

CLIMATE- AND HABITAT-MEDIATION OF
PREDATOR-PREY INTERACTIONS IN AN
INVASION CONTEXT

A thesis submitted in partial fulfilment of the requirements for

the Degree of

Master of Science

in Ecology

at the University of Canterbury

by Sophia Katherine Hunt

School of Biological Sciences,
University of Canterbury,
Christchurch, New Zealand

2015

Table of Contents

Preface.....	3
Research aims and outline	3
Abstract	4
Chapter One: General Introduction	6
INTRODUCTION.....	6
Invasions	6
Interacting drivers.....	7
Study system.....	7
CLIMATE CHANGE: Global and New Zealand impacts	9
Climate in New Zealand	9
CLIMATE CHANGE: Interactions with biotic invasions	10
Climate and invasion process	10
Changes at the species level	10
Altered interactions between species.....	11
Range shifts	11
Effects on local communities	13
Ecosystem effects	13
LAND-USE MODIFICATION: Interactions with biotic invasions	14
Land-use modification affects mosquito invasion success.....	15
Mosquitoes in NZ.....	16
WHERE TO NOW? Future research directions overview.....	17
Broader focus for climate research	17
Local knowledge.....	17
SUMMARY	17
LITERATURE CITED	18
Chapter two: Habitat modification influences invasion success by altering biotic interactions	25
INTRODUCTION.....	25
METHODS.....	28
Survey design	28
Statistical analyses	29

RESULTS.....	31
DISCUSSION	42
LITERATURE CITED	46
Chapter three: Climate change mediates mosquito success by affecting life history and predation dynamics	52
INTRODUCTION.....	52
METHODS.....	56
Experimental design	56
Experiment two: Warming	58
Statistical analyses	59
RESULTS.....	61
Experiment One: Drying, predator type and mosquito species	61
Experiment two: Warming and mosquito species	66
DISCUSSION	69
LITERATURE CITED	73
Acknowledgements.....	80

Preface

Research aims and outline

In my thesis I aimed to assess the role of climate change and land-use modification in mediating mosquito invasions in biotic communities in lentic freshwater habitats. This thesis has been written largely as two stand-alone scientific manuscripts (Chapters Two and Three) intended for publication, with a review of relevant literature (Chapter One) giving initial background. As a result, there is inevitably some overlap between chapters, but I have attempted to keep repetition to a minimum.

In Chapter One, I review literature addressing the role of climate change, land-use modification and biotic invasions on freshwater biotic communities, and address some mechanisms for how these drivers can interact.

Chapter Two considers the role of two scales of habitat modification, land use at the landscape scale, and abiotic and biotic characteristics of individual habitats, on freshwater communities containing mosquitoes.

Finally, in Chapter Three, I examine effects of two aspects of climate change, habitat drying and warming, on interactions between exotic *Aedes notoscriptus* and native *Culex pervigilans* mosquitoes and their predatory invertebrates.

Abstract

Ecosystems across the globe are facing a range of anthropogenically-driven changes, including biotic invasions, urbanisation and land-use alterations, which can affect ecosystem structure and stability. To manage both native species decline and invasive species spread it is imperative that we can accurately predict how current global environmental change will affect biotic communities.

I examined effects of different land uses at both landscape- and habitat-scales on native (*Culex pervigilans*) and exotic (*Aedes notoscriptus*) mosquito distributions in lentic (standing water) freshwater habitats. Because of the importance of land use on habitat characteristics, I expected different land uses would contain different biotic communities, and that mosquitoes would more likely be present in simple communities with fewer predators. Moreover, because habitat disturbance and modification can significantly influence community structure, I expected less diverse pond communities in habitats within highly modified urban and pasture land uses would also be more likely to contain mosquitoes. I found land use affects mosquito presence, and was likely strongly linked with land-use effects on predator presence and taxon richness. Predators were more common in habitats within native forest and tussock grassland, and mosquitoes were almost entirely restricted to urban and pasture habitats. Moreover, local habitat characteristics had a strong influence on both mosquito and predator presence, with deeper and more open habitats supporting greater predator abundance, thereby excluding mosquito larvae.

To further investigate the global of climate change on predator-prey interactions involving *Ae. notoscriptus* and *Cx. pervigilans*, I conducted two experiments. Firstly, I measured effects of habitat warming and short- and long-term habitat drying on interactions between the two mosquito species and three predatory invertebrates, *Anisops wakefieldi* backswimmers, *Austrolestes colenisonis* damselflies, and *Procordulia smithii* dragonflies, which represented predators characteristic of different habitat drying regimes. A second experiment further tested interactions between *A. wakefieldi* and the two mosquito species in a wider range of temperatures. There was little evidence that short-term habitat drying affected interaction strengths of any of the predator-prey combinations, but strong evidence for the importance of temperature-mediated predation rates which depended on both predator and prey identities. Here, predators characteristic of more temporary hydroperiods showed temperature-mediated

predation responses on the two mosquito species: increasing temperature resulted in greater predation on native *Cx. pervigilans* but not effect on predation on exotic *Ae. notoscriptus*. The second experiment revealed, again, that predation depended on both temperature and mosquito species with higher predation occurring at increased temperature, but also indicated life history traits could mediate the overall effect of temperature-mediated predation.

Overall, I have shown that interactions between temperature, predator identity and mosquito species will be very important in determining the potential for mosquitoes to invade under a changing climate. Considering effects of both climate change and land-use-driven habitat modification on the invasion potential of mosquitoes in freshwater communities will therefore be important for managing both native species decline and spread of invaders. Moreover, research and management decisions on critical species like mosquitoes will need to encompass multiple drivers of climate change at both global and local scales.

Chapter One: General Introduction

INTRODUCTION

To manage both native species decline and invasive species spread (Didham et al. 2007), it is imperative that we can accurately predict how current global environmental change will affect biotic communities. Species extinction rates are already at one hundred times their natural background rates due to anthropogenically-driven stressors, and are predicted to increase to one thousand times that rate by the end of the century, if not earlier (Pimm 2009). Global-change drivers including climate change, habitat modification, over-harvesting, biotic invasions, increased atmospheric carbon dioxide (CO₂) concentrations and nitrogen deposition (MEA 2005, Strayer 2012, WMO 2013), have already resulted in extinctions and altered distributions of species worldwide (MEA 2005, Tylianakis et al. 2008). Not only are ecosystems facing pressures from novel stressors, but these stressors are predicted to increase in intensity (Pimm 2009, Walther 2010). Therefore we need to understand how to manage ecosystems in response to these global changes sooner, rather than later.

Invasions

Invasive species can have significant effects on biotic communities, and can alter both ecosystem structure and functioning (Dukes and Mooney 1999, Melbourne et al. 2007, Strayer 2012). Invasive species can have detrimental effects on native species, through predation (Mack et al. 2000), competition (Dukes and Mooney 1999), disease transmission (Derraik and Calisher 2004), and by altering fundamental characteristics of the ecosystem itself (Strayer 2012). For example, invaders can affect nutrient cycling, habitat engineering and even disturbance regimes (Strayer 2012). Effects of invaders will depend on a range of factors, including habitat heterogeneity (Melbourne et al. 2007), disturbance regime (Diez et al. 2012), propagule transport and pressure (Diez et al. 2012), and characteristics of the invader itself (Melbourne et al. 2007). Understanding how invasions affect ecosystems is important for both management and conservation of native species, especially because invasions are increasing worldwide (Huang et al. 2011, Diez et al. 2012).

Interacting drivers

How ecosystems will respond to global change drivers has been investigated but much is still unknown, especially regarding the effects of interactions between drivers, which can be complex but important (Didham et al. 2007, Tylianakis et al. 2008, Pimm 2009, Greig et al. 2012). For example, Facon et al. (2006) suggest that to understand the effect and success of invasions, they need to be examined in the context of other global change drivers, such as climate change. Didham and colleagues (2007) show that interactions between global change drivers can be both additive and synergistic (Figure 1.1). This means that the effect of one driver on a biotic community, such as climate change, will depend on the effect of biotic invasions, and vice versa (Dukes and Mooney 1999, Thomas et al. 2006, Didham et al. 2007, Pimm 2009, Walther 2010, Greig et al. 2012). For example, an invader might increase in competitiveness due to altered habitat temperature caused by changing climatic conditions (Didham et al. 2007; Pimm 2009), or extreme climatic events that are predicted to increase in frequency and magnitude could increase invasion success by enhancing propagule pressure through transportation (for example in floods) (Diez et al. 2012).

Study system: ponds will be disproportionately affected by global environmental change

Both natural and artificial water bodies play an important role in regional biodiversity (Biggs et al. 2005, Rosset et al. 2010), but are at risk from biotic invasions and have high extinction rates (Dudgeon et al. 2006, Hamilton et al. 2013). In particular, the freshwater fauna of New Zealand has high numbers of endemic species (Allibone et al. 2010), so conserving biotic communities in these systems will be important for regional and global biodiversity. Anthropogenically-driven habitat changes caused by climate change, land-use modification and biotic invasions affect ecosystem structure and functioning, and native species diversity in freshwater systems. Land-use changes such as urbanisation and agricultural intensification can alter lentic habitat distribution and quality. For example, high nutrient levels associated with land-use modification can have strong impacts on species richness and rarity in freshwater pond ecosystems (Biggs et al. 2005). Land-use modification also alters habitat characteristics such as habitat area, isolation, vegetation abundance and pH, which are strongly correlated with species diversity and rarity (Biggs et al. 2005). Because changes to climate also affect these ecosystems through altered hydroperiod regimes (Brooks 2009, Zacharias and Zamparas 2010), there may be strong interactive effects of both land-use and climate change on native biotic community within these habitats.

Freshwater-based studies on anthropogenic impacts are more scarce than those in terrestrial systems (Rosset et al. 2010), so more research on the interactive effects of global environmental change will be important for the conservation of freshwater native species and management of invaders. Moreover, because of their small size and simple community structure, ponds can be used as early indicators of anthropogenic effects on larger aquatic systems (De Meester et al. 2005, Hulsmans et al. 2008).

To investigate this further, I will first outline likely current and future effects of climate change. I then review how these changes can affect biotic communities, especially in relation to biotic invasions in modified land use. I conclude with a short summary of areas for future research.

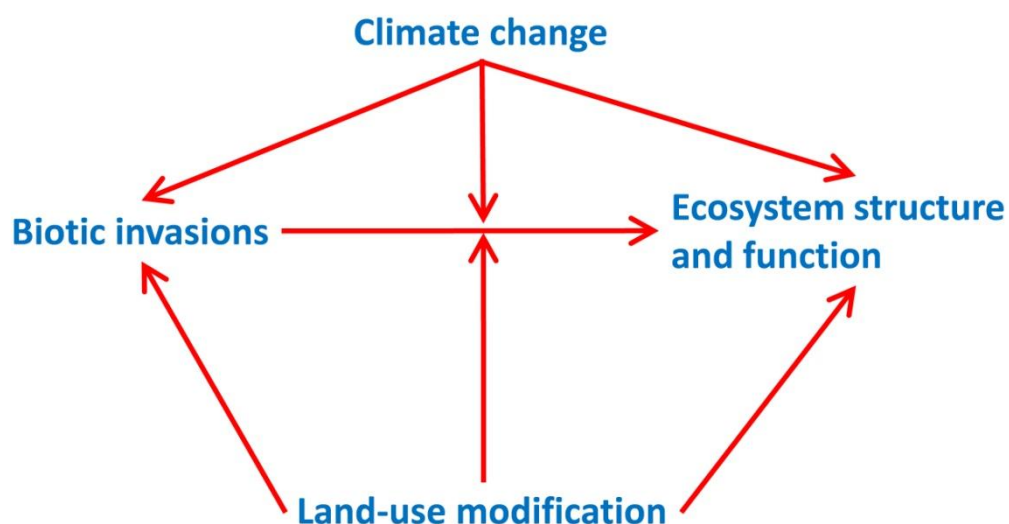


Figure 1.1. Climate change, land-use modification and biotic invasions can have direct effects on ecosystem structure and function. Climate and land-use change can also increase biotic invasions directly, and the magnitude of the per capita effect an invader has on an ecosystem. Figure adapted from Didham et al. (2007)

CLIMATE CHANGE: Global and New Zealand impacts

The planet is already experiencing precipitation and temperature changes associated with climate change (IPCC 2014, WMO 2013), and these are predicted to alter at increasing rates (Sala et al. 2000, WMO 2013). The most recent decade (2001 – 2010) was the warmest on record (WMO 2013), and mean global temperature is predicted to increase approximately 1 - 3.5°C by the end of the century (Dukes and Mooney 1999, IPCC 2014). Moreover, climate change will increase the likelihood of weather extremes such as droughts, heat waves, severe storms and floods, which are predicted to increase in frequency, intensity and duration (MfE 2008, Pimm 2009, Diez et al. 2012, WMO 2013, IPCC 2014). Although general predictions can be made about impacts of these climate changes on biotic communities (Strayer 2012), effects will not be homogeneous, resulting in varied conditions in both quality and intensity between different locations (Dukes and Mooney 1999; IPCC 2013). Although climate change is not novel, biotic communities in the past may have been more equipped to deal with climate-induced habitat changes because historical warming rates, such as in the post-Pleistocene warming (Pimm 2009), were usually slower than the current rate of climate warming (Pimm 2009, WMO 2013). Moreover, the impacts of climate change are now also amplified by other global change drivers such as biotic invasions and habitat loss (Sala et al. 2000).

Climate in New Zealand

Increases in both drying and precipitation are predicted for New Zealand, and the magnitude of these changes is likely to vary between seasons (Reisinger et al. 2010, IPCC 2013). Temperature in New Zealand is expected to increase at about 70 % of the global rate of increase, due to the buffering capacity of the oceans surrounding the country (IPCC 2013). Extremes of temperature and precipitation have the potential to be more important to biotic communities than changes to means (Reisinger et al. 2010). However, global climate models still do not have the resolution to make accurate within-region predictions in New Zealand, especially in relation to precipitation, which will be arguably more important for freshwater ecosystems than just temperature change (MfE 2008, Reisinger et al. 2010). Local studies on the effects of climate change on biotic communities will therefore be important for accurately predicting ecosystem responses to these perturbations.

CLIMATE CHANGE: Interactions with biotic invasions

There are a variety of ways that the changing climate can affect biotic communities. Temperature and habitat alteration put pressure on individual organisms which can affect populations, communities and also whole ecosystem structure and functioning (Greig et al. 2012, Diez et al. 2012, Strayer 2012, Rall et al. 2012). Consequently the predicted changes in climate will likely have a variety of complex effects on biodiversity (e.g. Dossena et al. 2012, Greig et al. 2012).

Climate and invasion process

Climate also plays an important role in mediating the invasion process, thereby directly and indirectly influencing the structure and function of ecosystems (Strayer 2012, Vaz-Pinto et al. 2013). Increasing establishment success of invaders can be partly attributed to increased transport associated with increased human movements, however increased invasion success is also likely to be associated with climate change, especially extreme climatic events (Rahel and Olden 2008, Huang et al. 2011, Diez et al. 2012). For example, Diez et al. (2012) showed that disturbances and resource pulses were linked, and therefore climate change, especially ECEs, will potentially affect rates of invasion, through processes such as increased propagule transport through floods (Walther et al. 2009). Extreme climatic events may also decrease resistance of the local community to invaders, facilitating invasive species establishment (Melbourne et al. 2007, Rahel and Olden 2008, Diez et al. 2012). For example, Petes et al. (2007) showed that a heat wave resulted in much greater mortality of native compared to introduced mussels in a New Zealand marine ecosystem, enhancing populations of invasive mussel, even after recovery from the weather event.

Changes at the species level

Habitat warming has direct effects on individual organisms, such as increases in activity, metabolism, respiration, digestion and growth (Vucic-Pestic et al. 2011, Lang et al. 2012, Grigaltchik et al. 2012, Wagner et al. 2013), but these effects of habitat warming are unlikely to be the same for all species (Vucic-Pestic et al. 2011, Greig et al. 2012, Rall et al. 2012). For example, larger species are often more susceptible to altered environmental conditions driven by climate change due to their large body size and associated energetic demands (Woodward et al. 2005, Rall et al. 2012).

Altered interactions between species

Because climate change will affect species in different ways, interactions between species will also change (Lang et al. 2012, Rall et al. 2012, Wagner et al. 2013). Species interactions may be altered through the increasing competitiveness of one species, by increasing predation of one species on another, or by altering the spread of diseases (Dukes and Mooney 1999, Rahel and Olden 2008). Climate change will also influence species' abiotic environment and again these abiotic changes will not affect all species in the same way (Rahel and Olden 2008, Walther et al. 2009). For example, Ewald et al. (2013) found *Chirocephalus diaphanous* fairy shrimp grew best at higher temperatures, but that when an ostracod predator, *Heterocypris incongruens*, was introduced, prey had reduced growing time and increased predation rate. This resulted in the optimal temperature for *C. diaphanous* growth being less when predators were present compared to when absent. This sort of interaction also has implications for the effect of invasions, because the same abiotic changes may cause the habitat to become more appropriate for other species, allowing them to invade (Walther et al. 2009). This creates challenges in making accurate predictions about how global change drivers might alter interactions between species, because changes to individual organisms as a result of climate change will have flow-on effects to the rest of the community (Grigaltchik et al. 2012, Rall et al. 2012). These are likely to be most identifiable as changes in predator-prey interactions, such as altered consumption rates (Wagner et al. 2012, Rall et al. 2012), prey handling time (Lang et al. 2012), and encounter rates (Rall et al. 2012).

Range shifts

Interactions between species can also occur due to range shifts, which are spatially and temporally altered species distributions (Dukes and Mooney 1999, Walther et al. 2009, Gallardo and Aldridge 2013). Range shifts occur when species move either spatially or temporally to stay in ideal habitats, such as their thermal optima (Walther et al. 2009, Gallardo & Aldridge 2013), because either habitat becomes unsuitable for an organism or opportunities are provided in the form of new suitable habitat (Walther et al. 2009). Many species are already responding to the changing climate by shifting ranges (Walther et al. 2009).

It is predicted that warmer temperatures will cause the ranges of species to shift poleward or higher in elevation (Dukes & Mooney 1999). For example, Hongoh et al. (2012) modelled

climate effects on mosquito populations in Canada, finding that a *Culex* species' range expanded northward as a result of warming. Such range shifts have implications for spread of diseases, because species like mosquitoes are vectors for a range of diseases and parasites, including malaria and West Nile virus (Derraik and Calisher 2004, Hongoh et al. 2012).

Not all species can, or will, shift range with the shifting climate, however (Dukes and Mooney 1999). For example, because of the rate of current climate change, fast-moving species will likely be more successful in expanding to new habitat than slow-moving species (i.e. there will be a difference in the responses of species with short generation times compared to long generation times) (Dukes and Mooney 1999). Species will also have different responses to change. For example, Loarie et al. (2008) predicted the Californian flora would react in a variety of ways to altered climate. While some species ranges will shift up in altitude, others will shift in latitude, resulting in novel species interactions and altered ecosystem structure. Because there are species in already restricted ranges, either through living in a naturally constricted habitat such as mountaintop or habitat loss, climate change will, at the minimum, cause significant declines in species (Pimm 2009).

Climate change may also cause temporal range shifts, primarily caused by temperature increases (Harper and Peckarsky 2006, Greig et al. 2012). Temporal shifts are already occurring due to increases in spring air temperature (Walther 2010). For example, for migratory pied flycatchers, changing temporal ranges have resulted in a key food resource for nestlings, caterpillars, peaking in population size earlier than in the past, leading to population declines of the bird species (Both et al. 2006). Harper and Peckarsky (2006) also demonstrated that warming resulted in mayfly emergence occurring earlier in spring. Change in temperature can either directly affect the thermal optimum of a species (Walther 2010), or may affect their food supply (Winder and Schindler 2004), and effects may be non-linear in response (Walther 2010). Range shifts may also have implications for invasive species, because local communities will lose some species and gain others (Walther et al. 2009). Implications of this may be either a loss of ecosystem functioning due to key species losses, or losses to native biodiversity due to exotic species' expansion into new habitats (Walther et al. 2009). These examples show the importance of considering indirect impacts of range-shifts on species assemblages.

Effects on local communities

Although some studies have found no direct effects of climate on biodiversity (e.g. Dossena et al. 2012), global change drivers do not act in isolation (Didham et al. 2007). Climate change is occurring both in conjunction with and enhancing biotic invasions. For example, as mentioned earlier, extreme climatic events, which are predicted to increase in frequency and magnitude, can increase invasion success by enhancing propagule pressure through transportation (e.g. floods) (Diez et al. 2012). Extreme climatic events may also cause a decrease in resistance of the local community to invaders, enabling invasive species establishment where it may not have occurred before (Melbourne et al. 2007, Diez et al. 2012). For example, Kane and colleagues (2010) showed that drought in North America suppressed invasive grasses, but was only short-term. With fast recovery the non-native grasses were expected to invade areas of juniper or pine die-off after the drought. Climate-moderated invasions will therefore need to be considered when predicting both climate and invasion community impacts because of their capacity to interact.

Ecosystem effects

Effects of climate change and biotic invasions can also occur at an ecosystem level. For example, range shifts cause novel species interactions which can have whole-ecosystem effects. Changing interactions can affect ecosystem functioning, such as through altered nutrient cycling and trophic cascades (Walther 2010, Dossena et al. 2012). Warmer spring water temperatures over the last few decades in Lake Washington in North America have resulted in a timing mismatch between when phytoplankton bloom and zooplankton herbivores are present. This resulted in significant declines in *Daphnia* abundance, a keystone herbivore, affecting whole lake nutrient cycling (Winder and Schindler 2004).

