Environmental change and the structure and functioning of invertebrate communities

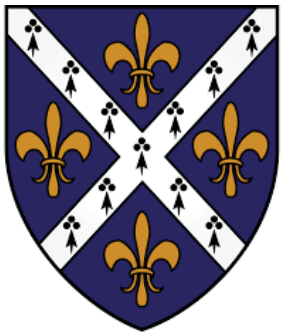
Moya L. Burns



University of Oxford

Department of Zoology

St Hugh's College



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Abstract

Land-use change and climate change are considered to be the greatest threats to biodiversity globally. The conversion of natural habitats into agricultural land with remnant patches of the original habitat left embedded within an anthropogenic matrix is one of the main land-use changes. This has been shown to alter species richness and abundance, depending on factors such as remnant area and isolation. Climate change has caused species to shift their distributions, alter their phenologies or risk going extinct. The interaction of habitat fragmentation and climate change exacerbates these problems when the lack of suitable habitat within a species dispersal limits prevents a species from tracking changing climates, forcing its adaptation or extinction. One method attempting to remedy this is to restore habitats in a network across landscapes in order to reduce the isolation between natural communities and increase connectivity across landscape. These areas have been largely assessed using a species-centred approach. In this thesis I investigate these elements of environmental change, and the potential mitigation process of habitat restoration, using a food web and functional approach to assess how these factors affect the structure and functioning of invertebrate communities.

In Chapter 2 I describe the results of a landscape scale study into the effects of habitat fragmentation on sub-tropical rainforest communities in Australia. Using cavity-nesting bees, wasps and their parasitoids as a study community I show that fragmentation effects such as fragment area, isolation and edge effects can impact different trophic levels to different extents, but that this does not necessarily result in a change to the ecosystem function of parasitism.

Using a field-based manipulative experiment, In Chapter 3 I investigate the effects of altered rainfall regimes which may be a consequence of climate change on host-parasitoid food webs and parasitism in a temperate grassland. I show that changes to precipitation regimes disrupts host-parasitoid synchrony between a common grassland leaf-mining insect *Stephensia brunichella* and its parasitoid *Pholetesor arisba*. These changes do not cause food web changes at the scale studied, but demonstrate the potential for climate change to alter host-parasitoid synchrony and hence the ecosystem service of parasitism.

Utilising a long-term experiment into the effects of different grazing regimes on the restoration of lowland calcareous grassland in the UK on former arable land, in Chapter 4 I address the impacts of restoration on quantitative food web structure and parasitism. I show that although grazing regime can affect trophic level composition differentially, this does not translate into overall changes in food web structure or parasitism at the field scale studied.

Using the same field experiment, and a novel method for assessing soil ecosystem feeding activity by invertebrates, I investigate the impacts of seasonal grazing regime on soil ecosystem function (Chapter 5). I show that the season of grazing has an impact on the vertical profile of soil ecosystem functioning. I discuss the potential implications of this novel finding for the future of restoration studies and the importance of including below ground processes in ecological studies of environmental change.

This thesis shows that research into the effects of anthropogenically induced environmental change can benefit from a food web and ecosystem functioning approach. However, experimental field studies at larger spatial scales and the inclusion of species traits are needed to fully address these questions.

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Chapter 1

General Introduction

1.1 Environmental change in the 21st Century

We are living through a period of unprecedented levels of human-induced environmental change, causing global declines in biodiversity (Pimm *et al.* 1995). Many people have now concluded that we are in the midst of the sixth mass extinction event, often referred to as the Anthropocene (Steffen *et al.* 2011a). The Millennium ecosystem assessment (2005) identified five major causes of anthropogenically induced environmental change: land-use change, chemical release, climate change, over-harvesting and species invasions (McGill *et al.* 2015). Of these land-use change and climate change are thought to pose the greatest threats to the future persistence of biodiversity (Chapin *et al.* 2000; Mora *et al.* 2007) and are the focus of this thesis.

1.1.1 Land-use change

Land-use change is defined as "the arrangements, activities and inputs people undertake in a certain land cover type to produce, change or maintain it" (UNEP, 1999). The term is usually used to refer to the conversion of natural or semi-natural habitats to agricultural or urban use. This typically results in the fragmentation and degradation of remaining natural habitats and consequent losses of biodiversity (Foley *et al.* 2005). The conversion of natural habitats to agricultural use is the greatest cause of habitat fragmentation (Vitousek et al 1997, Tilman et al 2001) and overall the proportion of land globally subjected to transformation or degradation by humans is estimated to be somewhere between 39 to 50% (Vitousek *et al.* 1986).

1.1.2 Climate change

After land-use change climate change is considered to be the greatest threat to biodiversity, producing changes not only in global temperatures but also in rainfall patterns (Allan & Soden 2008). There is now a widespread consensus that numerous species, across many taxa are shifting their ranges, phenologies and behaviour in response to recent climate warming and alterations in rainfall regimes (Merrill *et al*, 2008; Franco *et al*, 2006; Parmesan *et al*, 1999; Warren *et al*, 2001; Hickling *et al*, 2006, Walther *et al*, 2002; Parmesan & Yohe, 2003, Wilson *et al*, 2007). For instance 63 % of European non-migratory butterfly species have shifted their range northwards during the last century (Parmesan *et al.* 1999) and 78 % of European leafing, fruiting and flowering records are showing phenological shifts to occurring earlier in the season, in line with increasing temperatures (Menzel *et al.* 2006).

The effects of climate change and land-use change do not occur in isolation and will have interacting effects on future levels of biodiversity (Oliver & Morecroft 2014). For instance over the coming century the impacts of climate warming are expected to be exacerbated by restrictions to species movements caused by fragmented landscapes (Mora *et al.* 2007), with many species unable to shift their ranges to follow warming climates due to the lack of suitable habitats within their new climatic envelope (Warren *et al.* 2001).

1.1.3 Restoration

With the increasing loss of natural habitat worldwide there is a growing awareness that protecting remaining habitat will not be enough to ensure the preservation of future biodiversity and ecosystem functioning (Rodrigues *et al.* 2004). There is a pressing need to reverse some of this loss of habitat through the restoration of native habitats on degraded lands (Hobbs & Harris 2001). There is still much debate as to the most effective method of restoring biodiversity, structure and ecosystem function to anything close to that of original habitats (Janzen 1988, Parrotta et al. 1997, Kanowski et al. 2003). However, there is great potential for restoration science to not only mitigate some of the effects of habitat loss, but also by careful planning of restoration sites to ameliorate some of the effects of climate change by providing appropriate new habitats for species shifting locations due to changing conditions (Shoo *et al.* 2011). For this reason I also address restoration in this thesis.

1.2 Assessing the effects of environmental change on biodiversity

Biodiversity, and in particular the richness and abundance of species, has long been the measure by which community response to natural variations in environments have been measured (Gaston 2000; Purvis & Hector 2000). Biodiversity is thus also the natural choice for assessing the pressures on natural environments due to global anthropogenic environmental change (Chapin *et al.* 2000). Below I discuss how the environmental changes investigated in this thesis have been shown to affect biodiversity.

1.2.1 Habitat fragmentation

The study of fragmentation effects has usually been based on the species-area relationships and island biogeography (MacArthur & Wilson 1967a) and metapopulation dynamics theories which consider the extent to which isolated fragments can be colonised, and the frequency with which they experience extinctions (Hanski 1998). Smaller fragments are predicted to be less able to support a wide variety of habitat niches and hence species (McGuinness 1984) whilst more isolated fragments are thought to be more vulnerable to extinctions due to stochastic processes and less likely to be colonised by species from adjacent habitats due to the greater dispersal distances required (Hanski 1998) leading to the consensus that smaller and more isolated fragments should support lower species diversity.

In reality, the effects of habitat fragmentation on biodiversity is far more complicated with positive, neutral and negative responses of species richness to habitat fragmentation being widely reported (Ewers & Didham 2006), due to the difference among species in their ability to utilise different habitats, their dispersal distances and their ability to perceive different levels of fragmentation at different spatial scales (Tscharntke & Brandl 2004; Ribas *et al.* 2005).

These biodiversity predictions based on biogeography theory assume that fragmented habitats exist as islands in a hostile wider environment, when in reality the fragmentation of landscapes leads to the opening up of a matrix environment and the creation of greater edge environment, where the original habitat meets the surrounding habitat. Some species

will favour the new edge environment and increase in abundance in this zone, which can lead to maintenance or even the increase of species richness at the landscape scale due to the interacting effects of opening up the environment to edge or open habitat species (Laurance *et al.* 2002; Ewers & Didham 2006; Ewers & Didham 2007).

1.2.2 Climate change

As the climate changes, species are faced with the option of adapting to altered environmental conditions *in situ* (through phenotypic plasticity or evolutionary adaptation; Parmesan *et al*, 2006), shifting their phenologies (Parmesan & Yohe 2003), or shifting their ranges to different latitudes and/or elevations in order to remain within their climatic limits (Root *et al*, 2003). However, some species may not be able to track these changes due to restrictions to movement caused by other factors such as habitat availability (Opdam & Wascher 2004). Species unable to migrate and unable to adapt within their current location will face extinction (Chevin, Lande & Mace 2010), meaning that overall climate change is predicted to lead to a global decline in biodiversity (Sala *et al.* 2000b; Bellard *et al.* 2012).

1.2.3 Restoration

Restoration involves the purposeful removal of a factor causing habitat degradation or the reestablishment of processes which maintained a desirable ecosystem (Benayas *et al.* 2009). Restoration as a scientific discipline was founded in plant community ecology and thus its theoretical roots lie in community assembly theory (Young 2000; Young, Chase & Huddleston 2001) with positive outcomes often judged in terms of the restoration of

plant species richness and composition comparable to reference sites (Young, Petersen & Clary 2005; Brudvig 2011) or an overall increase in levels of biodiversity (Ruiz-Jaen & Aide 2005). In reality achieving full restoration of an ecosystem is difficult, with restored sites often developing a species composition at an intermediate state between those found in degraded lands and that of target communities (Benayas *et al.* 2009).

Over the last decade there has been a move to focus restoration efforts on invertebrates, particularly charismatic species such as butterflies (Schultz, Russell & Wynn 2008) and bumblebees (Goulson, Lye & Darvill 2008; Redpath-Downing *et al.* 2013). Although some of the restoration practices implemented have had notable success for target species (Thomas, Simcox & Clarke 2009), restoration of invertebrate communities as a whole suffers from the same problems facing plant communities in that restored sites often reach an intermediate level of biodiversity before plateauing (Grimbacher *et al.* 2007; Woodcock *et al.* 2012b) and show significant time lags between implementation of restoration management and the development of a community approaching that of the target sites (Woodcock *et al.* 2012a), reminding us that restoration cannot be a panacea against continued degradation of natural habitats (Brudvig 2011).

1.3 Assessing environmental change on ecological communities using a food web approach

Environmental change does not always result in species loss and in fact a more pervasive effect of environmental change may be alterations to the structure of natural communities

via changes in relative abundances of different species as they respond to environmental perturbations (Chapin *et al.* 2000). These changes in communities of organisms due to environmental change can result in alterations to interactions between species and thus food web structure (Tylianakis *et al.* 2008).Many studies investigating environmental change to-date have focused on single species and yet we know that species respond differently to change (Davis *et al.* 1998). Thus, responses across whole food webs are likely to differ greatly from predictions made using single species (Petchey et al 1999).

A food web traditionally describes all the feeding links between species in a community and was first used under the term "food chain" by Charles Elton (Elton 1927). Early food webs were constructed using binary matrices of interaction between species in communities, where either an interaction existed (1) or did not (0) (Pimm 1982) and from these qualitative descriptors of food webs were developed (Lawton 1989). However, it became apparent that these binary matrices which gave equal weight to all interaction regardless of their frequency did not reflect real world food webs (Paine 1988; Goldwasser & Roughgarden 1997). Authors began to emphasise the need for quantitative descriptors of food webs which took into account the intensity of interactions (Pimm & Kitching 1988; Winemiller & Polis 1996), culminating in the development of now widely used quantitative descriptors of food webs to replace the previous qualitative descriptors (Bersier, Banašek-Richter & Cattin 2002).

The use of quantitative food webs in the applied analysis of the effects of environmental change on natural communities has undergone an explosion in the last decade (Memmott

2009). I will discuss how the food web approach has been used to gain insight into the effects of the environmental changes addressed in this thesis.

Food webs can be subdivided into three broad types: 'traditional' binary food webs, mutualistic networks (such as plant-pollinator networks) and antagonistic networks (such as host–parasitoid webs) (Ings *et al.* 2009). Since different types of interaction networks will illuminate different responses to environmental change (Tylianakis *et al.* 2008), in this thesis I focus my research on the impacts of environmental change on host-parasitoid food webs.

1.3.1 Fragmentation and food web alteration

It was Holt who first called for the consideration of a spatial element to food webs and their application to questions such as fragmentation (Holt 1996). Since then Tylianakis et al. (2007) showed that the quantitative food web approach could demonstrate the impacts of land-use change on communities which a traditional biodiversity approach would have missed. Valladares et al. (2012) conducted the first real world landscape scale quantitative food web study and found that increasing levels of fragmentation led to food web contraction around a small number of highly connected species, with consequent impacts on trophic processes dependent on trophic levels and individual traits of the species studied (Valladares, Salvo & Cagnolo 2006b).

1.3.2 Climate change and food web alteration

As with land-use changes, the differential ability of species to respond to climatic changes are predicted to translate into changes in food web structure (Petchey *et al.* 1999). Climate change studies often use altitudinal transects as a 'natural experiment' to try to understand the effects changing climates may have on biodiversity (Körner 2007) and thus real world food web studies on food web alteration with climate change have thus far been focused on altitudinal transects.

The first of these studies (Morris, Sinclair & Burwell 2014) on cavity-nesting Hymenoptera and their parasitoids in sub-tropical Australia found that food webs became less even at higher elevations as networks became more specialised. Maunsell et al. (2015) studying leaf-mining herbivores and their parasitoids discovered a similar result, showing that food web evenness declined with increasing elevation and declining temperature, independently of elevational changes to plant species composition.

The impacts of climate change are not limited to increases in global temperatures, but also to predicted alterations in rainfall regimes which are likely to affect the timing of interactions between species (Harrington, Woiwod & Sparks 1999) and hence have the potential to affect food web structure. No studies that I know of have yet attempted to determine the effects of altered rainfall regimes on quantitative food webs and hence I tackle this question using data from an existing climate change experiment in this thesis.

1.3.3 Restoration and food web alteration

A review by (Brudvig 2011) found that 88% of restoration studies focus on biodiversity levels as the outcome. However, in recent years there has been a great deal of interest in the restoration of food webs and particularly plant-pollinator webs.

A study on the restoration of hay meadows in the UK found that plant-pollinator webs on restored sites were less complex, showing lower levels of connectance, compared to ancient heathlands (Forup *et al.* 2008b). This is a concern since lower connectance is theoretically predicted to result in less robust communities (Dunne, Williams & Martinez 2002). A further study on the restoration of heathland communities found that higher trophic levels showed a lag in returning to restored sites compared to lower trophic levels, resulting in altered food web structure (Henson, Craze & Memmott 2009).

Albrecht et al. (2007) comparing the food web structure of cavity-nesting Hymenoptera on restored meadows and adjacent intensively managed meadows in Switzerland, found that interaction diversity of cavity-nesting Hymenoptera and their parasitoids were significantly higher in restored meadows. This suggests that although, as the Forup et al. and Henson et al. studies show, restored communities may not demonstrate the same food web structure as target sites, they can still improve community food web structure in comparison to heavily managed environments.

The existing restoration studies show that food web structure can be affected by restoration. However, no studies that we know of have compared the impacts of different restoration management practices on food web structure. Since it is known that the

outcomes of a restoration practise depends on the management being implemented (Hobbs & Harris 2001) I apply a food web approach to compare different restoration techniques in this thesis.

1.4 Ecosystem functioning

Ultimately whilst we are interested in the structure of communities, the functioning of the communities is of critical importance. However, fewer studies have addressed the effects of environmental change on ecosystem functioning. Parasitism is an important ecosystem function providing biological control of lower trophic level insects in natural and managed environments (Hawkins and Cornell 1994). For this reason I largely focus my research in this thesis onto the effects of environmental change on parasitism and discuss the known impacts of environmental change on this ecosystem function.

1.4.1 Effects of fragmentation on parasitism

Parasitoids are predicted to be more greatly affected by fragmentation due to their higher trophic position (Simberloff 1974). This proposition has been supported by field experiments which have shown a greater impact of reduced patch size and increased isolation on parasitoids compared to their hosts and consequent declines in rates of parasitism (Kruess & Tscharntke 1994b; Kruess & Tscharntke 2000). However, caution in the widespread application of the results of such experiments is advised due to the fact that individual parasitoids species will experience the landscape at different spatial scales

(Roland & Taylor 1997) and will be affected by the wider landscape context in which they are studied (Thies, Steffan-Dewenter & Tscharntke 2003).

Landscape scale studies of the effects of habitat fragmentation on parasitism are still rare. For this reason I conduct a large-scale investigation into fragmentation effects on parasitism in this thesis.

1.4.2 Effects of climate change on parasitism

Understanding the impacts of climate change on parasitism has important consequences for human activities such as forestry and agriculture, since climate variability may uncouple host-parasitoid dynamics leading to a greater frequency of pest outbreaks (Stireman *et al.* 2005; Thomson, Macfadyen & Hoffmann 2010).

Altitudinal studies on rates of parasitism generally find that parasitism rates are higher at warmer, lower elevations (Péré, Jactel & Kenis 2013; Morris, Sinclair & Burwell 2014) indicating that as climate warms we may expect increasing levels of parasitism. However, an experimental study by Maunsell et al. (2015) in which a leaf-mining herbivore was moved to a lower latitude than its existing range, did not show an increase in parasitism, indicating that responses to global warming may depend on the abilities of parasitoids to adapt to new hosts undergoing range shifts (Grobler & Lewis 2008).

The general consensus is that climate change could also affect parasitism rates by causing spatial and phenological mis-match between hosts and parasitoids as they respond differently to warming (Klapwijk *et al.* 2010; Jeffs & Lewis 2013). Experimental studies

into climate change effects on parasitism beyond simply warming are rare, therefore in this thesis I look at the effect of rainfall changes, another potential consequence of climate change, on parasitism.

1.4.3 Effects of restoration on parasitism

As in other forms of perturbation, higher trophic levels are predicted to return more slowly to restored sites due to their higher trophic level (Heatwole & Levins 1972). Evidence for a slower return of parasitoids to restored sites compared to their hosts has been found in a range of systems from tropical forests (Maeto et al. 2009) to temperate heathlands (Henson, Craze & Memmott 2009).

Despite a recent shift towards the inclusion of functional outcomes in restoration science (Ruiz-Jaen & Aide 2005), investigations into the effects of habitat restoration on parasitism are rare and hence I address this in this thesis.

