulated by the initial level of connectivity between host patches and became the driving force that shaped all results in this experiment (Fig. 1). The size of meta-populations formed by individuals successfully finding and settling in host patches adjacent to the point of introduction, were higher at highly connected patches (5 m between each host patch) than those with a medium (15 m between each host patch) or low level of connectivity (30 m between each host patch). This is in agreement with model findings that organisms should target their movement to the nearest patch, especially when patches become rare and movement in the matrix becomes more costly (Barton et al., 2009; Poethke et al., 2011). Alternatively, this result (larger meta-populations in patches located nearer to each other) is simply a probabilistic response whereby closer patches have a greater chance of being discovered.

Removal of the middle patches from host removal treatment sites at week six did not result in an immediate lowering of meta-population sizes, as the middle patches were mostly depleted by this time and harboured very few adults. The reduced resources and connectivity level at host removal treatment sites influenced the meta-population size of *N. ogloblini* at highly connected sites only. At these sites, the mean meta-population size was initially significantly higher than at the corresponding control sites but was reduced over time to a similar level as control sites at week 13 (Fig. 2a and 2b). This was potentially due to the combination of initially high population levels and reduced resources that increased intraspecific competition and forced adult dispersal from the outlaying patches resulting in dispersal loss.

The fact that connectivity levels after host removal did not influence population growth and survival suggested that adults, once settled in a suitable patch with sufficient food resources, were reluctant to move between patches or search for other host patches or conspecifics (to actively aggregate). As settling into another patch would again involve the extra costs associated with patch location, dispersal, exposure to predators, and potential starvation (Bonte et al., 2012), leaving a high-quality patch would have to be associated with high reward.

For some species known to exhibit an Allee effect, density dependent dispersal has been found to conform to a roughly U-shaped function, with a balance between high dispersal rate at low densities to ensure necessary intraspecific interactions, and high dispersal rate at high densities driven by resource competition (Fronhofer et al., 2015; Zhang et al., 2018). For example, Fronhofer et al. (2015) found negative density dependence dispersal at low population densities and positive density dependence dispersal at high population densities due to local competition in a freshwater protist *Tetrahymena* cf. *pyriformis*. Another species known to actively emigrate from low-density situations to overcome Allee effects is the six-spot burnet moth (*Zygaena filipendulae*) which is more likely to disperse from a patch with low conspecific numbers towards patches with higher densities (Menéndez et al., 2002).

This U-shape density dependent pattern had not been observed for *N. ogloblini.* In Chapter 3, where the relationship between mating success and population size was studied, 39% of adults were not recovered after three weeks in the field. Higher disappearance rates were only observed at high densities, suggesting positive density-dependent dispersal as motivated by competition. The absence of higher dispersal rates at low population densities indicate that *N. ogloblini* adults do not disperse to search for conspecifics and therefore do not actively aggregate in an attempt to overcome the Allee effect. Results from the current study suggest that adults are attracted to plant volatiles released by conspecifics feeding on hosts (Chapter 4) to attract dispersing adults to their location, rather than moving out of a high-quality patch. Such an informed, density-dependent dispersal strategy is considered to be evolutionary-explicit because it provides advantages to individual fitness (Hovestadt et al., 2010; Travis et al., 2009). Populations of *N. ogloblini* therefore tend to take on clumped distributions under field conditions, thereby minimizing the consequences of Allee effects. In very low population density situations however, for example when populations are newly introduced or at the forefront of the invasion, *N. ogloblini* would be vulnerable to the Allee effect. This is advantageous to eradication attempts where host removal at the epicentre would result in lower population densities and isolation of remaining patches will render populations vulnerable to Allee effects and stochastic events.

In meta-population dynamics of established and stable populations, the probability of extinction of a local population decreases as population connectivity and size increases (e.g., Baguette et al., 2013;

Coudrain et al., 2014; Fourcade & Öckinger, 2017; Hanski, 1999; Hill et al., 1996). For example, Hill et al. (1996) found that relatively small, isolated areas of suitable habitat for the butterfly *Hysperia comma* were not populated because the emigration rate was too high for the local birth rate to maintain a resident population. Thus, when patches are lost or reduced in size, among-patch distances can increase such that dispersal is reduced or eliminated, and settlement or re-settlement of areas that are otherwise suitable habitat is prevented.

However, in the non-equilibrium context of the initial stages of an invasion and at the onset of the formation of a meta-population, increased connectivity has a potentially adverse effect on survival (Morel-Journel, et al., 2016; Parlato & Armstrong, 2013; Skelsey, 2013). For example, Parlato and Armstrong (2013) used data from multiple reintroductions of the North Island robin (*Petroica longipes*) and found that high connectivity at the introduction site weakened initial populations and increased establishment failure. Morel-Journel et al. (2016) studied establishment and persistence of the parasitoid *Trichogramma chilonis* in a microcosm experiment, and showed that increased connectivity decreased initial persistence by increasing early emigration from the introduced population, but also promoted persistence in the long run by favouring the formation of a meta-population. Their laboratory microcosm results were also supported by model simulations (Morel-Journel, et al., 2016).

In this experiment, meta-population size was the only observed variable that was correlated with per capita population growth rate and the probability of survival. High connectivity (before host removal) supported a higher degree of dispersal success than sites with medium or lower connectivity levels. But similar to findings by the above authors, Parlato and Armstrong (2013) and Morel-Journel et al. (2016), host removal induced additional dispersal at high connectivity host removal treatment sites only, significantly reducing meta-population size and thereby reducing per capita growth rate and probability of survival.

Thus, the strategic removal of host plant patches to limit and isolate resources at the point of introduction (or areas of high population densities) of a new invasion, could be an effective tool to achieve eradication of invasive species. Firstly, targeting and removing heavily-infested host plants results in an immediate reduction of population sizes (potentially below the Allee threshold). Secondly, by limiting and isolating remaining host patches, dispersal propensity in higher populations are increased because of competition and dispersal success between patches is reduced, resulting in reduced population sizes. These populations could then be subjected to an Allee effect or to tactics that exploit an Allee effect.

**Table 1:** Linear regression estimates of the relationship between per capita population growth rate ($\ln(N_0/N_1)$) of *N. ogloblini* meta-populations and connectivity level (high, medium, low), treatment (control, host removal), and meta-population size before host removal.

| Explanatory variable | Estimate (β) | SE | t | p |
|---|---|---|---|---|
| Intercept | -7.149 | 0.982 | -7.277 | <0.001 |
| Treatment – Patch removal | -0.088 | 0.624 | -0.142 | 0.888 |
| Connectivity – Medium | 1.298 | 0.951 | 1.365 | 0.182 |
| Connectivity – Low | 0.695 | 1.034 | 0.672 | 0.506 |
| Meta-population size | 0.189 | 0.053 | 3.582 | 0.001 |

**Table 2**: Various linear regression models fitted to examine the relationship between per capita population growth rate ($\ln(N_0/N_1)$) of *N. ogloblini* meta-populations and connectivity level (high, medium, low), treatment (control, host removal), and meta-population size before host removal.

| Parameters fitted | AICc | Adj. $R^2$ |
|---|---|---|
| **~meta-population size *** | **145.6** | **0.36** |
| ~meta-population size + treatment | 148.1 | 0.34 |
| ~meta-population size + connectivity | 148.5 | 0.37 |
| ~meta-population size + connectivity + treatment | 151.3 | 0.35 |
| ~meta-population size * treatment | 149.0 | 0.36 |
| ~meta-population size * connectivity | 150.9 | 0.38 |

* best model

**Table 3:** Maximum likelihood estimates from logistic regression of the probability of survival of *N. ogloblini* meta-populations as a function of connectivity level (high, medium, low), treatment (control, host removal), and meta-population size before host removal.