Climate may also moderate invasion success through indirect ecosystem effects. Because ecosystems are linked through the exchange of resources (Nakano and Murakami 2001), changes to one ecosystem can affect adjacent ecosystems (Massol et al. 2011, Greig et al. 2012). Greig et al. (2012) showed that warming increased the strength of the interaction between terrestrial and aquatic pond systems by increasing flux of aquatic insect emergence due to a decrease in fish predation. Thus, a potential increase in temporary ponds associated with climate change may result in an overall decrease in proportion of ponds containing fish, and therefore increase flux of aquatic insect emergence from ponds into terrestrial habitat

(Greig et al. 2012). This insect flux may include species such as mosquitoes, which would have implications for human health (Derraik and Calisher 2004).

Ecosystems themselves can also differ in how they respond to the interaction of climate change and biotic invasions (Rahel and Olden 2008, Thomas et al. 2008, Sorte et al. 2013). When climate change is taken into account, aquatic systems may be more affected by biotic invaders than terrestrial systems (Sorte et al. 2013). These researchers found that in terrestrial systems native and non-native species responded similarly to environmental changes, while in aquatic systems non-native species had increased performance compared with native in increased temperature and CO₂ scenarios (Sorte et al. 2013). Rahel and Olden (2008) also found that warming can increase growth rates in temperate systems, but may exacerbate drought in more arid systems, promoting drought-tolerant species. These examples show that the interaction between invasions and climate change can be more pronounced for aquatic than terrestrial systems.

LAND-USE MODIFICATION: Interactions with biotic invasions

Land-use modification through urbanisation and agricultural intensification is another important driver of ecosystem change in freshwater systems, because it can alter habitat size, permanence and conditions which directly impact biotic community structure (Malmqvist and Rundle 2002, Saunders et al. 2002). For example, agricultural intensification has resulted in increased nitrate inputs to freshwater systems globally (Edwards et al. 2000, Bleken et al. 2005), altering primary production and species assemblages within affected habitats (Thompson and Townsend 2005, McHugh et al. 2015). Land-use modification can also alter a range of other habitat characteristics, including habitat connectivity, disturbance regime, shade intensity, pH, temperature, decomposition, terrestrial subsidies and hydrology (Wetzel et al. 1995, Leisnham et al. 2004, Patz et al. 2004, Derraik & Slaney 2005, Thompson and Townsend 2005, Leisnham et al. 2006). This can alter biotic community structure (Murrell and Juliano 2008, Rahel and Olden 2008, Murrell et al. 2014), which combined with altered abiotic habitat characteristics can increase the invasion potential of the community (Kennedy et al. 2002, Byers and Noonburg 2003, Pokorny et al. 2005). The range of effects of changing land-use need to be considered when assessing impacts on biotic communities in freshwaters, as effects can be multiplicative and extensive (Griffiths et al. 2014).

Land-use-driven habitat modifications such as urbanisation and agricultural intensification directly affect freshwater habitats and can increase the potential for biotic invasions (González-Moreno et al. 2015), which can occur through increased propagule pressure associated with areas of high human activity (Lockwood et al. 2009, Blackburn et al. 2013), or through altered habitat disturbance regimes (Bennett et al. 2012). Land-use can alter both duration and size of lentic freshwater habitats, and this will impact biotic communities by altering the structure of the food-web within that community. For example, in a large survey of bromeliad aquatic habitats, Srivastava et al. (2008) showed that habitat size was more important for predicting predator diversity than diversity of prey species. Smaller habitats were less likely to contain predators, so invasion could be more successful if the invader were otherwise limited by predation. Habitats in modified land-uses also often have more frequent disturbance regimes than natural areas, which is correlated with increased invader presence (Bennett et al. 2012). Understanding the mechanisms that permit invader presence in a community will be an important step in mitigating or managing potential ecological consequences.

Land-use modification affects mosquito invasion success

Mosquitoes are an invasive taxon of global relevance, and modification of aquatic habitats through changes in land use can affect invasion success. Many mosquitoes have the potential to vector viruses and parasites that can cause serious human illness, and land-use modification can increase risk of invasion. Human-alteration of the natural environment increases the potential for mosquito invasions by creating novel mosquito habitats (Norris 2004), or by altering current habitat characteristics so they become suitable for mosquitoes (Dian and Changxing 2001, Norris 2004). For example, urbanisation can support both *Aedes* and *Culex* invasion success because of increased habitat availability, such as artificial containers and storm-water drains (Kay et al. 2000, Norris 2004), and sedimentation associated with agricultural development and deforestation can slow or block stream flow, increasing habitat suitability for mosquitoes (Dian and Changxing 2001).

Different land uses affect larval mosquito densities (Leisnham et al. 2005), with mosquitoes being more common in highly disturbed environments with high propagule pressure (Lockwood et al. 2009, Blackburn et al. 2013). Land use also affects the abiotic environment of larval mosquitoes. For example, temperature changes with increased solar radiation in pasture compared to forested land use decrease mosquito development time (Clements 2000,

Norris 2004). Leisnham et al. (2004) found that both shade intensity and detritus level altered *Cx. pervigilans* abundances in a study conducted in the North Island of New Zealand. Greater mosquito densities were found in open habitats, rather than shaded or forested, and medium detritus loads also resulted in increased mosquito abundance. Land-use-induced changes to biotic characteristics of habitats also affect mosquito distribution and development, and have been found to have increased presence with increasing bacteria and dissolved organic carbon (Leisnham et al. 2005), and decreased presence with increasing predator presence (Leisnham et al. 2005). Thus, land use modification will likely affect mosquito invasion success, and will be important at both landscape and local habitat scales.

Mosquitoes in NZ

There are currently twelve endemic mosquito species present in New Zealand, and three exotic species. While there has not yet been any local transmission of mosquito-borne human disease in New Zealand, some of the species present may have the potential to vector disease in the future (Weinstein et al. 1997). *Aedes notoscriptus* (Skuse), an exotic mosquito from Australia, is a known vector of Barmah Forest virus and Ross River virus (Kay et al. 2007) and has been implicated as a dengue fever vector (Watson and Kay 1999). Native *Culex pervigilans* Bergroth is a known vector of Whataroa virus in Westland, which infects birds (Dumbleton 1968), and may be a vector for avian malaria (Holder 1999). Although these species do not currently vector human disease in New Zealand, habitat alterations driven by climate change, land-use modification and increased globalisation mean that it is likely that New Zealand will host mosquito-borne disease at some stage in the future. This is supported by the establishment and subsequent eradication of *Aedes camptorhynchus* (Disbury and Cane 2011), and the interception of more than 30 other mosquitoes at ports (Derraik 2004). Because mosquitoes spend the early stages of their life cycle in standing water habitats, identifying how factors which mediate mosquito invasions alter with climate in these habitats is integral to understanding mosquito invasion risk.

WHERE TO NOW? Future research directions overview

Broader focus for climate research

Although there are a wealth of studies looking at the effects of temperature change on ecological communities (e.g. Walther et al. 2009, Dossena et al. 2012, Greig et al. 2012) there are far fewer looking at how altered precipitation regimes will affect ecosystems, in particular freshwater systems (Pimm 2009, Walther et al. 2009, but see Chase 2007). Because drying directly affects habitat area, and indirectly affects water temperature, dissolved oxygen and evapotranspiration, it could be considered a more important influence on biotic systems than just temperature change (Chase 2007, Aldous et al. 2011). This is one area that would be useful to develop further, as it would broaden the scope of the knowledge about climate change effects on ecosystems.

Local knowledge

Because there is so much variability in species' responses to changing climate, if we are to gain an adequate understanding of how to manage climate change effects it is important that we rely not just on global models, but also on local experiments and predictions (Pimm 2009, Rosset et al. 2010, Walther 2010, Greig et al. 2012). For example, although predictions might show an increase in mean rainfall, there will be local precipitation variation (IPCC 2013, Diez et al. 2012, WMO 2013). The Intergovernmental Panel on Climate change (IPCC) (2007) show that coastal areas in Argentina have had an increase in mean rainfall, while areas closer to the Andes have not. This shows that local climate predictions need to be combined with local empirical studies to gain an accurate understanding of how the changing climate can affect specific ecosystems (Pimm 2009).

SUMMARY

This literature synthesis demonstrates the importance of a holistic approach to understanding and managing ecosystem change. By integrating climate change knowledge with that of biotic invasions we will be more able to make accurate predictions about species' responses to ecosystem change, which will help inform effective management and conservation of native species.

LITERATURE CITED

- Aldous, A., J. Fitzsimons, B. Richter, and L. Bach. 2011. Droughts, floods and freshwater ecosystems: evaluating climate change impacts and developing adaptation strategies. *Marine and Freshwater Research* 62:223.
- Allibone, R., B. David, R. Hitchmough, D. Jellyman, N. Ling, P. Ravenscroft, and J. Waters. 2010. Conservation status of New Zealand freshwater fish, 2009. *New Zealand Journal of Marine and Freshwater Research* 44:271–287.
- Bennett, J. R., P. W. Dunwiddie, D. E. Giblin, and P. Arcese. 2012. Native versus exotic community patterns across three scales: roles of competition, environment and incomplete invasion. *Perspectives in Plant Ecology, Evolution and Systematics* 14:381–392.
- Biggs, J., P. Williams, M. Whitfield, P. Nicolet, and A. Weatherby. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15:693–714.
- Blackburn, T. M., T. A. A. Prowse, J. L. Lockwood, and P. Cassey. 2013. Propagule pressure as a driver of establishment success in deliberately introduced exotic species: fact or artefact? *Biological Invasions* 15:1459–1469.
- Bleken, M. A., H. Steinshamn, and S. Hansen. 2005. High nitrogen costs of dairy production in Europe: worsened by intensification. *Ambio* 34:598–606.
- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–3.
- Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change* 95:469–483.
- Byers, J. E., and E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84:1428–1433.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104:17430–4.
- Clements, A.N. 2000. *The biology of mosquitoes: sensory reception and behaviour*. Wallingford, UK: CABI Publishing.
- Derraik, J. G. B. 2004. Exotic mosquitoes in New Zealand: a review of species intercepted, their pathways and ports of entry. *Australian and New Zealand Journal of Public Health* 28:433–444.
- Derraik, J. G. B., and C. H. Calisher. 2004. Is New Zealand prepared to deal with arboviral diseases? *Australian and New Zealand Journal of Public Health* 28:27–31.

- Derraik, J. G. B., and D. Slaney. 2005. Container aperture size and nutrient preferences of mosquitoes (Diptera: Culicidae) in the Auckland region, New Zealand. *Journal of Vector Ecology* 30:73–82.
- Dian, Z., and S. Changxing. 2001. Sedimentary causes and management of two principal environmental problems in the lower Yellow River. *Environmental Management* 28:749–760.
- Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22:489–96.
- Diez, J. M., C. M. D'Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. B. Sorte, D. M. Blumenthal, B. A. Bradley, R. Early, I. Ibáñez, S. J. Jones, J. J. Lawler, and L. P. Miller. 2012. Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment* 10:249–257.
- Disbury, M., and R. P. Cane. 2011. The national exotic saltmarsh mosquito surveillance programme. *Surveillance* 38:44–46.
- Dossena, M., G. Yvon-Durocher, J. Grey, J. M. Montoya, D. M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B* 279:3011–9.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews of the Cambridge Philosophical Society* 81:163–82.
- Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.
- Edwards, A. C., Y. Cook, R. Smart, and A. J. Wade. 2000. Concentrations of nitrogen and phosphorus in streams draining the mixed land-use Dee Catchment, north-east Scotland. *Journal of Applied Ecology* 37:159–170.
- Ewald, N. C., S. E. Hartley, and A. J. A. Stewart. 2013. Climate change and trophic interactions in model temporary pond systems: the effects of high temperature on predation rate depend on prey size and density. *Freshwater Biology* 58:2481–2493.
- Facon, B., B. J. Genton, J. Shykoff, P. Jarne, A. Estoup, and P. David. 2006. A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology and Evolution* 21:130–5.
- Gallardo, B., and D. C. Aldridge. 2013. Evaluating the combined threat of climate change and biological invasions on endangered species. *Biological Conservation* 160:225–233.
- González-Moreno, P., J. M. Diez, D. M. Richardson, and M. Vilà. 2015. Beyond climate: disturbance niche shifts in invasive species. *Global Ecology and Biogeography* 24:360–370.

- Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Global Change Biology* 18:504–514.
- Griffiths, J. I., P. H. Warren, and D. Z. Childs. 2014. Multiple environmental changes interact to modify species dynamics and invasion rates. *Oikos*:1EV–11EV.
- Grigaltchik, V. S., A. J. W. Ward, and F. Seebacher. 2012. Thermal acclimation of interactions: differential responses to temperature change alter predator-prey relationship. *Proceedings of the Royal Society B* 279:4058–64.
- Hamilton, D. P., C. G. McBride, D. Özkundakci, M. Schallenberg, P. Verburg, M. de Winton, D. Kelly, C. Hendy, and W. Ye. 2013. Effects of climate change on New Zealand lakes. Pages 337–366 *Climate Change and Inland Waters: Impacts and Mitigation for Ecosystems and Societies*.
- Harper, M. P., and B. L. Peckarsky. 2006. Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. *Ecological Applications* 16:612–21.
- Holder, P. 1999. The mosquitoes of New Zealand and their animal disease significance. *Surveillance* 26:12–15.
- Hongoh, V., L. Berrang-Ford, M. E. Scott, and L. R. Lindsay. 2012. Expanding geographical distribution of the mosquito, *Culex pipiens*, in Canada under climate change. *Applied Geography* 33:53–62.
- Huang, D., R. A. Haack, and R. Zhang. 2011. Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. *PloS ONE* 6:e24733.
- Hulsmans, A., B. Vanschoenwinkel, C. Pyke, B. J. Riddoch, and L. Brendonck. 2008. Quantifying the hydroregime of a temporary pool habitat: A modelling approach for ephemeral rock pools in SE Botswana. *Ecosystems* 11:89–100.
- Kane, J. M., K. A. Meinhardt, T. Chang, B. L. Cardall, R. Michalet, and T. G. Whitham. 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecology* 212:733–741.
- Kay, B. H., A. M. Boyd, P. A. Ryan, and R. A. Hall. 2007. Mosquito feeding patterns and natural infection of vertebrates with Ross River and Barmah Forest viruses in Brisbane, Australia. *American Journal of Tropical Medicine and Hygiene* 76:417–423.
- Kay, B. H., P. A. Ryan, B. M. Russell, J. S. Holt, S. A. Lyons, and P. N. Foley. 2000. The importance of subterranean mosquito habitat to arbovirus vector control strategies in north Queensland, Australia. *Journal of Medical Entomology* 37:846–853.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–8.

- Lang, B., B. C. Rall, and U. Brose. 2012. Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *The Journal of Animal Ecology* 81:516–23.
- Leisnham, P., P. Lester, D. Slaney, and P. Weinstein. 2004. Anthropogenic landscape change and vectors in New Zealand: effects of shade and nutrient levels on mosquito productivity. *EcoHealth* 1:306–316.
- Leisnham, P. T., P. J. Lester, D. P. Slaney, and P. Weinstein. 2006. Relationships between mosquito densities in artificial container habitats, land use and temperature in the Kapiti-Horowhenua region, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 40:285–297.
- Leisnham, P. T., D. P. Slaney, P. J. Lester, and P. Weinstein. 2005. Increased larval mosquito densities from modified landuses in the Kapiti region, New Zealand: vegetation, water quality, and predators as associated environmental factors. *EcoHealth* 2:313–322.
- Loarie, S. R., B. E. Carter, K. Hayhoe, S. McMahon, R. Moe, C. A. Knight, and D. D. Ackerly. 2008. Climate change and the future of California's endemic flora. *PloS ONE* 3:e2502.
- Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15:904–910.
- Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. *Environmental Conservation* 29:134–153.
- Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14:313–23.
- McHugh, P. A., R. M. Thompson, H. S. Greig, H. J. Warburton, and A. R. McIntosh. 2015. Habitat size influences food web structure in drying streams. *Ecography* 37:1EV–13EV.
- De Meester, L., S. Declerck, R. Stoks, G. Louette, F. Van De Meutter, T. De Bie, E. Michels, and L. Brendonck. 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15:715–725.
- Melbourne, B. A., H. V. Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H. Yokomizo. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10:77–94.
- Murrell, E. G., A. R. Ives, and S. a Juliano. 2014. Intrinsic and extrinsic drivers of succession: Effects of habitat age and season on an aquatic insect community. *Ecological Entomology* 39:316–324.

- Murrell, E. G., and S. A. Juliano. 2008. Detritus type alters the outcome of interspecific competition between *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae). *Journal of Medical Entomology* 45:375–383.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98:166–170.
- Norris, D. E. 2004. Mosquito-borne diseases as a consequence of land use change. *EcoHealth* 1:19–24.
- Patz, J. A., P. Daszak, G. M. Tabor, A. A. Aguirre, M. Pearl, J. Epstein, N. D. Wolfe, A. M. Kilpatrick, J. Foufopoulos, D. Molyneux, and D. J. Bradley. 2004. Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. *Environmental Health Perspectives* 112:1092–1098.
- Petes, L. E., B. a. Menge, and G. D. Murphy. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *Journal of Experimental Marine Biology and Ecology* 351:83–91.
- Pimm, S. L. 2009. Climate disruption and biodiversity. *Current Biology* 19:R595–601.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:448–459.
- Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22:521–33.
- Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367:2923–34.
- Rosset, V., A. Lehmann, and B. Oertli. 2010. Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. *Global Change Biology* 16:2376–2387.
- Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–4.
- Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater for Protected Areas : Strategies Conservation. *Conservation Biology* 16:30–41.
- Sorte, C. J. B., I. Ibáñez, D. M. Blumenthal, N. a Molinari, L. P. Miller, E. D. Grosholz, J. M. Diez, C. M. D’Antonio, J. D. Olden, S. J. Jones, and J. S. Dukes. 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters* 16:261–70.

- Srivastava, D. S., M. K. Trzcinski, B. A. Richardson, and B. Gilbert. 2008. Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. *The American Naturalist* 172:761–71.
- Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15:1199–210.
- Thomas, C. D., A. M. A. Franco, and J. K. Hill. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution* 21:415–6.
- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137–148.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Vaz-Pinto, F., C. Olabarria, I. Gestoso, E. Cacabelos, M. Incera, and F. Arenas. 2013. Functional diversity and climate change: effects on the invasibility of macroalgal assemblages. *Biological Invasions* 15:1833–1846.
- Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* 17:1301–1310.
- Wagner, A., S. Hülsmann, W. Horn, T. Schiller, T. Schulze, S. Volkmann, and J. Benndorf. 2013. Food-web-mediated effects of climate warming: consequences for the seasonal *Daphnia* dynamics. *Freshwater Biology* 58:573–587.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2019–24.
- Walther, G.-R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pysek, I. Kühn, M. Zobel, S. Bacher, Z. Botta-Dukát, H. Bugmann, B. Czúcz, J. Dauber, T. Hickler, V. Jarosík, M. Kenis, S. Klotz, D. Minchin, M. Moora, W. Nentwig, J. Ott, V. E. Panov, B. Reineking, C. Robinet, V. Semchenko, W. Solarz, W. Thuiller, M. Vilà, K. Vohland, and J. Settele. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution* 24:686–93.
- Watson, T. M., and B. H. Kay. 1999. Vector competence of *Aedes notoscriptus* (Diptera: Culicidae) for Barmah Forest virus and of this species and *Aedes aegypti* (Diptera: Culicidae) for dengue 1-4 viruses in Queensland, Australia. *Journal of Medical Entomology* 36:508–514.
- Weinstein, P., M. Laird, and G. Browne. 1997. Exotic and Endemic Mosquitoes in New Zealand As Potential Arbovirus Vectors. Pages 1–16 *Ocasional paper*, Ministry of Health, Wellington. Wellington.
- Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100–2106.

- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20:402–9.
- Zacharias, I., and M. Zamparas. 2010. Mediterranean temporary ponds. A disappearing ecosystem. *Biodiversity and Conservation* 19:3827–3834.

Chapter two: Habitat modification influences invasion success by altering biotic interactions

INTRODUCTION

Ecosystems across the globe are facing a range of anthropogenically-driven changes, including biotic invasions, urbanisation and land-use alterations, which can affect ecosystem structure and stability (Sala et al. 2000, Malmqvist and Rundle 2002, Saunders et al. 2002, Melbourne et al. 2007). Species extinction rates are already at one hundred times natural background rates due to anthropogenically-driven stressors, and are predicted to increase to one thousand times that rate by the end of the century (Pimm 2009, Barnosky et al. 2011). There can be strong interactive effects of environmental drivers on invasion success. (Didham et al. 2007, Griffiths et al. 2014). Therefore, considering effects of both land-use-driven habitat modification and biotic invasions on native biotic communities will be important for managing both native species decline and spread of invaders (Kennedy et al. 2002, Didham et al. 2007).

Changes to land use through deforestation, agricultural intensification, damming, and urbanisation are especially influential in freshwater ecosystems, and can alter both the structure and functioning of biotic communities within those systems (Malmqvist and Rundle 2002, Saunders et al. 2002, Dudgeon et al. 2006). Effects of these changes can be observed at multiple scales, from regional land-use changes altering the dispersal potential of species, to micro-habitat changes affecting the ability of a species to persist in that habitat (Yeiser and Richter 2015). For example, Thompson and Townsend (2005) found a gradient of algal productivity in streams in different land uses which altered which functional feeding groups were present in the community. Moreover, land-use-driven changes to habitats can interact, generating complex outcomes. In a study manipulating multiple habitat characteristics, Griffiths et al. (2014) found species responses depended on the magnitude of change of other environmental characteristics. These examples illustrate the importance of considering the range of possible effects of changing land use when assessing impacts on biotic communities in freshwaters; changes to abiotic habitat characteristics will have flow-on effects to local biotic community structure and can be complex (Griffiths et al. 2014).