1.4.4 Effects of restoration on soil ecosystem function

The impacts of global environmental change on below ground organisms and processes has received very little attention compared to above ground ecosystems (Blankinship, Niklaus & Hungate 2011). Despite its high importance for the outcome of terrestrial restoration (Cramer, Hobbs & Standish 2008) studies on the impacts of restoration on the soil fauna are very rare (Brudvig 2011). However evidence is mounting that the above ground outcomes of restoration are intrinsically linked to below ground processes

(Bardgett & Wardle 2003; Bardgett & van der Putten 2014). For this reason I expand the scope of my thesis in respect to restoration to include below ground ecosystem function.

Soil feeding activity is used as an indication of the functioning of the soil fauna (Römbke *et al.* 2006). Understanding how restoration activities, such as grazing, affects below ground faunal composition and functioning is important as changes below ground can in turn feed-back to a change in above ground species composition by altering competitive interactions between species and functional groups (Eisenhauer *et al.* 2010). This means a change in below ground fauna with grazing management, can feed-back into altered above ground community structure (Mortimer, Van der Putten & Brown 1999), which could ultimately influence the outcome of a restoration treatment (Verschoor *et al.* 2002; Bardgett & Wardle 2003).

For these reasons I investigate the little studied area of the impacts of restoration on nematode densities and soil ecosystem function.

1.5 Aims and thesis overview

The studies in this thesis assess the effects of different forms of environmental change on invertebrate communities and ecosystem functioning and on one of the proposed solutions to these environmental changes: habitat restoration. I consider a range of different taxa and study systems allowing a broad overview of the effects of environmental change, in particular addressing the effects of habitat fragmentation, climate change and restoration on community structure and rates of parasitism.

Additionally, due to its scarcity in the literature and to take advantage of a unique long term existing experiment I also include the impacts of habitat restoration on soil ecosystem function. Throughout my thesis I take advantage of natural experiments and long term manipulative experiments to gain a better understanding of the impacts of these environmental changes.

The main questions driving my thesis are:

- Is a community and ecosystem approach beneficial to our understanding of environmental change on natural communities?
- Do the impacts of environmental change affect different trophic levels to different extents?
    - If so, do these change at different levels result in changes to food web structure and ecosystem function?
- Does habitat restoration affect food web structure and ecosystem function?
- Can our understanding of environmental changes be enhanced by considering the below ground environment and its ecosystem processes?

In Chapter 2, I describe a landscape scale study into the effects of habitat fragmentation on sub-tropical rainforest communities in Australia. Using cavity-nesting bees and wasps and their parasitoids as a study community I show that fragmentation effects such as fragment area, isolation and edge effects can impact different trophic levels to different extents, but that this does not necessarily result in a change to the ecosystem function of parasitism.

In Chapter 3, I investigate the effects of climate change on host-parasitoid food webs and rates of parasitism in temperate grassland. Using data from a manipulative climate change experiment I construct quantitative leaf-miner – parasitoid food webs and examine the impacts of altered precipitation regimes on their structure. I show that changes to precipitation regimes which may follow climate change have the potential to disrupt host-parasitoid synchrony. These changes do not cause food web changes at the scale studied, but show the potential for climate change to alter host-parasitoid synchrony and hence the ecosystem service of parasitism.

In Chapter 4, I utilise a long-term experiment into the effects of different grazing regimes for the restoration of lowland calcareous grassland in the UK. By constructing host-parasitoid food webs of leaf-mining herbivores and their natural enemies I examine the impacts of the season of grazing on food web structure and parasitism rate. I show that although grazing regime can affect trophic level composition differentially, this does not translate into overall changes in food web structure or parasitism at the field scale studied.

In my final data chapter (Chapter 5) I investigate the impacts of seasonal grazing regime on soil ecosystem function. I show that the season of grazing has an impact on the vertical profile of soil ecosystem functioning and discuss the potential of this novel finding for the future of restoration studies.

My results are discussed in the context of the wider literature in Chapter 6.

Chapter 2

Landscape-scale rainforest fragmentation shows little impact on the structure and functioning of cavity-nesting Hymenoptera communities

Abstract

- Habitat fragmentation poses a significant threat to the maintenance of biodiversity, yet its impact on the functioning of ecosystems is still poorly understood. This threat is particularly acute in mega-diverse rainforests which provide global ecosystem services such as carbon storage and oxygen production.
- In this study I investigate the effects of landscape-scale fragmentation of subtropical rainforest on communities of cavity-nesting Hymenoptera and their parasitoids, which perform important functional roles as pollinators and predators. I expected higher trophic levels to be more negatively impacted by fragmentation, resulting in a decline in the ecosystem service of parasitism.
- Although individual species show species-specific response to fragmentation, these did not translate into changes in rates of parasitism, due to the study system being dominated by a single, generalist parasitoid.
- The most abundant individual species present in this study appear to respond to fragmentation at different spatial scales, indicating that the trophic level response of species may be less important than by individual species traits.

2 Landscape-scale rainforest fragmentation shows little impact on the structure and functioning of cavity-nesting Hymenoptera communities

2.1 Introduction

The increasing loss of natural habitats worldwide is believed to be the greatest threat to future global biodiversity (Sala *et al.* 2000a; Rands *et al.* 2010). Habitat loss leads to increasingly fragmented landscapes in which remnant habitat patches remain within an anthropogenically created matrix. Whilst the amount of habitat lost has the greatest direct effect on biodiversity decline, biodiversity within remaining habitat patches will be subject to compounding factors such as reduced quality of the matrix habitat, the area and isolation of remaining fragments and the magnitude and strength of edge effects, all of which can affect biodiversity (Fahrig 2003).

Beyond the concern of habitat fragmentation causing biodiversity decline, there is the further question of whether declines in biodiversity will lead to changes in the functioning of ecosystems (Haddad *et al.* 2015). Work in experimental ecosystems has demonstrated that declining biodiversity can impact on many measures of ecosystem functioning (Balvanera *et al.* 2006; Cardinale *et al.* 2006). However, these findings have been drawn largely from small-scale experiments in often artificially created ecological communities subjected to random species loss (Diaz *et al.* 2003). Such artificial communities lack the complexity of naturally assembled communities over multiple trophic levels (Duffy *et al.*

2007; Cardinale *et al.* 2009). This has led to a call for more research on how changes in real world environments may impact biodiversity and in turn, ecosystem functioning, across multiple trophic levels (Didham *et al.* 1996; Srivastava & Vellend 2005; Reiss *et al.* 2009). Over the last decade this call has been met with increasing research on biodiversity-ecosystem functioning relationships being carried out in large-scale field studies (Valladares, Salvo & Cagnolo 2006b).

Ecosystem functioning research to date has been largely focused on plant ecosystem services such as productivity (Loreau et al. 2001), with few studies looking at impact at higher trophic levels, such as parasitism. Parasitism is an important ecosystem function providing biological control of lower trophic level insects in natural and managed environments (Hawkins and Cornell 1994). There are several ecological theories relevant to understanding how parasitoids and the ecosystem function they perform will be affected by habitat fragmentation. Island biogeography theory (MacArthur & Wilson 1963; MacArthur & Wilson 1967b) predicts that declining habitat area will lead to a decline in the species richness of parasitoids and, due to complementary resource use (Loreau 1998), a consequent decline in parasitism.

The trophic rank hypothesis predicts that species at a higher trophic rank, such as parasitoids and predators, will be more affected by declining area and increasing isolation caused by fragmentation due to their dependence on the existence of lower trophic rank species and their lower population size (Holt *et al.* 1999). Many field studies have supported this prediction (Kareiva 1987; Kruess & Tscharntke 1994a; Roland & Taylor 1997; Zabel & Tscharntke 1998; Kruess & Tscharntke 2000), although the level of

specialisation of the parasitoid or predator also influences its response to fragmentation (Valladares, Salvo & Cagnolo 2006a; Cagnolo *et al.* 2009).

Island biogeography theory assumes that habitat fragments are uniform and embedded within a hostile matrix. In reality, habitat fragments are subject to edge effects, where the meeting of the fragment habitat and matrix can cause changes in microclimate such as light availability and temperature (Nicotra, Chazdon & Iriarte 1999; Laurance 2004), habitat structure (Faria *et al.* 2009) and consequently impact species interactions and ecosystem processes (Fagan, Cantrell & Cosner 1999; McGeoch & Gaston 2000; Valladares, Salvo & Cagnolo 2006a; Riutta *et al.* 2012). Different insect species can have positive, negative or neutral response to habitat edges, often dependent on their level of generalisation or specialisation (Peyras *et al.* 2013), leading to distinct edge communities (Ries *et al.* 2004). Furthermore, the nature of the matrix habitat and the variation in the ability of individual species to persist within it is a further crucial factor influencing species within habitat fragments (Ricketts 2001; Laurance *et al.* 2012) meaning species less able to cross the matrix habitat are those most likely to be lost from isolated fragments.

Since tropical and sub-tropical rainforests harbour the greatest levels of global terrestrial biodiversity (Myers et al. 2000), yet continue to be broken into ever smaller fragments embedded in agricultural mosaics (Skole and Tucker 1993), understanding fragmentation effects on rainforest community dynamics is more pressing than ever (Turner and Corlett 1996, Bawa et al. 2004). In particular, the rich and complex invertebrate communities of

rainforests, which carry out vital ecosystem services, such as pollination and biological control (Blanche et al. 2006, Olschewski et al 2006), offer potentially tractable study systems with which to investigate multi-trophic effects and how landscape-level fragmentation effects including area, isolation and edge effects may interact (Ewers, Thorpe & Didham 2007). In light of this, I set out to investigate the effects of habitat fragmentation on the interactions between cavity-nesting Hymenoptera and their parasitoids in a fragmented landscape of sub-tropical forest remnants in eastern Australia. The host Hymenoptera include a variety of solitary bees (which are often important pollinators of native and crop plants) and predatory wasps (which may be important in controlling prey populations) (Klein et al. 2003; Klein et al. 2004). These aspects make trap-nesting studies extremely valuable for investigating food web interactions and ecosystem functioning (Tscharntke et al. 1998, Steffan-Dewenter 2002, Tylianakis et al. 2005, 2006a,b, 2007).

I addressed the following questions:

- Are species richness, abundance and community composition, of hosts and parasitoids, affected by habitat area, connectivity and changes across the rainforest-matrix boundary?
- Are parasitoids more affected by habitat area, connectivity and edge effects than their hosts?
- What are the consequences of these landscape-level fragmentation effects for the ecosystem function of parasitism?

2.2 Methods

2.2.1 Study system

Cavity nesting Hymenoptera are solitary insects which naturally nest in hollow twigs, holes in trees or the ground, and often crevices in walls and fence posts. Each adult insect will construct a nest containing a series of cells with a single egg laid into each cell. The adult insect will provision each cell with food, pollen for bees and spiders or immature insects such as caterpillars for wasps (Evans 1966). After an egg has been laid in each cell and a food source provided the adult insect will block off the nest entrance with mud, resin or grass. Cavity nesting Hymenoptera are subject to parasitism by parasitic wasps, which usually attack during the nest building stage, but some species will also attack closed nests. They are also attacked by cleptoparasites, which feed on the food resources with which the Hymenoptera provision their nests (Tylianakis, Tscharntke & Klein 2006). This group make an ideal study system as they can be surveyed using trap nests, which provide artificial nesting sites, mimicking the crevices and hollow twigs that they would naturally seek out. The use of trap nests allows the observer to remove whole nests from a site and, on rearing up the host and parasitoid species, to determine the structure and functioning of communities.

2.2.2 Study location

This study was carried out in north-eastern New South Wales, Australia, in an area known as “The Big Scrub”. This was once the largest area of lowland subtropical rainforest in Australia, covering 750 square kilometres (Figure 1a). In the 1840s the clearing of the area by European settlers began and by 1900 the majority of the forest cover had been

removed (Figure 1b). Today just 0.13 % of the original forest area remains as fragments spread across the landscape within a matrix dominated by cattle- grazed pasture and macadamia plantations (NSW National Parks and Wildlife Service, 2001).

The lowland rainforests of subtropical Australia are listed as a critically endangered ecological community under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) Australia. This ecological community is primarily situated in north-eastern New South Wales and south-eastern Queensland, occurring on soils derived from basalt or alluvium, at altitudes less than 300 m above sea level. This ecological community typically occurs in areas with high annual rainfall (>1300mm) where the mean maximum temperature is 25.5^{o}C. Rainforests of this region are characterised by white booyong *Heritiera trifoliolata*, black bean *Castanospermum australe*, native tamarind *Diploglottis australis*, white bolly gum *Neolitsea dealbata*, red cedar *Toona ciliata*, and epiphytes such as *Platycerium* spp. and *Asplenium australasicum* (bird's nest fern).

Approximately fifty remnants of the Big Scrub exist today, most having an area of less than 5 hectares (Figure 1). The clearing of the Big Scrub was so rapid that little is known about the flora and fauna of the original forest. Early military maps show that most existing remnants have been in their current form for at least fifty years. The majority of remnants are on private land with six of the largest remnants under the management of New South Wales National Parks and Wildlife Service.

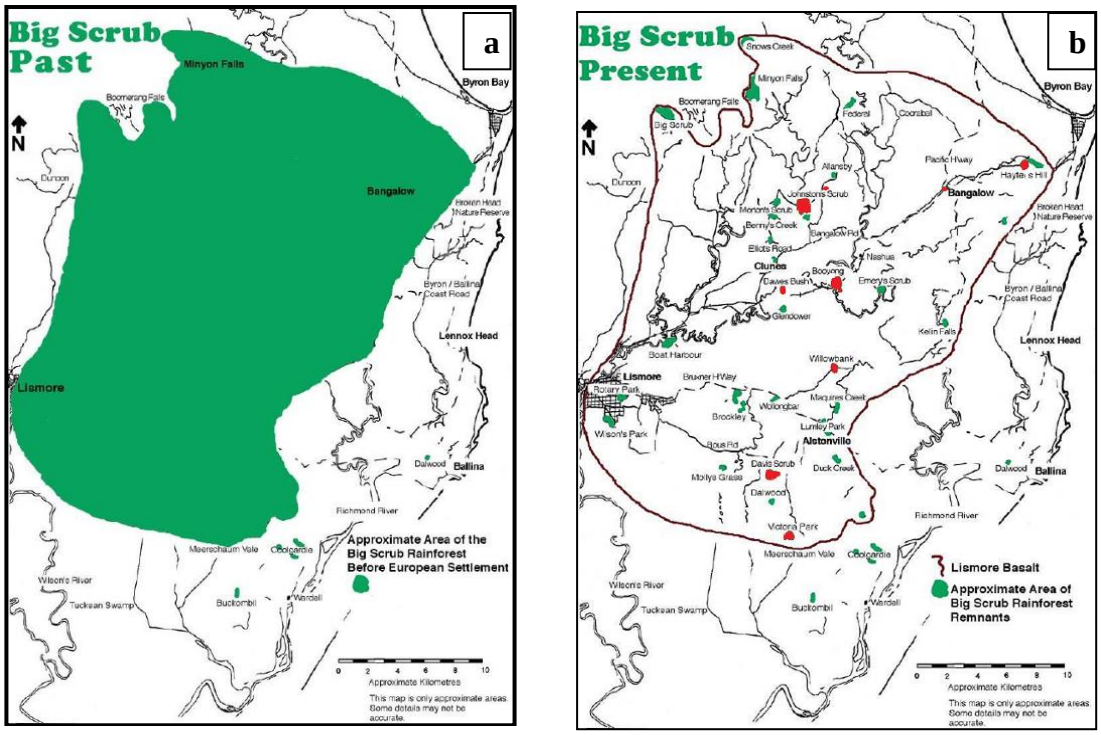


Figure 1. Study location showing approximate extent of "Big Scrub" lowland sub-tropical rainforest before European settlement (a) and remaining fragments today (b). Fragments marked in red are included in this study. Image from www.rainforestrescue.org.au

2.2.3 Study sites

Nine fragments were chosen to form a gradient from very small fragments (0.36 ha) up to the largest available fragment (20.66 ha). All sites were at less than 150 metres elevation and each fragment was bordered by pasture along at least 50 % of its perimeter. The criterion for site selection was to cover a wide range of areas whilst keeping fragment shape, matrix characteristics and current habitat management as uniform as possible. All chosen fragments have been fenced to prevent access by grazing cattle from the pasture matrix.

2.2.4 Transect positioning

Four transects, each containing ten trap nests spaced five metres apart, were set up at each of the seven larger and reference sites and three transects at the two smallest sites. Larger fragments contained a central forest, inner forest, forest edge and pasture transect (Figure 2). The two smallest fragments contained only a central, edge and pasture transect, as due to their small size the central transect also represented the inner transect. The central transect was placed as close as possible to the centre of the fragment, or at least 50 m from the edge in the largest fragments. The edge transect was attached to the outermost row of trees where the forest met the pasture boundary. The inner transect was placed 10-25 m into the fragment from this edge. This distance was chosen as Fox et al. (1997) had shown this to be the distance beyond which edge effects were not evident in the flora of a series of Australian forest remnants. A pasture transect was placed 10-25 m out into pasture from this edge. The exact distance of each trap from the edge depended on the availability of suitable trees. In some pasture sites where insufficient trees were available some traps were attached to fence posts.

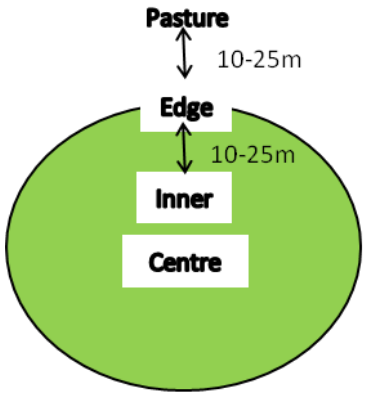


Figure 2. Diagram illustrating position of trap-nest transects across the rainforest-pasture boundary in fragments of the "Big Scrub", New South Wales, Australia. Not to scale.

Trap nests contained 25- 30 pieces of bamboo with diameters from 5 mm to 50 mm encased in a PVC tube. A variety of bamboo diameters was offered since this has been shown to maximise the diversity of solitary Hymenoptera that will occupy a trap nest (Matsumoto & Makino 2011). Trap nests were 25 cm length by 10 cm diameter. Traps were attached by rope to the trunks of trees at a minimum of 1.5 m above the ground. Tape coated in Tanglefoot® was placed on the tree above and below each trap to deter ants.

2.2.5 Sampling

Trap nests sampling was conducted for three months from the end of January to the end of April 2010. Occupied nests were removed from the field monthly and replaced with fresh bamboo nodes of the same diameter as those removed. Removed nests were stored in individual plastic bags in ambient conditions in a shed close to the field site. These nests were checked weekly for emergent adults, which were killed by freezing and then stored at the Queensland Museum for identification.

Insect rearing and species identification was carried out by Dr Chris Burwell at the Queensland Museum, Brisbane, with the assistance of Dr Aki Nakamura.