| Explanatory variables | Estimate (β) | SE | $e^{\beta}$ (Odds ratio) | z | p |
|---|---|---|---|---|---|
| Intercept | -1.774 | 1.421 | 0.170 | -1.249 | 0.212 |
| Treatment – Patch removal | -0.272 | 0.933 | 0.762 | -0.291 | 0.771 |
| Connectivity – Medium | 0.007 | 1.349 | 1.007 | 0.005 | 0.996 |
| Connectivity – Low | 0.273 | 1.398 | 1.314 | 0.195 | 0.845 |
| Meta-population size | 0.286 | 0.110 | 1.3331 | 2.595 | 0.009 |

**Table 4**: Various logistic regression models fitted to examine the relationship between the probability of survival of *N. ogloblini* meta-populations and connectivity level (high, medium, low), treatment (control, host removal), and meta-population size before host removal.

| Parameters fitted | AICc | $R^2$ # |
|---|---|---|
| **~meta-population size *** | **36.6** | **0.35** |
| ~meta-population size + treatment | 38.9 | 0.35 |
| ~meta-population size + connectivity | 41.4 | 0.35 |
| ~meta-population size * treatment | 36.8 | 0.45 |
| ~meta-population size * connectivity | 45.5 | 0.38 |

* best model

# McFadden's Pseudo $R^2$ values (the logistic regression equivalent of the coefficient of determination)

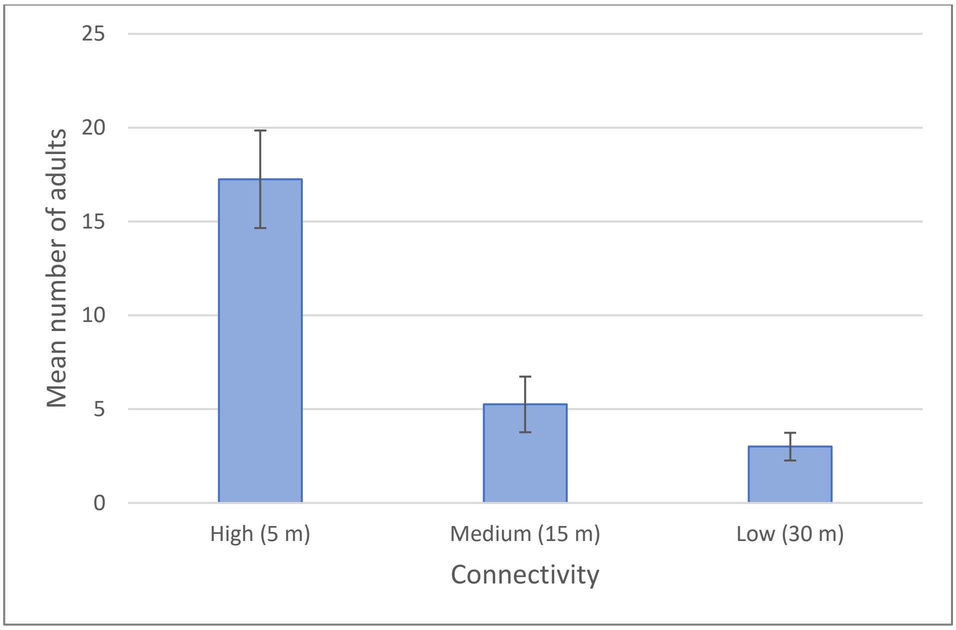

**Figure 1:** Influence of connectivity level on meta-population size at sites before host removal treatment. Meta-populations thus consist of adults found on all three patches at each site. Error bars represent standard error.

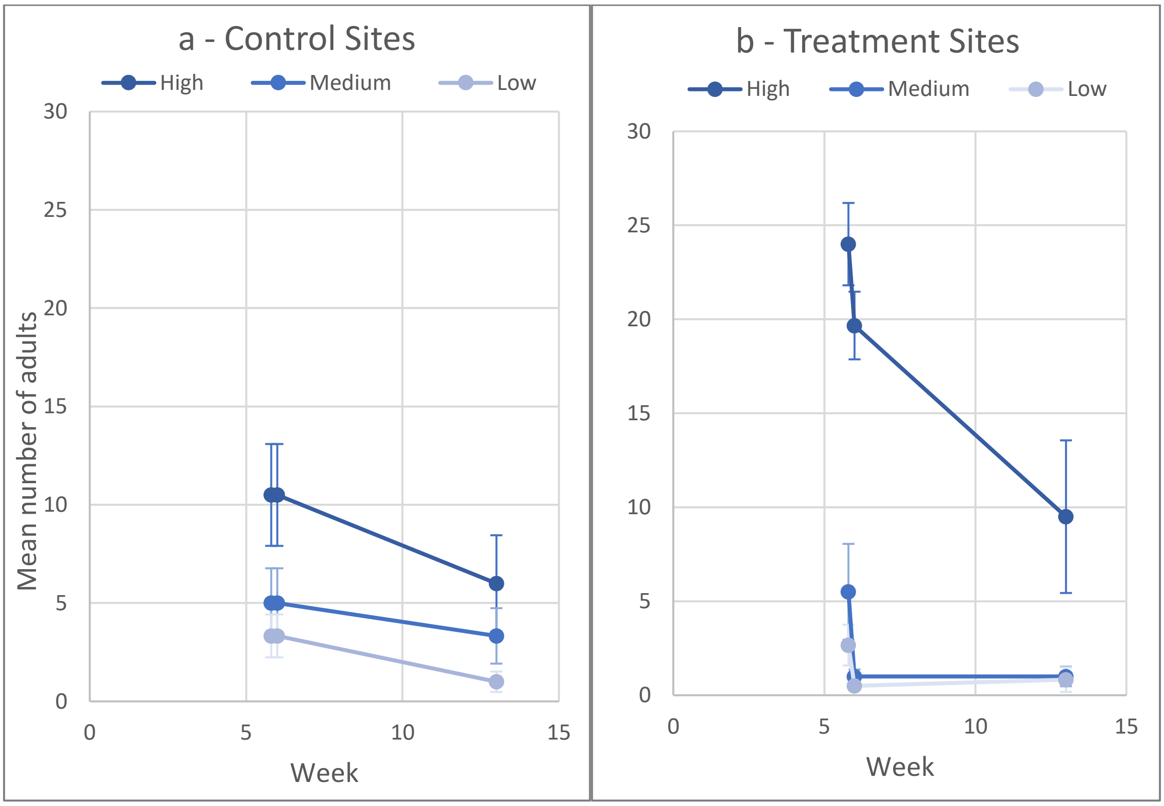

**Figure 2a and 2b**: Mean meta-population sizes at a) control and b) host removal treatment sites: i) just before host removal treatment (6 weeks into experiment; left-hand data point); ii) after host removal treatment (6 weeks into experiment; middle data point); and iii) at census two (13 weeks after the start of the experiment; right-hand data point). Error bars indicate standard error.

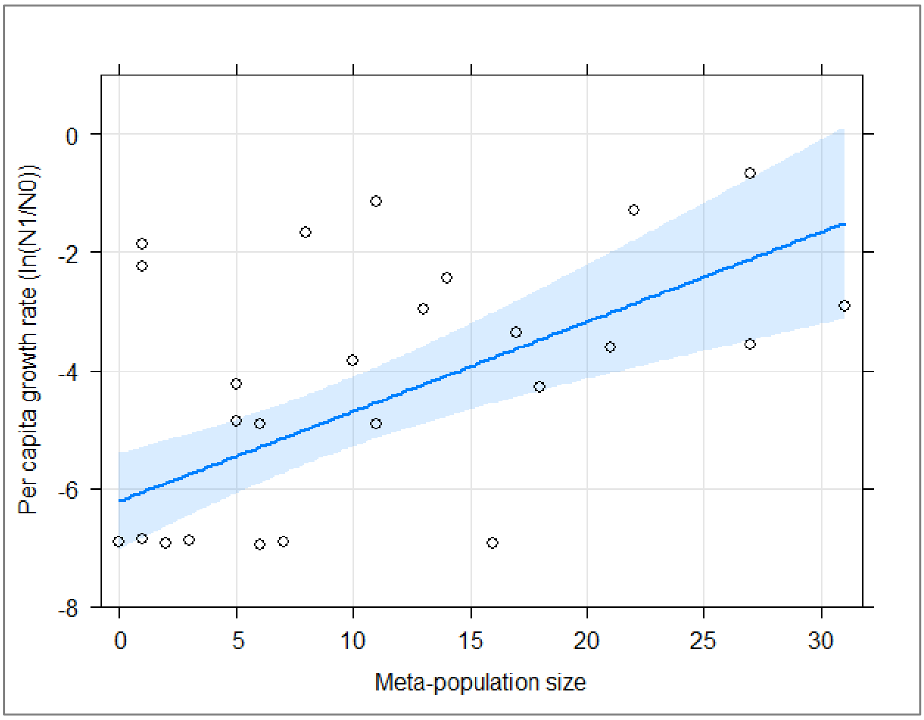

**Figure 3:** The relationship between meta-population size (as formed before host removal) and per capita growth rate (ln($N_1/N_0$)) as predicted by linear regression. The shaded area is a pointwise confidence band for the fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. The circles are partial residuals points.