Habitat modifications such as urbanisation and agricultural intensification directly affect freshwater habitats and can increase the potential for biotic invasions (González-Moreno et al. 2015). This can occur through increased propagule pressure associated with areas of high human activity (Lockwood et al. 2009, Blackburn et al. 2013), as well as through altered habitat disturbance regimes (Bennett et al. 2012). Habitats in modified land uses often have more frequent disturbance regimes than natural areas, and invasive species are often more common in these disturbed habitats (Bennett et al. 2012). More frequent disturbance can change both the strength and pattern of interactions between species within those habitats (Zacharias and Zamparas 2010), altering the potential for an exotic species to become established. For example, in aquatic systems frequent drying disturbances and increased solar radiation can decrease habitat size and permanence (Brooks 2009), which decreases biotic community size (McHugh et al. 2015). Smaller and more temporary aquatic communities are also less likely to include top predators than large permanent habitats (Srivastava et al. 2008). This thereby may increase the potential for an invader to persist in communities in small, temporary habitats, especially if the invader is tolerant to disturbance (Romanuk et al. 2009). Thus, there is a large potential for land-use-driven alteration to also affect biotic interaction, and ultimately invasion potential.

Identifying the scale at which these interactions occur and at which species distribution is determined is important for managing invasive species spread and native species decline (Byers and Noonburg 2003, Saunders et al. 2002, Urban 2004, Hogg and Daane 2013, Yeiser and Richter 2015). For example, Weaver et al. (2012) found altitude and annual precipitation determined *Cygnus olor* mute swan distribution at large scales, but that local distribution was determined by habitat size, road density and percent forest. Moreover, Nolen et al. (2014) found native and exotic crayfish distribution in southern Missouri and Northern Arkansas to be both species- and scale-dependent. At the landscape scale, land-use change can alter habitat connectance, thereby affecting dispersal potential (Urban 2004, Chase 2007, Massol et al. 2011), and can also alter fundamental characteristics of biotic communities, such as species diversity (Hogg and Daane 2013). On a smaller scale, abiotic characteristics such as habitat temperature and shade level will affect the potential for a species to persist in the habitat (Thompson and Townsend 2005, Shurin et al. 2012). This will be important for invasion success by affecting not only the potential of the invader to persist in the abiotic environment, but also the potential to persist as part of the biotic community that is present (Murdoch et al. 1984).

Many biotic invaders threaten both natural biodiversity and human health, and freshwater systems have particularly high rates of biotic invasions (Dukes and Mooney 1999, Sala et al. 2000, Melbourne et al. 2007). Of particular importance are invaders that carry human disease, such as mosquitoes, which spend part of their life cycle in standing water habitats (Derraik and Calisher 2004, Norris 2004, Strayer 2012). *Aedes* and *Culex* are two mosquito genera that have high invasion potential worldwide, and can carry viruses that cause serious human diseases such as Ross River Virus, West Nile virus, and dengue virus (Norris 2004). Risk of infection by mosquitoes is increasing worldwide, through frequent international air travel and mosquito range expansions (Gubler 2002, Dauphin et al. 2004, Semenza et al. 2014). For example, *Aedes albopictus* is a competent vector of dengue fever; originating from Southeast Asia it is now considered one of the world's worst invaders, present in 15 countries and almost all continents (Lowe et al. 2000, Semenza et al. 2014).

Species interactions are an important determinant of invasion success, and biodiversity can sometimes be an effective barrier to invasions (Kennedy et al. 2002, Byers and Noonburg 2003, Pokorny et al. 2005). Habitat size and permanence directly affects biotic community size, with smaller habitats supporting fewer species (Thompson and Townsend 2005, McHugh et al. 2010, McHugh et al. 2015), which is important for mosquitoes, because they spend part of their life cycle in standing water habitats such as ponds. Because smaller habitats are likely to have lower species diversity, the potential for invasion of small, temporary ponds is likely to be higher than that of larger, more permanent habitats. For example, because predators are more likely to occur in larger habitats, and because predators in standing water habitats often prefer dipteran prey, especially mosquito larvae (Murdoch et al. 1984, Klecka and Boukal 2012), the effectiveness of a mosquito invader will in part depend on the predator community in the habitat, which will be affected by habitat size. Therefore, understanding how habitat size changes with land-use will be an important step in managing invasive species such as mosquitoes.

To investigate the potential for land use and associated abiotic characteristics to alter both community diversity and mosquito presence, I surveyed for two mosquitoes, exotic *Aedes notoscriptus* and endemic *Culex pervigilans*, in standing water habitats across different land uses in the South Island of New Zealand. Both *Culex* and *Aedes* genera have global distributions, so using two representatives of these genera currently established in New Zealand is an effective way of investigating population responses of future invaders to different land use. It is also useful towards enhancing understanding about how these current

species distributions are affected by land use. Because land use directly affects abiotic habitat characteristics, I expected different land uses would contain different biotic communities, and that mosquitoes would more likely be present in simple communities with fewer predators. Moreover, because habitat disturbance and modification can significantly influence community structure, I expected less diverse pond communities in habitats within highly modified urban and pasture land uses would also be more likely to contain mosquitoes.

METHODS

Survey design

I surveyed standing water habitats and measured both biotic communities and a range of key abiotic variables in 190 potential mosquito habitats. The survey took place during early summer (October to December) in 2013 in Canterbury and Westland, in the South Island of New Zealand (Figure 2.1). Both regions support a range of land uses, including native forest (primarily beech and podocarp/broadleaved forests), pasture, urban and natural tussock grasslands, and sites sampled were spread across these four categories. In total, 34 sampling sites were visited, with a maximum of seven habitats sampled at each site (Table 2.1). Number of habitats sampled at each site was determined by randomly locating a point within the property to sample, and sampling up to seven habitats within a 100 m radius. I visually searched the area for standing water, and if there were more than seven standing water habitats within the 100 m radius, the closest seven to the centre point were sampled. Potential mosquito habitats were defined as any standing water habitat, either temporary or permanent (Laird 1988, Norris 2004).

Land uses at sampling sites were classified as either: (1) pasture, consisting of open cultivated exotic pasture grasses, generally stocked with cattle; (2) urban, consisting of mainly suburban land-use with a range of exotic and native flora and fauna; (3) native forest, being either beech or podocarp forest with few exotic species, or (4) grassland, consisting of mainly ungrazed natural grasslands, primarily native but with some invasive grass species. Land uses were defined using visual assessments both on-site and with Google Earth.

For each habitat, surface area (m^2), mean depth (m) and shade level were estimated, and dissolved oxygen ($\text{mg O}_2 \text{ L}^{-1}$, ± 0.01 , DO), pH (± 0.01), specific conductivity ($\mu\text{S}_{25} \text{ cm}^{-1}$, \pm

0.01), and temperature ($\pm 0.1^{\circ}\text{C}$) were measured. Latitude, longitude and altitude were also recorded at each habitat. Shade was measured by visually assigning one of three levels, 1 (full shade), 2 (medium shade) or 3 (full sun) (Figure 2.2). Surface area was estimated by measuring width and length of each habitat at approximately middle widths and lengths, and depth was measured by taking three random depth measurements and taking the average. For habitats too large to measure, a visual estimate was made of both area and depth. Conductivity and pH were measured using a YSI 63 meter, and temperature and DO using a YSI 55a meter (YSI, Yellow Springs, USA). Latitude, longitude and altitude were measured using a Garmin GPS.

Biotic communities were measured through three D-net (1 mm mesh; for habitats 0.3 m wide or larger) or aquarium net (1 mm mesh; for habitats between 0.13 and 0.3 m wide) sweeps targeted in different representative micro-habitats. For habitats that were too small for either of the nets (< 0.13 m wide), the entire contents of the habitat were removed using a turkey baster and washed through the aquarium net. Samples were stored in 70 % ethanol, and all invertebrates counted and identified in the laboratory using relevant keys (mosquitoes: Belkin 1968; other insects: Winterbourn et al. 2006; Crustacea: Chapman et al. 2011). Invertebrates were classified as predators based on a review by Greig (2008). For habitats where fish were present, fish captured in nets were restrained briefly for visual identification purposes.

Statistical analyses

To initially evaluate the differences in community composition in different regions and under different land-use scenarios, a non-metric multidimensional scaling (NMDS) ordination of communities was carried out using Bray-Curtis dissimilarity with 50 restarts, using the ‘vegan’ package in R (Oksanen et al. 2013). Environmental variables were related to the NMDS ordination axes using an analysis of similarities (ANOSIM) to identify underlying habitat gradients in community structure, and ellipses representing the 95 % C.I. of sites with and without predators were fitted.

To further unravel impacts of land use on biotic communities, I investigated the effect of habitat characteristics at two scales, surrounding land use and local abiotic characteristics, on species diversity, predator presence and mosquito presence, after testing all abiotic variables for correlation (to avoid multicollinearity in multivariate models). To investigate the effects of land use and associated abiotic variables on species diversity, I used a generalised linear

model (GLM) with quasi-Poisson distribution, and for both mosquito and predator presence at both land-use and local abiotic scales I used GLMs with binomial distributions.

Mosquitoes were found almost entirely in pasture and urban sites, so I subsequently tested how abiotic variables determined mosquito and predator presence in these two land uses using GLMs with binomial distributions. All statistical analyses were performed in the programme ‘R’ version 3.1.1 (R Core Team 2014).

Table 2.1. Number of sites, samples and percent of sampled habitats containing mosquitoes and mosquito predators from four land-use types in a survey of potential mosquito habitats in Canterbury and Westland, New Zealand.

Land use	Pasture	Urban	Native forest	Grassland
<i>n</i> sites	11	11	5	6
<i>n</i> samples	65	69	30	26
% samples containing mosquitoes:	40 %	23 %	0 %	3 %
% samples containing predators:	26 %	7 %	35 %	83 %

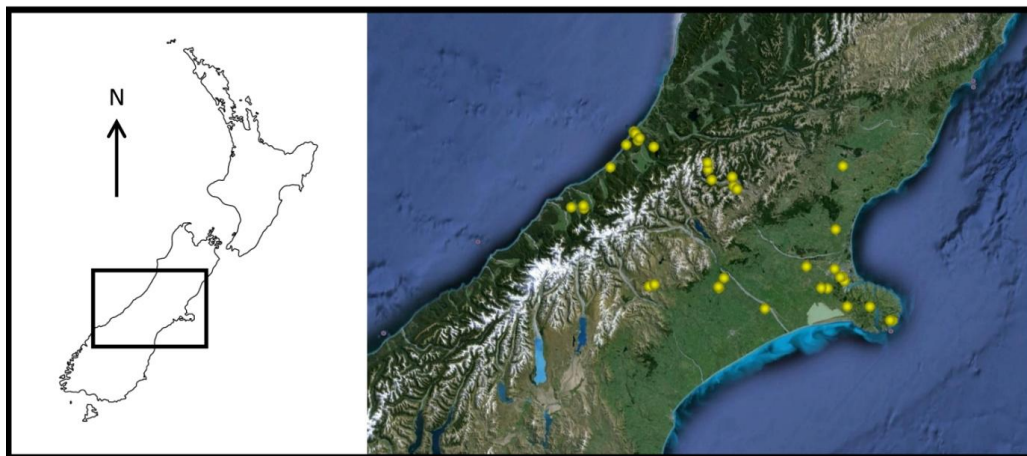


Figure 2.1. Survey sampling site locations in Westland and Canterbury, New Zealand (yellow symbols). A maximum of seven habitats were sampled at each of these site locations.

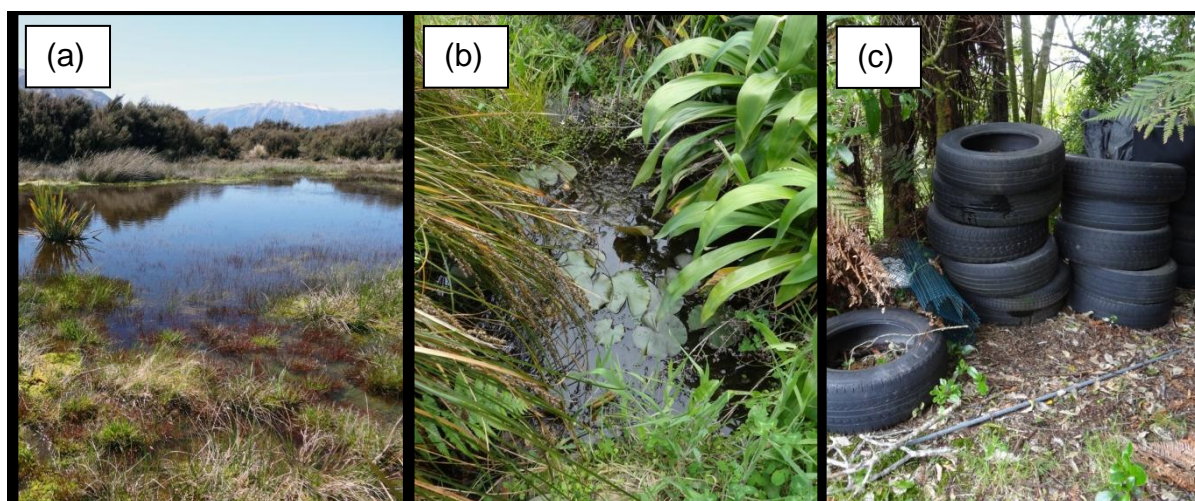


Figure 2.2. Examples of habitats in different shade levels (low, medium and high) of standing water habitats surveyed in Canterbury and Westland, New Zealand, including: (a) temporary pond in natural grassland, Canterbury (full sun), (b) pond in urban land use in Canterbury (medium shade) and (c) tyres in urban land use, Westland (full shade).

RESULTS

The NMDS ordination plots of the small standing water body communities sampled and associated ANOSIM showed communities with predators differed significantly from those without, and communities with predators were more likely to occur in habitats in natural grassland, forest and pasture, and unlikely to occur in habitats in urban land use (NMDS, $k = 2$, stress = 0.233; Table 2.2; Fig. 2.3a). Predators included a range of taxa, including odonate nymphs (Aeshnidae, Corduliidae, Lestidae and Coenagrionidae), and both adult and larval Hemiptera (*Anisops* sp.) and Coleoptera (Dytiscidae and Hydrophilidae). When fish were seen or known to be in the habitat they were also included. Mosquito larvae presence or non-detection in communities was not strongly associated with land use; mosquitoes were very rare in forest and grassland land use and common in pasture and urban areas (Table 2.2; Fig. 2.3b). Moreover, plotting only sites containing mosquitoes showed predators were generally rare within those communities; predators only co-occurred with mosquitoes in five out of 190 total habitats, 41 which contained mosquitoes (Fig. 2.3c). The species ordination (Fig. 2.4) indicated both mosquito species were associated with high axis 1 scores, and communities associated with native *Cx. pervigilans* although variable were similar to those associated with exotic *Ae. notoscriptus* mosquitoes (Fig. 2.3c).

ANOSIM indicated habitat depth, area, pH, shade, altitude and longitude were associated with the NMDS axes, with altitude and shade negatively associated with axis 1, and depth (+), area (+), longitude (-) and pH (-) associated with axis 2 (Table 2.2b; Fig. 2.4). Thus, mosquito presence was associated with open lower altitude habitats. Testing indicated strong correlation among abiotic variables with habitat shade, depth and conductivity providing relatively independent measures of abiotic conditions (Table 2.4).

To investigate effects of land use on pond invertebrate taxon richness, a generalised linear model (GLM) was conducted. This revealed richness was significantly related to land use. Richness declined across the land-use gradient from grassland to forest, pasture and urban land use (Table 2.3a; Fig. 2.5a). A subsequent GLM analysis showed this relationship was similar for predator presence with predators more common within the grassland and forest land use habitats (Table 2.3a).

Subsequent analyses of the effects of abiotic habitat characteristics within all land uses on both taxon richness and predator presence showed both habitat depth and habitat shade were independently and positively associated with taxon richness and a greater likelihood of predator presence. Moreover, taxon richness and likelihood of predator presence were greater in deeper and more open habitats (Taxon richness: Table 2.3a; Figure 2.5b & c; Predator presence: Table 2.3a; Figure 2.6a & b).

To further tease apart the effects of land use and predator presence on mosquito presence, a GLM was conducted. This showed mosquito presence was significantly affected by both land use and predator presence when all four land uses were considered (Table 2.3a; Fig. 2.7). As previously mentioned, there were only five habitats that contained both mosquitoes and predators. Also, mosquitoes were found almost exclusively in habitats within pasture and urban land use: only one habitat in natural grassland contained mosquitoes, and no mosquitoes were found in native forest (Table 2.1). The one grassland habitat that contained mosquitoes was excluded from further analyses due to its proximity to a large urban centre (within 2 km). Predators were more abundant in grassland and forested locations (Table 2.1). Thus, mosquitoes were largely absent from standing water habitats in more natural land uses, possibly due to predation being more common in standing water habitats occurring in more natural land uses.

Further insight into the drivers of mosquito and predator distribution was gained by investigating mosquito and predator presence separately in the urban and pasture land uses where mosquitoes were most common. Mosquito presence was significantly affected by depth in urban habitats, but there was no relationship with depth in pasture (GLM with binomial distribution and logit link, $p = 0.003$ and $p = 0.524$, respectively; Figure 2.8a & c). This pattern was possibly driven by the relationship between predator presence and habitat depth (Fig. 2.9b): habitats in pasture were generally deeper than those in urban (Table 2.3b; Fig. 2.9b), and because predator presence was significantly affected by habitat depth, predators were less common in habitats in urban compared to pasture land uses (Table 2.1; Fig. 2.6b). This weaker relationship between depth and predator presence in urban compared to pasture (GLM with binomial distribution and logit link, $p = 0.003$ (urban) & $p = 0.006$ (pasture); Figure 2.8b & d) was probably due to the small numbers of urban sites containing predators, which in turn allowed mosquito density to respond to depth in urban areas.

Analyses using further GLMs showed shade intensity probably also influenced both predator and mosquito presence, with mosquitoes being more common in fully shaded habitats, and predators more common in open (Table 2.3a). In analyses examining pasture and urban land uses individually, shade was important for predator presence in urban but not pasture habitats (GLM with binomial distribution and logit link, $p = 0.001$ [urban]; $p = 0.112$ [pasture]; Fig. 2.10b & d), and shade did not have a significant effect on mosquito distribution when individual land uses were examined (GLM with binomial distribution and logit link, $p = p = 0.131$ [urban]; $p = 0.176$ [pasture]; Fig. 2.10a & c). Thus, the overall effects of shade and habitat depth on both mosquito and predator presence are likely due to the strong effect of land use on shade at a habitat (Fig 2.9a), with only pasture sites having enough un-shaded open sites to influence the effect of shade on predator presence.

Table 2.2. ANOSIM analysis of land use (a), abiotic (b), and biotic variables (c) contributing to differences in community structure a survey of standing water habitats in Canterbury and Westland, New Zealand. Variables significantly contributing to community structure are indicated with *, and continuous variables significantly correlated with NMDS ordination axes 1 or 2 are indicated.

	Variable	R-squared	<i>P</i> value	NMDS ordination axis correlation
(a)	Land use (4 types)	0.22	0.001 *	
(b)	Depth	0.18	0.001 *	Axis 2 (+ve)
	Area	0.18	0.002 *	Axis 2 (+ve)
	DO	0.04	0.147	
	Temperature	0.03	0.312	
	Conductivity	0.03	0.275	
	pH	0.17	0.001 *	Axis 2 (-ve)
	Shade	0.23	0.001 *	Axis 1 (-ve)
	Altitude	0.29	0.001 *	Axis 1 (-ve)
	Latitude	0.05	0.090	
	Longitude	0.12	0.005 *	Axis 2 (-ve)
(c)	Predator presence	0.33	0.001 *	
	Mosquito presence	0.02	0.211	
	Mosquito species	0.04	0.116	

Units: Temperature (°C), DO (mg O₂ L⁻¹), Conductivity (µS₂₅ cm⁻¹), Area (m²), Depth (m), Shade (3 levels).

Table 2.3. Analysis of taxon richness, predator presence and mosquito presence (a), and abiotic variables (b), in four land-use types, pasture, urban grass and forest and with two abiotic variables, habitat depth and shade intensity, using generalised linear models, or analyses of variance. All GLMs used logit link function. When number of land uses is 4 analyses included pasture, urban, grass and forest, and when 2, only pasture and urban were included in the analyses.

	Response	Variable	Number of land uses	Test used	Distribution	<i>P</i> value
(a)	Taxon richness	Land use	4	GLM	Quasi-Poisson	< 0.001 *
		Habitat depth	4	GLM	Quasi-Poisson	< 0.001 *
		Shade	4	GLM	Quasi-Poisson	0.001 *
		Conductivity	4	GLM	Quasi-Poisson	0.864
	Predator presence	Land use	4	GLM	Binomial	< 0.001 *
		Habitat depth	4	GLM	Binomial	< 0.001 *
		Shade	4	GLM	Binomial	< 0.001 *
		Conductivity	4	GLM	Binomial	0.235
	Mosquito presence	Predator presence	4	GLM	Binomial	0.002 *
		Land use	4	GLM	Binomial	< 0.001 *
		Habitat depth	2	GLM	Binomial	0.026 *
		Shade	2	GLM	Binomial	0.021 *
	Predator presence	Conductivity	2	GLM	Binomial	0.632
		Habitat depth	2	GLM	Binomial	< 0.001 *
		Shade	2	GLM	Binomial	< 0.001 *
		Conductivity	2	GLM	Binomial	0.741
(b)	Habitat depth (m)	Land use	4	ANOVA	F	< 0.001 *
	Habitat area (m ²)	Land use	4	ANOVA	F	< 0.001 *
	Shade intensity	Land use	4	ANOVA	F	< 0.001 *

Note: F = F statistic and *P* is significant at < 0.05; units: Temperature (°C), DO (mg O₂ L⁻¹), Conductivity (μS₂₅ cm⁻¹), Area (m²), Depth (m), Shade (3 levels).

Table 2.4. Correlations between variables measured in the survey of 141 potential mosquito habitats. Significant correlation indicated with *. Conductivity and pH were not measured at all sites.