2.2.6 Measures of fragment size and isolation

The area of each fragment was obtained from data supplied by the Big Scrub Landcare Group. Coordinates of all 52 known fragments of the Big Scrub were supplied by the Big

Scrub Landcare Group and these were used to assess the connectivity of each fragment in this study using the connectivity index S_i (Hanksi, 1994), calculated as:

$$S_i = \mathbf{\Sigma} \exp(-\alpha d_{ij}) p_j A_j$$

d_{ij} represents distance between patches in km, p_j represents patch occupancy, A_j patch area in m^2, and α is a measure of dispersal ability (1/average dispersal distance). The dispersal distances of the insects in this study are unknown, so a value of 0.5 was used for α based on an estimated average migration of 2 km as used in other similar studies (Bruckmann et al, 2010). Tests on the robustness of the connectivity measure were made by varying the value of α and it was found that the Si value was robust to large variations in α and thus that using our estimate of dispersal would not affect the results.

2.3 Analyses

All statistical analyses were carried out using R (R Core Team, 2012). Generalised linear models with quasi-poisson errors (due to over-dispersion in the data) were used to analyse the relationship between the abundance and species richness of hosts and parasitoids and the predictor variables of fragment area, connectivity and transect location within the forest remnant (Central forest, Inner forest and Edge forest) and any interaction between these factors. The models were simplified by removing non-significant terms until arriving at a minimum adequate model. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. The minimum adequate model was then checked to test all model assumptions had been met.

Generalised linear models with quasi-binomial errors (due to over-dispersion in the data) were used to analyse the relationship between the rates of parasitism and the predictor variables of fragment area, connectivity and transect location within the forest remnant (Central forest, Inner forest and Edge forest) and any interaction between these factors. Models were simplified and checked to see that they met the assumptions as described above.

The abundance of host individuals was calculated as the abundance of occupied nest cells of a given Hymenoptera species per transect. Natural enemy abundance was recorded as the number of cells parasitised, irrespective of whether the parasitoid was gregarious or not. Parasitism is represented graphically as a proportion but in the models was calculated using cbind in R (R Core Team, 2012) of parasitised versus unparasitised cells, to account for the variation in the total abundance of hosts and parasitoids between transects.

Changes in community composition of hosts across the rainforest-pasture boundary were investigated using the Bray-Curtis distance measure. This is a widely used measure which reflects difference in samples due to differing taxon composition and abundance, and is considered to be robust to any skew caused by data sets dominated by individual species (Clarke & Warwick 2001).

2.4 Results

1544 brood cells were collected from 439 hymenopteran nests over the study period. Nests within forest fragments were dominated by four species of spider-hunting wasps (Pompilidae) from the genus *Fabriogenia*, but also contained small numbers of nests from one Vespidae species in the genus *Rhynchium*. Nests collected in pasture contained additional species including two species of Sphecidae from the genera *Isodontia* and *Pison* and one species of leaf-cutter bee (Megachilidae).

Natural enemies were dominated by the ectoparasitoid *Melittobia australica* (Eulophidae), which accounted for 95% of all parasitism events. *Melittobia australica* is a gregarious parasitoid which rapidly produces hundreds of offspring per parasitism event. Since each adult female *Melittobia australica* is believed to attack only one host in her lifetime (Trexler, 1985), each brood cell attacked by *M. australica* was recorded as one parasitism event, rather than counting the individual parasitoid offspring. The remaining parasitism came from a small number of cleptoparasitoids in the family Chrysididae and Diptera from the family Sarcophagidae. Species biology and their locations in this study are summarised in Table 1 and 2.

Table 1. Summary of Hymenoptera species surveyed in the "Big Scrub" region of New South Wales, Australia and their biology (Pers. Comm. Chris Burwell).

	Family	**Species**	**Biology**
Wasps	Pompilidae	*Fabriogenia Sp. A*	Solitary, spider-hunting wasp
		Fabriogenia Sp. B	Solitary, spider-hunting wasp
		Fabriogenia Sp. C	Solitary, spider-hunting wasp
		Fabriogenia Sp. D	Solitary, spider-hunting wasp
	Vespidae	*Rhynchium Sp. A*	"Potter wasp" Solitary, spider-hunting wasp.
	Sphecidae	*Isodontia Sp. A*	"Grass-carrying wasp" Solitary wasp provisioning cells with grasshoppers.
		Pison Sp. A	Solitary spider-hunting wasp
Bees	Megachilidae	*Megachile Sp. A*	Solitary leaf-cutter bee
Natural Enemies	Eulophidae	*Melittobia australica*	Gregarious ectoparasitoid
	Chrysididae	*Chrysididae Sp. A*	"Cuckoo wasp" Clepto-parasite of solitary wasps and bees
	Diapriidae	*Diapriidae Sp. A*	Solitary parasitoid wasp
	Sarcophagidae	*Miltogramminae Sp. A*	Clepto-parasitic fly

Table 2. Summary of Hymenoptera species abundances by fragment and transect in the "Big Scrub" region of New South Wales, Australia.

Fragment	Area (ha)	Transect	Host species								Natural enemies				
			Fabriogenia				*Rhynchium Sp. A*	*Pison Sp. A*	*Isodontia Sp. A*	*Megachile Sp. A*	*Melittobia australica*	*Chrysididae Sp. A*	*Diapriidae Sp. A*	*Miltogramminae Sp. A*	*Indet. Dipteran parasitoid*
			Sp. A	*Sp. B*	*Sp. C*	*Sp. D*									
Wilton's Scrub	0.36	Centre	0	0	0	0	0	0	0	0	0	0	0	0	0
		Edge	0	0	0	0	0	0	0	0	0	0	0	0	0
		Pasture	0	0	0	0	0	0	0	0	0	0	0	0	0
Noble's Scrub	1.45	Centre	0	0	0	0	0	0	0	0	0	0	0	0	0
		Edge	2	0	28	0	0	0	0	0	6	1	0	0	0
		Pasture	0	0	0	0	0	0	0	0	4	0	0	0	0
Willowbank	2.65	Centre	0	0	0	0	0	0	0	0	0	0	0	0	0
		Inner	24	0	0	0	5	0	0	0	8	0	0	0	0
		Edge	42	6	8	0	0	0	0	0	17	0	0	0	0
		Pasture	0	0	0	0	0	0	0	0	0	0	0	0	0
Hayter's Hill West	5.02	Centre	37	7	4	0	0	0	0	0	8	0	0	0	0
		Inner	25	0	25	0	0	0	0	0	14	0	0	0	0
		Edge	19	0	23	5	0	0	0	0	17	0	0	0	0
		Pasture	4	0	0	0	0	0	0	0	3	0	0	0	0
Dawe's Bush	7.16	Centre	7	0	4	0	0	0	0	0	4	0	0	0	0
		Inner	54	0	6	0	0	0	0	0	18	0	0	0	0
		Edge	16	0	24	0	0	0	0	0	1	0	0	0	0
		Pasture	0	0	0	0	0	0	149	27	25	0	0	0	6

Fragment	Area (ha)	Transect	Host species								Natural enemies				
			Fabriogenia				*Rhynchium Sp. A*	*Pison Sp. A*	*Isodontia Sp. A*	*Megachile Sp. A*	*Melittobia australica*	*Chrysididae Sp. A*	*Diapriidae Sp. A*	*Miltogramminae Sp. A*	*Indet. Dipteran parasitoid*
			Sp. A	*Sp. B*	*Sp. C*	*Sp. D*									
Davis Scrub	14.36	Centre	62	9	24	0	1	0	0	0	20	0	0	0	0
		Inner	49	0	0	0	0	0	0	0	0	0	0	0	0
		Edge	98	1	46	0	25	0	0	0	29	0	0	0	0
		Pasture	4	0	0	0	23	5	10	0	0	0	0	0	0
Booyong	15.82	Centre	2	0	0	0	0	0	0	0	2	0	0	0	0
		Inner	13	1	15	0	0	1	0	0	7	0	0	0	0
		Edge	33	0	0	0	8	0	0	0	19	0	0	0	0
		Pasture	0	0	0	0	9	0	0	43	23	0	0	0	0
Victoria Park	16.99	Centre	48	5	0	0	0	0	0	0	30	0	0	0	0
		Inner	44	2	0	0	8	0	0	0	34	0	0	0	0
		Edge	44	0	0	0	10	0	0	0	38	0	0	0	0
		Pasture	5	19	11	0	0	0	0	0	10	0	0	0	0
Johnston's Scrub	20.66	Centre	83	0	0	8	0	0	0	0	37	0	0	0	0
		Inner	42	0	0	0	0	0	0	0	8	0	0	0	0
		Edge	38	0	0	0	0	0	0	0	3	0	0	0	0
		Pasture	9	7	11	0	9	0	0	0	7	0	0	0	0

2.4.1 Abundance and species richness

Both host and natural enemy species richness was low, ranging from one to five host species and 1 to 4 natural enemy species per fragment and demonstrated no significant relationship with fragment area, connectivity or position across the rainforest-matrix boundary (Figure 3, Table 3). Abundance of hosts showed no significant relationships with area, connectivity of forest fragment or any significant interactions of these with position within the fragment (Figure 3, Table 3). Natural enemy abundance showed a significant positive relationship with fragment area, but not connectivity or position across the rainforest-matrix boundary (Figure 3, Table 3).

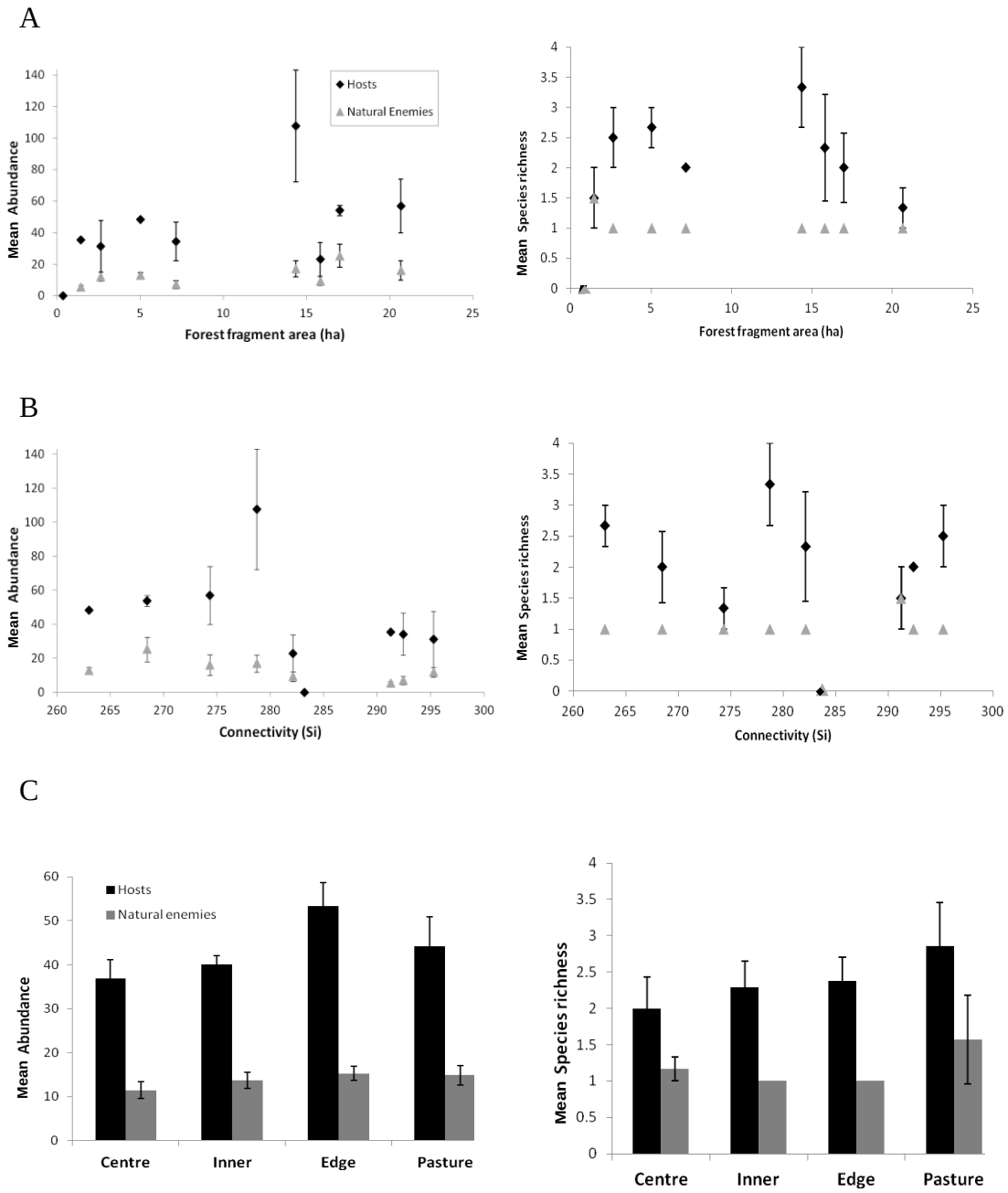


Figure 3. Effect of fragment area (A), connectivity (B), and position across the rainforest-matrix boundary (C) on Hymenoptera host and natural enemy abundance and species richness in the "Big Scrub" region, New South Wales, Australia. Error bars show standard error of the mean (s.e.m).

Table 3. Generalised linear models of host and natural enemy abundance and species richness in relation to fragmentation in the "Big Scrub" region, New South Wales, Australia. Natural enemy species richness was not modelled as it was almost universally 1.

Model	DF	F	P-value	Error structure
Host Abundance~				
Area*Connectivity*Location	13	0.141	0.870	Quasi-poisson
Area*Connectivity	15	0.089	0.769	
Area*Location	16	0.485	0.624	
Connectivity*Location	18	0.830	0.452	
Connectivity	20	0.4230	0.523	
Location	21	0.560	0.580	
Area	23	4.041	0.0563	
Natural enemy abundance~				
Area*Connectivity*Location	13	0.334	0.722	Quasi-poisson
Area*Connectivity	15	1.574	0.229	
Connectivity*Location	16	0.0930	0.912	
Area*Location	18	1.797	0.194	
Location	20	0.214	0.809	
Connectivity	22	3.144	0.090	
Area	23	8.321	0.008	
Species richness~				
Area*Connectivity*Location	13	0.440	0.653	Quasi-poisson
Area*Location	15	0.151	0.860	
Connectivity*Location	17	0.776	0.476	
Location	19	0.669	0.524	
Area*Connectivity	21	2.789	0.110	
Connectivity	22	0.353	0.559	
Area	23	1.252	0.275	

2.4.2 Community composition

Although mean species richness showed little variation across the rainforest-matrix boundary, absolute species richness was greater in pasture transects with seven host species occurring in the matrix compared to five within fragments. Forest transects were fairly uniform in their species composition, whilst pasture transects showed a different community structure was present just 20 metres outside the fragment borders (Figure 4).

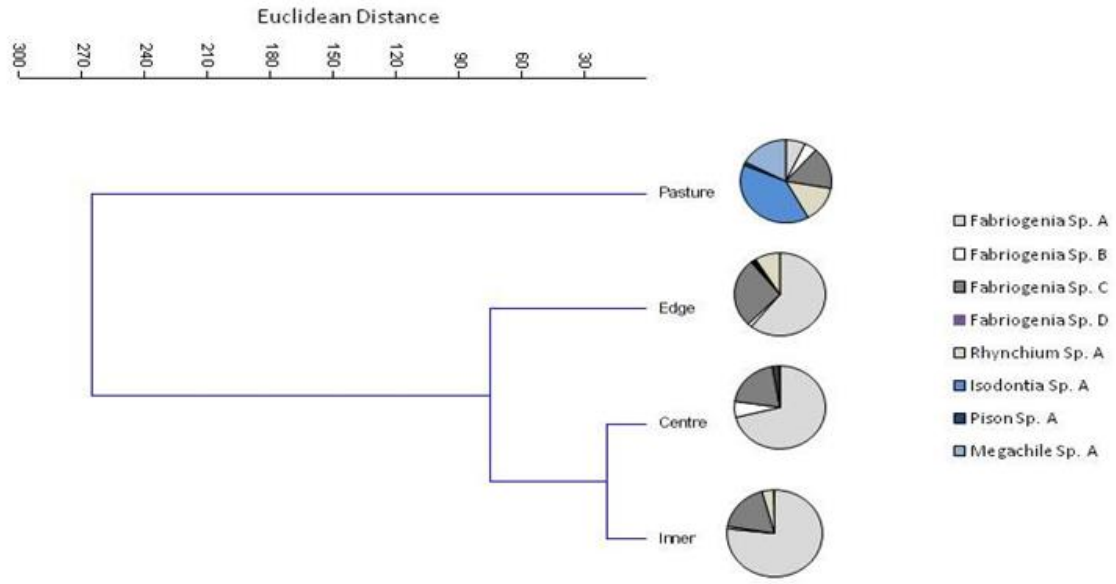


Figure 4. Cavity-nesting Hymenoptera species composition as a proportion of total abundance across the rainforest-matrix boundary in fragments of the "Big Scrub", new South Wales, Australia.

The host community of cavity-nesting Hymenoptera was dominated by two species of spider-hunting pompilid wasps, *Fabriogenia* species A and C, accounting for 72 % of all individuals recorded (Fabriogenia species A 52%, Fabriogenia species C 20%). Looking at the response of these species to area, isolation and position from the edge separately

showed that these two species were responding differently to fragmentation. *Fabriogenia* A was found to increase in abundance with fragment area (Figure 5, table 4) whilst *Fabriogenia* species C did not demonstrate a significant relationship (figure 5, table 4). Neither species showed a significant response to connectivity or position from the edge (Figure 5, table 4)

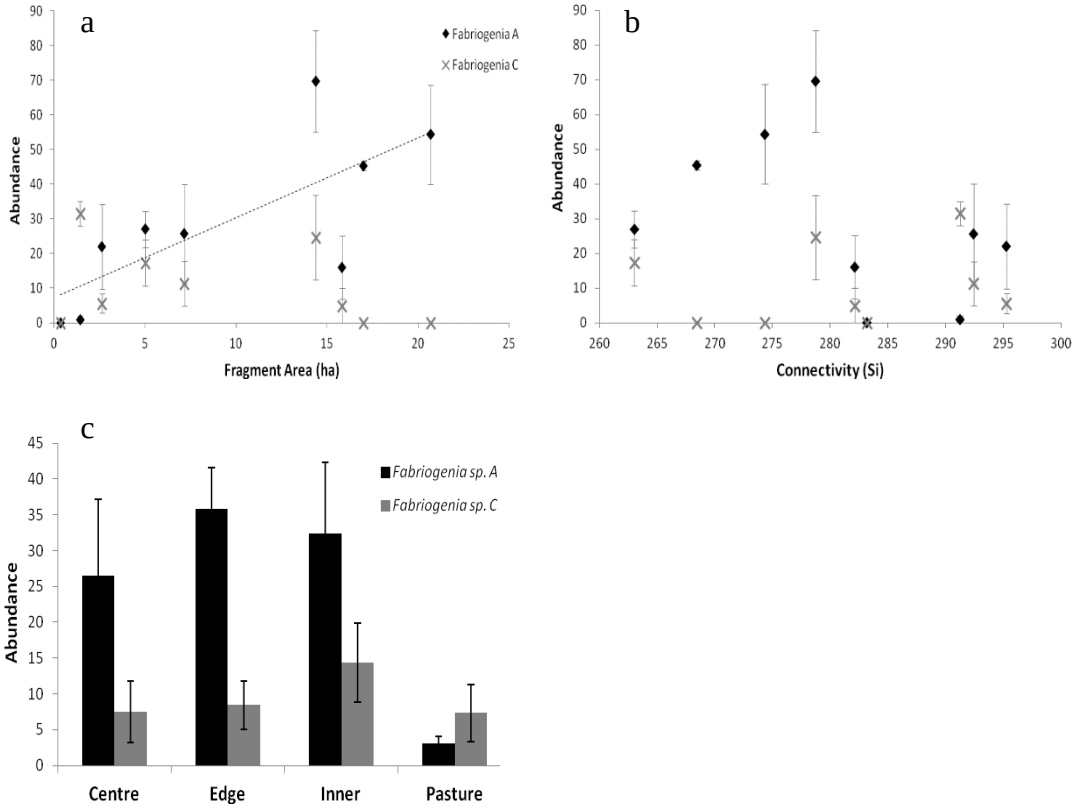


Figure 5. Response of *Fabriogenia* species A and C to fragment area (a), connectivity(b) and position across the rainforest-matrix boundary (c) in fragments of the "Big Scrub", New South Wales, Australia. Error bars show s.e.m.