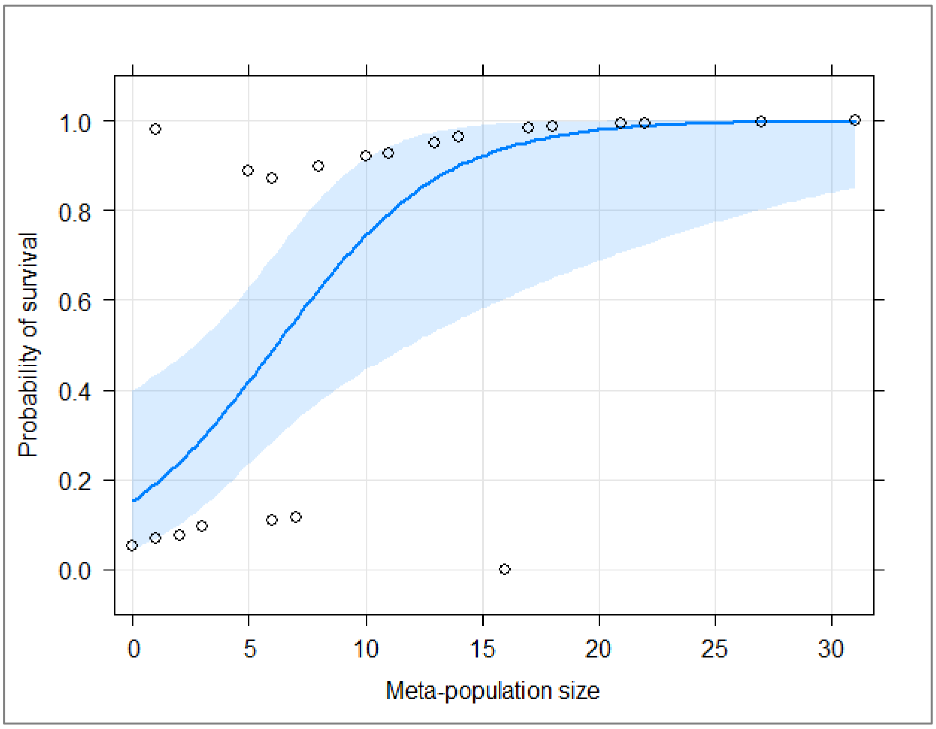

**Figure 4:** The relationship between mean meta-population size (as formed before host removal) and probability of survival (sites where populations survived (1), sites where populations were eradicated (0) following host removal) as predicted by binomial regression. The shaded area is a pointwise confidence band for the fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. The circles are partial residuals points.

# Chapter 6 – Synthesis and Conclusion

The intent of this thesis was two-fold. Firstly, to examine the role of the Allee effect in the establishment success of insect pest populations during the early phases of invasion. Secondly, to examine how spatial management at the point of introduction could render populations more vulnerable to the Allee effect and facilitate in their eradication. Both aims are important, as despite strong theoretical findings that demographic Allee effect can prevent small founder population establishment, empirical evidence is limited (Dennis et al., 2016; Gregory et al., 2010; Hutchings, 2015; Walter et al., 2017). Additionally, social pressure is demanding alternative 'greener' tools to achieve eradication of new incursions (Brockerhoff et al., 2010; Goldson et al., 2015; Liebhold & Kean, 2019; Tobin et al., 2014; Villalta et al., 2018).

In this thesis, I investigated the impact of propagule size on establishment success and found evidence that cautiously supports the existence of a strong demographic Allee effect governing the establishment of a model insect pest species (Chapter 2). I then explored potential mechanisms of component Allee effects that are likely to lead to a demographic Allee effect (Chapter 3). In chapter 4, I demonstrated how cues used by the model species allow dispersing individuals to locate suitable patches of its host plant, influence population distribution, potentially negating the Allee effect (Chapter 4). Finally, I investigated the impact of host removal as a management strategy to reduce populations below the Allee threshold and thereby potentially achieving eradication (Chapter 5).

## General application to prevention and management of future invasions

In Chapter 2, results of my field experiment demonstrated that propagule size was an important factor in determining the establishment success of species and conform to the assertion that propagule pressure is a consistent predictor of invasion success (Colautti et al., 2006; Lockwood et al., 2005). Propagule pressure affects establishment success by moderating the stochastic processes (demographic, environmental, genetic or Allee effects) to which small, introduced populations are particularly vulnerable (Blackburn et al., 2015). This supports phytosanitary regulations and policy as an effective way of limiting the establishment of non-native species by reducing the number of individuals arriving in a new area (Brockerhoff et al., 2014; Eschen et al., 2015; Reaser et al., 2008). Accordingly, as long as individual introductions are as small as possible, establishment should fail, though, high arrival frequency of small populations over a short time period may still result in establishment (Lockwood et al., 2005; Wittmann et al., 2014).

The Allee effect has been described as a "strongly theoretical, sparingly empirical framework that encompasses the dynamics of small, declining and recovering populations" (Hutchings, 2015), and other researchers have questioned the prevalence of demographic Allee effects in natural populations (Gregory et al., 2010; Matter & Roland, 2013). Strong empirical evidence have been found for component Allee effects, but less so for demographic Allee effects (Gregory et al., 2010; Kramer et al, 2009). Results of my experiment in Chapter 2 indicated a reduced per capita population growth rate at smaller population sizes, but as the influence of demographic stochasticity could not be completely removed from that of a demographic Allee effect in the data, I concluded that the extinction probability of the experimental populations of *N. ogloblini* was driven by both a demographic Allee effect and stochasticity. My study thus contributes to empirical evidence for a demographic Allee effect under field conditions. Further investigation found evidence for at least one component Allee effect in small populations of *N. ogloblini*; that is, mate-finding failure. Predator-exclusion trials revealed a high level of generalist predation on the immature stages of *N ogloblini* (Chapter 3). These results, as well as observations during the propagule size experiment in Chapter 2, suggest that generalist predation potentially contributed to the demographic Allee effect, but additional studies are needed to confirm it constitutes a predator-driven Allee effect.

As the Allee effect plays an important role in the dynamics of newly established and low-density populations by driving small populations to extinction, it is critical in influencing outcomes of eradication efforts (Blackwood et al., 2012; Liebhold et al., 2016). The Allee effect, together with other processes occurring at low population sizes (e.g., demographic stochasticity), eliminate the need for removal of all individuals in a population during management actions (Blackwood et al., 2012; Liebhold et al., 2016). Blackwood et al. (2012) modelled interactions between multiple control tactics used against gypsy moth, to determine their impacts on the strength of the demographic Allee effect and cost-effectiveness. The authors found that generalist predation created relatively low Allee thresholds, indicating that augmentation of predator populations was unlikely to result in eradication when implemented alone. In addition, little benefit was gained in including predator augmentation together with either pesticide application or mating disruption (Blackwood et al., 2012). In contrast, my study suggested generalist predation to be strongly influential in establishment success and survival of small populations of *N. ogloblini* (Chapter 2 and 3).