	Shade	Mean temp	DO	Conductivity	pH	Area	Depth
Temperature	0.21 *						
DO	0.41 *	0.26 *					
Conductivity	-0.19	-0.19	-0.12				
pH	0.47 *	0.36 *	0.58 *	0.17			
Area	0.19 *	0.04	0.25 *	-0.01	0.29 *		
Depth	0.12	-0.09	-0.1	0.09	-0.06	0.32 *	
Latitude	-0.13	0.25*	-0.18*	0.17	-0.03	0.03	-0.12
Longitude	-0.13	0.23*	-0.05	-0.14	0.08	0.11	-0.05
Altitude	-0.05	0.09	-0.06	-0.04	-0.08	-0.06	-0.10

	n	df
Mean temp	141	139
DO	141	139
Conductivity	69	67
pH	69	67
Area	141	139
Depth	141	139
Latitude	141	139
Longitude	141	139
Altitude	141	139

Units: Temperature (°C), DO (mg O₂ L⁻¹), Conductivity (μS₂₅ cm⁻¹), Area (m²), Depth (m)

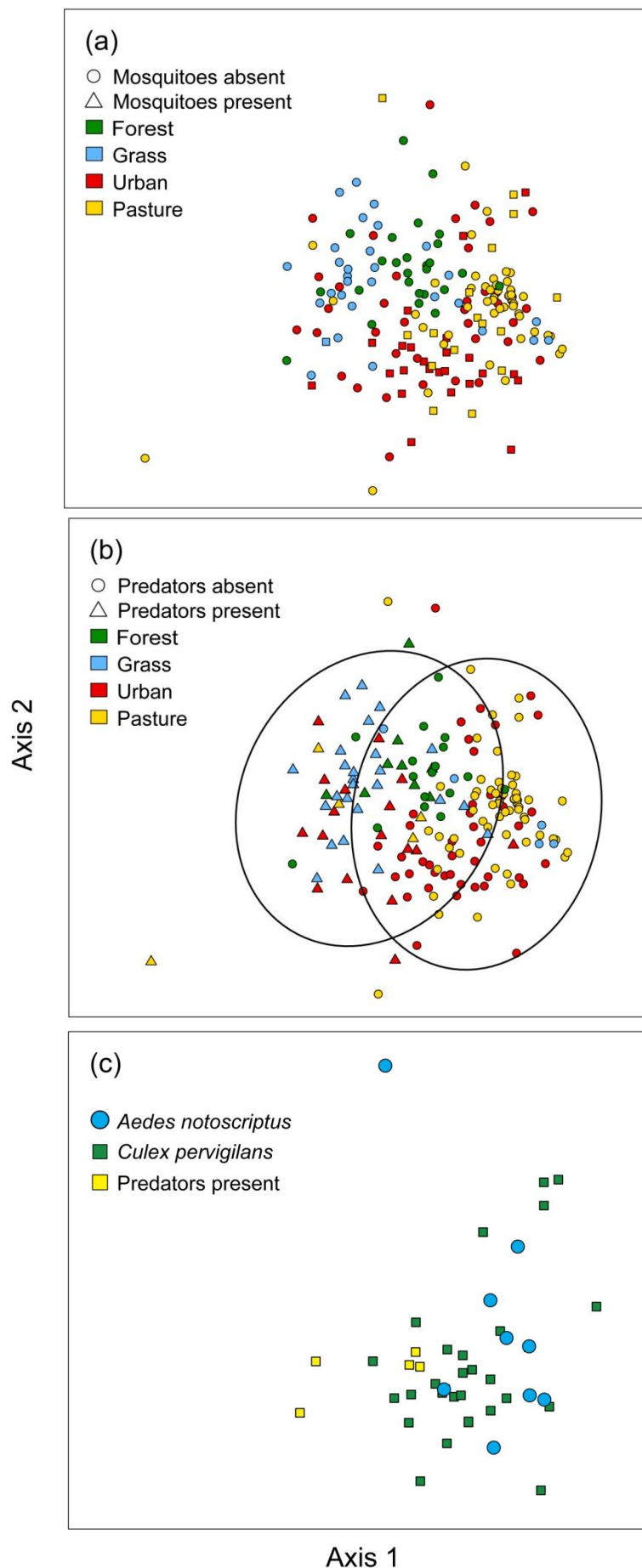


Figure 2.3. Plot of a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis matrix of dissimilarities from invertebrate abundance of aquatic communities inhabiting standing water habitats in native forest (green, $n = 26$), tussock grassland (blue, $n = 30$, urban (red, $n = 69$) and pasture (yellow, $n = 69$) land uses in relation to (a) mosquito presence, (b) predator presence and (c) for only sites containing *Ae. notoscriptus* (circles) or *Cx. pervigilans* (squares) mosquitoes with (yellow) and without (green and blue) predators. Ellipses show significant differences in communities containing predators compared to those without, according to ANOSIM.

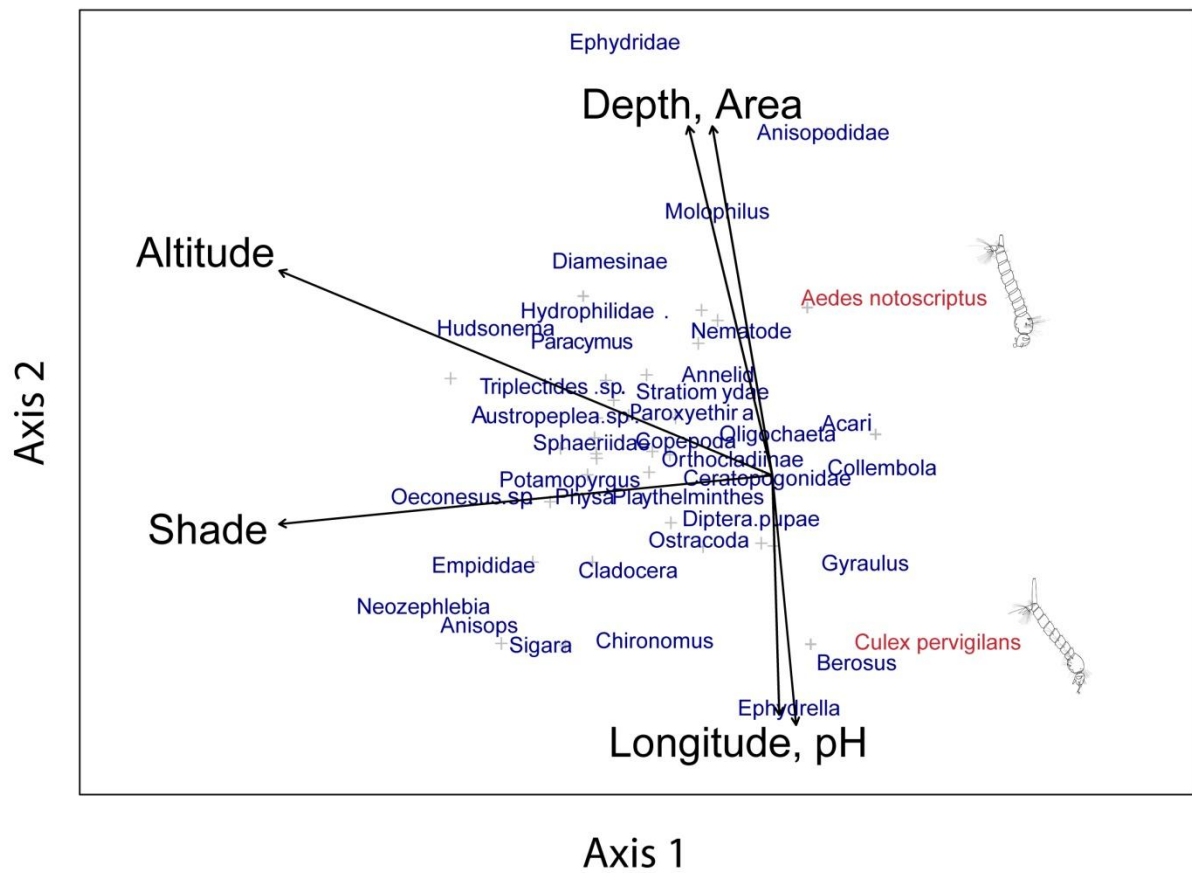


Figure 2.4. NMDS ordination of species in standing water habitats, showing abiotic variables significantly associated with axes of community composition, as determined by ANOSIM. Most abundant taxa are shown, and mosquito illustrations show locations in ordination of the two mosquito species (red labels).

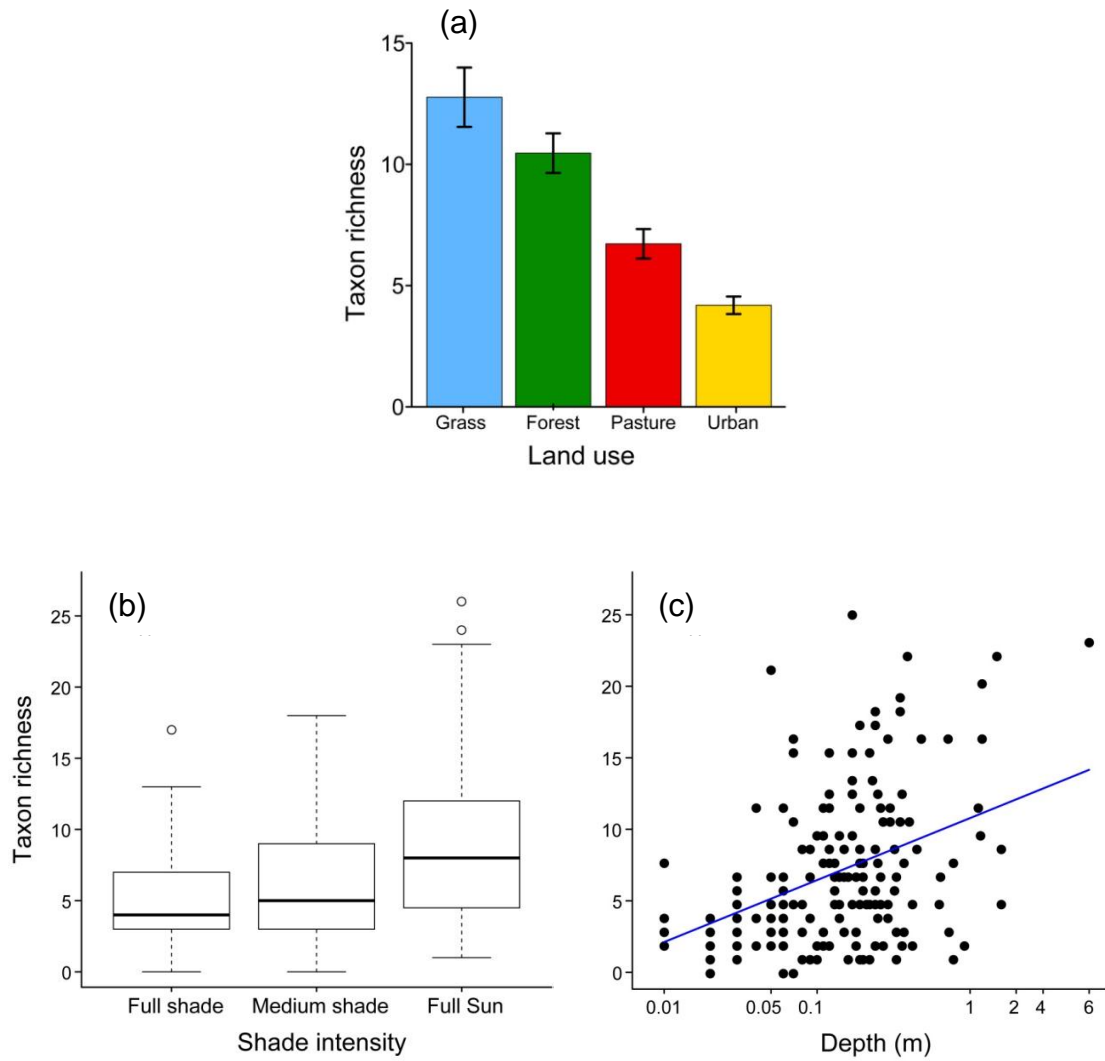


Figure 2.5. Taxon richness in habitats differing in (a) land use, (b) depth and (c) shade intensity from a survey of 190 standing water habitats in Canterbury and Westland, New Zealand. Error bars are SE and taxon richness is number of taxa found in a habitat.

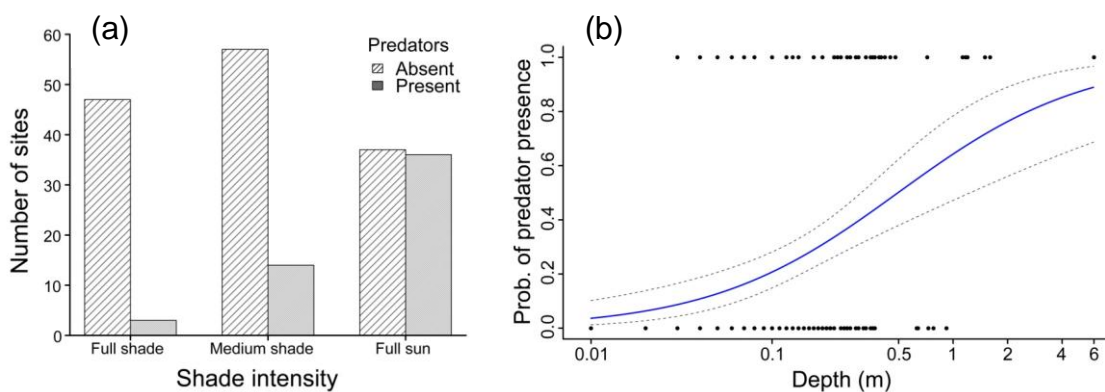


Figure 2.6. Predator presence in standing water habitats in (a) different shade intensities and (b) different depths in a survey of 190 potential mosquito habitats in Canterbury and Westland, New Zealand. Dashed grey lines are 95 % CI.

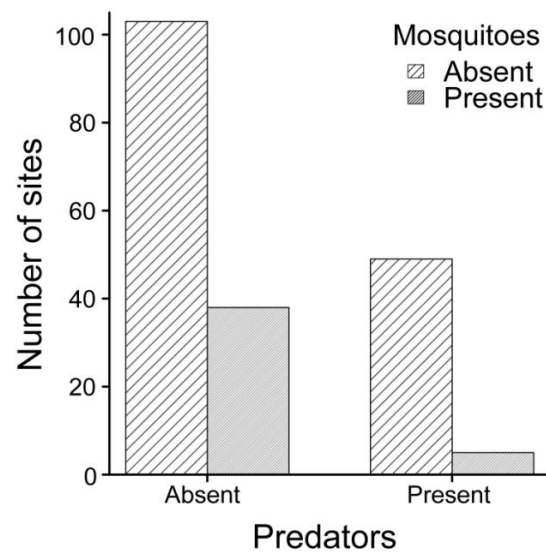


Figure 2.7. Number of habitats containing mosquitoes in relation to mosquito predator presence in a survey of 190 standing water habitats in Canterbury and Westland, New Zealand.

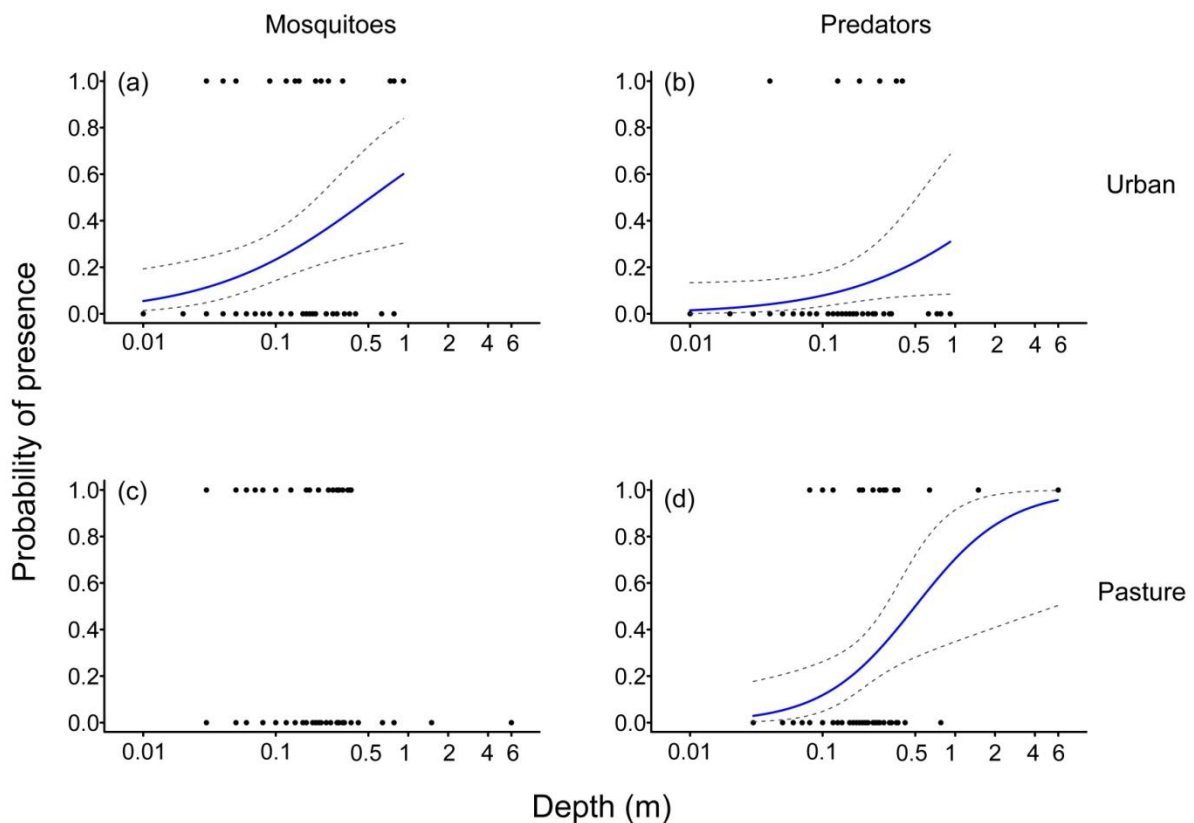


Figure 2.8. Probability of mosquito and predator presence at different depths in standing water habitats in a) and b) urban land uses and c) and d), pasture land uses. Plotted line indicated significant effect of depth on presence. Grey dashed lines are 95 % CI.

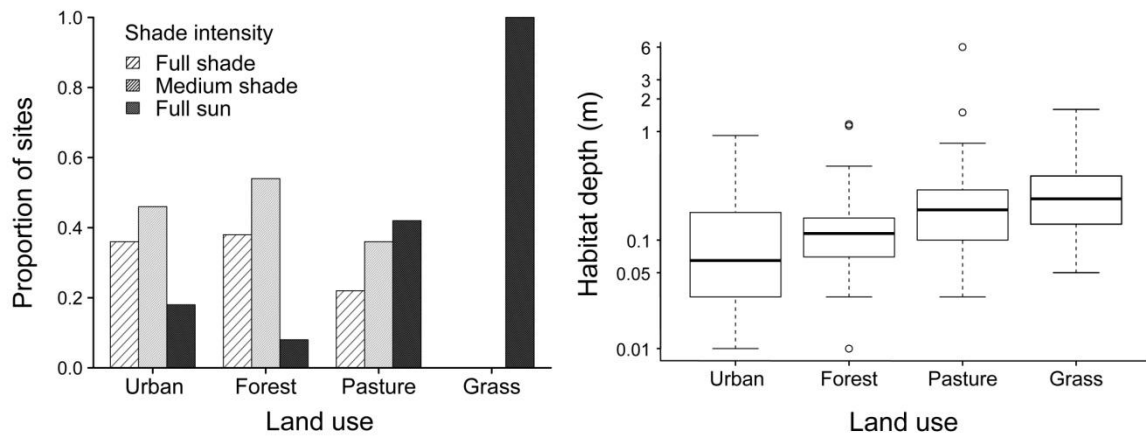


Figure 2.9. Shade intensity and habitat depth in four land-uses from a survey of 190 standing water habitats in Canterbury and Westland, New Zealand. Box and whisker plots show medians and ranges.

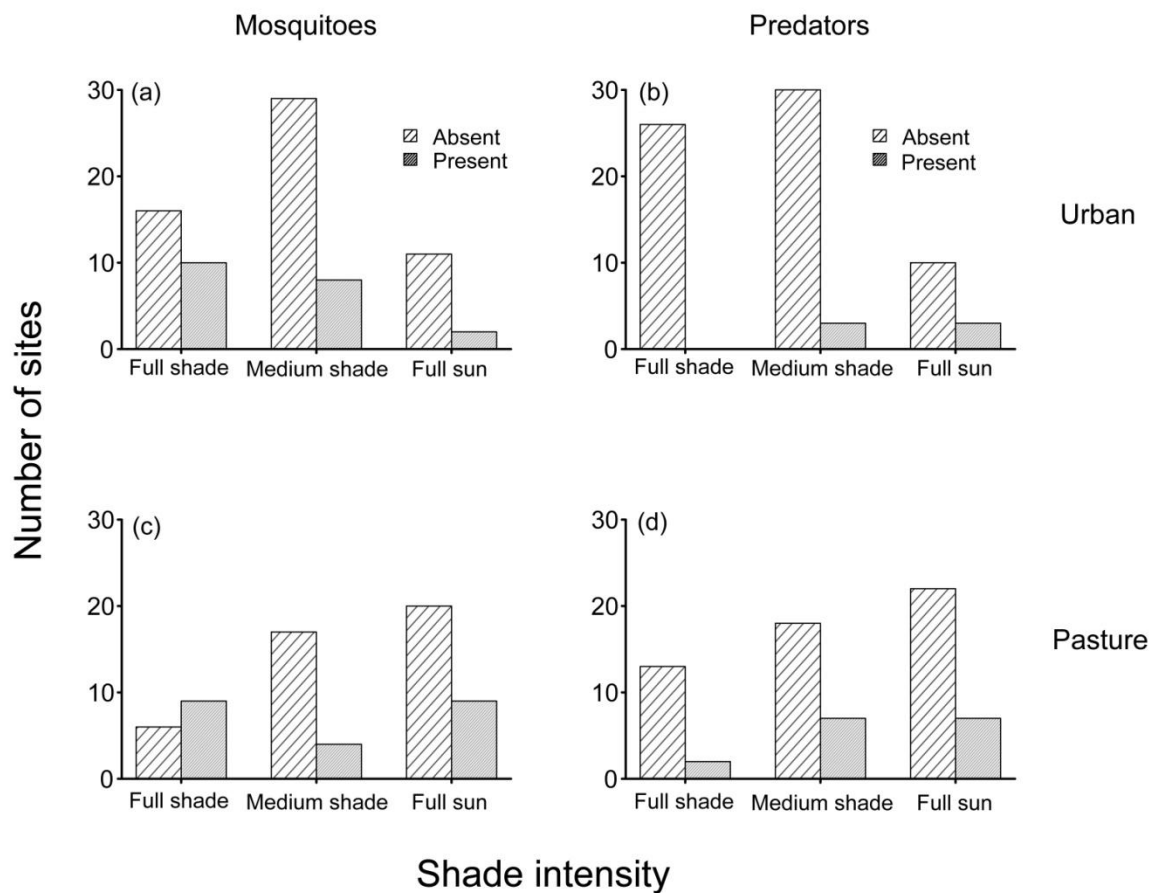


Figure 2.10. Frequency of habitats containing mosquitoes (a and c) and predators (b and d) in different shade intensities in standing water habitats in a) and b) urban land uses and c) and d), pasture land uses.