Table 4. Generalised linear models of the abundance of *Fabriogenia* species A and C in response to fragment area, connectivity and position within fragment.

Model	DF	F	P-value	Error structure
Fabriogenia sp. A abundance~				
Area*Connectivity*Location	13	0.301	0.745	Quasi-poisson
Area*Connectivity	15	0.162	0.693	
Connectivity*Location	16	1.830	0.192	
Connectivity	18	0.312	0.583	
Area*Location	20	1.726	0.205	
Location	21	0.158	0.855	
Area	23	11.367	0.003	
Fabriogenia sp. C abundance~				
Area*Connectivity*Location	13	0.282	0.759	Quasi-poisson
Area*Connectivity	15	1.368	0.261	
Area*Location	16	0.203	0.819	
Connectivity*Location	18	0.218	0.807	
Connectivity	20	0.023	0.882	
Location	21	0.557	0.581	
Area	23	1.712	0.204	

Fabriogenia species A and C also responded differently to the rainforest-matrix boundary, though not to transect position within forest remnants themselves. *Fabriogenia* species A was less abundant in pasture than in forest transects (Figure 5), whereas *Fabriogenia* species C did not differ in abundance between these habitats.

The relative proportions of *Fabriogenia* species A and C changed with regards to the size of the fragment. *Fabriogenia* species C dominated both edge and central transects in small fragments, but was absent from very large fragments. In contrast *Fabriogenia* species A is present in lower proportions in the smaller fragments and dominated all transects in larger fragments (Figure 6).

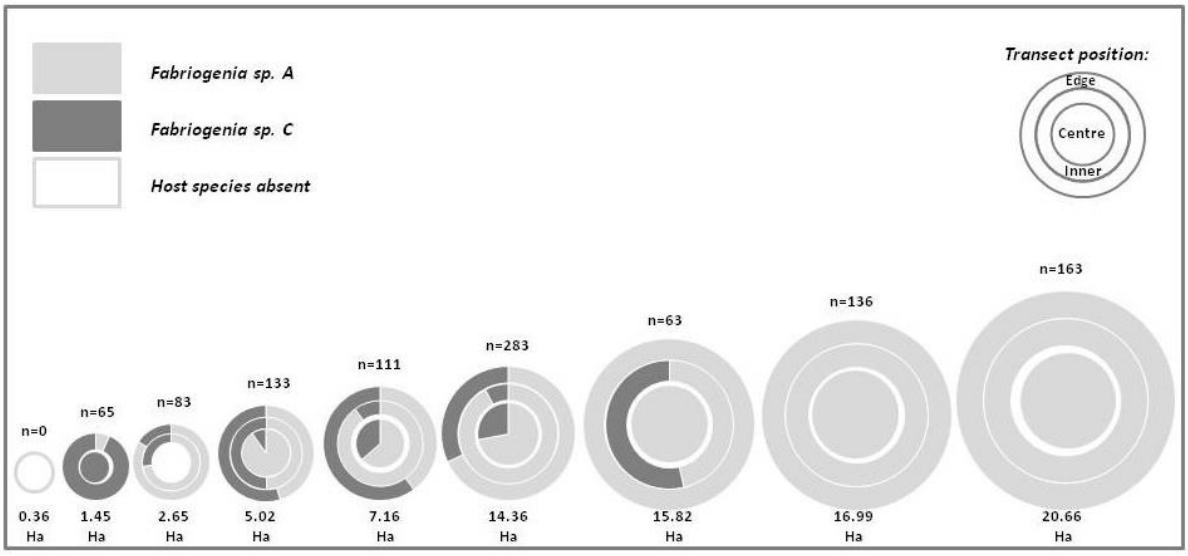


Figure 6. Relative proportion of *Fabriogenia* species A and C by transect and fragment area of rainforest fragments in the "Big Scrub", New South Wales, Australia. Symbols representing fragment sizes are not to scale and are illustrative only.

2.4.3 Parasitism

Overall parasitism varied from 15% to 50% showing no significant relationship with fragment area, isolation, position across the rainforest-matrix boundary, or interactions between these variables (Figure 7, Table 5).

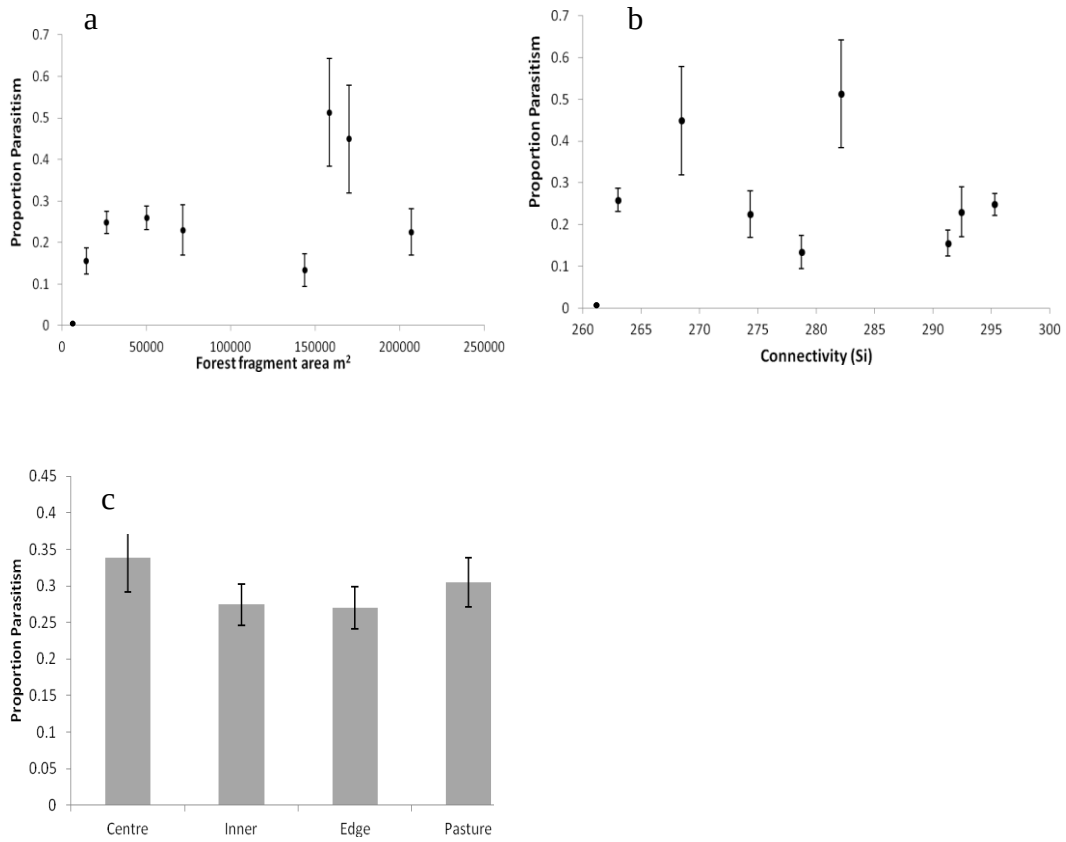


Figure 7. Parasitism rates of cavity-nesting Hymenoptera in response to fragment area (a), isolation (b) and position across the rainforest-matrix boundary (c) in fragments of the "Big Scrub", New South Wales, Australia. Error bars show s.e.m.

Table 5. Generalised linear model with quasi-poisson errors of overall parasitism rates of cavity-nesting Hymenoptera in response to fragment area, connectivity and position within fragment, in the "Big Scrub" region, New South Wales, Australia.

Model	DF	F	P-value	Error structure
Parasitism~				
Area*Connectivity*Location	10	0.7	0.519	Quasi-binomial
Connectivity*Location	12	0.578	0.576	
Area*Connectivity	14	2.8734	0.112	
Area*Location	15	0.127	0.882	
Location	17	0.084	0.92	
Area	19	0.3801	0.545	
Connectivity	20	2.0834	0.164	

Parasitism rates of the two dominant *Fabriogenia* hosts shows no significant relationships with fragment area, connectivity or position across the rainforest-matrix boundary (Figure 8, Table 6).

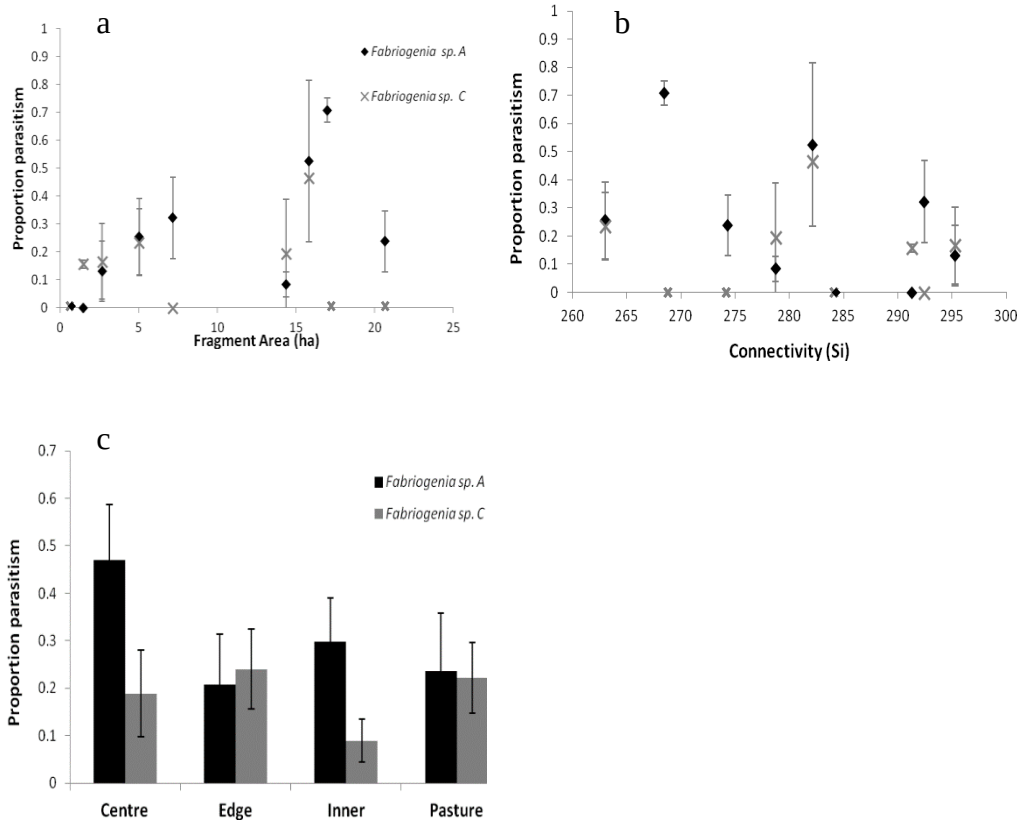


Figure 8. Proportion parasitism of the two dominant hosts *Fabriogenia* A and C in response to (a) fragment area, (b) connectivity, and (c) position across the rainforest-matrix boundary in fragments of the "Big Scrub", New South Wales, Australia. Error bars show s.e.m.

Table 6. Generalised linear model with quasi-binomial errors of parasitism rates of Fabriogenia A and C in response to fragment area, connectivity and position within the fragment in the "Big Scrub" region, New South Wales, Australia.

Model	DF	F	P-value	Error structure
Fabriogenia sp. A parasitism~				
Area*Connectivity*Location	9	0.471	0.639	Quasi-binomial
Connectivity*Location	11	0.223	0.804	
Area*Connectivity	13	2.440	0.142	
Area*Location	14	0.711	0.508	
Location	16	0.078	0.925	
Connectivity	18	1.192	0.289	
Area	19	1.810	0.194	
Fabriogenia sp. C parasitism~				
Area*Connectivity*Location	2	0.384	0.723	Quasi-binomial
Connectivity*Location	4	2.626	0.187	
Area*Connectivity	6	0.592	0.471	
Area*Location	7	4.000	0.0694	
Area	9	0.115	0.742	
Connectivity	10	2.655	0.134	
Location	11	2.804	0.104	

The attack rate of the dominant parasitoid *Melittobia australica* was independent of the host density of its most abundant hosts *Fabriogenia* species A and C (Figure 9, Table 7).

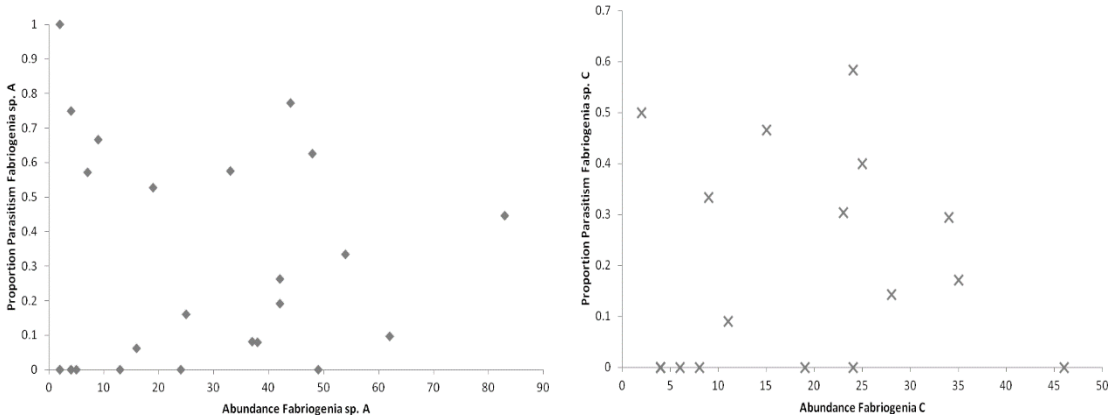


Figure 9. Proportion parasitism of (a) *Fabriogenia* A and (b) *Fabriogenia* C in relation to host abundance.

Table 7. Generalised linear models with quasi-binomial errors of attack rate of *Melittobia australica* on *Fabriogenia* A and C in response to host abundance.

Model	DF	F	P-value	Error structure
Fabriogenia sp. A Melittobia attack rate~				
Abundance Fabriogenia sp. A	19	0.07	0.78	Quasi-binomial
Fabriogenia sp. C Melittobia attack rate~				
Abundance Fabriogenia sp. C	12	1.14	0.31	Quasi-binomial

2.5 Discussion

I found no overall response of host or parasitoid species richness or parasitism, and only a small impact on abundance, to fragmentation in this landscape. Contrary to the trophic level hypothesis, the parasitoid species in this study showed minimal response to fragmentation, whereas their hosts showed individual responses that differed among species. Our results are consistent with the findings of Valladares et. al. (2010) and Schnitzler et al. (2011) that trophic level is likely to be less important in influencing responses to fragmentation than other individual species traits.

2.5.1 Species richness and abundance

I expected smaller habitat fragments to have lower species richness since smaller populations are more vulnerable to extinctions due to stochastic processes (Hanski 1998, Hanski & Ovaskainen 2000, Fahrig 2003). In contrast I found no overall effect of habitat fragment area on species richness. Small fragments were populated by edge and matrix-inhabiting species, making their overall species richness similar to that of large fragments (Ewers & Didham 2006).

Overall host abundance did appear to increase with fragment size and was close to significance ($p=0.056$, Table 3) whilst natural enemy abundance did show a positive relationship with area ($p=<0.01$, Table 3), although since parasitism rate appeared to be

fairly constant in relation to host density the increase in natural enemy abundance was most likely caused by the increase in host abundance.

2.5.2 Community composition

There was a clear change in community composition across the habitat boundary with pasture having the greatest diversity and central and inner rainforest the lowest (Figure 4). This result is consistent with that of Tylianakis et al. (2006), who found that cavity-nesting Hymenoptera diversity was greater in pasture than in forest habitats across a tropical land-use gradient.

The central and inner rainforest contained only nests from the spider hunting wasp family Pompilidae. This result is likely due to the availability of prey. Klein et al. (2002) found that spider densities increased in shaded environments. Klein et al. (2004) showed that Pompilidae foraging time increased with light intensity. This indicates that nesting in shaded environments would be profitable for Pompilidae species as it would reduce the foraging distance required from the nest, which has been shown to benefit the progeny of cavity-nesting Hymenoptera (Petersen & Roitberg 2006).

The bee family (Megachilidae) found in this study nested only in pasture. A study by Morris et al. (2015) found that cavity nesting bee abundance was significantly greater in the rainforest canopy than in the understory. As this study is only being carried out in the understorey it may be that there are bee species present in the fragments that are not being sampled. Klein et al. (2004) showed that the brood cell density of bees was positively correlated with light intensity, which would suggest that the preference for nesting in the

canopy and in pasture is likely due to the beneficial microclimate in these locations compared to the rainforest interior.

The edge transects contained an intermediate composition (Figure 3) between pasture and rainforest, suggesting that species from each habitat are interacting at the convergence of the zones.

Variations in community structure within forest fragments were primarily driven by changes in the proportion of *Fabriogenia* species A and C, two closely related species which appear to be responding differently to fragmentation. *Fabriogenia* C appears to be an edge species which can be found in central and inner transects of small to medium sized fragments as at this size these transects are likely to retain more "edge" like conditions. As fragment size increases *Fabriogenia* A dominates and *Fabriogenia* C is lost from inner and eventually edge transects (Figure 6).

2.5.3 Parasitism

Stronger negative effects of fragmentation on parasitoids relative to their hosts (and hence reductions in parasitism rates) have been documented in a number of observational studies (Kruess and Tscharntke 2000, Thies et al. 2003). However, Roth et al. (2006) experimentally manipulated densities of the forest tent caterpillar *Malacosoma disstria* in fragmented versus continuous forest in Canada and found no evidence to support the generally held view that parasitism rates will be reduced in fragmented landscapes. Maeto et al. (2009) studying the effects of environmental change on parasitic wasps in tropical

habitats found that responses differed among parasitic guilds, perhaps accounting for the differing responses of parasitism to environmental perturbation observed in these studies.