Apart from population size, the spatial distribution of the individuals in the population also strongly impact establishment and persistence (Drury et al., 2007; Garnier et al., 2012; Kanarek et al., 2013; Morel-Journel et al., 2016). Increased aggregation of individuals allows necessary interactions (mating, predator dilution, etc.) and minimizes the negative impacts of the Allee effect (Kanarek et al., 2013). My study indicated that adults of *N. ogloblini* potentially utilize feeding-induced plant volatiles as a cue to find their host, thereby increasing dispersal success among host patches and aggregation on host plant patches (Chapter 4). Furthermore, landscape connectivity within the invaded area affects individual dispersal and spatial distribution of individuals, thereby shaping variations in population density and consequently the prevalence of the Allee effect (Chapter 5).

In Chapter 5, limited resources at the point of introduction motivated dispersal to adjacent host patches. A higher number of adults successfully located and settled on host patches that were closer (5 m) to the point of introduction (higher connectivity level) than sites where adjacent patches were further away (medium connectivity (15 m away) or low connectivity (30 m)). Subsequent host removal of patches at the point of introduction induced additional dispersal at high connectivity treatment sites only, significantly reducing meta-population size. Meta-population size correlated significantly positively with probability of survival and per capita population growth rate. Therefore, management actions that reduces landscape connectivity (limiting and isolating host patches), and consequently population size, could subject remaining populations to the Allee effect and achieve eradication.

An important element of the landscape connectivity is the matrix as unsuitable habitat surrounding host patches has been shown to enable or hinder movement among host patches (Eycott et al., 2012). Structurally complex matrices decreased dispersal success of *N. ogloblini* adults (Chapter 4), suggesting that during host removal, the distances left between host patches surrounded by open grass areas needed to be larger to achieve sufficient isolation of surviving populations. Additionally, prioritizing host patches in structurally simple matrices for removal and leaving host patches in complex matrices would maximize population reduction through dispersal loss.

## Management of invasive species with similar characteristics

Despite the fact that *N. ogloblini* presents none of the 'typical' life history characteristics that are often associated with species susceptible to the Allee effect (e.g., sessile species or social species reliant on co-operative breeding and defence) (Courchamp et al., 2008), results of my study revealed a strong demographic Allee effect in small populations of the beetle species.

Different species, depending on life history and other abiotic and biotic effects, could be subjected to vastly different mechanisms of an Allee effect; thus, the causes and implications of an Allee effect mean that some species are more susceptible than others (Tobin et al., 2009). Currently, empirical evidence for the demographic Allee effect is still sparse and consequently also the type of life histories represented. Results of my study indicated the presence of a mate-finding component Allee effect, as well as high levels of generalist predation on immature stages in small populations of *N. ogloblini*. At low population size, the low daily reproductive rates of females were not able to withstand generalist predation pressure and this life history characteristic was potentially the highest contributor to the Allee effect.

Any strategy to eradicate an invasive species should therefore consider the extent to which the life history and species interaction contribute to an Allee effect. The ubiquity of generalist predation implicates that, for species with an existing component Allee effect, the combination would make small populations of these species more vulnerable to extinction. Any management action reducing population size of these species to a level where the two processes interact to drive the population below the Allee threshold could potentially result in eradication. Results of my study indicated that spatial habitat manipulation of reducing and isolating resources will reduce population size through dispersal loss and subject remaining populations to generalist predation. It must be noted though that if predation pressure is insufficient, it may not interact with an existing component Allee effect to produce a demographic Allee effect. Populations of the particular generalist predator species involved in the interaction may differ in space and time and be subjected to various trophic interactions influencing their behaviour and density (Bellone et al., 2017; Birkhofer et al., 2008; Larsen et al., 2018; Walter et al., 2017). Therefore the impact of generalist predation can vary, and needs to be taken into consideration with pest management actions (Berec et al., 2007; Liebhold et al., 2016).

Practically all species that require sexual recombination for reproduction may be expected to exhibit some form of a mate-finding Allee effect (Courchamp et al., 1999; Gascoigne et al., 2009). Yamanaka and Liebhold (2009b) compared the effectiveness of three eradication strategies enhancing mating-failure (mating disruption, mass trapping and sterile male release) in Coleopteran pest species using a spatially implicit model. These species have life history characteristics such as: long-lived adults; multiple mating events; and low daily reproductive rates stretched over a relatively long time period. The authors found the sterile male release method the most effective to eradicate Coleopteran pest species, mainly due the negative effect of copulation with sterile males persisting until females mate with wild males (Yamanaka & Liebhold, 2009b). In the case of species that do not produce long-range sex pheromone (such as *N. ogloblini*), sterile male release would be the only effective method to reduce mating success.

## Benefits to the field of Biological Control

In this thesis I utilised an invasive weed biocontrol agent as study organism and this had the added advantage of contributing information to the benefit the biocontrol programme specifically using *N. ogloblini*, but also to biocontrol in general.

The initial establishment of biocontrol agent populations is a critical step toward successful biocontrol and establishment failure has often been linked to small release size (Grevstad, 1999b; Hayes et al., 2013; Memmott et al., 1998; Shea & Possingham, 2000; Spafford et al., 2008). In biocontrol programmes, the number of individuals available for release is often limited due to rearing difficulties or limited resources (Grevstad et al., 2011; Paynter et al., 2016). Practitioners thus have to choose between release strategies of either many (smaller) releases that provide more chances to establish, or larger (fewer) releases that may have a higher chance of establishment per release (Grevstad, 1999b). Theoretical models have revealed that the optimal release strategy depends on the comparative influences of the Allee effect (and its strength) and environmental variability on the colonizing populations (Grevstad et al., 2011). In the presence of an Allee effect, establishment success strongly depend on population size and the optimal release strategy is to make fewer, large releases (Grevstad et al., 2011). When environmental variability has the larger influence, a strategy of many, smaller releases is optimal (Grevstad et al., 2011). In the presence of a strong Allee effect and low environmental variability, a few large releases should maximize establishment rate (Shea & Possingham, 2000). When the Allee effect is weak, but environmental variability is high, an intermediate number of smaller releases will be optimal (Fauvergue et al., 2012). In invasive weed biocontrol programmes in New Zealand, agent establishment success was correlated with the numbers released, with higher success rate resulting from releases of >200 individuals (Paynter et al., 2016).

In New Zealand, difficult-to-rear approved agents were, in the past, often directly released using field-collected material, enabling larger release sizes (Paynter et al., 2016). Since 1984 though, the regulatory requirement for agents to be screened for the presence of pathogenic organisms have resulted in limited numbers available for direct releases, resulting in smaller release sizes (<400 individuals) (Paynter et al., 2016). Similarly, in Australia new stock of any previously released agents must be bred for at least one generation before field release, while in Canada direct releases are discouraged and it is preferred that F1 or later generations be released to safeguard against diseases and parasitism (Hunt et al., 2008). In these circumstances limited numbers of individuals may be available, and the potential role the Allee effect could play in successful establishment should be taken into account when planning releases.

Results of my study confirmed the positive relationship between release size and establishment success, and the Allee effect as one of the processes underpinning this relationship. Since the presence of an Allee effect is often not known, an adaptive approach is to perform a number of releases over a range of population sizes to gain information that can be used to optimize later releases.