DISCUSSION

Land-use modification is altering natural ecosystems worldwide, and may increase invasion potential of important invaders in aquatic systems like mosquitoes. To investigate the importance of land use and associated abiotic characteristics on biotic control of communities potentially containing mosquitoes, I surveyed potential mosquito habitats in Canterbury and Westland, New Zealand. My hypothesis, that different land uses would contain different biotic communities, and that mosquitoes would be present in more simple communities with fewer predators, was supported by my results. Taxon richness was highest in natural land uses (forest and grassland), and lowest in more human-modified land uses (pasture and urban), and the opposite relationship was true for mosquitoes. Mosquitoes, both native and exotic, were almost entirely restricted to habitats in pasture and urban land uses. Within these habitats, habitat depth and shade intensity were important in determining mosquito presence likely via their effects on the predators of mosquitoes. These same abiotic characteristics had a strong influence on overall taxon richness and predator presence. Predators were more common in habitats in natural land uses, forest and tussock grassland, and less common in modified land uses, urban and pasture. This relationship with land use in-part driven by altered habitat depth and shade associated with the different types of aquatic habitat available in these areas.

Thus, overall the ultimate driver of mosquito distribution appeared to be land use and its associated high taxon richness and predator presence. Predation pressure is a known determinant of mosquito persistence in freshwater habitats (Murdoch et al. 1984), and predator presence was significantly greater in forest and grassland sites, compared to pasture and urban, with the opposite true for mosquitoes. My finding, that predator presence depended on habitat depth, supports other research indicating habitat size is an important influence on aquatic community structure (Greig 2008, McHugh et al. 2010, McHugh et al. 2015), but also highlights the importance of applying this knowledge in an invasion context. Because urban areas had smaller freshwater habitats than other land uses, the potential for invasion success of a mosquito species in urban areas is likely greater than in other land uses characterised by deeper or more permanent habitats. Moreover, shallower habitats are more likely to dry more often than deeper habitats (Brooks 2009), which can exclude species that need longer hydroperiods to complete their life cycles, such as many predatory aquatic invertebrates (Wissinger et al. 2009, Chapter 3). Because invasion potential can be dependent

on the top predator within a habitat (Murdoch et al. 1984, DeRivera et al. 2005), the altered habitat depths associated with changes in land use that I found will be an important influence on invasions. If habitat physical characteristics exclude predators, then they also increase the chance that an exotic species strongly affected by biotic interaction will successfully invade.

Habitat size is also important to biotic communities in freshwater systems because it affects community structure (McHugh et al. 2015), which could subsequently alter the invasion resistance of the community. Higher species diversity can increase invasion resistance of a community (Kennedy et al. 2002, Byers and Noonburg 2003, Pokorny et al. 2005). However, because community structure and diversity alter along habitat permanence gradients in aquatic systems, with increasing predator diversity associated with more permanent habitats (Poff et al. 1996, Wellborn et al. 1996, Greig 2008), the decreased habitat size and increased disturbances associated with modified land uses may mean food webs in urban and agricultural land uses are likely to be affected. For example, in drying streams McHugh et al. (2015) found smaller webs with shorter food chains, lower species diversity and fewer predators as streams got smaller. This has implications for biotic community in shallow habitats, such as those I found in urban land use, because they generally had lower taxon richness than large habitats. More permanent and larger habitats have, in general, greater species diversity than temporary habitats, and more food-web complexity, and this increased food-web complexity likely affects interaction strength between species (Greig 2008, McHugh et al. 2010, Greig et al. 2013, McHugh et al. 2015) possibly stabilising food webs.

Weak interactions can be stabilising factors in food-webs (May 1972, McCann 2000, Kokkoris et al. 2002, Greig et al. 2013), due to the presence of interactions such as intraguild predation and omnivory (Emmerson and Yearsley 2004, Sánchez-Carmona et al. 2012). The stability that is associated with large biotic communities with many weak interactions between species may thereby increase invasion resistance (Case 1990). My finding, that urban environments contain more shallow habitats than those in natural landscapes, and that these smaller habitats contained fewer taxa than larger habitats, show that these sort of food-web dynamics are likely to be highly relevant in modified urban systems where invasion risk is high. Increasing characteristics that promote large communities, such as increasing habitat depth of aquatic systems, may enhance the likelihood of more diverse communities that are more resistant to invasion and are more likely to contain predators.

Other physical factors were also important (e.g., shade) in driving the land-use affected patterns of biotic interactions which drove mosquito distribution. Shade was likely important for taxon richness, as well as predator and mosquito presence, because of the variety of biotic and abiotic factors it influences, including microbial decomposition, water temperature, evapotranspiration, and if generated by foliage cover, effects on terrestrial subsidies into the habitat (Thompson et al. 2012). Shade can also be an indicator of shelter from wind, which affects adult mosquito oviposition ability (Reiter 2001). Wind facilitates adult mosquito dispersal (Midega et al. 2012), but oviposition is not possible in sites that are too windy (Clements 1999). Thus, predators were present in a smaller proportion of shaded habitats than mosquitoes, especially in habitats located within urban land use. It is also likely that predators were limited from more shaded habitats in urban habitats, thereby increasing the potential for mosquitoes to persist.

Neither habitat depth nor shade intensity associated with land use fully explained predator presence. Predator presence was positively associated with habitat openness and depth, but while habitats in forest and pasture had similar depths, forest habitats were much more shaded. This pattern was likely driven by habitat characteristics that alter with shade, but were not measured, such as habitat productivity and terrestrial detritus input. These influences likely directly impact which invertebrate functional feeding groups are present (Cummins et al. 1989, Remor et al. 2013), and may also influence mosquito development. This is especially relevant where shade is generated by riparian cover, because riparian habitat regularly influences species composition within the freshwater habitat (Kennedy et al. 2000, Lecerf et al. 2005, Remor et al. 2013). For example, Yee and Juliano (2006) showed that mosquito development and competitive ability was affected by terrestrial subsidies, and that the relative proportion of leaf compared to insect food subsidy addition to the habitat was important. Thus, while there were likely strong land-use influences on mosquito presence due to altered predator-prey interactions this was not the whole story and other land-use related effects on mosquitoes were also likely to have contributed.

Another mechanism by which mosquito presence in habitats within forest and natural grassland land-uses may have been limited is through the lack of habitat connectivity. Habitat connectivity can limit invasive species distributions in both terrestrial and freshwater environments (Benjamin et al. 2007, Minor et al. 2009, Pilliod et al. 2013). Suitable standing water habitats in urban and pasture were often more common and evenly spread than those in

grassland and forest. Although there can be many habitats in one location in grassland and forest, these land uses often have greater distances between habitat complexes (S. Hunt, personal obs.). Unless carried by wind, adult mosquitoes are limited to short dispersal distances (Clements 2000), so any lack of habitat connectance may account for their absence, and this is an area that would benefit from further research.

Even though other physical characteristics associated with land use will be influential, biotic interactions between mosquitoes and their competitors and predators, and the effects of land use on these, will likely be of primary importance in determining their invasion success because they are very strong interactions. The two mosquito species found in my survey, while found in a similar range of habitat types (Figure 3c), only co-occurred in one habitat. Competition occurs between *Aedes* and *Culex* mosquitoes (Winters and Yee 2012, Yee and Skiff 2014), and likely explains this lack of co-occurrence. Moreover, for the five sites where predators were present together with mosquitoes, these co-occurrences only involved native *Cx. pervigilans*, and not exotic *Ae. notoscriptus* mosquitoes. Thus *Ae. notoscriptus* may be more vulnerable to predation than *Cx. pervigilans*. These observations highlight the importance of biotic interactions for mosquitoes, and were investigated further with experimental manipulation of predator-prey interactions (Chapter 3).

Overall, small pond communities, in part because they have more simple food webs, play an important role in biotic invasions, especially those involving mosquitoes. Pond communities worldwide are important sources of regional biodiversity (Biggs et al. 2005, Céréghino et al. 2013), but because of their small size and frequent drying regimes they typically have fewer species than larger habitats. This means the invasion potential of small ponds is greater than large habitats, especially for species such as mosquitoes that have life-histories adapted to frequent habitat drying (Norris 2004). Because higher species richness and the associated many weak trophic interactions are both mechanisms for community resistance to invasions, focusing habitat restoration efforts on maintaining water in small ponds will have the benefit of both increasing native biodiversity and decreasing the change of invasions of species such as mosquitoes. Public education about the potential for standing water habitats to support mosquito populations, combined with increased establishment of larger habitats that support predators, will also help to both decrease invasion potential and increase native biodiversity in these important habitats.

Finally, although my study has focused on mosquitoes, an important invader of small standing water habitats, it illustrates a more important general issue: habitat modification due to land-use change, which affects biotic interactions, can have a profound influence on biodiversity. In an era where multiple global changes are happening, there is a need to learn more about them and how biotic communities may respond. In general, habitat size changes which affect predators will be very important for both the spread of invasive species and the decline of native biodiversity.

LITERATURE CITED

- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51–57.
- Belkin JN. 1968. Mosquito studies (Diptera: Culicidae) VII. The Culicidae of New Zealand. *Contributions to the American Entomology Institute* 3: 1–182.
- Benjamin, J. R., J. B. Dunham, and M. R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. *Transactions of the American Fisheries Society* 136:875–888.
- Bennett, J. R., P. W. Dunwiddie, D. E. Giblin, and P. Arcese. 2012. Native versus exotic community patterns across three scales: roles of competition, environment and incomplete invasion. *Perspectives in Plant Ecology, Evolution and Systematics* 14:381–392.
- Biggs, J., P. Williams, M. Whitfield, P. Nicolet, and A. Weatherby. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15:693–714.
- Blackburn, T. M., T. A. A. Prowse, J. L. Lockwood, and P. Cassey. 2013. Propagule pressure as a driver of establishment success in deliberately introduced exotic species: fact or artefact? *Biological Invasions* 15:1459–1469.
- Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change* 95:469–483.
- Byers, J. E., and E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84:1428–1433.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the United States of America* 87:9610–9614.

- Céréghino, R., D. Boix, H.-M. Cauchie, K. Martens, and B. Oertli. 2013. The ecological role of ponds in a changing world. *Hydrobiologia* 723:1–6.
- Chapman, A., M. H. Lewis, and M. J. Winterbourn. 2011. Guide to the freshwater crustacea of New Zealand. New Zealand Freshwater Sciences Society, Christchurch, New Zealand. 188p.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104:17430–4.
- Clements, A.N. 1999. *The Biology of Mosquitoes, Vol. 2: Sensory Reception and Behavior*. CABI Publishing, New York.
- Clements, A.N. 2000. *The biology of mosquitoes: sensory reception and behaviour*. Wallingford, UK: CABI Publishing.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and Riparian Vegetation. *BioScience* 39:24–30.
- Dauphin, G., S. Zientara, H. Zeller, and B. Murgue. 2004. West Nile: Worldwide current situation in animals and humans. *Comparative Immunology, Microbiology and Infectious Diseases* 27:343–355.
- DeRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364–3376.
- Derraik, J. G. B., and C. H. Calisher. 2004. Is New Zealand prepared to deal with arboviral diseases? *Australian and New Zealand Journal of Public Health* 28:27–31.
- Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22:489–96.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews of the Cambridge Philosophical Society* 81:163–82.
- Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.
- Emmerson, M., and J. M. Yearsley. 2004. Weak interactions, omnivory and emergent food-web properties. *Proceedings of the Royal Society B* 271:397–405.
- González-Moreno, P., J. M. Diez, D. M. Richardson, and M. Vilà. 2015. Beyond climate: disturbance niche shifts in invasive species. *Global Ecology and Biogeography* 24:360–370.

- Greig, H. S. 2008. Community assembly and food web interactions across pond permanence gradients. PhD Thesis, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand.
- Greig, H. S., S. A. Wissinger, and A. R. McIntosh. 2013. Top-down control of prey increases with drying disturbance in ponds: a consequence of non-consumptive interactions? *The Journal of Animal Ecology* 82:598–607.
- Griffiths, J. I., P. H. Warren, and D. Z. Childs. 2014. Multiple environmental changes interact to modify species dynamics and invasion rates. *Oikos*:1EV–11EV.
- Gubler, D. J. 2002. The global emergence/resurgence of arboviral diseases as public health problems. *Archives of Medical Research* 33:330–342.
- Hogg, B. N., and K. M. Daane. 2013. Contrasting landscape effects on species diversity and invasion success within a predator community. *Diversity and Distributions* 19:281–293.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–8.
- Kennedy, T. B., A. M. Merenlender, and G. L. Vinyard. 2000. A comparison of riparian condition and aquatic invertebrate community indices in central Nevada. *Western North American Naturalist* 60:255–272.
- Klecka, J., and D. S. Boukal. 2012. Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PloS ONE* 7:e37741.
- Kokkoris, G. D., V. A. A. Jansen, M. Loreau, and A. Y. Troumbis. 2002. Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology* 71:362–371.
- Laird, M. 1988. The natural history of larval mosquito habitats. Academic, San Diego, CA.
- Lecerf, A., M. Dobson, C. K. Dang, and E. Chauvet. 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* 146:432–442.
- Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15:904–910.
- Lowe, S., M. Browne, S. Boudjclass, and M. De Poorter. 2000. 100 of the world's worst invasive alien species. Page 12 Published by The Invasive Species Specialist Group ISSG a specialist group of the Species Survival Commission SSC of the World Conservation Union IUCN 12pp First published as special liftout in Aliens.
- Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. *Environmental Conservation* 29:134–153.

- Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14:313–23.
- May, R. M. 1972. Will a large complex system be stable? *Nature* 238:413–414.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* 405:228–233.
- McHugh, P. a., A. R. McIntosh, and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters* 13:881–890.
- McHugh, P. A., R. M. Thompson, H. S. Greig, H. J. Warburton, and A. R. McIntosh. 2015. Habitat size influences food web structure in drying streams. *Ecography* 37:1EV–13EV.
- Melbourne, B. A., H. V Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H. Yokomizo. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10:77–94.
- Midega, J. T., D. L. Smith, A. Olotu, J. M. Mwangangi, J. G. Nzovu, J. Wambua, G. Nyangweso, C. M. Mbogo, G. K. Christophides, K. Marsh, and P. Bejon. 2012. Wind direction and proximity to larval sites determines malaria risk in Kilifi District in Kenya. *Nature Communications* 3:674.
- Minor, E. S., S. M. Tessel, K. A. M. Engelhardt, and R. Todd. 2009. The Role of Landscape Connectivity in Assembling Exotic Plant Communities : A Network Analysis. *Ecology* 90:1802–1809.
- Murdoch, W. W., M. A. Scott, and P. Ebsworth. 1984. Effects of the general predator, *Notonecta* (Hemiptera) upon a freshwater community. *Journal of Animal Ecology* 53:791–808.
- Nolen, M. S., D. D. Magoulick, R. J. DiStefano, E. M. Imhoff, and B. K. Wagner. 2014. Predicting probability of occurrence and factors affecting distribution and abundance of three Ozark endemic crayfish species at multiple spatial scales. *Freshwater Biology* 59:2374–2389.
- Norris, D. E. 2004. Mosquito-borne diseases as a consequence of land use change. *EcoHealth* 1:19–24.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens and H. Wagner. 2013. *vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Pilliod, D. S., R. S. Arkle, and B. A. Maxell. 2013. Persistence and extirpation in invaded landscapes: Patch characteristics and connectivity determine effects of non-native predatory fish on native salamanders. *Biological Invasions* 15:671–685.
- Pimm, S. L. 2009. Climate disruption and biodiversity. *Current Biology* 19:R595–601.

- Poff, N. L., S. Tokar, and P. Johnson. 1996. Stream hydrological and ecological responses to climate change assessed with an artificial neural network. *Limnology and Oceanography* 41:857–863.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:448–459.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reiter, P. 2001. Climate change and mosquito-borne disease. *Environmental Health Perspectives* 109:141–161.
- Remor, M. B., C. Santos, S. C. Sampaio, L. F. Sgarbi, and M. Sorace. 2013. The effects caused by the replacement of native riparian forest with *Eucalyptus* sp. on the benthic macro-invertebrate community. *Journal of Food, Agriculture and Environment* 11:1444–1448.
- Romanuk, T. N., Y. Zhou, U. Brose, E. L. Berlow, R. J. Williams, and N. D. Martinez. 2009. Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364:1743–54.
- Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–4.
- Sánchez-Carmona, R., A. Rodríguez-Ruiz, L. Encina Encina, M. V. Rodríguez-Sánchez, and C. Granado-Lorencio. 2012. Consequences of species grouping for food web structure. *Applied Ecology and Environmental Research* 10:333–347.
- Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater for protected areas: strategies conservation. *Conservation Biology* 16:30–41.
- Semenza, J. C., B. Sudre, J. Miniota, M. Rossi, W. Hu, D. Kossowsky, J. E. Suk, W. Van Bortel, and K. Khan. 2014. International dispersal of dengue through air travel: importation risk for Europe. *PLoS Neglected Tropical Diseases* 8:e3278.
- Shurin, J. B., J. L. Clasen, H. S. Greig, P. Kratina, and P. L. Thompson. 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367:3008–17.
- Srivastava, D. S., M. K. Trzcinski, B. A. Richardson, and B. Gilbert. 2008. Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. *The American naturalist* 172:761–71.
- Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning. *Ecology letters* 15:1199–210.

- Thompson, R. M., J. A. Dunne, and G. Woodward. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology* 57:1329–1341.
- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137–148.
- Urban, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology* 85:2971–2978.
- Weaver, J. E., T. M. Conway, and M.-J. Fortin. 2012. An invasive species' relationship with environmental variables changes across multiple spatial scales. *Landscape Ecology* 27:1351–1362.
- Wellborn, G. a., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Winterbourn, M. J., K. L. D. Gregson, and C. H. Dolphin. 2006. Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand* 14:108 p.
- Winters, A. E., and D. A. Yee. 2012. Variation in performance of two co-occurring mosquito species across diverse resource environments: insights from nutrient and stable isotope analyses. *Ecological Entomology* 37:56–64.
- Wissinger, S. A., H. Greig, and A. McIntosh. 2009. Absence of species replacements between permanent and temporary lentic communities in New Zealand. *Journal of the North American Benthological Society* 28:12–23.
- Yee, D. A., and S. A. Juliano. 2006. Consequences of detritus type in an aquatic microsystem: effects on water quality, micro-organisms and performance of the dominant consumer. *Freshwater biology* 51:448–459.
- Yee, D. A., and J. F. Skiff. 2014. Interspecific competition of a new invasive mosquito, *Culex coronator*, and two container mosquitoes, *Aedes albopictus* and *Cx. quinquefasciatus* (Diptera: Culicidae), across different detritus environments. *Journal of Medical Entomology* 51:89–96.
- Yeiser, J. M., and S. C. Richter. 2015. Microhabitat conditions influence mesohabitat associations and distribution of larval salamanders in headwater streams. *Hydrobiologia*. Article in Press.
- Zacharias, I., and M. Zamparas. 2010. Mediterranean temporary ponds. A disappearing ecosystem. *Biodiversity and Conservation* 19:3827–3834.

Chapter three: Climate change mediates mosquito success by affecting life history and predation dynamics

INTRODUCTION

Global-change drivers such as climate change, urbanisation, and biotic invasions are increasingly altering natural ecosystems and may interact, generating unexpected outcomes for biological communities (Sala et al. 2000, Didham et al. 2007, IPCC 2014). The most recent decade (2001 – 2010) was the warmest on record (WMO 2013), and mean global temperature is predicted to increase approximately 1 - 3.5°C by the end of the century (Dukes and Mooney 1999, IPCC 2014). Moreover, climate change will increase the likelihood of weather extremes such as droughts, heat waves, severe storms and floods, which are predicted to increase in frequency, intensity and duration (MfE 2008, Pimm 2009, Diez et al. 2012, WMO 2013, IPCC 2014). To manage both native species decline and invasive species spread it is imperative to accurately predict how these climate changes affect biotic communities at risk of invasion (Didham et al. 2007). Making local predictions about extreme climatic events is difficult, and natural climate variability caused by events such as El Niño-Southern Oscillation (ENSO) make predicting ecological responses to climate change even more challenging (Pall et al. 2006, Pimm 2009, WMO 2013). Climate predictions for New Zealand show large inter-regional variability in both temperature and precipitation, so making accurate predictions about climate effects on biological communities will require consideration of this variability (Heino et al. 2009).