These results support the conclusions of other studies (e.g Valladares et al. 2006, Scnitzler et.al 2011) which have shown that in general parasitoids appear to show an individual response to fragmentation, rather than a group response associated with their trophic level. In particular it has been suggested that diet breadth is likely to be a better indicator of a parasitoid species' response to fragmentation that its trophic position (Valladares et al. 2006) meaning that generalist parasitoids such as the one in this study (*Melittobia australica*), which are able to attack many host species, do not decline with increasing fragmentation, although specialist parasitoids may. It was not possible to test the diet breadth hypothesis directly as only one parasitoid species was found in our study in high enough numbers to analyse; meaning comparisons with specialist parasitoids were not possible. Given the greater number of parasitoid taxa found in the only other cavity-nesting Hymenoptera study in this region (Morris et al., 2015) it may be that specialised parasitoids were lost during the fragmentation process.

2.5.4 The importance of landscape context and management history

The nature of the edge between the habitat and matrix will affect climatic changes between the two (Denyer, Burns & Ogden 2006; Wright *et al.* 2010) and hence the depth and strength of edge effects. In this study we only focused on the impacts at the rainforest-pasture boundary, and although we found a distinct edge community we did not find any changes in the rates of parasitism. It seems that the hosts and parasitoids in this study are responding to the landscape at different spatial scales with *Melittobia australica* not

showing any evidence of responding to this particular habitat boundary, whilst its host does. This does not mean however that *Melittobia australica* may not respond to other boundaries such as those between the rainforest and macadamia plantations, which were not investigated in this study.

An important caveat to our results stems from the fact that studies have shown that fragmentation effects on ecological communities can often not be fully understood without taking into account land management history (Brudvig & Damschen 2011). Unfortunately, no such data exist for this landscape, meaning this parameter could not be studied directly, though very likely continues to affect the current structure of this community.

2.6 Conclusions

This study adds to the growing evidence that real-world communities do not respond to fragmentation according to expectations based on trophic level alone. Rather they show a range of individual responses, likely driven by individual species traits, which may not always result in overall changes to ecosystem functions such as parasitism. Cavity-nesting Hymenoptera communities have been shown to respond to fine-scale local habitat structures, including habitat complexity and management, and it may be these, rather than large-scale landscape effects, which drive community changes in this study location (Morato & Martins 2006; Loyola & Martins 2009).

Chapter 3

Experimental climate change alters host-parasitoid synchrony but not food web structure

Abstract

- Anthropogenically induced climate change has led to an increase in global mean temperatures and alterations to rainfall regimes. These changes are leading to range shifts in species distributions, changed phenologies of key ecological phenomenon and extinctions where species are unable to move or adapt.
- The differential response of species to these pressures induced under climate change have the potential to disrupt interactions between species, altering community structure and function.
- In this study I use a field experiment manipulating rainfall regimes under different climate change scenarios to investigate the impacts of these treatments on the quantitative food web structure and functioning of grassland leaf-mining insect communities and their parasitoids.
- I show that alterations to rainfall regime alters the host-parasitoid synchrony between the dominant species in this community, but that this does not translate into overall food web or functional changes.
- Demonstrating the principal that host-parasitoid synchrony can be altered by shifts in rainfall patterns has implications for the ecosystem service of pest control by parasitoids should these asynchronies become sufficiently large to completely de-couple relationships.

3 Experimental climate change alters host-parasitoid synchrony but not food web structure

Statement of contributions:

The data for this chapter were collected by Professor Owen Lewis in 2001. Professor Lewis planned and carried out the field work and mounted the specimens. I processed the data from Professor Lewis' field note books, identified host insects, carried out the data analysis, interpretation and presentation. Professor Charles Godfray and Dr Mark Shaw identified the parasitoids. Dr Rebecca Morris and Professor Owen Lewis gave guidance on analysis and interpretation.

3.1 Introduction

Anthropogenic climate change is expected to be the greatest challenge for managing our environment in the upcoming century (Steffen et al. 2011b). While increasing mean global temperatures have received particular attention, rainfall patterns are also likely to alter dramatically, and the variance in both temperature and rainfall is expected to increase significantly. For example, in southern England climate model projections envisage drier summers and wetter winters, with more rainfall falling in heavy events (Alexander & Jones 2000; Murphy et al. 2009). These changing rainfall patterns are already evident in meteorological records (Osborn & Hulme 2002) and will have marked social and economic consequences (Fowler & Kilsby 2003; Jones et al. 2013) as well as affecting biodiversity and associated ecosystem processes (Morecroft et al. 2002; Stenseth et al. 2002).

In this context there is a need for research exploring the range of potential impacts climate change may generate (Dawson et al. 2011). Climate research has focused on using current trends to predict future scenarios (Pereira et al. 2010) or using species and community niche models to predict how organisms will respond to projected future changes in environmental conditions (Jackson et al. 2009). However, it is increasingly recognised that responses to climate change are likely to be complex and difficult to predict. One aspect of this is that evolutionary changes and interspecific interactions need to be better understood (Lavergne et al. 2010). Changes to climate can affect organisms in a variety of ways such as inducing changes in phenology and distribution (Penuelas et al. 2013). Since these changes are likely to be species-specific. Differential responses of organisms to altered climate will inevitably result in the de-coupling of some interactions and the strengthening of others (Yang & Rudolf 2010). Thus, in order to understand the likely consequences of future changing climates for ecological communities, a multi-species approach is needed.

There has been a move to investigate how the environmental effects of changing climatic conditions may cascade up and down food webs via alterations to trophic interactions (Schmitz et al. 2003). For example, shifts in plant-herbivore interactions have been shown to alter vegetation structure and thus availability of nesting sites for birds, with far reaching consequences for the wider ecological community which would not have been obvious from a single species approach (Auer & Martin 2013). Many studies have begun to look at how insect host-parasitoid relationships may be affected by changing climates and the possible implications this could have for the ecosystem service of pest control of arable crops (Estay, Lima & Labra 2009; Romo & Tylianakis 2013). A recent summary

by Jeffs and Lewis (2013) highlighted that climate warming is likely to produce complicated changes in host-parasitoid interactions, which will be influenced in particular by the dispersal ability and host specificity of parasitoids.

Here, we use a long-term manipulative field experiment in a lowland calcareous grassland at Wytham (Oxfordshire, UK) to investigate how changes in precipitation affect the interactions between insect herbivores and their parasitoids. We assess the effects of experimental drought and supplementary rainfall treatments on the phenology, abundance and species richness of leaf mining insects and their parasitoids and the network of trophic interactions among hosts and parasitoids, assessed in terms of quantitative food web structure. Earlier work at the site showed that increased rainfall increased plant productivity and reduced rainfall decreased productivity (Morecroft et al., 2004). There was also a change in the plant species composition, with drought reducing the proportion of grass species within the sward and an increase in deep rooted species and short-lived ruderal species (Morecroft et al., 2002). These altered the quantity and quality of resource available for different leaf miner species and that these changes could alter the relative densities of different herbivores (Staley *et al.* 2006). In the context of these findings the current study concentrated on the potential cascading influence of these herbivore effects on higher trophic levels (parasitoids) and the structure of host-parasitoid food webs.

The hypotheses tested were:

1) Different density and species richness responses to rainfall regimes by hosts and parasitoids will result in altered food web structure and rates of parasitism.

2) Different phenological responses of host and parasitoids to changes in rainfall regimes will de-couple interactions, altering food web structure and ecosystem functioning

3.2 Methods

3.2.1 Experimental Design

The Wytham climate change experiment (Masters et al., 1998; Grime et al., 2000) was established under the TIGER (Terrestrial Initiative in Global Environmental Research) programme in 1993 to investigate the impact of climate change on a calcareous grassland community (Cummins *et al.* 1995). The experiment was located within limestone grassland at Wytham Woods, Oxfordshire, U.K. within 1 ha of a 10 ha ex-arable field, in which cultivation ceased in 1982 (Gibson 1986). The experimental area was fenced to exclude deer and sheep. The original study design consisted of six climate treatments (Control; Summer Drought; Summer Rainfall; Winter Warming; Winter Warming + Summer Drought; Winter Warming + Summer Rainfall) applied once in each of five blocks, coded A to E. Warming treatments of an increase of 3°C was applied using 1 kW heating cables at the soil surface annually from 1st November to 30th April. Summer drought treatments were applied from 1 July to 31st August each year by mobile, non-invasive rain shelters. Summer rainfall treatments were applied from 1st June to 30th September each year with 20% increased rainfall supplementation applied over the 10-year average for the period by spraying deionised water evenly across plots weekly. Treatments began in 1993. Heating treatments ceased in 1998 but rainfall treatments continued until 2004 and were active at the time of the current investigation; hence this study only focuses on changes in precipitation.

3.2.2 Field sampling

Field work began on 25th May 2001 and ended on 29th August 2001. Sampling involved a 'hands-and-knees' search of all plots, to count and collect tenanted mines and identify their host plants. Trampling was minimised by kneeling on the margin of each plot. All living miners in 1/3 of each 3m x 3m plot were collected on a ten day rotation. Thus, it was typically 30 days before each section was revisited.

3.2.3 Rearing

Leaves containing living miners were placed in sealed plastic tubs to rear hosts or parasitoids. This was done in a laboratory at the John Krebs Field Station at Wytham, 2 km from the collection site. Diapausing hosts and parasitoids were over-wintered at ambient temperatures in a well-ventilated outdoor shed in the field station grounds. Emerging hosts and parasitoids were documented, preserved and mounted for later identification.

3.2.4 Identification

Leaf miners were identified using a combination of mine shape, seasonal emergence and reference to the British Leafminers website (www.leafmines.co.uk). Parasitoids were identified by Professor Charles Godfray and Dr Mark Shaw.

3.2.5 Food web metrics

Quantitative food web metrics (Vulnerability, Generality, Connectance, Linkage Density, and Interaction Evenness) were calculated using the formulae of (Bersier, Banasek-Richter & Cattin 2002) in the Bipartite package for R (R Core Team). These metrics are defined as Vulnerability: the mean number of consumers per prey; Generality: the mean

number of prey per consumer; Connectance: the realised proportion of possible links; Linkage Density: the mean number of links per species and Interaction Evenness: the quantitative evenness of interactions based on the Shannon index. These statistics incorporate information on the frequencies of trophic interactions making them much less sensitive to sampling biases than conventional binary food web statistics, and are now widely used metrics in quantitative food web analyses (Albrecht et al. 2007; Tylianakis, Tscharntke & Lewis 2007; Van Veen et al. 2008). However, although quantitative network metrics are less prone to sampling effects than their qualitative counterparts, they can still be biased by sampling intensity (Bluthgen *et al.* 2008) and food web size (Morris *et al.* 2014).

3.2.6 Statistical analysis

Host and parasitoid abundance and species richness were investigated using generalised linear mixed effects models with Poisson error structure. Rainfall treatments were included in the models as a fixed effect and block as a random effect. Parasitism was investigated using a generalised linear mixed effect model with binomial error structure, rainfall treatment as a fixed effect and block as a random effect.

Food web metrics were analysed using linear mixed effects models with rainfall treatments as a fixed effect and block as a random effect. Food web metrics were log-transformed to improve the normality of residuals.

Insect phenology was analysed using linear mixed effects models. Host and parasitoid emergence dates were assessed separately in relation to rainfall treatment as a fixed effect and block as a random effect.

All analyses began with the maximal model from which non-significant fixed effects were removed until a minimum adequate model was obtained. P-values of fixed effects were obtained by likelihood-ratio tests of the full model with the explanatory variable included versus excluded. The residual plots of the minimum adequate model were then visually inspected to check that the requirements for homoscedasticity and normality had been met.

Since matrix size (the total number of interactions recorded between individuals) can affect quantitative food web statistics (Morris *et al.* 2014) we tested for any such effect in our models. This was achieved by including matrix size as a fixed effect in our maximal models and then comparing it to a reduced model excluding matrix size to test for significance.

3.3 Results

3.3.1 Community Composition

Fourteen leaf mining species were across the rainfall treatments. The samples were dominated by *Stephensia brunichella* (Linnaeus), a Lepidoptera species which feeds on wild basil (*Clinopodium vulgare* Linnaeus) and which accounted for 80% of all host individuals. Sixteen species of parasitoids in total were reared from these hosts (Table 7).

Table 7. Summary of leaf miner and parasitoid species occurrence by rainfall treatment in the TIGER experiment, Upper Seeds, Oxfordshire, 2001.

Hosts	**Control**	**Summer Drought**	**Summer Rain**
Stephensia brunichella	221	368	461
Agromyza idaeiana	1	4	3
Arrhenatherum host	1	0	0
Chromatomyia ramosa	22	21	29
Ectodemia septembrella	6	8	34
Elachista rufocinerea	4	0	0
Eucalybites auroguttella	3	0	0
Liriomyza congesta	9	0	18
Mniophyllum muscorum	4	3	3
Phytomyza centaurii	11	4	34
Phytomyza crassiseta	0	1	2
Phytomyza obscura	1	0	0
Trachys scrobiculatus	1	0	0
Trifolium host	4	1	29
Parasitoids	**Control**	**Summer Drought**	**Summer Rain**
Pholetesar arisba	63	130	145
Celis sp.	1	0	1
Chelonus contractus group	0	1	2
Chorebus dagda	0	0	7
Chorebus misellus	0	0	4
Chorebus sp.1	0	0	3
Chorebus sp.2	0	2	0
Chorebus tanis	13	0	7
Eulophidae	0	0	0
Mirax rufilabris	4	0	7
Opius sp.1	0	1	1
Phaedrotoma sp.	0	0	0
Phaedrotoma sp.1	0	1	4
Phaedrotoma sp.2	3	6	10
Phaedrotoma sp.3	0	1	0
Sympiesis notata	0	1	2

3.3.2 Density and species richness

The density of host insects averaged 10 mines per square metre, but was highly variable, ranging from 2 to 24 mines per m^2. Host species richness per plot ($9m^2$) ranged from 3 to 8 species, whilst parasitoid species richness ranged from 1 to 10 species. There was no significant effect of rainfall treatment on host density and species richness or parasitoid species richness (Table 8).

Table 8. Results of generalised linear mixed effects models with Poisson error structure and block as a random factor for host abundance (per 9m2 sampling area), host species richness and parasitoid species richness in relation to rainfall treatment.

	Chisq	**Degrees of freedom**	**P**
Host abundance	4.167	2	0.125
Host species richness	0.674	2	0.714
Parasitoid species richness	2.295	2	0.317

3.3.3 Parasitism

Parasitism rates averaged 60%, ranging from 37 % to 82 % across replicates, but were not found to differ significantly between treatments (Table 9).

Table 9. Results of generalised linear mixed effects models with binomial error structure and block as a random factor for parasitism in relation to rainfall treatment.

	Chisq	**Degrees of freedom**	**P**
Parasitism	4.33	2	0.12

3.3.4 Food web structure

Summary quantitative trophic webs are given in Figure 10. Food web stucture was found to be similar across treatments, consisting of a web dominated by the interaction between the lepidopteran *Stephensia brunichella* (Linnaeus) and its parasitoid *Pholetesar arisba* (Nixon) which did not attack any other host in this study. Overall, 813 interactions were recorded in this study, of which 688 were between *S. brunichella* and *P. arisba* (85% of all interactions observed).

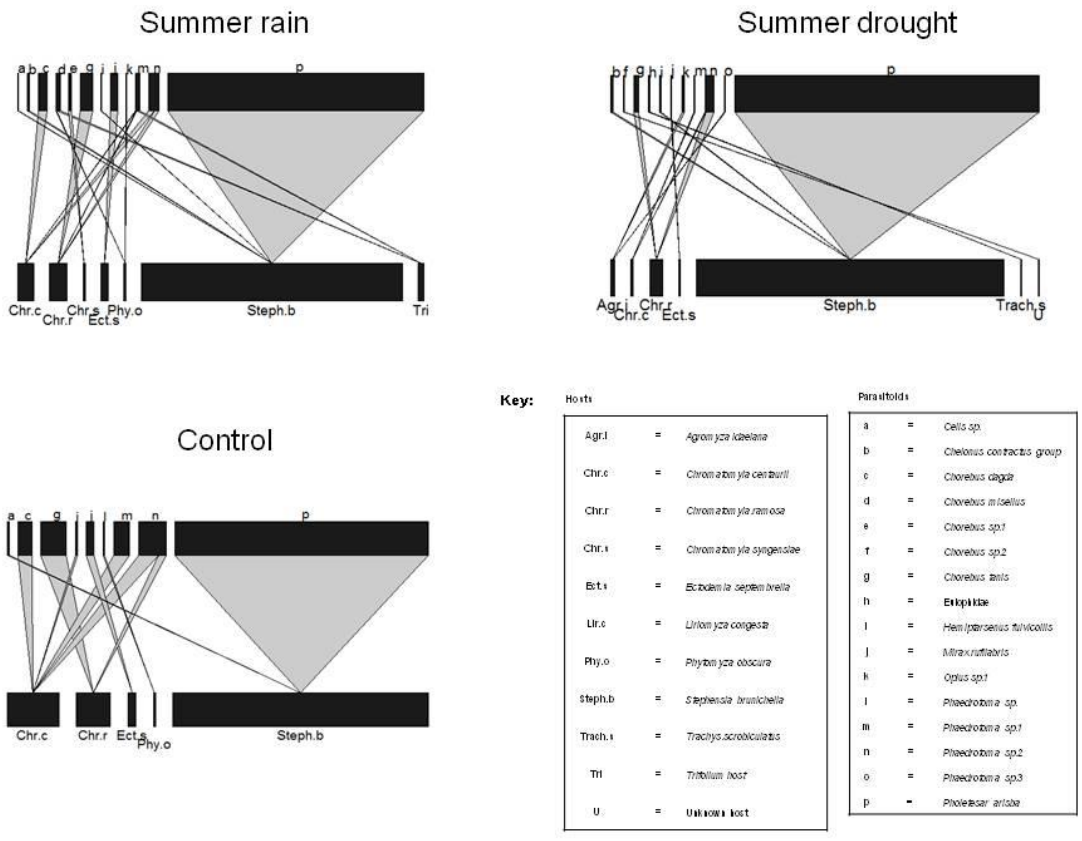


Figure 10. Summary food webs for interactions between leaf mining insects and their parasitoids across rainfall treatments in the TIGER programme, Upper Seeds, Oxfordshire, 2001. The thickness of the bars represents the relative abundance of that species.

3.3.5 Food web metrics

Connectance, linkage density, generality, vulnerability and interaction eveness showed no significant response to rainfall treatments (Figure 11, Table 10). Generality is not depicted as this was consistently 1. Interaction evenness approached statistical significance in these analyses (p=0.06), so Cohen's d was calculated to investigate the effect size (Nakagawa & Cuthill 2007). This revealed that any effect of treatments on interaction evenness was small (Control-SD, d=0.32; Control-SR, d= 0.22).