Generalist predation has been identified as a factor influencing establishment success and impact of many biocontrol agents (Heimpel & Mills, 2017; Paynter et al., 2018). Insect species presenting adaptations to protect themselves against predators and parasitoids are often prioritized as potential weed biocontrol agents (Paynter et al., 2018). Species of Chrysomelidae beetles display a remarkable array of defences against predation including crypsis, cyclo-alexy, stridulation, regurgitations, glandular and anal secretions, distasteful or toxic haemolymph, and host plant-sequestered or derived offensive chemicals (Begossi & Benson, 1988; Chaboo et al., 2007; Ferguson & Metcalf, 1985; Hilker, 1992). In addition, larvae use their faeces and skin moults as a material resource for constructing protective shields (Bacher & Luder, 2005; Bottcher et al., 2009; Morton & Vencl, 1998). Larvae of the closely-related species *Neolema sexpunctata* and *Lema trilinear* carry their skin moults and faeces in a shield on their backs, and host-derived compounds in their faeces protect the larvae from attack by a generalist predator, the ant *Formica subsericea* (Morton & Vencl, 1998). *Neolema ogloblini* similarly display a number of these behaviours (e.g., adults stridulate when handled, larvae regurgitate fluids, retain exuviae and faeces in a shield on their backs and would sometimes move the shield when disturbed; HE Williams unpublished data). Despite these presumed adaptations to resist predation and parasitism, my study revealed high levels of predation by generalist predators (potentially spiders and predatory mites) in small populations of *N. ogloblini*. As a biocontrol agent, *N. ogloblini* has been very successful in New Zealand, with releases of approximately 200 beetles resulting in establishment and subsequent spread at especially the warmer North Island sites (L. Hayes, personal communication, June 2019). Consequently, despite severe impact of generalist predators on immature survival that could potentially interact with the mate-finding component Allee effect, successful establishment of larger populations of *N. ogloblini* indicate a population threshold above which both these processes are overcome.

As generalist predation is such a pervasive ecological process, its interaction with potential component Allee effects (such as mate-limitation) could put small populations of many biocontrol agents at risk of extinction. This urges the practice of not only testing for the Allee effect during early releases or the release of larger populations, but also to provide protection to initial populations and/or to make releases with the least vulnerable life stage (Paynter et al., 2016; Spafford et al., 2008). An alternative approach is to compensate for predation through the release of very large numbers of agents and to make releases at times when populations of predators are less active. If this approach is used, it is important to consider other parameters influencing the release strategy, such as intra-specific competition, agent dispersal behaviour and release patch size that could promote early dispersal.

The ultimate goal of weed biocontrol is to reduce the vigour, reproductive capacity, or density of the target invasive weed in the invaded range (Thomas & Reid, 2007). As the distribution of biocontrol agent populations may have a significant effect upon their impact on the target weed, thus understanding the mechanisms regulating these distributions are of great interest. The aggregated distribution *N. ogloblini* populations adopt on host patches ensures not only conditions to overcome the Allee effect, but should also increase the damage level on the target weed patch. Following resource depletion, adults in dense populations should disperse to colonize new host patches and by using and responding to cues from successfully dispersed conspecifics, dispersal success is maximized to adjacent host patches. The successful spread of biocontrol agents depends crucially on the rate of population growth at small population size. An agent will successfully spread only when individuals that disperse beyond the current range limit establish viable populations. When an Allee effect is present in the population, individuals dispersing beyond the current range limit of the population need to form population sizes above the Allee threshold. In this instance effective dispersal cues, resulting in aggregated distributions, would be to the benefit of agent spread.

Invasive weed biocontrol is conducted on heterogeneous landscapes that are medleys of host and non-host plant patches. Once establishment has been achieved at the release site, the interaction between an agent's dispersal ability, landscape connectivity and the interlaying matrix will influence the spread to and attack of adjacent host patches. Results of my study indicate that immigration to and colonization of adjacent host patches are dependent upon the type of matrix separating source and destination host patches, as well as size and isolation between patches. An important consequence for weed biocontrol is that release strategies may differ depending on the type of landscape encountered. Matrices that decrease dispersal and colonization success will mean individual releases should be made at a finer scale than matrices promoting dispersal and colonization. Care should also be taken on release patch size, as a combination of resource-limited patches and high release sizes could promote intraspecific competition and early dispersal.

## Benefits of study to future research

### *i. Theoretical Modelling to define and explore Allee effect*

Overall, the empirical data on the influence of population size, individual behaviour, spatial structure of the population, and landscape heterogeneity on population establishment and survival presented in this thesis can be used as baseline data in future theoretical models exploring the role of the Allee effect in population persistence and spread.

### *ii. Herbivore-induced plant volatiles as surveillance tool*

Eradication programmes rely on an effective survey tool to initially detect and demarcate nascent populations while they are still small, and to also confirm eradication success (García-Díaz et al., 2017; Liebhold & Kean, 2019). Semio-chemicals such as insect sex pheromones and aggregation pheromones (on their own or in combination with host compounds) are frequently used as survey tools (Baker et al., 2013; Liebhold et al., 2016; Poland & Rassati, 2019). Eradications of Diptera (primarily fruit flies) and Lepidoptera (largely gypsy moths) have had a high success rate due to effective and cost-efficient semio-chemical lures (Liebhold et al., 2016). In contrast, success rate for Coleoptera are lower and likely reflects the higher diversity of taxa targeted for eradication and the lack of effective surveillance tools (Liebhold et al., 2016). Improved methods are critically needed to facilitate early detection of insect taxa that do not produce long-range pheromones (Liebhold et al., 2016). Both males and females of *N. ogloblini* have shown to be attracted to feeding-induced plant volatiles (Chapter 4). Blends of feeding-induced plant volatiles differ both quantitatively and qualitatively depending on the herbivore species (Halitschke et al. , 2008; Poelman & Dicke, 2014; Reddy & Guerrero, 2004). For example, Cai et al. (2014) studied the tea plant volatiles induced by a leafhopper *Empoasca vitis* and a geometrid moth *Ectropis oblique* and found that feeding (chewing) by the geometrid induced more complex volatile blends than did leafhopper infestation (piercing-sucking). Feeding-induced plant volatiles thus provide specific and detailed information about the identity of both the plant and the attacking herbivore and this information has been applied in agricultural pest management (Miresmailli et al., 2009; Szendrei & Rodriguez-Saona, 2010). Feeding-induced host-plant volatiles (or synthetic equivalents) may thus be a potential ingredient in surveillance lures and traps for species that do not produce sex or aggregation pheromones. However, success of these lures and traps would be dependent on their competitiveness with natural sources of attraction (El-Sayed et al., 2006).

## Limitations of study

Per capita population growth rate was either negative or generally low in both the establishment (Fig, 4, Chapter 2) and host removal (Fig, 3, Chapter 5) experiments. It is probable that the minimum patch size required to maintain populations throughout the duration of the experiment, is considerably larger than what was provided in these experiments. Limited patch size could have resulted in earlier emigration than what would have occurred at larger patch sizes, resulting in lower population sizes and the overall lower per capita growth rates. In the establishment experiment in Chapter 2, a quadratic relationship was found between per capita growth rate and population size, indicating the presence of interspecific competition at higher population sizes. It is thus clear that with small patches, the population size range between the Allee threshold and carrying capacity of the patch is very narrow and populations were easily tipped from a positive density dependent situation to a negative density situation, lowering survival in small patches. With no other host patches in the vicinity (apart from what was provided in the experimental layout), any adult that dispersed away was effectively lost to the population and thus no opportunity for the 'rescue effect' through immigrating adults. Although the above is a limitation of the study, on the other hand, it supports the concept that host removal, resulting in small and isolated host patches, could subject small populations to the Allee effect and achieve eradication.

## Conclusion

Increasing trade and transportation of goods and materials between countries are drastically accelerating the arrival of non-native species in novel environments. As a result, the world's ecosystems are facing unparalleled pressures from novel interactions that can result in species loss and the transformation of ecosystem structure and functioning. Research on biological invasions is at an all-time high, aiming to provide government and policy makers with the necessary guidance to deal with future incursions through socially-accepted tools. The work conducted in this thesis indicates that small founder populations will usually go extinct if they remain below an Allee threshold, thus policy aimed at minimizing the number of individuals can be a key management tool to prevent further establishments of exotic species. Furthermore, generalist predation can interact with existing component Allee effects and contribute to a demographic Allee effect, thereby expanding the pool of species potentially vulnerable to a demographic Allee effect. Finally, spatial management at the point of introduction could render populations more vulnerable to the Allee effect and facilitate in their eradication.

## APPENDIX A – A comparison between the suitability of *Tradescantia fluminensis* and *Tradescantia mundula* as host species for *Neolema ogloblini*

**Aim:** To ensure *T. mundula* would be a suitable substitution for *T. fluminensis* as a host plant under field conditions.