Climate change will affect ecosystems at multiple levels, from changing behaviour, size and life history of individual species (Dossena et al. 2012, Vaz-Pinto et al. 2013, Mas-Martí et al. 2014), to whole community changes, by altering nutrient cycling and trophic cascades (Walther 2010, Greig et al. 2012, Kratina et al. 2012, Dossena et al. 2012). These changes can result in a variety of complex effects on ecosystems, such as range shifts, creating novel species interactions (Greig et al. 2012, Dossena et al. 2012, Gallardo and Aldridge 2013), and altering native community resilience to disturbances (Macdougall and Turkington 2005). Climate change will influence all ecosystems, but freshwater systems are particularly vulnerable to predicted changes in precipitation and temperature (Heino et al. 2009, Sorte 2013). Altered freshwater habitat size, availability and conditions will directly influence the

biotic communities in those habitats (Norris 2004, Thompson and Townsend 2005, McHugh et al. 2015), and in particular, lentic systems that rely on rainfall rather than groundwater inputs will be more sensitive to changes in climate than other freshwater systems (Bates et al. 2008, Brooks 2009).

Understanding how communities respond to climate-driven habitat changes is important, because it may mediate the success of an invader. This is particularly relevant in freshwater systems because not only are they vulnerable to climate change, but they also have high rates of biotic invasions (Dukes and Mooney 1999, Sala et al. 2000, Melbourne et al. 2007). A wealth of evidence shows that climate plays an important role in mediating invasion, especially through increased weather extremes and habitat modification that accompanies such events. Moreover, freshwater systems are more sensitive to the combined pressures of climate change and biotic invasions than terrestrial ecosystems (Sala et al. 2000, Rahel and Olden 2008, Heino et al. 2009, Diez et al. 2012, Bennett et al. 2012, Sorte 2013). For example, Sorte et al. (2013) found that in terrestrial systems, native and non-native species responded similarly to environmental changes, whereas in aquatic systems non-native species had increased performance compared with native in increased temperature and CO₂ scenarios. Furthermore, Rahel and Olden (2008) found that while warming can increase growth rates in temperate systems, it may also exacerbate drought in more arid systems, promoting drought-tolerant species. These examples show that not only will climate change likely result in an increase in invasion success, but subsequent effects will likely be more pronounced in freshwater than terrestrial systems.

New Zealand has a disproportionately large number of exotic species due to both deliberate and accidental introductions (Atkinson and Cameron 1993, Laird 1995, Lee et al. 2008, Norton 2009). Some of these species are beneficial to humans, but a vast majority have resulted in losses to native flora and fauna (Atkinson and Cameron 1993, Norton 2009). Because invasion is an ongoing process, understanding how local communities respond to invaders is important. Of particular importance are invaders that carry human disease, such as mosquitoes (Derraik and Calisher 2004, Strayer 2012). Globally mosquitoes vector a range of serious human diseases, including dengue fever, Ross River virus, West Nile virus and chikungunya fever, and risk of infection is increasing in many areas (Gubler 2002, Dauphin et al. 2004, Charrel et al. 2007). New Zealand has twelve native and three exotic mosquitoes, none of which currently are vectors for serious human diseases in New Zealand (Weinstein et al. 1997). However, as was shown by the invasion and subsequent eradication of the salt

marsh mosquito, *Aedes camptorhynchus*, and interceptions of many more non-native mosquitoes at ports, the likelihood that countries like New Zealand will receive more mosquito invaders is high (Weinstein et al. 1997, Disbury et al. 2008, Disbury and Cane 2011). Because mosquitoes spend the early stages of their life cycle in standing water habitats, identifying how factors which mediate mosquito invasions alter with climate in these habitats is integral to understanding mosquito invasion risk.

Both habitat drying and warming are likely to alter the potential for invasion of freshwater habitats, but effects of warming have received significantly more attention than habitat drying (Walther 2010, Dossena et al. 2012, Kratina et al. 2012, Strayer 2012, Vaz-Pinto et al. 2013, but see Chase 2007, Greig et al. 2013, Strachan et al. 2014). Examining both short- and long-term drying in these systems is important, because short-term drying affects prey density, habitat size and duration, resource availability and water chemistry, and alters encounter rates between predators and their prey (Brooks 2009, Greig et al. 2013, Strachan et al. 2014), while long-term drying, or drought, can remove the habitat entirely, affecting which species can persist (Wissinger et al. 2009). For freshwater habitats that have the potential to dry, such as temporary and semi-permanent ponds, and artificial habitats (e.g. stock water containers and urban rubbish), intra-annual rainfall variability will likely play a more important role in determining the duration of the habitat than will mean annual rainfall. New Zealand's climate already results in more unpredictable hydroperiods than other, well-studied areas such as North America and Europe (Schneider et al. 2014, Wellborn et al. 1996, Brooks 2009, Greig 2008, MfE 2008). Moreover, climate models for New Zealand predict increasing inter- and intra-regional variability in precipitation, meaning that what is already a variable, unpredictable system will likely become more so (MfE 2008, IPCC 2013). Smaller water volumes also experience greater temperature fluctuations, with potential for higher upper temperatures and lower cold temperatures than do larger water volumes (Carrington et al. 2013). Thus, New Zealand's high invasion rates of exotic species and unpredictable hydroperiods make its ponds and other small water bodies particularly vulnerable under global climate change.

Examining predator-prey interactions, especially those involving invaders, will help reveal how these freshwater communities will be affected by climate change (Dukes and Mooney 1999, Rall et al. 2010, Thompson et al. 2012). Climate change will affect species in different ways, such as by directly affecting species' metabolism, or indirectly affecting species through altered habitat characteristics (Lang et al. 2012, Rall et al. 2012, Wagner et al. 2013).

These changes to individual organisms will subsequently alter interactions between species, which will affect whole community dynamics, including the community's response to an invader (Rahel and Olden 2008, Walther et al. 2009). These changes are likely to be most identifiable as changes in predator-prey interactions, such as altered consumption rates (Rall et al. 2012, Wagner et al. 2013), prey handling time (Lang et al. 2012), and encounter rates (Rall et al. 2012). Because climate change will alter predator-prey interactions both directly, through climate effects on habitats, and indirectly, through altered prey life-history strategies (van Uitregt et al. 2013), it will be important to consider both direct and indirect mechanisms determining the outcome of climate change on predator-prey interactions, and therefore communities.

To unravel effects of both short- and long- habitat drying and warming on biotic interactions potentially affecting mosquitoes, I conducted two predator-prey experiments involving native (*Culex pervigilans*) and exotic (*Aedes notoscriptus*) mosquitoes and their invertebrate predators. Backswimmers (*Anisops wakefieldi*), damselfly nymphs (*Austrolestes colenisonis*) and dragonfly nymphs (*Procordulia smithii*) all prey on mosquito larvae in freshwater habitats (Graham 1939, Zuharah and Lester 2010, Klecka and Boukal 2012), and were chosen for this study because they vary in habitat drying tolerance (Greig 2008, Wissinger et al. 2009). Backswimmers are found in a large range of freshwater habitats, from very temporary to permanent, whereas *A. colenisonis* are rarer in temporary compared to permanent habitats (Greig 2008, Wissinger et al. 2009). *P. smithii* are restricted to even more permanent habitats (Wissinger et al. 2009; Fig. 3.1). Thus, altered precipitation regimes predicted for New Zealand will likely alter the distributions of these predatory insects by changing the proportion of temporary to permanent habitats, thereby affecting the potential for predator-prey interactions involving these species to affect mosquito invasion success.

The two mosquito species I chose for these experiments, *Cx. pervigilans* and *Ae. notoscriptus*, were selected to allow comparison of native and exotic mosquito species' responses to climate change and associated effects on species interactions. The two species have similar habitat preferences and are the most common mosquitoes in New Zealand (Laird 1995, Derraik 2005a, Derraik and Slaney 2007). However, while native *Cx. pervigilans* mosquitoes have evolved in the variable New Zealand climate with both frequent rainfall and drying events, exotic *Ae. notoscriptus* have invaded from Australia, where in most regions periods between rainfall events are typically longer than in New Zealand (Williams and Rau 2011, van Uitregt et al. 2013). Thus, I predicted that introduced *Ae. notoscriptus* mosquitoes

may more successfully respond to habitat drying than *Cx. pervigilans* by altering behaviour and growth rate (Williams and Rau 2011, Melbourne et al. 2007). I also predicted that native and introduced mosquito larvae would respond differently to the combined pressures of temperature change, habitat drying and predation, with overall success, or emergence, of *Ae. notoscriptus* being greater than that of *Cx. pervigilans*.

METHODS

Experimental design

Experiment One: Drying

Firstly, I conducted a mesocosm experiment to investigate the effects of both short- and long-term drying on vulnerability of exotic *Ae. notoscriptus* and native *Cx. pervigilans* mosquito larvae to predation by *P. smithii* dragonfly larvae, *A. colenisonis* damselfly larvae and *A. wakefieldi* backswimmers. These predators were selected to represent predation pressures experienced in temporary, semi-temporary and semi-permanent habitats. Short-term drying was simulated by applying three different drying rates: no drying, slow and fast drying, to the mesocosms.

Each mesocosm contained one predator (either *P. smithii*, *A. colenisonis* or *A. wakefieldi*), and either 100 *Cx. pervigilans* or 100 *Ae. notoscriptus* (instars two to four, identified using the Belkin (1968) key). Drying was manipulated twice a day, with the slow drying treatments losing one litre of water per day, and the fast drying two litres per day. The fast drying treatments finished the experiments with two litres of water left, because the aim was to investigate the effects of drying, not drought, on the interaction between the predators and their prey. Water level was manipulated by altering the angle of a pipe that drew water from the bottom of the experimental container (Fig. 3.2a & b). Habitat structure was included in each mesocosm to allow refuges for both *Ae. notoscriptus* and *Cx. pervigilans* (rocks and plastic aquarium plants).

One replicate of all predator combinations was run at a time, including a predator-free control for each drying and mosquito species combination, with a total of four replicates of all treatment combinations conducted in total. Predators were starved for 24 hours prior to the

experiment, and both predators and prey were acclimatised for one hour in closed containers before being released into the mesocosm. Based on a preliminary trial which measured predator satiation at different prey densities, 100 prey was selected as the optimum prey density for this experiment to ensure that predation rate was not affected by changes in encounter rate over time.

Experimental mesocosms were 24 15-L plastic containers, containing 12 L water, including a 2-L microorganism inoculum (water collected from artificial container habitats containing mosquito larvae and detritus filtered through a 40- μ m sieve). Two crushed pellets of rabbit food (Weston Milling Stock feed) were added to the water 24 hours prior to the experiment as an additional food for mosquito larvae.

All predators were collected from the Groynes Recreation Reserve, Christchurch, New Zealand (43°27'01.88"S, 172°36'20.32"E), through repeated D-net (1-mm mesh) sweeps in the littoral zone. Second to fourth instar larvae of the two species of mosquito, *Ae. notoscriptus* and *Cx. pervigilans*, were collected in a range of locations in the Christchurch area using targeted D-net or aquarium net (< 1 mm mesh) sweeps. First instar larvae are difficult to identify to species so were not used.

The experiment was set up outside in an enclosure on the University of Canterbury campus, in Christchurch, New Zealand (43°31'22.77"S, 172°34'59.21"E). Because mesocosms were subject to diurnal temperature and light fluctuations, I measured light intensity and temperature hourly for the duration of the experiment, using data loggers (Onset HOBO pendant loggers UA-002-64, Bourne, MA, USA).

Adult mosquitoes were removed daily using an aspirator for the six day experiment. At the conclusion of the experiment dead mosquito larvae, pupae, live larvae and adults were counted. Larvae and pupae were stored in 70% ethanol, and adults were frozen. Each individual predator was photographed and measured, then released back to original habitat (although samples of the predators were kept to verify identification).

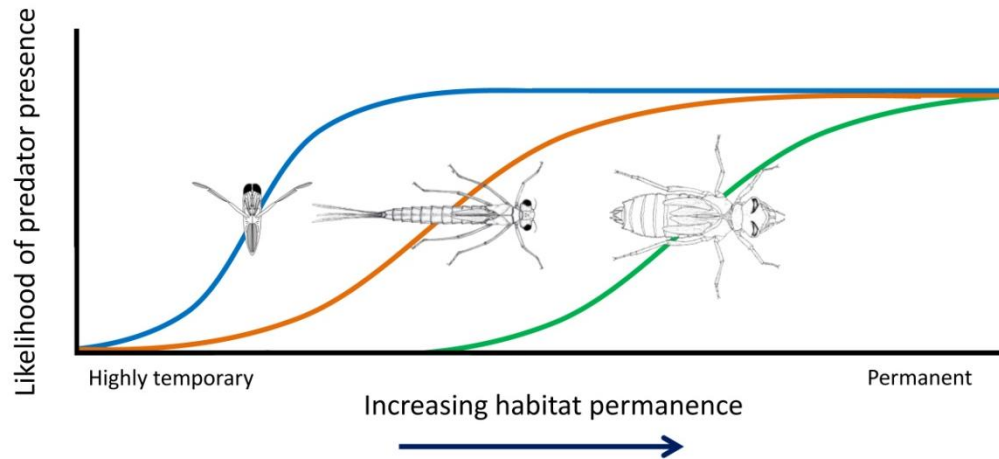


Figure 3.1. Established habitat permanence requirements for three predatory invertebrates, *A. wakefieldi* backswimmer, *A. colenisonis* damselfly, and *P. smithii* dragonfly, based on Wissinger et al. (2009). Highly temporary habitats dry at least annually, and permanent habitats do not dry, and increasing lentic freshwater habitat permanence is associated with greater predator diversity (Greig 2008, Wissinger et al. 2009).

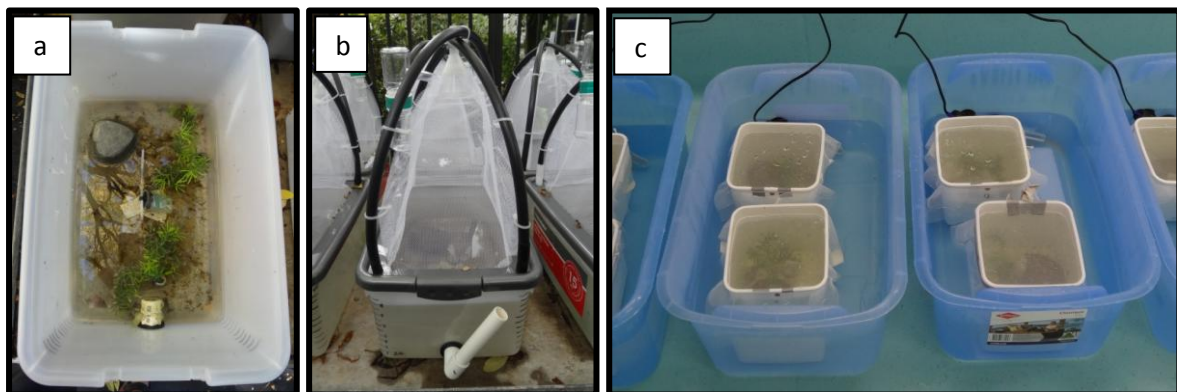


Figure 3.2. Experimental mesocosm containers showing a) habitat structure and HOBOT data logger in a fast-drying container at the end of the drying experiment, b) mesocosm with pipe to release water and emergence trap to catch adult mosquitoes, and c) water baths containing mesocosms for the warming experiment, with aquarium heaters to provide warming.

Experiment two: Warming

To further investigate the effect of temperature on the interaction between the predatory *A. wakefieldi* found in the most temporary habitats and the two mosquito species, I conducted a habitat-warming experiment. Experimental mesocosms were constructed from 15 five-litre

ice-cream containers containing 4.5 L tap water, each including a 1-L microorganism inoculum and one pellet of rabbit food (Weston Milling Stock feed). The mesocosms were set up in a temperature control room (photoperiod LD 14 : 10 hours, 13 °C) at the University of Canterbury, Christchurch, NZ, where containers were placed in water baths heated using an aquarium heater (Aqua One, 100-W Heater, Australia). Each bath contained two mesocosms, one with a predator and one predator-free control (Fig. 3.2c). Five temperatures, each with three replicates, were targeted (12, 20, 22, 26 and 30 °C). Due to the variability in the room (proximity to fan, door and heaters), actual mean temperatures had a range evenly spread from 13.5 °C to 30.4 °C. Thus, instead of three replicates at four levels we had a continuous temperature gradient. Habitat structure (rocks and plastic aquarium plants) was included to provide refuges for both *Ae. notoscriptus* and *Cx. pervigilans*.

Each mesocosm contained one predatory *A. wakefieldi* and 25 *Cx. pervigilans* and 25 *Ae. notoscriptus* mosquito larvae as prey. Predators were starved for 24 hours prior to the experiment, and both predators and prey were acclimatised for one hour in closed containers before being released into the mesocosm. After 48 hours, the number of dead mosquito larvae, pupae, live larvae and adults was counted. Larvae were counted and stored in 70% ethanol, and adults frozen. Remaining pupae were kept and reared to adult stage, where they were identified to species using the key of Belkin (1968).

Statistical analyses

For the drying experiment, the effects of three categorical (drying rate, predator identity and mosquito species) and one continuous covariate (mean temperature) on predation and mosquito pupation rates were analysed in a fully factorial design using analyses of variances. After removing any non-significant interactions I conducted homogeneity of slopes tests followed by either analyses of covariance (ANCOVA), for non-significant interactions, or individual regressions, where interactions were significant. For the significant three-way interaction I conducted three separate sets of analyses on the three predator treatments, with subsequent homogeneity of slopes tests and either ANCOVA or individual regressions. Two blocks experienced unusually cold temperatures well outside the range of the other blocks, so were therefore excluded from the model (Table 3.1).

Due to low adult emergence, the number emerged was added to the number of pupae, hereafter referred to just as pupae. Although predators do prey on pupae as well as larvae,

pupation is often used as a measure of adult productivity, being the penultimate stage before adult emergence (Leisnham et al. 2005). Therefore, I refer to ‘pupae’ as the total number of pupae plus total number of adults.

Because I was interested in determining how pupation rates altered both additively and independently of predation rate in changing conditions, I conducted my analyses using both the final counts of both pupae (‘pupation rate’) and using responses adjusted to account for changes in mosquito abundance due to predation (‘adjusted pupation rate’). Adjusted pupation rate was calculated as

$$Pup_A = \frac{n\ pup}{(n\ pup + n\ larv)}$$

where Pup_A is the adjusted pupation rate for each mesocosm, $n\ pup$ the number of pupae, and $n\ larv$, the number of larvae remaining at the end of the experiment.

To confirm normality and homogeneity of variances of response variables Levene tests and Shapiro-Wilk tests were conducted and qqnorm plots of all models were created. All responses in the drying experiment met the assumptions of normality and homogeneity of variances.

For the warming experiment, the effect of *A. wakefieldi* backswimmer predator on predation and pupation rates of *Ae. notoscriptus* and *Cx. pervigilans* at different temperatures was analysed using analyses of variance involving homogeneity of slopes tests followed by either analyses of covariance (ANCOVA), for non-significant interactions, or individual regressions, where interactions were significant. Levene tests and Shapiro-Wilk tests were conducted to assess variances from normality and heterogeneity of responses, and where responses did not meet normality or homogenous variances (‘predation rate’ and ‘adjusted pupation rate’) they were transformed using an arcsine square root transformation. Blocking was not deemed necessary, as the only significant variability in the room was temperature, which was included in the statistical analyses. All statistical analyses were performed in the programme ‘R’ version 3.1.1 (R Core Team 2014).

Table 3.1. Total replicates in each level of microcosm experiment after removal of cold blocks

	No drying		Slow drying		Fast drying	
	<i>Cx. pervigilans</i>	<i>Ae. notoscriptus</i>	<i>Cx. pervigilans</i>	<i>Ae. notoscriptus</i>	<i>Cx. pervigilans</i>	<i>Ae. notoscriptus</i>
<i>Austrolestes</i>	4	3	4	3	4	3
<i>Anisops</i>	4	3	4	2	4	3
<i>Procordulia</i>	4	3	4	3	4	2

RESULTS

Experiment One: Drying, predator type and mosquito species

In Experiment One, the number of mosquito larvae consumed by predators was influenced by a three-way interaction between predator identity, mosquito species and average temperature (Fig. 3.3; Table 3.2a), but there was no effect of drying on predation rate (Table 3.2a). Subsequent analyses indicated this three-way interaction occurred because the effects of mosquito species and temperature changed according to predator. *P. smithii* consumed a greater number of mosquito larvae than either *A. colenisonis* or *A. wakefieldi* (predator main effect Table 3.2a), but consumption increased with temperature and was similar for the two mosquito species (Fig. 3.3a; ANCOVA of *P. smithii* expts: temperature, $F_{1, 15} = 16.34$, $p = 0.001$; species: $F_{1, 15} = 0.03$, $p = 0.863$). *Austrolestes colenisonis*, on the other hand, consumed slightly greater numbers of *Ae. notoscriptus* than *Cx. pervigilans*, with consumption of both increasing with temperature (Fig. 3.3b; ANCOVA of *A. colenisonis* expts: temperature, $F_{1, 15} = 18.96$, $p < 0.001$; species: $F_{1, 15} = 4.85$, $p = 0.044$). Finally, *A. wakefieldi* consumption of *Ae. notoscriptus* increased with temperature, but consumption of *Cx. pervigilans* did not change with temperature (Fig. 3.3c; homogeneity of slopes test, $F_{1, 14} = 8.67$, $p = 0.011$; *Cx. pervigilans* liner regression: $F_{1, 10} = 1.04$, $p = 0.332$; *Ae. notoscriptus* linear regression: $F_{1, 6} = 16.19$ $p = 0.007$). Thus, each predator had a different pattern of interaction with temperature and mosquito species, and consistently no effect of drying.