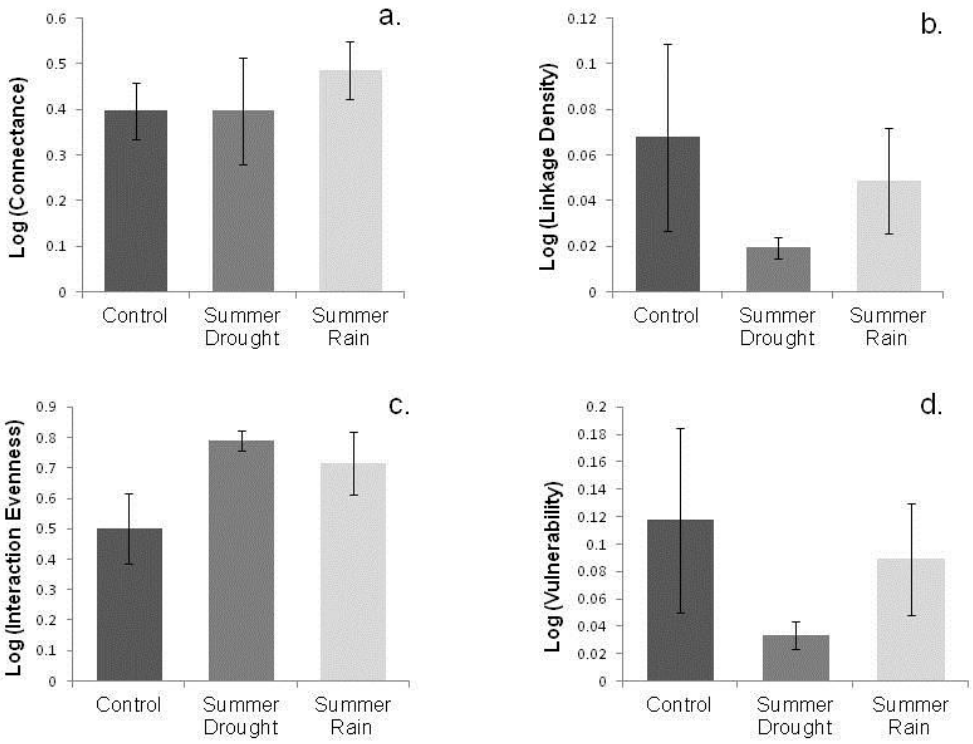


Figure 11. Food web metrics in response to rainfall treatments in the TIGER programme, Upper Seeds, Oxfordshire: a. log (connectance); b. log (linkage density); c. log (interaction evenness); d. log (vulnerability). Error bars show standard error of the means.

Table 10. Results of linear mixed-effects models analysing food web metrics in relation to rainfall treatment in the TIGER programme, Upper Seeds, Oxfordshire. Matrix (web) size did not have a significant effect on the food web metrics and so was removed from all models.

	Chisq	Degrees of freedom	P
Log (Interaction evenness)			
Web Size	0.896	1	0.344
Treatment	5.488	2	0.06
Log (Vulnerability)			
Web Size	1.471	1	0.225
Treatment	3.27	2	0.195
Log (Connectance)			
Web Size	0.293	1	0.588
Treatment	0.906	2	0.636
Log (Linkage Density)			
Web Size	1.401	1	0.237
Treatment	2.926	2	0.232

3.3.6 Phenology

Phenology was solely assessed for interactions between the dominant Lepidopteran host *Stephensia brunichella* (Linnaeus) and its specialist parasitoid *Pholetesor arisba* (Nixon) since these accounted for 85% of all interactions observed, with insufficient replicates of other species interactions present for analysis.

Stephensia brunichella (Linnaeus) had a peak emergence of the 6-7thth of August under all treatments (Figure 12). Its parasitoid *Pholetesor arisba* (Nixon) consistently emerged earlier than its host, peaking at the 4th to 5th of August under the control treatment. Under the summer drought treatment peak parasitoid emergence shifted forwards to the 2nd of August, and under the enhanced summer rainfall treatment it moved further forwards to the 30th-31st July. This effect of rainfall treatment on parasitoid emergence was significant (Table 11).

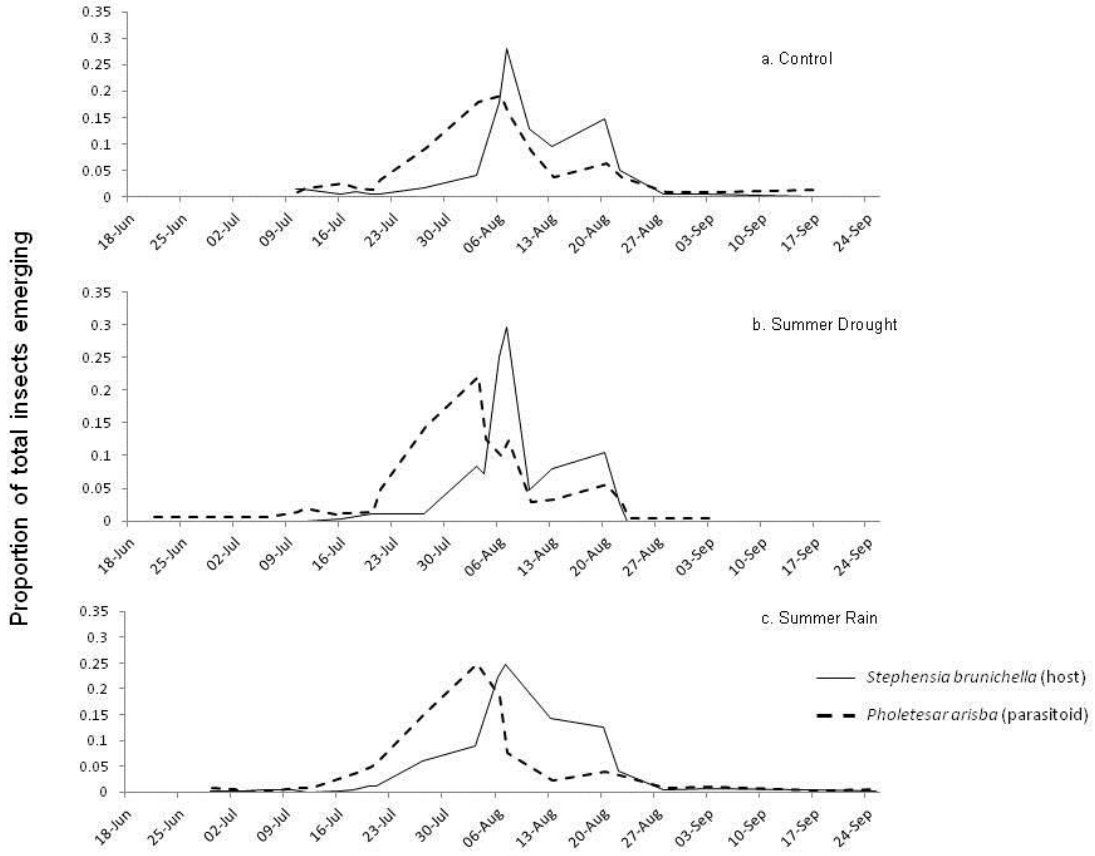


Figure 12. Proportion of total insects emerged by date for *Stephensia brunichella* (solid line) and its parasitoid *Pholetesor arisba* (dashed line) in relation to rainfall treatment in the TIGER programme, Upper Seeds, Oxfordshire, 2001.

Table 11. Results of generalised linear mixed effects models of host and parasitoid emergence date in relation to rainfall treatment in the TIGER programme, Upper Seeds, Oxfordshire. Block was included in the models as a random effect.

	Chisq	**Degrees of freedom**	**P**
Host emergence date	3.1	2	0.37
Parasitoid emergence date	10.9	2	0.004

Post-hoc Tukey tests showed that parasitoid peak emergence under the enhanced summer rainfall treatment was significantly different to the unmanipulated control (p=0.004),

whereas the change in parasitoid peak emergence date under the summer drought conditions was not significantly different from the control treatments (p=0.08).

3.4 Discussion

Rainfall treatments simulating alternative climate change scenarios did not significantly affect the abundance or species richness of either leaf-mining insects or their parasitoids. However, we found that rainfall treatments have the potential to de-couple the interaction between the abundant host *Stephensia brunichella* (Linnaeus) and its parasitoid *Pholetesor arisba* (Nixon) due to differential effects on insect phenologies. The host plant for this interaction *Clinopodium vulgare* was dominant across all plots. Altered rainfall regimes had no effect on peak host emergence, whereas enhanced summer rainfall led to a shift in the peak emergence of parasitoids by 7 days. However, these altered phenologies did not alter rates of parasitism, nor could they be detected in measures of quantitative food web structure.

3.4.1 Abundance

Previous entomological studies on the TIGER plots have shown interesting indirect effects of both increased and decreased rainfall on insect herbivore abundance (Masters *et al.* 1998). Increased precipitation leads to a denser sward, which can directly support higher insect abundance; however decreased rainfall also leads to higher insect herbivore abundance than un-manipulated controls, but via a different mechanism. Drought results in a poorer sward of stressed plants which leads to increased nutrient levels in leaves

(Hale *et al.* 2005). This increase in nutrient levels can result in a greater number of insect herbivores surviving to adulthood due to increased performance related to improved food quality (Hale *et al.* 2003). Furthermore, Staley et al. (2006) found that the different precipitation treatments had species-specific effects on the density and parasitism rates of leaf-mining insects, again highlighting the difficulty of making generalisations, even across species in the same feeding guild.

In contrast to these previous studies, we observed no significant effect of the rainfall treatments on insect density. One possible explanation for the discrepancy between our results and those of Staley et al. (2006) is the spatial scale of investigation. Staley et al. (2006) selected five focal plants per plot and looked at density per plant, finding that it increased under both summer rainfall and summer drought treatments. It may be that *Stephensia brunichella* (Linnaeus) responds to environmental conditions on a finer spatial scale than we investigated, with individuals aggregating on high-quality plants.

The literature (Gripenberg *et al.* 2010) shows that leaf-mining insects do show some preference for ovipositing on leaves of better quality. Both the summer drought and summer rainfall treatments have previously been found to result in higher-quality foliage, but via different mechanisms. Enhanced summer rainfall results in larger leaves, offering a greater resource for leaf miners, whereas summer drought results in leaves of higher nutritional status (Staley, 2006). However, female herbivorous insects are also known to engage in "bet-hedging" behaviour (Hopper 1999), meaning that although they do show an overall preference for ovipositing on leaves of better condition, they will also lay some eggs on leaves of poor quality, and so density at the patch scale may appear unchanged.

3.4.2 Phenology

Studies of plant-aphid-parasitoid dynamic responses to drought stress have found measurable reduction in parasitism attack rates resulting from changes in aphid phenology, which in turn are caused by alterations in plant nutrient content (Aslam, Johnson & Karley 2013). However studies have also shown that plant-insect herbivore responses to drought stress are species-specific (Hale *et al.* 2005), which highlights the challenges to predicting community responses to alterations in precipitation. Our study revealed that climate manipulations were affecting insect phenology, but that the effects differed between trophic levels: a specialised parasitoid had significantly earlier emergence under the elevated summer rainfall treatment, but its host was unaffected. The mechanism underlying this result is unknown. Altered rainfall regimes can result in changes to plant growth and nutrient status and these changes may be passed up the food chain. Although we did not find any effect of increased rainfall on host density, it may have increased host quality. In particular, if elevated rainfall allows leaves to grow larger, hosts may be able to reach a greater size due to increased food availability. Larger hosts might be expected to enhance development rates for parasitoids (Sequeira & Mackauer 1992).

3.4.3 Food web metrics

Previous studies of host-parasitoid communities have revealed pronounced changes in quantitative food web structure in response to environmental change (Tylianakis, Tscharntke & Lewis 2007). Such changes are of interest because the structure of networks

has implications for their dynamics and stability, and because such changes may not be reflected in simpler community metrics such as richness, diversity or species composition. The phenological shifts in parasitoid emergence we observed did not lead to any detectable shifts in food web structure or rates of parasitism. One potential explanation for the lack of foodweb-level effects is that most parasitoids were host specific, limiting the opportunity for shifts in the incidence and frequency of species interactions of the type documented by Tylianakis et al. (2008). High levels of specialisation also mean that there was little potential for indirect interactions between hosts via shared parasitoids, making it less likely that changes to particular host or parasitoid species driven by the experimental treatments will have wider repercussions within the network. We suggest that food webs dominated by specialist consumers, such as this one, may be less likely than those with more generalist species to show altered food web structure under climate change and other anthropogenic perturbations; or at least that any such effects will be manifest largely by direct alterations to the frequencies of tightly-coupled interacting species within the network.

Like many climate change experiments, for practical reasons the manipulations in this experiment were carried out at a relatively small spatial scale. One problem with this form of experiment for studies of mobile organisms such as leaf miners and their parasitoids, is that it is likely to reflect the foraging decisions of these organisms rather than their demographic responses (Moise & Henry 2010). Furthermore, the effects of experimental treatments on host-parasitoid interactions may depend on landscape context (Martin *et al.* 2013) and underlying environmental conditions (Cummins *et al.* 1995; Johnson *et al.* 2011). However, such experiments can still provide valuable insights into the differential

effects of climate treatments on host and parasitoid development, and the potential cascading effects of altered plant quality on higher trophic levels.

This experiment demonstrated that alterations to future rainfall regimes under climate change may have different effects on insects at different trophic levels. Of particular concern is the finding that more frequent and more extreme summer drought conditions, which are predicted for the UK, have the potential to cause the de-coupling of the phenologies of herbivorous insects and their parasitoids. Changes in phenology with climate change are often assumed to be primarily driven by temperature and evidence that precipitation changes can also affect phenology are much rarer (Thackeray *et al.* 2010). Such effects, if observed more widely in ecological communities, might lead to a range of community-wide consequences, such as more frequent outbreaks of pest insects (Estay, Lima & Labra 2009; Estay *et al.* 2012).

Chapter 4

Host-parasitoid food web structure is unaffected by changes in seasonal grazing regime during grassland restoration

Abstract

- Restoring habitats to their original state is a growing area of research with the potential to mitigate some of the effects of anthropogenically caused habitat losses and climate change. Restoration studies have shown that whilst recreating habitats to their original state is extremely difficult, an intermediate state which increases biodiversity levels is possible.
- Whether restoration can restore the structure of communities and important ecosystem functions provided by insects such as pollination and pest control is a more difficult question.
- In this study I use a long-term grassland restoration experiment to assess the impact of different grazing regimes on the quantitative food web structure and ecosystem function of parasitism on leaf-mining insect communities.
- I show that grazing regime alters the leaf-mining insect communities, but not the parasitoids that attack them at the spatial scale of this experiment.
- Grassland leaf-miner-parasitoid food webs show robustness in their structure and function to alterations in grazing regimes. However these results must be interpreted with caution due to the small scale of this experiment, with larger scale experiments being needed to fully address this question.

4 Host-parasitoid food web structure is unaffected by changes in seasonal grazing regime during grassland restoration

4.1 Introduction

The loss and degradation of natural habitats worldwide is the greatest driver of global biodiversity decline (Butchart *et al.* 2010). Conservation of remaining habitat fragments in protected areas is unlikely to stop this decline (Bengtsson *et al.* 2003). In Europe it is now recognised that biodiversity must be maintained and natural habitats restored beyond protected areas if the loss of species and habitats is to be halted (Young *et al.* 2006). The field of restoration ecology has grown in recent decades to respond to this need (Dobson, Bradshaw & Baker 1997; Young, Petersen & Clary 2005), but our understanding of ecological restoration is still insufficient to manage the competing pressures for space and resources on our landscapes (Rands *et al.* 2010; Montoya, Rogers & Memmott 2012).

One of the limitations of terrestrial restoration ecology to date has been its focus on plant species recovery. There has been an assumption that recovery by insects and other animals will follow, although this has often been shown not to be the case (Maeto et al. 2009, Babin-Fenske & Anand 2010). Even when lower trophic level insects such as herbivores have been successfully restored it does not mean that higher trophic level insects will necessarily follow (Maeto et al. 2009), since higher trophic levels such as parasitoids are often more vulnerable to habitat loss and degradation than their hosts (Kruess and Tscharntke 1994, Klein et al. 2006, Shaw 2006). Furthermore even when species appear to have been successfully restored, their interactions may not be restored,

ultimately meaning that full restoration of the structure and functioning of a habitat has been unsuccessful (Memmott *et al.* 2007; Henson, Craze & Memmott 2009).

To tackle this bias towards documenting the restoration of species over the restoration of the structure and functioning of communities the growing field of quantitative food web ecology is beginning to be applied to the field of restoration science. The use of quantitative food web studies in applied questions of conservation and management is a fledgling discipline (Forup & Memmott 2005; Forup *et al.* 2008a; Lohaus, Vidal & Thies 2013) with more research in this area being encouraged (Ings *et al.* 2009).

The loss of a species due to habitat change can often result in unforeseen secondary extinctions cascading through food webs as inter-species connections are lost or altered (Sole & Montoya 2001; Dunne, Williams & Martinez 2002; Ives & Cardinale 2004; Memmott, Waser & Price 2004; Montoya, Pimm & Sole 2006). During habitat restoration we may therefore expect to see a reverse process with species unable to recolonise until facilitated by the re-establishment of inter-dependent species. The unpredictability of which species interactions may be most affected during habitat loss implies that the same will be true of habitat restoration meaning that a consideration of whole ecosystems over individual species is needed (Ives & Cardinale 2004).

It has been shown that the restoration of plant-herbivore interactions can be successful over relatively short time periods (Watts & Didham 2006), but that herbivore–parasitoid interactions, which appear to be more affected by habitat loss (Kruess and Tscharntke 1994) and form a vital role in ecosystem structuring by providing population control

(Hawkins, Cornell & Hochberg 1997) may not be restored as easily (Henson, Craze & Memmott 2009). In this chapter I use a long-term grassland restoration experiment to address whether different grazing regimes result in different host-parasitoid food web structures in temperate grassland.

Temperate calcareous grassland is one of the richest habitats in Europe for plants and invertebrates (Prendergast *et al.* 1993; Partel & Zobel 1999; Poschlod & WallisDeVries 2002; WallisDeVries, Poschlod & Willems 2002). The area of semi-natural or unimproved grassland in the UK has declined sharply over the past fifty years largely due to agricultural intensification and urbanisation (Hodgson *et al.* 2005). Low intensity seasonal grazing is now a widely used management practise for grassland restoration (Roach 1995; Walker *et al.* 2004; Whyte 2012), as it has been found to be one of the most natural and cost-effective methods available (Gibson & Brown 1991; Walker *et al.* 2004; Klimek *et al.* 2007; Maccherini & Santi 2012). Short periods of seasonal grazing can be applied in either spring or autumn, both resulting in similar plant species richness but with altered sward heights during the peak period of invertebrate activity during the summer months. Spring grazing produces a short even turf structure during the summer months, while autumn grazing will allow the sward to reach greater heights over the summer grazing period. Insect abundance tends to increase with sward height and thus autumn grazing is considered to be a positive management practise in terms of maintaining food for grassland birds (Vickery *et al.* 2001).