### Introduction

As an invasive weed species, *T. fluminensis* is listed on the National Pest Plant Accord, which indicates that it is an unwanted organism under the Biosecurity Act 1993 and cannot be distributed or sold in New Zealand (NPPA, n.d.). Therefore, potted specimens could not be used during field trials. A closely related species, *Tradescantia mundula* Kunth (Commelinaceae), was evaluated to determine if it could be used as a substitute host species for field experiments.

During quarantine studies to determine the suitability of *N. ogloblini* as a biocontrol agent for *T. fluminensis*, similar levels of adult feeding damage and oviposition as well as larval development were found on both *T. fluminensis* and *T. mundula* (Fowler et al., 2013). The researchers concluded *T. mundula* to be part of the beetle's fundamental or physiological host range (Fowler et al., 2013). The fundamental host range includes all the plant species that an agent is capable of accepting and/or utilising (Van Klinken, 2000). The fundamental host range is not always realized under field conditions and could be due to several reasons. For example, all the necessary host detection cues may not be made available during host range testing under quarantine laboratory conditions, whereas, under field conditions, inclusion of these cues may result in only a small subset of the fundamental host range be utilized under field conditions. Other reasons could be that the potential host species and agent species may not be co-occurring geographically (due to different abiotic requirements) or temporally (correct phenological state not available to support development). Therefore, the realized host range is how the fundamental host range is actually expressed under field conditions (Van Klinken, 2000).

To determine if *T. mundula* is part of the realized host range of *N. ogloblini* and would support populations of the beetle to the same degree as *T. fluminensis*, a series of experiments were done. These consisted of:

- Adult choice field trials to ensure that females would recognise and accept *T. mundula* as a potential host for feeding and oviposition;
- Female oviposition output during first five weeks of adult life span in generation F1, F3 and F4 to ensure that *T. mundula* would maintain female fecundity over several generations;
- Multi-generation larval development trials (F1- F4) to ensure *T. mundula* would maintain larval development over several generations.

## Materials and Methods

*Adult choice field trials:*

To determine if adults recognised *T. mundula* as a suitable host species for feeding and oviposition, both in the absence and presence of *T. fluminensis*, adults were given a choice between the two species under natural field conditions. Paired choices thus consisted of:

i) *T. fluminensis* vs *T. mundula*;

ii) *T. fluminensis* vs *T. fluminensis;* and

*iii) T. mundula* vs *T. mundula*.

Single, potted specimens of the appropriated species were placed 4m apart under trees at Landcare Research facility in Lincoln, New Zealand. Fifty sexually mature adults were collected from the general population into a 100ml vial containing wood shavings. The vial was chilled for a few minutes at 5 C and then placed in the middle between the pair of plants. The adults could freely choose among the two species for suitable feeding and oviposition sites. After four days each plant was carefully searched through, and the number of adults and eggs on each plant recorded. There were 8 replicates.

*Average number of eggs produced per day by females during first five weeks of adult life span*

Populations of *N. ogloblini* were reared on both plant species for several generations (F1 to F4), with generations kept separate. As larvae of each generation matured and pupated, a group of at least 30 pupae were collected and kept in square plastic food containers (≈1l) with moist paper towel linings. When adults emerged, five groups of eight females and four males were collected and caged with a potted plant of each host plant species. Plants were searched approximately every 5 days to count the numbers of adults and eggs present. All eggs were removed, and adults were returned to the cage.

This was done for 35 days for each generation. As the number of females did not stay consistent throughout the 35 days (some died or disappeared), the number of eggs found every 5 days were totalled and then divided by the number of females found on the plant. This gave an average number of eggs per female for the 5 days. At the end of 35 days, the average number of eggs per female every 5 days were summed and then divided by 35 days to give an average number of eggs per female per day.

*Multi-generation larval development trials:*

Populations of *N. ogloblini* were reared on both plant species for several generations (F1 to F4), with generations kept separate. When females of each generation started laying eggs, five groups of ten females were collected and caged with a potted plant of each host plant species. After 24h the females and excess eggs were removed to obtain 15 eggs per plant. Eggs were allowed to hatch, and the larvae allowed to develop to the adult stage. The development time to adulthood of each larva and the number of larvae developing to adulthood were recorded.

## Statistical Analysis

*Adult choice field trials:*

The non-parametric Wilcoxon Rank-Sum test was used to compare the means between the number of adults or eggs found on each plant species.

*Multi-generation female oviposition output in first five weeks of adult life span:*

A linear model was used to test whether the number of eggs laid by females per day in the first five weeks of adult lifespan differed between the two species and differed between the generations tested (F1, F3 and F4). To test whether oviposition output was maintained by both host species over the generations tested, the interaction between species and generation was included in the model.

*Multi-generation larval development trials:*

Generalized linear models were used to test both the influence of host species and generation on development time as well as the number of larvae surviving to the adult stage. To test whether development time and number surviving were maintained by both host species over the generations tested, the interaction between species and generation was included in the models.

## Results

*Adult paired-choice field trials:*

There were no significant differences between the number of adults recovered from (W=24.0; p=0.429), or eggs laid (W=27.5; p=0.666) on the two different species when given a choice between *T. fluminensis* and *T. mundula* (Fig. 1 – grey palette).

When given a choice between two specimens of *T. mundula*, significantly higher number of adults were found on one plant than on the second plant (W=61.5; p=0.002) (Fig. 1 – blue palette). This could be due to adults making use of herbivore-induced plant volatiles (by conspecifics) to find their host plant, resulting in aggregation on a selected host patch (for more information see Chapter 4). There was no significant difference between the number of eggs laid on each of the two specimens (W=46.5; p=0.105).

When given a choice between two specimens of *T. fluminensis*, although not significantly different, the number recovered from one specimen were much higher than from the other (W=51.0; p=0.052) (Fig. 1 – green palette), echoing the trend found on *T. mundula*. There was no significant difference between the number of eggs laid on the two specimens of *T. fluminensis* (W=40.0; p=0.410) (Fig. 1 – green palette).

*Multi-generation female oviposition output in first five weeks of adult life span:*

There was no significant difference between the average number of eggs produced by females (≈2 eggs per day) during the first five weeks of adult lifespan when reared on the two different species over all generations tested (F(1,24)=1.967; p=0.174) (Fig. 2).

For both species, oviposition was significantly different between generations (F(2,24)=8.716; p=0.001). Post-hoc testing (Tukey Honest Significant Differences) indicated a lower per daily oviposition rates in F3 when compared with either F1 ($p=0.005$) or F4 ($p=0.003$), irrespective of the species females were reared on (Fig. 2). This was possibly due to seasonal quality differences in host plants

No significant interaction between generation and species ($F(2,24)=0.494$; $p=0.616$), indicating that both host species supported egg production in a similar manner (Fig. 2).

*Multi-generation larval development trials:*

Development time: Both species ($\chi^2=33.514$, $p<0.0001$) and generation ($\chi^2=106.835$, $p<0.0001$) had a significant influence on development time to the adult stage. Results indicated that, on average, development took approximately 2 to 3 days longer on *T. mundula* than on *T. fluminensis* for generations F1, F2 and F4 (Fig. 3). For both species, development time was the shortest in the F3 generation, and significantly so on *T. fluminensis* (26.2 ± 0.2 days) when compared to *T. mundula* (31.2 ± 0.2 days) ($\chi^2=9.269$, $p<0.0001$).

Number developing to adult stage: Species significantly influenced the number of larvae developing to the adult stage ($F_{(1,37)}=17.459$, $p=0.0002$), with higher survival supported by *T. fluminensis* 94.7% (14.2 ± 0.2 larvae out of 15) than *T. mundula* 84.0% (12.6 ± 0.3 larvae out of 15) (Fig. 4). The number of larvae developing to the adult stage was not significantly influenced by generation ($F_{(3,33)}= 0.434$; $p=0.730$) and remained consistent over the four generations tested.

## Discussion

Recognition, acceptance and preference for a particular host plant species is a crucial step in the survival and proliferation of an insect species. A female's decision about where to lay her eggs can have serious consequences for her own reproductive fitness, as oviposition site affects offspring survival and performance, as well as potentially the survival of the ovipositing female (Refsnider & Janzen, 2010).