The number of mosquito larvae to pupate (adjusted) depended mostly on mean temperature, and an interaction between mosquito species and drying rate (Table 3.2b). Although there was a significant drying \times mosquito species interaction, this had relatively little effect on pupation rates (Fig. 3.4). Tukey HSD post-hoc tests showed that drying rate did not significantly affect adjusted pupation rates for either *Cx. pervigilans* or *Ae. notoscriptus*. The

significant interaction appears to be driven by the slight but not significant decrease of *Ae. notoscriptus* pupation rate, and the slight but not significant increase of *Cx. pervigilans* pupation at slow drying rates (Fig. 3.4).

In a separate analysis considering mosquito species and temperature, *Ae. notoscriptus* pupated at faster rates than *Cx. pervigilans*, with similar increases in pupation rates associated with temperature in both species (ANCOVA: temperature: $F_{1, 53} = 8.94$. $p = 0.004$; mosquito sp.: $F_{1, 53} = 259.42$, $p < 0.001$; Fig. 3.5a).

The number of pupae remaining at the end of the experiment (i.e. unadjusted) depended only on mosquito species, with *Ae. notoscriptus* pupating at significantly faster rates than *Cx. pervigilans* (Fig. 3.2b; Table 3.2c). Thus, predator identity, drying rate and mean temperature all had no effect on overall, unadjusted for predation, pupation rate, but mosquito species had a large influence (Table 3.2c).

Table 3.2. Results of analyses of variance on a) predation rate, b) adjusted pupation rate and c) pupation rate of *Ae. notoscriptus* and *Cx. pervigilans* mosquitoes (mosquito sp., categorical treatment) subjected to predation by *A. wakefieldi*, *A. colensonis* and *P. smithii* predators (Predator treatment, categorical treatment) over a six day mesocosm experiment in which temperature varied (mean temp, continuous covariate). Pupation rate is final number of pupae, and adjusted pupation is rate adjusted for predation. *P* values < 0.05 are indicated with *.

a) Predation rate

Variable	MS	df	F	<i>P</i> value
Predator type	691.72	2	23.22	< 0.001 *
Mean temperature	847.07	1	28.43	< 0.001 *
Drying rate	11.29	2	0.38	0.687
Mosquito species	11.62	1	0.39	0.535
Mosquito species × Mean temp	11.53	1	0.39	0.537
Mosquito species × Predator	115.07	2	3.86	0.028 *
Mean temperature × Predator	64.34	2	2.16	0.127
Mean temp × Mosquito sp. × Predator	147.63	2	4.96	0.011 *
Error	29.79	46		

b) Adjusted pupation rate

Variable	MS	df	F	<i>P</i> value
Predator type	0.008	2	1.59	0.214
Mean temperature	0.051	1	9.75	0.003 *
Drying rate	0.003	2	0.50	0.611
Mosquito species	1.492	1	283.12	< 0.001 *
Mosquito species × Drying	0.018	2	3.42	0.040 *
Error	0.005	51		

c) Pupation rate

Variable	MS	df	F	<i>P</i> value
Predator type	71.0	2	2.00	0.145
Mean temperature	9.6	1	0.27	0.606
Drying rate	0.5	2	0.01	0.986
Mosquito species	11260.0	1	317.45	< 0.001 *
Error	35.5	53		

Note: MS = Mean Squares, df = degrees of freedom, F = F statistic and *P* is significant at < 0.05

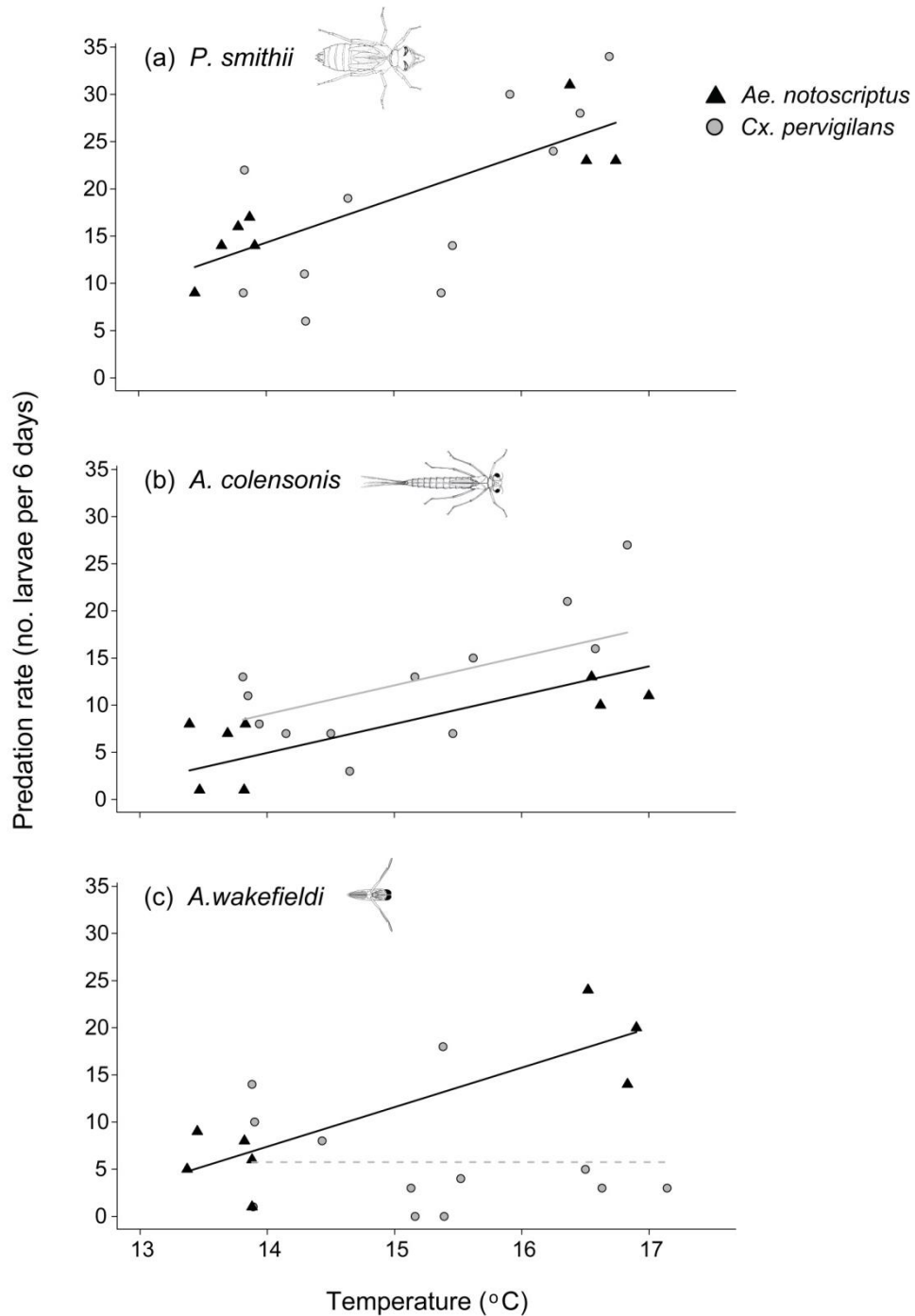


Figure 3.3. Predation rate by a) *P. smithii*, b) *A. colenisonis*, and c) *A. wakefieldi* on two mosquito species (*Ae. notoscriptus*: black triangles and *Cx. pervigilans*: grey circles) across different temperatures in a mesocosm feeding experiment. Regression lines were fitted by either ANCOVA (a & b) or linear regression (c). Solid line indicates significant effect and dashed line is mean response across the temperature range where linear regression was not significant. Multiple $R^2 = 0.480, 0.543$, and 0.520 for a) to c), respectively.

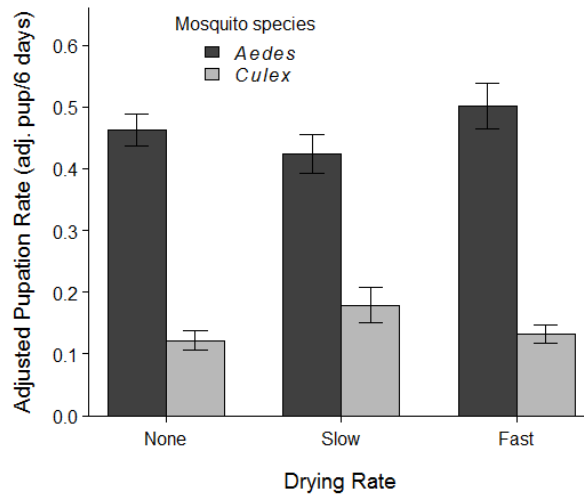


Figure 3.4. Adjusted pupation rates of *Ae. notoscriptus* (dark bars) and *Cx. pervigilans* (light bars) mosquitoes across different drying treatments, in a six day mesocosm feeding experiment. Fast drying treatments lost 2 L water per day, slow drying, 1 L and no drying none. Error bars are 95 % CI.

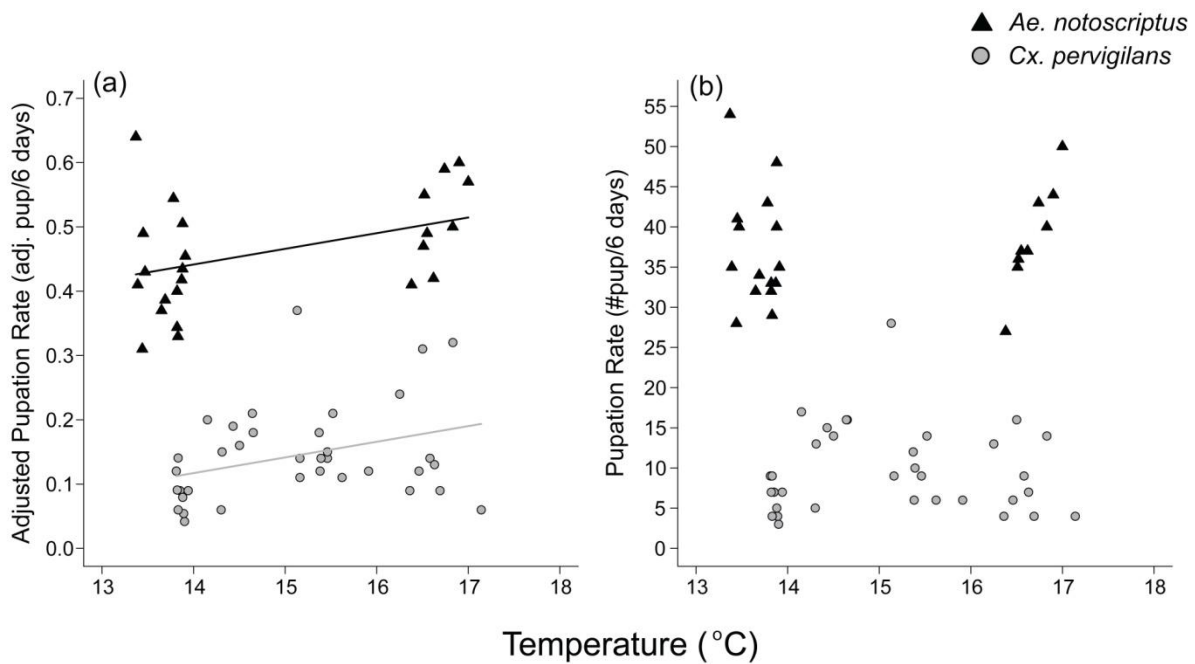


Figure 3.5. Pupation adjusted for predation (a) and unadjusted pupation rates (b) of *Aedes notoscriptus* (black triangles) and *Culex pervigilans* (grey circles) across different temperatures in a six day mesocosm feeding experiment. Adjusted pupae are the proportion of mosquitoes to pupate of those remaining to pupate (i.e. controlling for predation), and unadjusted pupae are counts of pupae remaining at the end of the experiment. Regression lines fitted by ANCOVA (*Ae. notoscriptus*: black and *Cx. pervigilans*: grey line). Multiple $R^2=0.821$

Experiment two: Warming and mosquito species

In the experiment investigating *A. wakefieldi* predation on the two mosquito species over a wider range of temperatures, the number of prey consumed was influenced by mosquito species and temperature (Fig. 3.6; Table 3.3a), and there was a possible interaction between mean temperature and mosquito species in the homogeneity of slopes test (Fig. 3.6; Table 3.3a). To further investigate temperature effects for the two mosquito species given the possibility of an interaction, I conducted separate linear regressions for each species. Increasing temperature significantly enhanced backswimmer predation rate on *Cx. pervigilans* ($F_{1, 13} = 14.24$, $p = 0.002$; Fig. 3.6), but temperature did not significantly affect predation on *Ae. notoscriptus* mosquitoes ($F_{1, 13} = 1.16$, $p = 0.301$). Predation by *A. wakefieldi* was consistently higher for *Ae. notoscriptus* than *Cx. pervigilans* regardless of temperature (Fig. 3.6).

There was no significant interaction in the homogeneity of slopes test, so the ANCOVA indicated that adjusted mosquito pupation rate increased with temperature (Fig. 3.7a; Table 3.3b), and was significantly different for *Aedes notoscriptus* and *Culex pervigilans* (Fig. 3.7a; Table 3.3b). Thus, based on adjusted pupation rates, *Ae. notoscriptus* pupated at slightly faster rates than *Cx. pervigilans* across the ~ 20 °C range of temperatures. Overall mosquito pupation rate (i.e. not adjusted) increased with temperature, but did not differ between mosquito species (Fig. 3.7b; Table 3.3c).

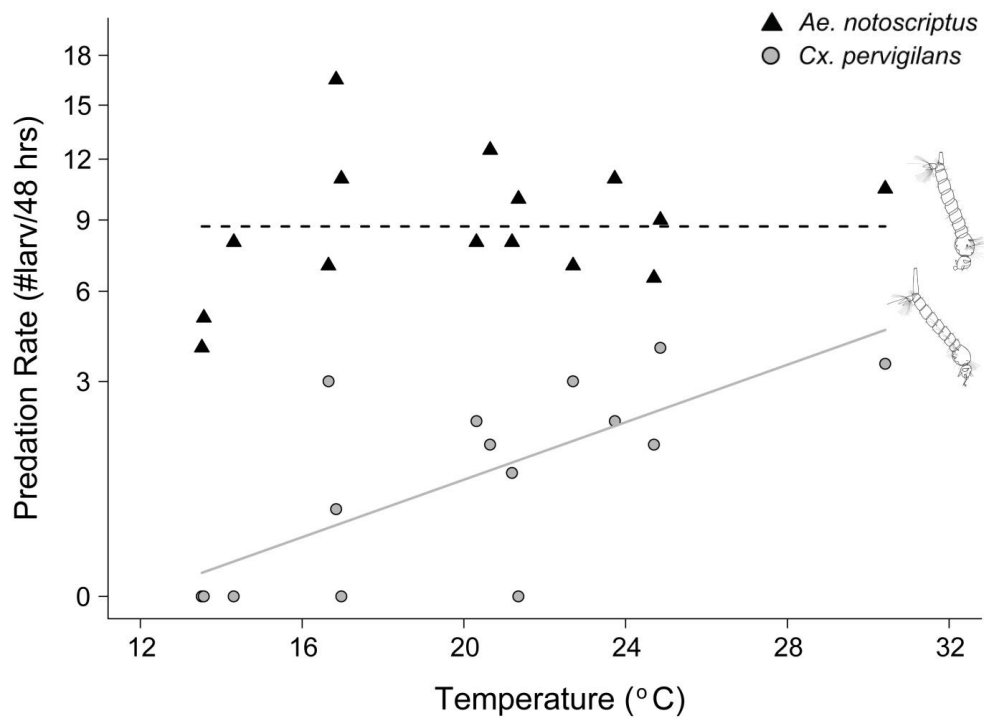


Figure 3.6. Predation rate on *Ae. notoscriptus* (black triangles) and *Cx. pervigilans* (grey circles) mosquitoes by backswimmer predators across different temperatures. Lines fitted by linear regression (*Ae. notoscriptus*: black and *Cx. pervigilans*: grey line). Solid line indicates significant effect and dashed line is mean response across the temperature range for *Ae. notoscriptus*. Multiple $R^2 = 0.753$.

Table 3.3. Results of homogeneity of slopes tests and ANCOVAs on a) predation rate by predatory *A. wakefieldi*, on *Ae. notoscriptus* and *Cx. pervigilans* mosquitoes (arcsine square-root transformed data, categorical treatment), b) adjusted pupation rate (arcsine square-root transformed data), and c) mosquito pupation rate over a 48 hour laboratory mesocosm experiment where temperature (continuous covariate) was manipulated. Adjusted pupae are the proportion of mosquitoes to pupate of those remaining to pupate (i.e. controlling for predation), and unadjusted pupae are counts of pupae remaining at the end of the experiment. *P* values < 0.05 are indicated with *.

a) Predation rate

Variable	MS	df	F	<i>P</i>
Mean temperature	0.036	1	11.92	0.002 *
Mosquito species	0.311	1	103.06	< 0.001 *
Mean temp × Mosquito sp.	0.011	1	3.79	0.062
Error	0.003	26		

b) Adjusted pupation rate

Variable	MS	Df	F	<i>P</i>
Mean temperature	0.015	1	60.36	< 0.001 *
Mosquito species	0.002	1	6.81	0.015 *
Error	0.0002	27		

c) Pupation rate

Variable	MS	df	F	<i>P</i>
Mean temperature	349.6	1	63.64	< 0.001 *
Mosquito species	9.6	1	1.75	0.197
Error	5.5	27		

Note: MS = Mean Squares, df = degrees of freedom, F = F statistic and *P* is significant at < 0.05

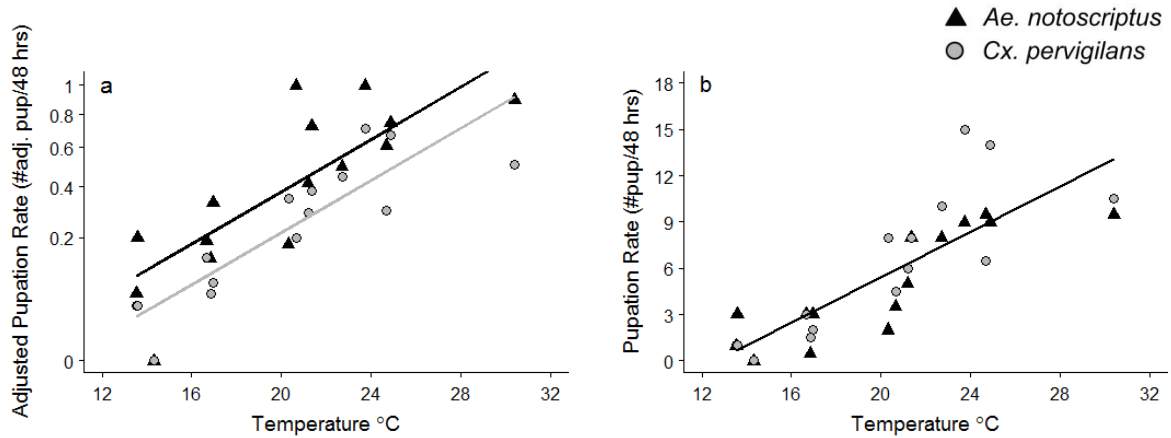


Figure 3.7. Adjusted pupation (a) and unadjusted pupation rates (b) of *Aedes notoscriptus* (black triangles) and *Culex pervigilans* (grey circles) across different temperatures in a 48-hour laboratory mesocosm experiment. Adjusted pupae are the proportion of mosquitoes to pupate of those remaining to pupate (i.e. controlling for predation by *A. wakefieldi*), and unadjusted pupae are counts of pupae remaining at the end of the experiment. Lines fitted by ANCOVA. Multiple $R^2 = 0.713$ and 0.689 for a) and b), respectively.

DISCUSSION

Interacting global change drivers such as climate change and biotic invasions are altering ecosystems at increasing rates, and their combined effect has received little attention in lentic systems. I therefore investigated whether altered habitat drying and increased temperature affected predation on native *Cx. pervigilans* and exotic *Ae. notoscriptus* mosquito larvae by three predatory invertebrates. I found little evidence that short-term habitat drying affected interaction strengths of any of the predator-prey combinations, but strong evidence for the importance of temperature-mediated predation rates which depended on both predator and prey identities. Predation rate generally increased with temperature, but the magnitude of the change depended on both predator and prey identity. *P. smithii* dragonflies were the most efficient predator, consuming both mosquito species at faster rates than the other two predators. *A. colensonis* damselflies preyed on *Cx. pervigilans* faster than *Ae. notoscriptus*, and the rate of predation on the two mosquito species by *A. wakefieldi* depended on temperature. Due to the narrow range of temperatures experienced and the lack of drying effects in the first experiment, I conducted a second experiment specifically investigating the interaction between backswimmer predators and *Ae. notoscriptus* and *Cx. pervigilans* across

a wide range of temperatures. I again found evidence for the importance of prey species in determining the effect of predator-prey interactions at different temperatures; while predation on *Cx. pervigilans* increased with temperature, predation on *Ae. notoscriptus* did not. These results, together with other studies indicate temperature is an important factor in mediating predator-prey interactions between mosquitoes and their predators (Williams and Rau 2011, van Uitregt et al. 2013). However, they also demonstrate that interactions between temperature, predator identity and mosquito species will be very important in determining the potential for mosquitoes to invade under a changing climate.