Studies have shown that changes to vegetation structure impact the composition of insect communities, not just the abundance (Robinson, 1981; Coll & Bottrell, 1996; Koricheva

et al., 2000). Since sward structure is known to affect the abundance and composition of phytophagous insects (Gibson et al., 1992; Borges & Brown, 2001) it might also impact parasitoid searching and oviposition behaviour (Meiners & Obermaier 2004; Obermaier *et al.* 2008) and thus food web structure. If the changes to habitat structure caused by grazing impact herbivores and parasitoids differentially, as the literature suggests, we would expect to see differences in food web structure under different grazing regimes.

A long-term experimental study on the effects of different sheep grazing regimes on the natural colonisation and establishment of species-rich grassland on former arable land has been running in Upper Seeds field, near Wytham Woods, Oxfordshire since 1985. This experiment provides an excellent opportunity to study the community and food web level consequences of different grazing regimes. In this chapter, I investigate assemblages of leaf miners and their associated parasitoids within the Upper Seeds experiment, and quantify trophic interactions between them to address the following specific hypotheses:

1. Due to their higher trophic level, the abundance, species richness and community composition of parasitoids will be more affected by changes in grazing strategy than the abundance, species richness and community composition of hosts.
2. The different response to grazing by parasitoids and hosts will result in altered food web structure under different grazing regimes.

4.2 Methods

4.2.1 Experimental design

The Upper Seeds grazing experiment is located in a 10 ha field, latitude (51°76'96.22"N, −01°33'05.25"W), which was cultivated mostly for cereals between 1960 and 1981. In 1981 a final crop of winter wheat was sown, after which the site was abandoned before harvest (Gibson et al. 1987). The soil is shallow (10cm) stony brown rendzina at an elevation of 150 mm. The mean annual temperature is 10°C and mean annual rainfall 680 mm.

The experiment is split across two Latin squares, each containing nine 30 x 30 metre paddocks fenced off from deer grazing. Three grazing regimes (ungrazed, short spring grazing and short autumn grazing), have each been replicated six times across these paddocks (Figure 13). Spring grazing has been applied using three ewes in each paddock for ten days in late April and autumn grazing has used the same stocking density for fourteen days in late September. Both grazing regimes have been applied annually since 1983. The ungrazed control plots were dominated by hawthorn (*Crataegus* sp.) scrub at the time of this study. Both the autumn grazed and spring grazed treatments were recognisably grassland, with interspersed patches of scrub being present.

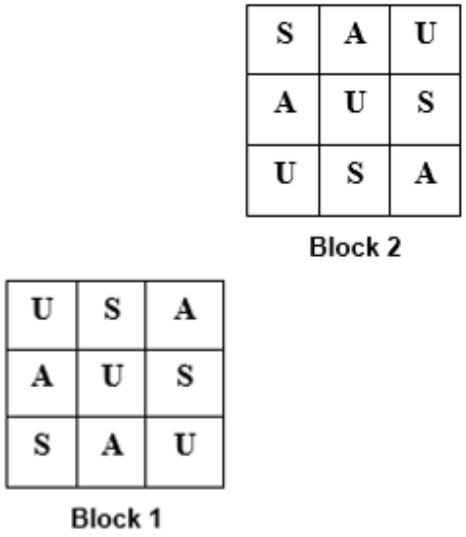


Figure 13. Experimental design of the three grazing treatments: autumn (A), spring (S) and ungrazed control (U) in Upper Seeds Field, Wytham Woods, Oxfordshire.

4.2.2 Study System

Leaf miners are herbivorous insects from the orders Lepidoptera, Coleoptera and Diptera which form galleries by feeding within the structure of leaves (Hespenheide, 1991). They are subject to high rates of attack by parasitoid wasps which play a vital role in their population control and the reduction of intraspecific competition on hosts plants (Hawkins, Cornell & Hochberg 1997; Faeth, & Simberloff, 1981). Leaf miners can be readily identified from the morphology of their mines and thus collected and reared to assess host-parasitoid relationships. For this reason they make ideal study systems for assessing environmental impacts across trophic levels and have been used successfully in a number of quantitative food web studies (e.g., Valladares et al. 2001, Morris et al. 2004, van Veen et al. 2006, Tylianakis et al. 2007).

4.2.3 Data Collection

Sixteen 1 m^2 quadrats were randomly surveyed in each plot per month in June, July and August 2011. In each quadrat all plants were examined for leaf mines. All leaf mines found were collected and taken back to the laboratory and checked under a microscope to see which contained live larvae. Leaf miners were reared individually in plastic containers at the John Krebs Field Station close to the collection site. Reared leaf-mining insects or parasitoid wasps were preserved by freezing and later mounted for identification.

Host insect species were identified by the author with reference to www.leafmines.co.uk. Parasitoids were identified by Professor Charles Godfray and Dr Mark Shaw. In some cases no hosts were successfully reared due to the propensity for some species of leaf-miners to exit the leaf as larvae to pupate in the soil. These individuals were not reared to adults in the laboratory and therefore could not be identified to species level. In these instances the hosts have been classified using morphospecies based on the host plant from which they were taken. Data were pooled over the survey period for analysis.

4.2.4 Food web metrics

Quantitative food web metrics were calculated following Bersier et al. 2002 using the Bipartite package (Dormann et al. 2009) in R (R Development Core Team 2015). The metrics used in this study were standard metrics of quantitative bipartite network architecture frequently used network comparisons: Linkage Density: the mean number of links per species; Connectance: the realized proportion of possible links; Vulnerability: the mean number of consumers per prey; Generality: the mean number of prey per

consumer; Interaction Evenness: the quantitative evenness of interactions based on the Shannon index (Tylianakis et al. 2007, Dormann et al. 2009) and H2': the weighted quantitative network specialisation (Blüthgen *et al*. 2006), which quantifies the deviation between observed interaction frequencies and those expected if interaction frequencies were random, reflecting the extent to which parasitoids discriminate among available host species. Since food web size is known to affect food web statistics (Morris et al. 2014), we included the size of the food web, in terms of the number of interactions observed, henceforth called matrix size, in all food web statistical models.

4.2.5 Community composition

De-trended Correspondence Analysis (DCA) (Oxanen & Minchin,1997) was used in the program PAST (Hammer, Harper & Ryan 2001) to assess the community structure of hosts and parasitoids under the different grazing treatments. Detrended Correspondence Analysis is a multivariate technique specifically designed for ecological data sets (Shaw 2003). It uses an iterative algorithm applied to a species matrix to find the main gradients in species data. This allows for a visual representation of the position of survey points in relation to one another.

Analysis of similarities (ANOSIM) was used to assess the significance of differences between the community composition of leaf-miners and parasitoids under the different grazing regimes. This is a non-parametric test which compares the species matrices between treatments (Clarke 1993) using a distance measure. The Bray-Curtis distance measure was used in the calculation of ANOSIM. This is a widely used measure which reflects difference in samples due to differing taxon composition and abundance, and is

considered to be robust to any skew caused by data sets dominated by individual species (Clarke & Warwick 2001).

Similarity Percentage (SIMPER) analysis was applied to the species matrices to assess which species were primarily responsible for the change in community composition. The Bray-Curtis similarity measure was used to calculate the taxon-specific dissimilarities between treatments (Clarke 1993) used in the SIMPER analysis.

4.2.6 Statistical Analysis

Generalised linear models with quasi-poisson error structure (due to over-dispersion in the count data) were used to investigate the effects of grazing regime on host and parasitoid abundances and species richness. Block was modelled as a fixed effect rather than a random effect due to the experimental set-up containing only two blocks. P-values of grazing effects were obtained by likelihood-ratio tests of the full model with the explanatory variable included versus excluded. Parasitism was analysed using generalised linear models with the same methodology as described but using quasi-binomial error structure (due to over-dispersion in the proportion data).

Generalised linear models were also used to investigate the effects of grazing on food web statistics. Block was modelled as a fixed effect. P-values were obtained as above. The residual plots of the minimum adequate model were visually inspected to check that the requirements for homoscedasticity and normality had been met.

Where models produced significant differences, post-hoc pair-wise comparisons between the three treatments were tested using the function testInteractions in the R post-hoc interaction analysis package phia (De Rosario-Martinez & Fox 2015).

4.3 Results

Twenty leaf mining insect species were recorded, from which seventeen species of parasitoid wasp emerged (Table 12). The autumn grazed and spring grazed grassland communities were dominated by *Stephensia brunichella* (Linnaeus), a Lepidopteran species that feeds on wild basil (*Clinopodium vulgare* Linnaeus), and *Phytomyza crassiseta* Zetterstedt, a Diptera that develops in Germander speedwell (*Veronica chamaedrys* Linnaeus). The ungrazed plots were dominated by a Lepidopteran leaf miner abundant on hawthorn (*Crataegus monogyna* Jacquin), which could not be identified due to larvae exiting the mine to pupate externally in soil and thus no adult specimens were reared.

Table 12. Summary of leaf-mining host and parasitoid species information by treatment (Spring-grazed, Autumn-grazed, Ungrazed) in the Upper Seeds experiment, Oxfordshire.

Host Species	**Family**	**Spring-grazed**	**Autumn-grazed**	**Ungrazed**
Agrimonia sp. host	Diptera	1	0	0
Chromatomyia 'atricornis'	Diptera	6	0	0
Chromatomyia horticola	Diptera	0	0	1
Chromatomyia ramosa	Diptera	1	0	0
Crataegus host	Unknown	89	39	211
Ectoedemia septembrella	Lepidoptera	7	7	1
Elachista obliquella	Lepidoptera	3	0	2
Eucalybites auroguttella	Lepidoptera	1	0	0
Lathyrus sp. host	Unknown	0	2	0
Oxyptilus pilosellae	Lepidoptera	3	10	0
Phytomyza crassiseta	Diptera	45	84	11
Phytomyza spondylii	Diptera	14	27	22
Phytomyza vitalbae	Diptera	34	18	31
Prunus spinosa host	Unknown	1	1	9
Ranunculus host	Unknown	5	0	0
Rubus sp. host	Unknown	0	1	0
Quercus host	Unknown	0	0	2
Stephensia brunichella	Lepidoptera	336	415	162
Trachys scrobiculatus	Coleoptera	32	35	7
Trifolium host	Unknown	23	8	9
Parasitoid Species				
Achrysocharoides atys	Hymenoptera	0	0	15
Agrimonia sp. parasitoid	Hymenoptera	1	0	0
Chrysocharis sp.	Hymenoptera	0	2	0
Chrysocharis pubicornis	Hymenoptera	9	0	2
Chrysocharis viridis	Hymenoptera	1	1	2
Cirrospilus vittatus	Hymenoptera	4	1	24
Crataegus sp. parasitoid	Hymenoptera	1	1	0
Diglyphus isaea	Hymenoptera	2	5	0
Knautia arvensis parasitoid	Hymenoptera	1	0	0
Mirax sp.	Hymenoptera	5	1	0
Oxyptilus pilosellae parasitoid	Hymenoptera	0	1	0
Pholetesar arisba	Hymenoptera	50	58	42
Pediobius sp.	Hymenoptera	0	2	12
Pnigalio sp.	Hymenoptera	9	18	0
Pnigalio pecticornis	Hymenoptera	2	3	5
Pnigalio soemius	Hymenoptera	0	6	2
Trachys scrobiculatus parasitoid	Hymenoptera	3	4	0

4.3.1 Abundance and species richness

The abundance of host leaf miners (Figure 13a) averaged around 80 to 100 mines per plot across treatments and did not vary significantly between treatments ($F_{2,16}$=1.49, p=0.26).

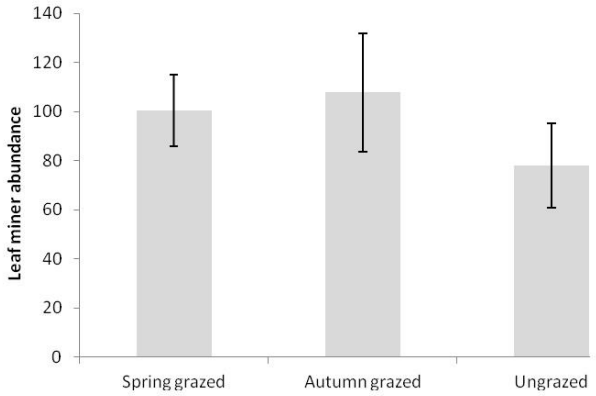


Figure 13a. Mean abundance of leaf mines per 30 x 30 metre plot under each grazing treatment in the Upper Seeds experiment, Oxfordshire. Error bars show standard error of the mean (s.e.m).

Host species richness ranged from 5 to 11 species per plot (Figure 14), and did not significantly differ between treatments (Table 13). Parasitoid species richness ranged from 2 to 6 species and also did not vary significantly between treatments.

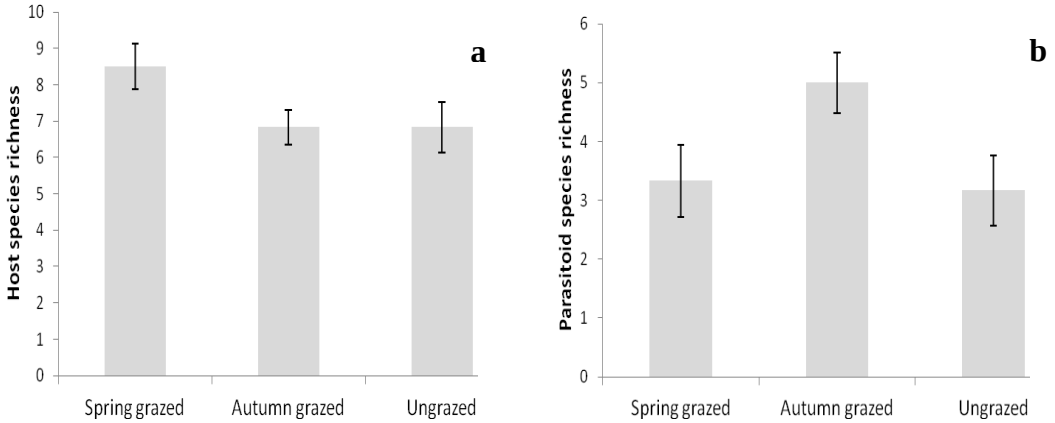


Figure 14. Mean host species richness (a) and parasitoid species richness (b) in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire. Error bars show s.e.m. Histograms do not represent quasi-poisson errors accurately and are illustrative only.

Table 13. Generalised linear models with quasi-poisson error structure of host and parasitoid species richness in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire. Test statistics given for grazing treatment are made by comparison of model specified against reduced model.

	Degrees of freedom	Variance	P
Host species richness~ grazing treatment + block	14	-1.47	0.48
Parasitoid species richness~ grazing treatment + block	14	-3.09	0.21

4.3.2 Parasitism

Overall parasitism across species ranged from 10% to 52% among plots and was on the borderline of significant difference among grazing treatments (

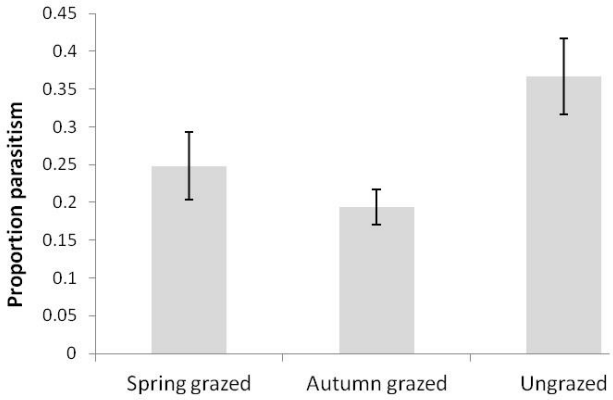


Figure 15, Table 14). Post-hoc pairwise analysis revealed that the parasitism rate in ungrazed treatments was significantly higher than in autumn grazed treatments (p=0.02) and approaching significance between ungrazed and spring grazed treatments (p=0.09). There was no significant difference in the parasitism rates between spring and autumn grazed treatments (p=0.54).

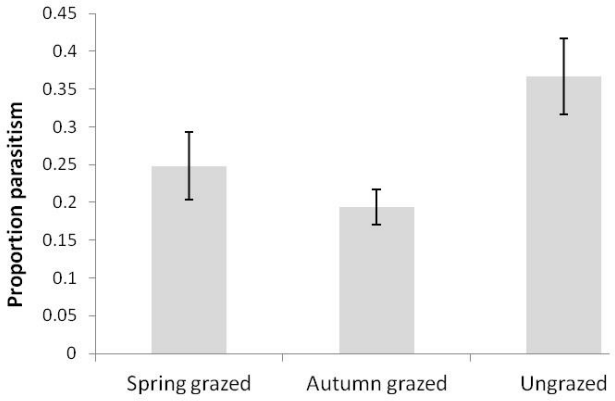


Figure 15. Parasitism rates of leaf-mining insects under different grazing treatments in the Upper Seeds experiment, Oxfordshire. Error bars show s.e.m.

Table 14. Generalised linear model with quasibinomial error structure of overall parasitism rate of leaf-mining insects in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire.

	Degrees of freedom	**F**	**P**
Parasitism~ grazing treatment + block	14	3.694	0.05

4.3.3 Community Composition

Detrended Correspondence Analysis showed that the host leaf miner communities were distinct under each grazing regime with some overlaps between spring and autumn grazed treatments and between spring grazing and ungrazed controls, whereas the parasitoid communities were similar in the three treatments (Figure 16).

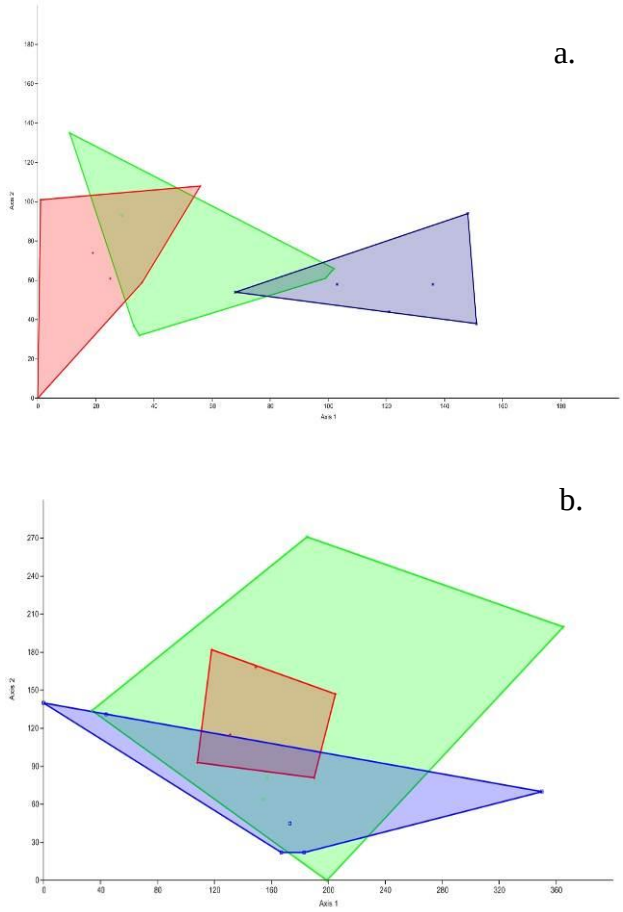


Figure 16. Detrended correspondence analysis representing community composition of host leaf miners (a) and parasitoids (b) under spring grazing (green), autumn grazing (red) and ungrazed control (blue) in the Upper Seeds experiment, Oxfordshire.