During the open field pair-choice tests, similar numbers of adults and eggs were found on both host species, indicating that females of *N. ogloblini* recognised and accepted *T. mundula* to the same degree as *T. fluminensis* as potential host plant. Additionally, neither the host species on which the females were reared, nor the generation of the adults influenced the average number of eggs laid per female in the first five weeks after eclosion. This indicated that both host species supported ovipositional output equally.

During the larval development trials, a higher number of larvae survived to the adult stage when reared on *T. fluminensis*, and larval development was significantly faster on this host species. The slow-growth, high-mortality hypothesis predicts that prolonged development in herbivorous insects results in greater exposure to natural enemies and/or adverse climatic events, which increases mortality risk and reduces fitness (Clancy & Price, 1987; Feeny, 1976; Murphy et al., 2018). Host species that support faster development shortens the duration of this vulnerable stage and is generally regarded to be higher quality host species (Larsson & Häggström, 1995).

This hypothesis has been tested many times with studies both supporting or rejecting it for various reasons. For example, Cornelissen and Stiling (2006) found that larvae of the leaf miners *Acrocercops albinatella* and *Brachys tesselatus* developed faster on higher quality plants, but neither quality nor natural enemy exclusion significantly affected mine survivorship or mortality caused by natural enemies. Singer et al. (2012) found herbivores on poor-quality host plants were more likely to be depredated, supporting the hypothesis, but only after they controlled for herbivore density.

Larsson and Häggström (1995) found elevated levels of predation on larvae of the leaf beetle species *Galerucella lineola* when reared on a suboptimal host *Salix dasyclados*. Larvae raised on this host were smaller and developed slower (73% slower), and survival rate was lower (45%) (Larsson & Häggström, 1995).

Results of the larval development trials on *N. ogloblini* indicated that larval survival on *T. mundula* was only 11.3% lower than on *T. fluminensis*, and development time only 15.5% slower.

Oviposition-site choice is a life-history trait of critical importance and females may have to balance several influences to optimize survival of the species (Refsnider & Janzen, 2010). The preference–performance hypothesis predicts that females will lay their eggs on species where offspring fitness will be maximized (for example, increased survival, faster growth, larger size, increased fecundity) (Jaenike, 1978). An alternative hypothesis, the fecundity-survival hypothesis, proposes that females will strike a balance between optimizing their own maternal fitness and/or survival and that of their offspring, even if it means selecting host plants that are suboptimal for offspring development.

In the case of *N. ogloblini*, female oviposition behaviour seems to follow the second hypothesis (fecundity-survival), where females ranked the optimization of their own maternal fitness and/or survival above optimizing habitat quality for their offspring. By following conspecific cues to find their host plant, females not only optimize host plant location, but ensure the presence of conspecifics for mating opportunities and protection against predation through the dilution effect (for themselves and their offspring).

Thus, although *T. mundula* is suboptimal for larval development, adult females recognized and accepted *T. mundula* to the same degree as *T. fluminensis* under field conditions. In addition, *T. mundula* also supported and maintained female oviposition output to the same extent as *T. fluminensis* over several generations. This plant species is thus deemed to be an acceptable host species, capable of supporting populations of *N. ogloblini* when encountered in the field and therefore part of the realized host range of *N. ogloblini*.

*Tradescantia mundula* is therefore a suitable substitution for *T. fluminensis* as a host plant species under field conditions.

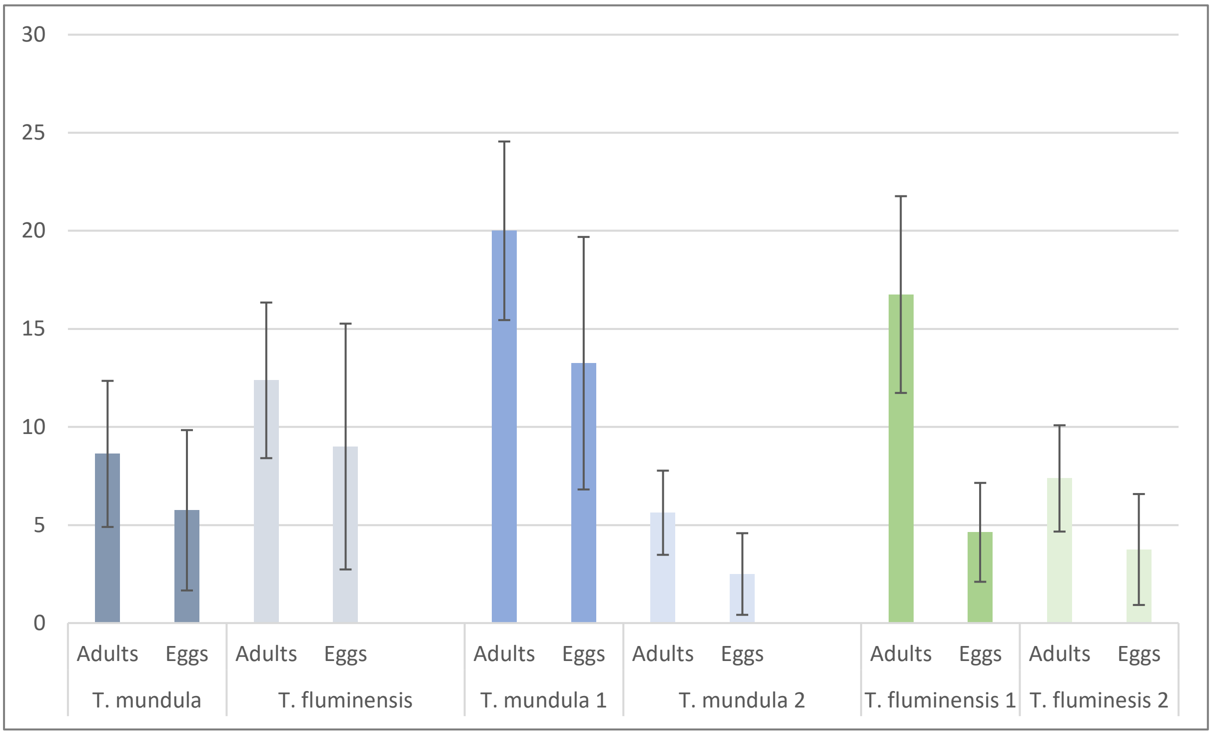

**Figure 1:** Host selection of *Neolema ogloblini* adults as determined by their mean (±SE) position and oviposition on different plant specimens, during paired-choice tests in open-field situations. (The columns in the grey palette a choice between *Tradescantia mundula* and *T. fluminensis*, the blue palette represents a choice between two *T. mundula* plants, and the green palette represents a choice between two *T. fluminensis* plants).