The differential effect of temperature on the defensive strategy of the two mosquito species likely explains these differences in predation rates. Metabolic activity increases with temperature, which will increase predator and prey activity due to increased oxygen and food demands (Reiter 2001, Lang et al. 2012). An effective behavioural defence against predation by both ambush predators and visual predators such as *A. wakefieldi* is for mosquito larvae to reduce activity in the presence of predators, but temperature-driven changes to metabolic activity mediate both predation intensity and defensive activities (van Uitregt et al. 2013, Culler et al. 2014). *Ae. notoscriptus* have significantly higher activity than *Cx. pervigilans* in the presence of *A. wakefieldi* predation cues (Zuharah and Lester 2010), likely explaining higher predation on *Ae. notoscriptus* than *Cx. pervigilans* in my experiment. However, van Uitregt et al. (2013) showed that *Ae. notoscriptus* activity decreased in the presence of predator cues, and this behavioural response increased with temperature (i.e., less activity at warmer temperatures). In summary, if the increased predation associated with rising temperature was balanced with an equal increase in defensive behaviour of *Ae. notoscriptus* but not *Cx. pervigilans*, then predation of *Cx. pervigilans*, but not *Ae. notoscriptus*, should increase with temperature, as I saw. Thus, even if native species appear better defended to native predators, higher habitat temperature may increase the defensive ability of invaders. So overall, species that may seem low-risk invaders due to efficient natural predation in recipient habitats may become higher risk as the climate warms.

In my experiments, temperature increases were usually associated with increased mosquito larvae pupation rates, with the magnitude of pupation increases depending on mosquito species. Both species decreased development time in the warming experiment, but invasive *Ae. notoscriptus* pupated faster than native *Cx. pervigilans*. Temperature increases affect both short- and long-term life history strategies (Peckarsky et al. 2002, Ewald et al. 2013), which has implications for mosquito fitness. Although increased development rates could

result in mosquitoes escaping predation faster and increased population productivity, faster development could decrease adult size, thereby decreasing adult fitness (McPeck and Peckarsky 1998, Williams and Rau 2011). Therefore, because *Ae. notoscriptus* developed faster than *Cx. pervigilans*, short-term results imply greater *Ae. notoscriptus* fitness through increased productivity. Long-term effects of this may mean *Cx. pervigilans* could have overall greater fitness, however, if the slower development resulted in greater adult fecundity. Further research on the long-term effects of habitat warming on mosquito populations would need to be conducted to identify which mosquito species would have greater fitness in prolonged warming.

Development rate will be a key factor in determining the survival of mosquito species, because this will affect how long they are exposed to predation as juveniles, but predation rate will also be important. The combined effects of predation and pupation in the warming experiment meant that overall success (i.e. development to penultimate adult stage) of the mosquito species was equal. In other words, the faster pupation rate of *Ae. notoscriptus* compared to *Cx. pervigilans* was balanced by the greater rate of predation on *Ae. notoscriptus* compared to *Cx. pervigilans*. My results highlight the need to incorporate life-history effects into predictions about climate warming effects on predator-prey interaction strengths. While considerable research has been conducted on climate effects on interaction strengths (Kokkoris et al. 2002, Rall et al. 2010, Vucic-Pestic et al. 2011), few address life history dynamics of prey species that spend part of their development in the terrestrial environment, such as mosquitoes (but see McPeck and Peckarsky 1998). Thus, my experiments highlight the importance of temperature-driven life history and behaviour differences in determining predation on mosquitoes. Moreover, climate warming effects on life history have the potential to alter community structure and function (Dossena et al. 2012), so understanding how climate affects combined life history and predation dynamics will be important for managing invasions.

To understand how mosquito distributions will change with climate change, we also need to know how altered habitat permanence, will affect predator abundance and distribution. Predicated temperature effects on predator-prey interactions involving mosquitoes will depend on which predators are present in mosquito habitats. Despite there being almost no effect of short-term habitat drying on predator-prey interactions in my first experiment, predicted climate change will significantly impact lentic freshwater systems through long-term drying, directly affecting which predators persist in a habitat. Climate models for New

Zealand, for example, predict an increase in the variability and distribution of rainfall, and this is likely to increase the proportions of temporary (i.e. subject to drying) freshwater habitats (Bates et al. 2008, MfE 2008, NZCCC 2010). Decreases in the proportion of more permanent habitats will exclude those species that require longer hydroperiod to complete their life cycle, such as dragonflies (Greig 2008, Wissinger et al. 2009). My finding, that predation rate on mosquitoes depended on predator species, highlights the importance of knowing how climate-driven habitat permanence drives predator distributions and abundances. Because predators consume mosquito species at different rates, knowing which predators are present will be an important part of identifying overall mosquito invasion success under a warming climate.

The context-dependent predator-prey interactions I have revealed are particularly relevant to New Zealand, because although New Zealand does not currently have mosquito-borne diseases (Derraik and Calisher 2004), warmer mean temperatures predicted for New Zealand combined with increased urbanisation and globalisation (MfE 2008, Lau et al. 2012, IPCC 2013) mean more mosquito species are likely to invade. Mosquito species that are currently excluded from New Zealand due to low temperature limitations, such as disease-transmitting *Aedes albopictus* and *Ochlerotatus japonicus*, will have a greater potential to invade successfully under climate warming (Reiter 2001, Disbury and Cane 2011). Moreover, while *Ae. notoscriptus* in New Zealand do not currently transmit any human diseases (Derraik and Calisher 2004), they have been implicated to do so in Australia (Kay et al. 2000). While local mosquitoes do not currently vector human disease, if there are enough human carriers a disease can become established in local mosquito populations (Lau et al. 2012). *Culex pervigilans* is a competent vector of Ross River Virus, a disease endemic to Australia (Harley et al. 2001, Kramer et al. 2011), so the risk of mosquito-borne diseases becoming established in New Zealand is high. This highlights the importance of having a detailed understanding of local habitat characteristics of potential invasion locations, because the effectiveness of invasion will be mediated by both predator presence and identity, as well as climate warming.

Potential invasion will also depend on human-created habitats. In most countries the public is largely unaware of the potential for standing water habitats to provide ideal habitats for both native and exotic mosquitoes (Derraik 2005b). Therefore, public education about the potential for mosquito-borne disease and awareness of the importance of native predators for natural biocontrol of mosquitoes will be an important step in limiting and controlling mosquito-borne disease. Moreover, understanding how native and exotic species responses

differ in vulnerability to predation by native species will be important in directing management and control resources, especially in the context of mosquito invasions. Because predators are an important control on mosquito populations, increasing the distribution of habitats that can support predators, and maintaining cool temperatures in these habitats, will increase biotic resistance to mosquito invaders.

LITERATURE CITED

- Atkinson, I. A. E., and E. K. Cameron. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology and Evolution* 8:447–451.
- Bates, B. C., Z. W. Kundzewicz, S. Wu, and J. P. Palutikof, (eds). 2008. Climate change and water. Page 210 Technical paper of the intergovernmental panel on climate change. Geneva.
- Belkin JN. 1968. Mosquito studies (Diptera: Culicidae) VII. The Culicidae of New Zealand. *Contributions to the American Entomology Institute* 3: 1–182.
- Bennett, J. R., P. W. Dunwiddie, D. E. Giblin, and P. Arcese. 2012. Native versus exotic community patterns across three scales: roles of competition, environment and incomplete invasion. *Perspectives in Plant Ecology, Evolution and Systematics* 14:381–392.
- Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change* 95:469–483.
- Carrington, L. B., M. V. Armijos, L. Lambrechts, C. M. Barker, and T. W. Scott. 2013. Effects of fluctuating daily temperatures at critical thermal extremes on *Aedes aegypti* life-history traits. *PLoS ONE* 8:e58824.
- Charrel, R. N., X. de Lamballerie, and D. Raoult. 2007. Chikungunya Outbreaks — The globalization of vectorborne diseases. *New England Journal of Medicine* 356:769–771.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104:17430–4.
- Culler, L. E., M. A. McPeck, and M. P. Ayres. 2014. Predation risk shapes thermal physiology of a predaceous damselfly. *Oecologia* 176:653–60.
- Dauphin, G., S. Zientara, H. Zeller, and B. Murgue. 2004. West Nile: Worldwide current situation in animals and humans. *Comparative Immunology, Microbiology and Infectious Diseases* 27:343–355.

- Derraik, J. G. B. 2005a. A tool for sampling mosquito larvae from phytotelmata. *Journal of Vector Ecology* 34:155–157.
- Derraik, J. G. B. 2005b. Mosquitoes breeding in container habitats in urban and peri-urban areas in the Auckland Region, New Zealand. *Entomotropica* 20:89–93.
- Derraik, J. G. B., and C. H. Calisher. 2004. Is New Zealand prepared to deal with arboviral diseases? *Australian and New Zealand Journal of Public Health* 28:27–31.
- Derraik, J. G. B., and D. Slaney. 2007. Anthropogenic environmental change, mosquito-borne diseases and human health in New Zealand. *EcoHealth* 4:72–81.
- Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22:489–96.
- Diez, J. M., C. M. D’Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. B. Sorte, D. M. Blumenthal, B. A. Bradley, R. Early, I. Ibáñez, S. J. Jones, J. J. Lawler, and L. P. Miller. 2012. Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment* 10:249–257.
- Disbury, M., and R. P. Cane. 2011. The national exotic saltmarsh mosquito surveillance programme. *Surveillance* 38:44–46.
- Disbury, M., R. Cane, and M. Singe. 2008. Post-border surveillance for exotic mosquitoes. In *Surveillance for Biosecurity: Pre-Border to Pest Management*. Froud, K.J., I. A. Popay, and S. M. Zydenbos (eds). New Zealand Plant Protection Society (Incorporated). Christchurch, New Zealand, 37-44.
- Dossena, M., G. Yvon-Durocher, J. Grey, J. M. Montoya, D. M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B* 279:3011–9.
- Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.
- Ewald, N. C., S. E. Hartley, and A. J. A. Stewart. 2013. Climate change and trophic interactions in model temporary pond systems: the effects of high temperature on predation rate depend on prey size and density. *Freshwater Biology* 58:2481–2493.
- Gallardo, B., and D. C. Aldridge. 2013. Evaluating the combined threat of climate change and biological invasions on endangered species. *Biological Conservation* 160:225–233.
- Graham, D. 1939. Mosquito life in the Auckland District. Report of the Auckland mosquito research committee on an investigation made by David H. Graham. *Transactions and Proceedings of the Royal Society of New Zealand* 69:210–224.
- Greig, H. S. 2008. Community assembly and food web interactions across pond permanence gradients. PhD Thesis, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand.

- Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Global Change Biology* 18:504–514.
- Greig, H. S., S. A. Wissinger, and A. R. McIntosh. 2013. Top-down control of prey increases with drying disturbance in ponds: a consequence of non-consumptive interactions? *The Journal of Animal Ecology* 82:598–607.
- Gubler, D. J. 2002. The global emergence/resurgence of arboviral diseases as public health problems. *Archives of Medical Research* 33:330–342.
- Harley, D., A. Sleight, and S. Ritchie. 2001. Ross River virus transmission , infection , and disease : a cross-disciplinary review. *Clinical Microbiology Reviews* 14:909–932.
- Heino, J., R. Virkkala, and H. Toivonen. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews of the Cambridge Philosophical Society* 84:39–54.
- IPCC. 2014. Summary for Policymakers. In: *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Edenhofer, O., R. Pichs-Madruga, Y. Sokona, E. Farahani, S. Kadner, K. Seyboth, A. Adler, I. Baum, S. Brunner, P. Eickemeier, B. Kriemann, J. Savolainen, S. Schlömer, C. von Stechow, T. Zwickel and J.C. Minx (eds)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Kay, B. H., P. A. Ryan, B. M. Russell, J. S. Holt, S. A. Lyons, and P. N. Foley. 2000. The importance of subterranean mosquito habitat to arbovirus vector control strategies in north Queensland, Australia. *Journal of Medical Entomology* 37:846–853.
- Klecka, J., and D. S. Boukal. 2012. Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PloS ONE* 7:e37741.
- Kokkoris, G. D., V. A. A. Jansen, M. Loreau, and A. Y. Troumbis. 2002. Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology* 71:362–371.
- Kramer, L. D., P. Chin, R. P. Cane, E. B. Kauffman, and G. Mackereth. 2011. Vector competence of New Zealand mosquitoes for selected arboviruses. *The American Journal of Tropical Medicine and Hygiene* 85:182–9.
- Kratina, P., H. S. Greig, P. L. Thompson, T. S. a Carvalho-Pereira, and J. B. Shurin. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* 93:1421–30.
- Laird, M. 1995. Background and findings of the 1993-94 New Zealand mosquito survey. *New Zealand Entomologist* 18:77–90.

- Lang, B., B. C. Rall, and U. Brose. 2012. Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *The Journal of Animal Ecology* 81:516–23.
- Lau, C., P. Weinstein, and D. Slaney. 2012. Imported cases of Ross River virus disease in New Zealand - a travel medicine perspective. *Travel Medicine and Infectious Disease* 10:129–34.
- Lee W.G., R. B. Allen, and D. M. Tompkins. 2008. *Ecological Studies*, Vol. 186. R.B. Allen, and W.G. Lee (eds). *Biological invasions in New Zealand*. Springer-Verlag Berlin Heidelberg 2006.
- Leisnham, P. T., D. P. Slaney, P. J. Lester, and P. Weinstein. 2005. Increased larval mosquito densities from modified landuses in the Kapiti region, New Zealand: vegetation, water quality, and predators as associated environmental factors. *EcoHealth* 2:313–322.
- Macdougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55.
- Mas-Martí, E., I. Muñoz, F. Oliva, and C. Canhoto. 2014. Effects of increased water temperature on leaf litter quality and detritivore performance: a whole-reach manipulative experiment. *Freshwater Biology* 60:184–197.
- McHugh, P. A., R. M. Thompson, H. S. Greig, H. J. Warburton, and A. R. McIntosh. 2015. Habitat size influences food web structure in drying streams. *Ecography* 37:1EV–13EV.
- McPeck, M. a., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: Combining mortality, growth, and fecundity effects. *Ecology* 79:867–879.
- Melbourne, B. A., H. V Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H. Yokomizo. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10:77–94.
- Ministry for the Environment (MfE). 2008. *Climate change effects and impacts assessment: a guidance manual for local government in New Zealand*. 2nd Edition. Mullan, B., D. Wratt, S. Dean, M. Hollis, S. Allan, T. Williams, G. Kenny, and MfE. Ministry for the Environment, Wellington. xviii + 149 pp.
- New Zealand Climate Change Centre (NZCCC). 2010. *Climate change adaptation in New Zealand: future scenarios and some sectoral perspectives*. Nottage, R. A. C., D. S. Wratt, J. F. Bornman, and K. Jones (eds). Wellington, 136 p.
- Norris, D. E. 2004. Mosquito-borne diseases as a consequence of land use change. *EcoHealth* 1:19–24.
- Norton, D. a. 2009. Species invasions and the limits to restoration: learning from the New Zealand experience. *Science* 325:569–71.

- Pall, P., M. R. Allen, and D. A. Stone. 2006. Testing the Clausius–Clapeyron constraint on changes in extreme precipitation under CO₂ warming. *Climate Dynamics* 28:351–363.
- Peckarsky, B. L., A. R. McIntosh, B. W. Taylor, and J. Dahl. 2002. Predator chemicals induce changes in mayfly life history traits: A whole-stream manipulation. *Ecology* 83:612–618.
- Pimm, S. L. 2009. Climate disruption and biodiversity. *Current Biology* 19:R595–601.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22:521–33.
- Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367:2923–34.
- Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. Temperature, predator-prey interaction strength and population stability. *Global Change Biology* 16:2145–2157.
- Reiter, P. 2001. Climate change and mosquito-borne disease. *Environmental Health Perspectives* 109:141–161.
- Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–4.
- Schneider, D. W., T. M. Frost, S. Journal, N. American, B. Society, and N. Mar. 2014. Habitat Duration and Community Structure in Temporary Ponds. *Journal of the North American Benthological Society* 15:64–86.
- Sorte, C. J. B. 2013. Predicting persistence in a changing climate: flow direction and limitations to redistribution. *Oikos* 122:161–170.
- Strachan, S. R., E. T. Chester, and B. J. Robson. 2015. Microrefuges from drying for invertebrates in a seasonal wetland. *Freshwater Biology* 59:2528–2538.
- Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning. *Ecology letters* 15:1199–210.
- Thompson, R. M., J. A. Dunne, and G. Woodward. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology* 57:1329–1341.

- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137–148.
- Van Uitregt, V. O., T. P. Hurst, and R. S. Wilson. 2013. Greater costs of inducible behavioural defences at cooler temperatures in larvae of the mosquito, *Aedes notoscriptus*. *Evolutionary Ecology* 27:13–26.
- Vaz-Pinto, F., C. Olabarria, I. Gestoso, E. Cacabelos, M. Incera, and F. Arenas. 2013. Functional diversity and climate change: effects on the invasibility of macroalgal assemblages. *Biological Invasions* 15:1833–1846.
- Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* 17:1301–1310.
- Wagner, A., S. Hülsmann, W. Horn, T. Schiller, T. Schulze, S. Volkmann, and J. Benndorf. 2013. Food-web-mediated effects of climate warming: consequences for the seasonal *Daphnia* dynamics. *Freshwater Biology* 58:573–587.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2019–24.
- Walther, G.-R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pysek, I. Kühn, M. Zobel, S. Bacher, Z. Botta-Dukát, H. Bugmann, B. Czúcz, J. Dauber, T. Hickler, V. Jarosík, M. Kenis, S. Klotz, D. Minchin, M. Moora, W. Nentwig, J. Ott, V. E. Panov, B. Reineking, C. Robinet, V. Semchenko, W. Solarz, W. Thuiller, M. Vilà, K. Vohland, and J. Settele. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution* 24:686–93.
- Weinstein, P., M. Laird, and G. Browne. 1997. Exotic and endemic mosquitoes in New Zealand as potential arbovirus vectors. Pages 1–16 *Ocasional paper*, Ministry of Health, Wellington. Wellington.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Williams, C. R., and G. Rau. 2011. Growth and development performance of the ubiquitous urban mosquito *Aedes notoscriptus* (Diptera: Culicidae) in Australia varies with water type and temperature. *Australian Journal of Entomology* 50:195–199.
- Wissinger, S. A., H. Greig, and A. McIntosh. 2009. Absence of species replacements between permanent and temporary lentic communities in New Zealand. *Journal of the North American Benthological Society* 28:12–23.
- World Meteorological Organisation (WMO). 2013. The global climate 2001-2010: a decade of extremes summary report. Geneva, 20 pp.

Zuharah, W. F., and P. J. Lester. 2010. The influence of aquatic predators on mosquito abundance in animal drinking troughs in New Zealand. *Journal of Vector Ecology* 35:347–53.

Acknowledgements

First and foremost I would like to thank my supervisor, Angus McIntosh. Angus has been an incredible mentor, providing inspiration and insight throughout both by undergraduate degree and now my MSc. I am also incredibly grateful to Mark Galatowitsch, who has fielded *so* many of my questions, and been incredibly patient and supportive of me these last two years.

I am incredibly grateful to my family, Ray Hunt, Biddy Flavell, Annabel Flavell and Lynette Low for a lifetime of support and encouragement.

One of my main reasons for choosing to do my Masters at the University of Canterbury was because to the Freshwater Ecology Research Group (FERG). As an undergraduate student FERG gave me many opportunities, and the camaraderie and support that the group has for its members is fantastic. I feel so lucky to have been a part of the group.

My thesis has given me a steep learning curve, especially in statistics, so I truly appreciate receiving assistance from Jon Harding, Helen Warburton, Simon Howard, Richard White, Jane Gosden, Amanda Klemmer, Jason Tylianakis, Melissa Broussard and Christoph Matthaei.

Thank you to those who have given me general support as I conducted my research (in no particular order): Ellen Hume, Mark Galatowitsch, Amanda Klemmer, Helen Warburton, Jane Gosden, Richard White, Robyn White, Michelle Lambert, Tom Swan, Nixie Boddy and Camille Coux, Biddy Flavell, Annabel Flavell, Lynette Low and Ray Hunt. I appreciate the assistance from Mark Disbury at Mosquito Consulting Services when I was planning my research, those pipettes were put to good use, as was the multitude of mosquito information. Thank you to Mark Galatowitsch for the illustrations of my study species.

Thank you to everyone who helped me to find mosquito larvae for my experiments, and to those of you who went a step further and set up mosquito farms (Paul Broady). Thanks to my dad for putting up with the mosquito farm I set up in his back yard (and thanks to his neighbours too!).

Technical support and expertise came from Linda Morris, Nick Etheridge, Dave Conder, Allan Woods, Dave Rutherford, and to the administrative support from Nicole Lauren-Manuera, Nikki Judson and Penny Moore.

Thank you to the University of Canterbury and Jenny Ladley for use of the field stations at Hari Hari and Cass, and to those that helped me in the field: Nixie Boddy, Robert Perry, Tom Swan, Amanda Klemmer, Mark Galatowitsch and Jane Gosden

I could not have conducted my survey without the help of many land owners, including Jane Gosden, Sharon Burrell-Smith, Tim Shaw, Ingrid Gruner, Terry Farrell, Suzie Breeze, Tom Belton, Rob Markillie, Sarah Sinton, Laura Williamson, Sarah Glasson, Ann Blackburne, Peg Gosden, Linda Morris, Graeme Boddy, Sophie Moloney, Jen Schori, Jackie, Bridget Armstrong, Christine and Mike White, Victoria and Murray Greig, Hugh Wilson at Hinewai, Paul Broady, Reijel Gardiner, Annabel Flavell, Lynette Low, Ray Hunt. Also thank you to the Department of Conservation, Christchurch City Council, the University of Canterbury and Plant and Food, for granting me land access.

Thank you also to Ellen Hume, Andrew Wallace, Aaron Chinnery-Brown, James Eagle and Andrew Matthews. Ellen you have kept me sane with your support and friendship, and Andrew thanks for all the games of Settlers of Catan in the evenings, and for sometimes letting me win.

I am extremely grateful to the Brian Mason Scientific and Technical Trust, for providing funding for my thesis, and to the Todd Foundation, Meadow Mushrooms, the Freemasons Charity, and the New Zealand Federation of Graduate Women for providing funding to support me as I conducted my research. Thank you to the New Zealand Ecological Society (NZES) for providing me with a travel grant to attend and present at the NZES 2013 conference.