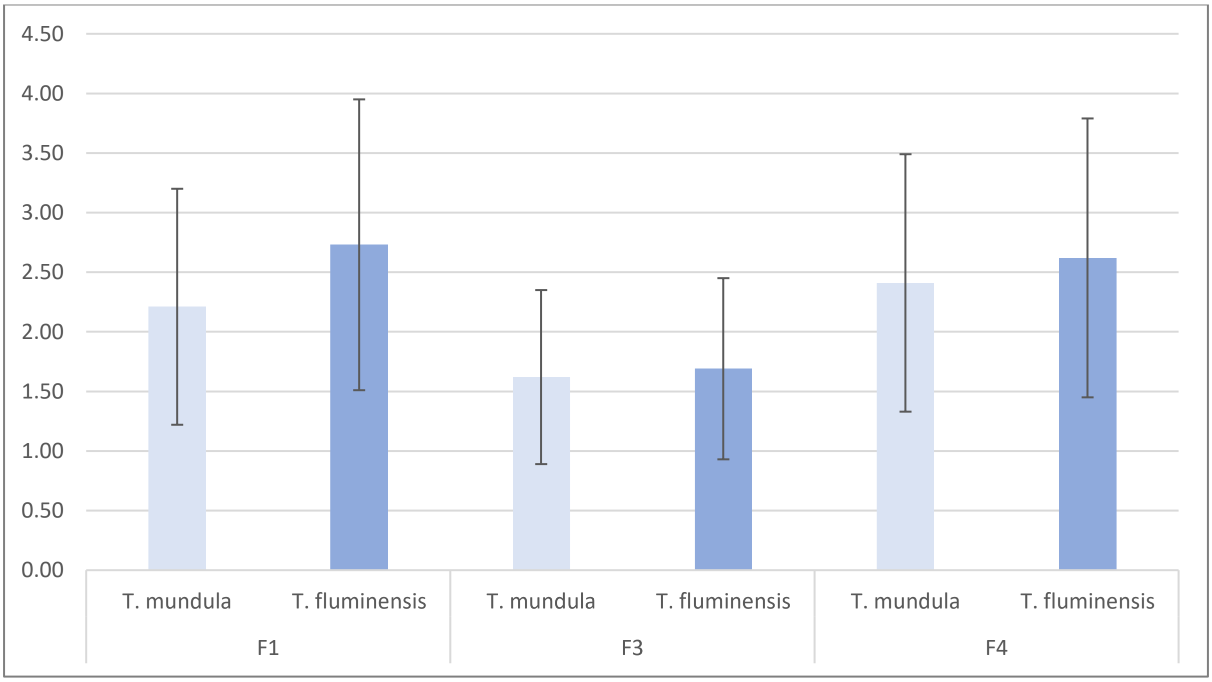

**Figure 2:** Average number of eggs laid per female (±SE) by *Neolema ogloblini* females during the first five weeks of their adult lifespan when reared on either *Tradescantia fluminensis* or *T. mundula* for successive generations.

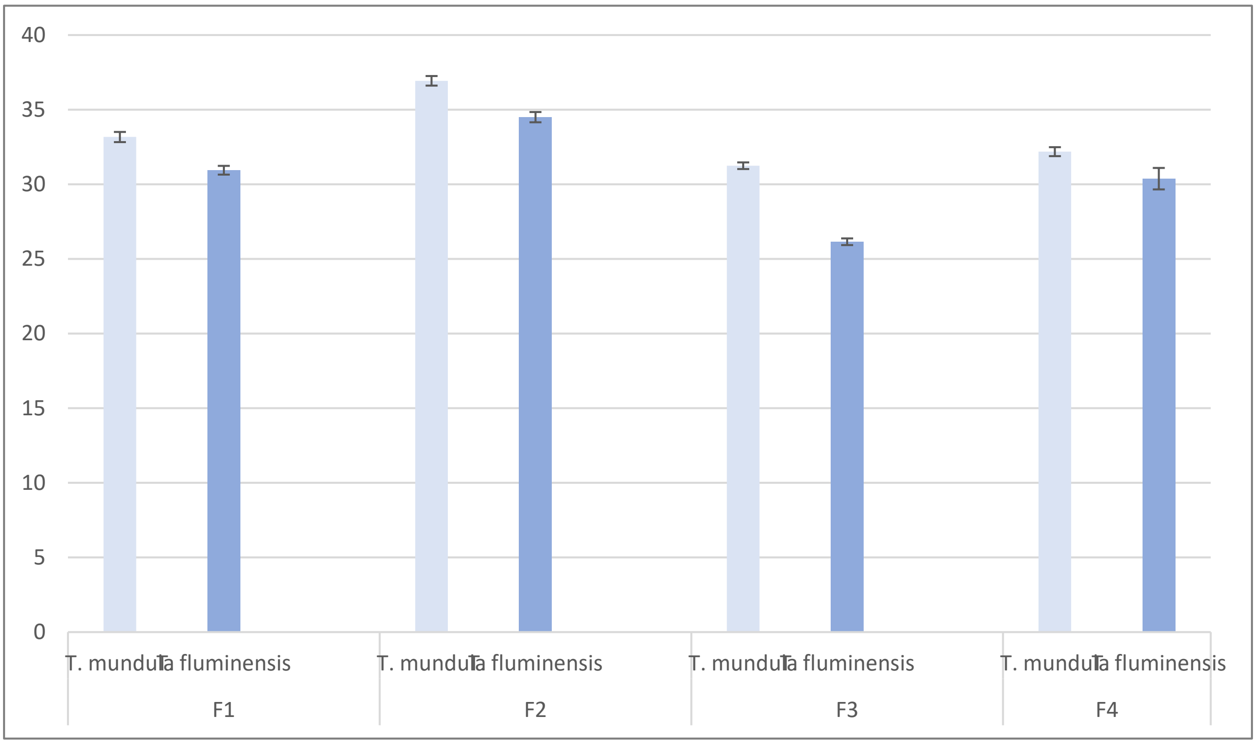

**Figure 3:** Average development time (±SE) of *Neolema ogloblini* larvae to the adult stage when reared on either *Tradescantia fluminensis* or *T. mundula* for successive generations.

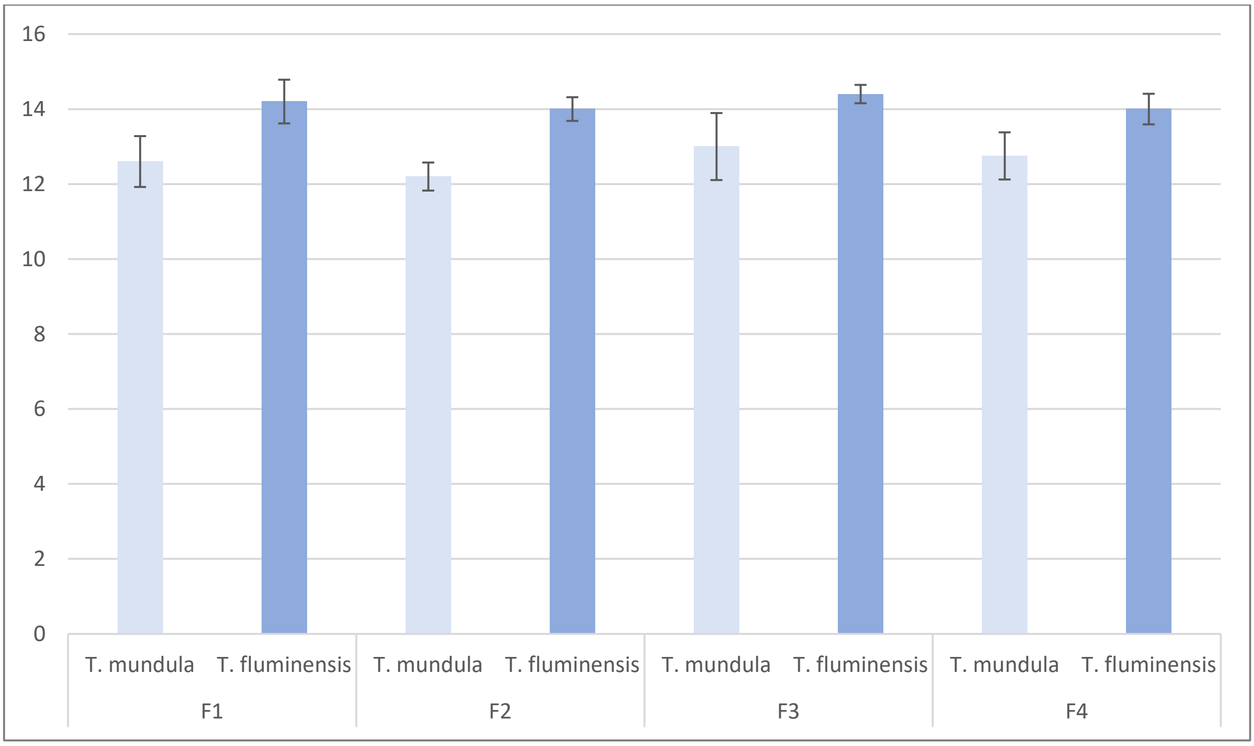

**Figure 4:** Average number (±SE) of *Neolema ogloblini* larvae developing to the adult stage when reared on either *Tradescantia fluminensis* or *T. mundula* for successive generations.

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