Analysis of similarity showed that host community was borderline significantly different between ungrazed and spring-grazed treatments ($p=0.05$) and differed significantly between ungrazed and autumn-grazed treatments ($p=0.004$) but not between spring and autumn grazed treatments ($p=0.55$).

Similarity percentage analysis showed that changes in the abundance of the dominant leaf-mining moth *Stephensia brunichella* and leaf miners on hawthorn *Crataegus sp*. were driving community differences between the ungrazed and grazed treatments (Table 15).

Table 15. Similarity percentage analysis of host leaf mining species between grazed and ungrazed treatments showing that differences in community composition are driven by *Stephensia brunichella* and *Crataegus sp*.

Spring grazed vs. ungrazed	**Average dissimilarity**	**% Contribution**	**Cumulative %**
Stephensia brunichella	19.61	37.33	37.33
Crataegus host species	13.95	26.55	63.88
Autumn grazed vs. ungrazed	**Average dissimilarity**	**% Contribution**	**Cumulative %**
Stephensia brunichella	24.36	39.83	39.83
Crataegus host species	15.26	24.95	64.78

For this reason these two species were analysed for their responses to grazing treatments separately. *Stephensia brunichella* dominated all paddocks, but its abundance was highly variable meaning no overall significant difference between grazing regimes was evident (Figure 17, Table 16). The proportion of *Stephensia brunichella* parasitised also showed no significant difference between grazing treatments. In contrast both the abundance (Table 16) and the parasitism rate (Table 17) of *Crataegus sp*. were affected by grazing treatment, being higher in the ungrazed paddocks (Figure 17).

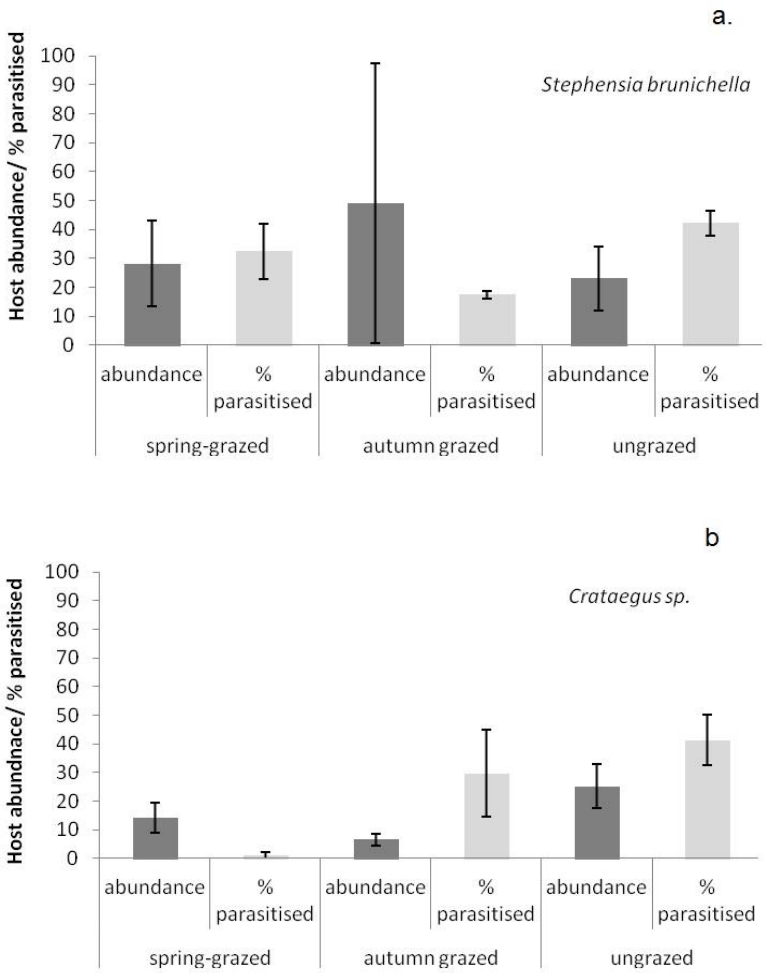


Figure 17. Abundance and parasitism rates of *Stephensia brunichella* (a) and *Crataegus* species (b) under the different grazing treatments in the Upper Seeds experiment, Oxfordshire.

Table 16. Generalised linear models with quasi-poisson error structure of individual dominant host species abundance in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire

	Degrees of freedom	**Deviance**	**P**
Stephensia brunichella abundance ~ grazing treatment + block	14	-65.219	0.181
Crataegus host species abundance ~ grazing treatment + block	14	-71.24	0.0247

Table 17. Generalised linear models with quasi-binomial error structure of individual dominant host species parasitism rates in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire.

	Degrees of freedom	**F**	**P**
Stephensia brunichella parasitism rate ~ grazing treatment + block	14	-2.58	0.111
Crataegus species parasitism rate ~ grazing treatment + block	14	13.488	<0.001

4.3.4 Food web structure

Food web structure was fairly uniform across all the grazing treatments. Summary webs are depicted in Figure 18 from which it can be seen that all three grazing regimes are dominated by the interaction between *Stephensia brunichella* and *Pholetesor arisba*. The ungrazed treatment in addition has the abundant *Crataegus* species of leaf miners and parasitoids. All three food webs are highly specialised with almost universal vulnerability and generality scores of 1 (Figure 19). There were no differences in connectance, interaction evenness, linkage density, vulnerability, generality and network specialisation across the grazing treatments (Figure 19, Table 18).

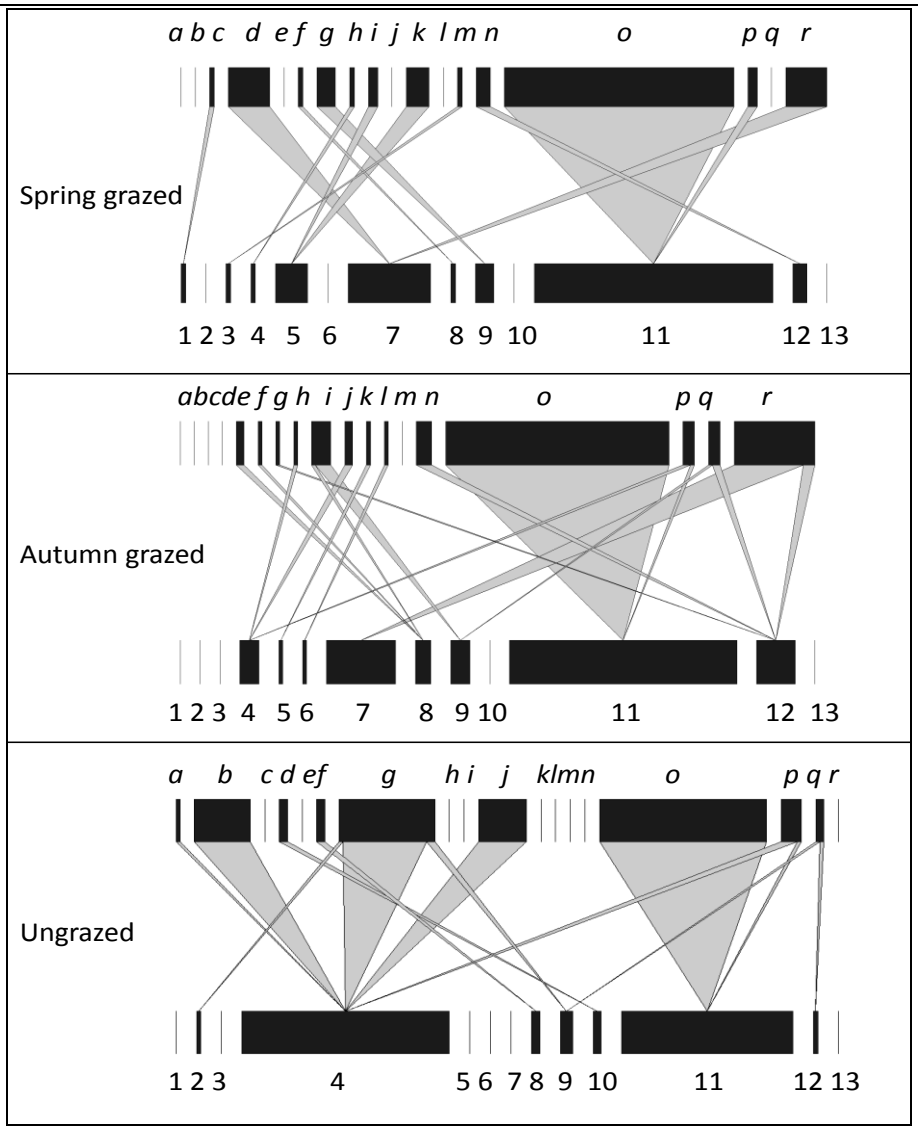


Figure 18. Summary host-parasitoid quantitative food-webs across different grazing regimes in the Upper Seeds experiment, Oxfordshire. Width of bars corresponds to relative abundance of that species. Light grey, unconnected bars represent absence of that species.

Hosts

1 *Agrimonia* host sp
2 *Prunus spinosa host*
3 *Chromatomyia ramosa*
4 *Craetagus host*
5 *Ectoedemia septembrella*
6 *Oxyptilus pilosellae*
7 *Phytomyza crassiseta*
8 *Phytomyza spondylii*
9 *Phytomyza vitalbae*
10 *Quercus* host
11 *Stephensia brunichella*
12*Trachys scrobiculatus*
13 *Trifolium* host

Parasitoids

a *Achrysocharoides suprafolius*
b *Achrysocharoides atys*
c *Agrimonia* parasitoid
d *Chrysocharis pubicornis*
e *Chrysocharis* sp.
f *Chrysocharis viridis*
g *Cirrospilus vittatus*
h *Crataegus* parasitoid
i *Diglyphus isaea*
j *Pediobius* sp.
k *Mirax* sp.
l *Oxyptilus pilosellae* parasitoid
m *Knautia arvensis* parasitoid
n *Trachys scrobiculatus* parasitoid
o *Pholetesor arisba*
p *Pnigalio pecticornis*
q *Pnigalio soemius*
r *Pnigalio sp.*

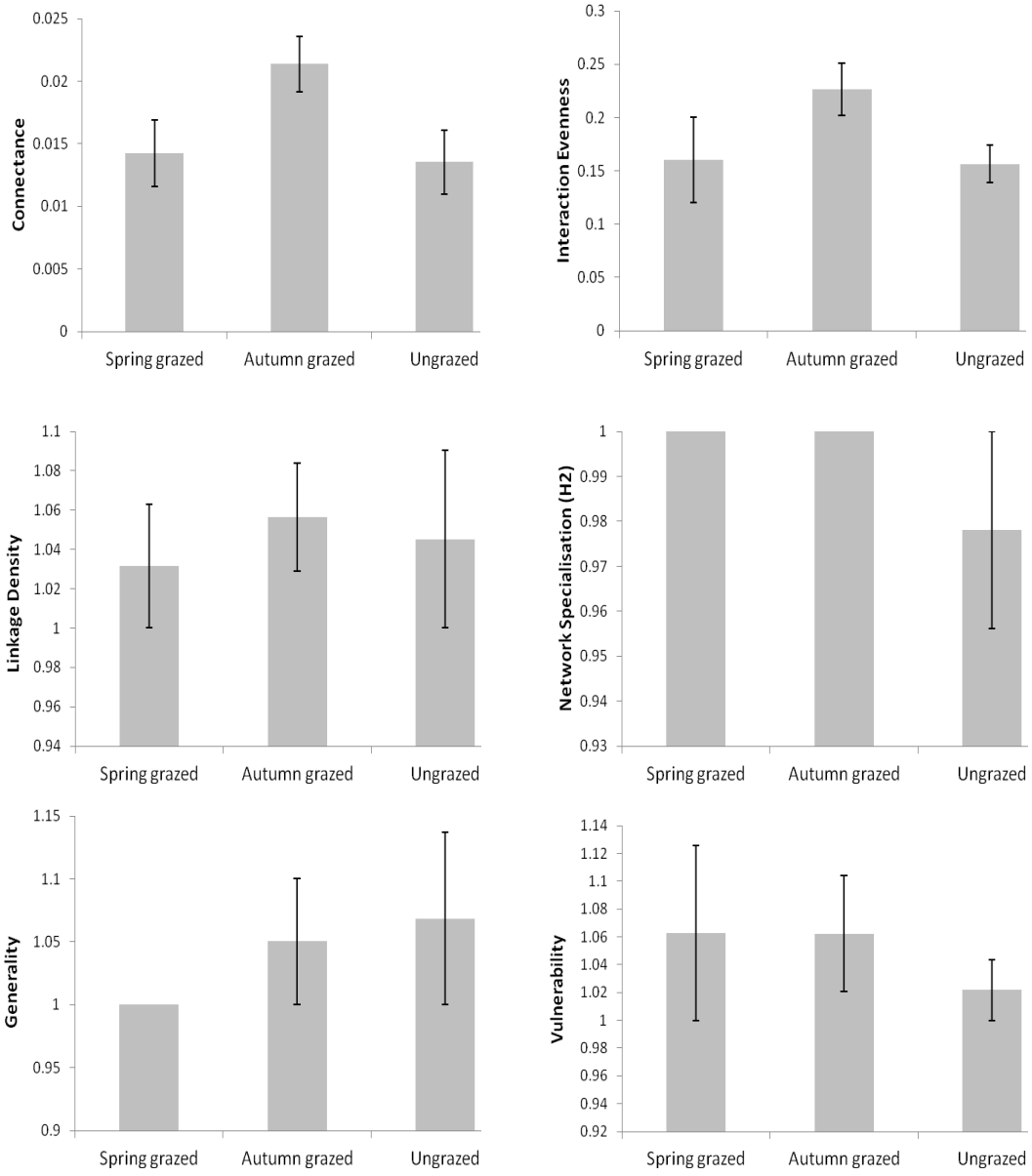


Figure 19. Food web statistics of leaf-mining insects and their parasitoids in relation to grazing treatments in the Upper Seeds experiment, Oxfordshire. Error bars show standard error of the mean. Where no error bars are present the food web statistic showed no variation under that treatment.

Table 18. Linear models of food web statistics for leaf-mining host-parasitoid insect webs under different grazing treatments in the Upper Seeds experiement, Oxfordshire.

		Degrees of freedom	**F**	**P**
Log (Connectance)	matrix size	14	3.21	0.097
	grazing treatment	16	2.87	0.090
Log(Interaction Evenness)	matrix size	16	0.63	0.44
	grazing treatment	14	1.70	0.28
Log(Linkage Density)	matrix size	16	0.66	0.43
	grazing treatment	14	0.13	0.8829
Log(H2)	matrix size	13	3.12	0.10
	grazing treatment	15	0.85	0.45
Log(Generality)	matrix size	16	0.39	0.54
	grazing treatment	14	0.56	0.58
Log(Vulnerability)	matrix size	16	0.32	0.58
	grazing treatment	14	0.25	0.78

4.4 Discussion

I found no significant differences between treatments in the abundance or species richness of either hosts or parasitoids; and only a trend towards higher parasitism in the ungrazed treatment. Despite this I found distinct responses to grazing treatment in terms of species composition by the lower trophic level, the leaf miners, but no such response to grazing treatment by the higher trophic level (parasitoid wasps). This is contrary to my expectation that parasitoids would show a greater response to the grazing treatment. Despite these differing responses to management treatment by the leaf miners and their parasitoids, the overall food web structure remained remarkably constant, again contrary to our expectations.

I found no effects of treatment on the abundance or species richness of leaf miners or parasitoids, contrary to a previous study showing the number of leaf miners was affected by treatment at the individual plant level (Staley *et al.* 2006). This may in part be due to the scale of study since in this study I looked at effects at the plot level. The host plants for the leaf miners were present in all the treatments, thus the species richness did not change across treatments. However, the abundance of individual plant species does differ across the treatments, with *Crataegus* being much more abundant in the ungrazed treatment. My food webs show that the same leaf miner and parasitoid species are present in each treatment, but those species differ in their abundance across treatments. In particular in the ungrazed treatment *Crataegus* sp. and consequently their parasitoids are much more abundant. Despite these differences in the abundant species in each treatment, the total abundance of leaf miners and their parasitoids did not change with grazing treatment.

Parasitism did show a response to management treatment, despite the fact that abundance and species richness did not respond to grazing regime, which indicate that this is a response to the effect of grazing on vegetation rather than insect densities directly. The spring grazing results in shorter average sward height during the summer peak season than the autumn grazed and the control treatments have become largely encroached by scrub, creating a more complex environment (See chapter 5). Experimental evidence that parasitoid host location rate is reduced in complex environments (Andow & Prokrym 1990) (Pimentel 1961, Gardner and Dixon 1985, Ables et al. 1980) led me to expect lower parasitism rates in the more complex vegetation of control plots than the simple short turf of spring grazed plots, when in fact I found the opposite. One reason for this could be that due to their small size, parasitoid wasps are vulnerable to disturbance by high winds and the more protected environment created by the scrub may enable a higher attack rate for parasitoids (Shaw, 2006).

Previous studies have found that the host community composition affects the composition of the associated parasitoid fauna in leaf-mining communities (Salvo, Valladares & Cagnolo 2011). This was not found in this study. I expected parasitoids to be more affected by grazing treatments than their hosts due to their higher trophic position making them more vulnerable to habitat change (Holt and Lawton, 1999). However, the reverse was found with hosts being affected by grazing regimes while parasitoids were unaffected. This may be due to the spatial scale of this experiment. In a study of this spatial scale involving mobile insects such as leaf miners and their parasitoids, any differences found are likely to reflect the foraging decisions of these organisms rather

than population level responses (Moise & Henry 2010). It appears that the leaf mining hosts and their parasitoids may be operating at different spatial scales, with the leaf miners responding to the 30 by 30m paddocks of different grazing regimes, whilst the parasitoids are unaffected by the changes to habitat structure at this scale. Both the connectivity of habitats and the dispersal ability of the organisms in question are key factors affecting food web structure, with greater food web complexity being found in more highly connected sites (Murakami, Hirao & Kasei 2008).

These different responses to habitat change by the hosts and parasitoids did not translate into changes in food web structure, in contrast to a study by Tylianakis (2007) showing that food webs can be significantly altered by habitat changes across habitat modification from rice fields to agroforest and rainforest. Studies looking at the restoration of pollinator communities however, have found little food web structural difference between restored and pre-existing habitats (Forup & Memmott 2005; Forup et al. 2008a), which hints at the relative robustness of mutualistic networks to changes implemented during restoration treatments. However, it may be that in my study as well, as in the Forup et al. studies, that the change in habitat was far less extreme than in the Tylianakis et al. (2007) study, and not enough to cause changes in food web structure.

By the necessity of experimental design, the treatments in this experiment were applied over small areas, which may have affected the response by the insect communities, as discussed above. In particular, leaf miners are usually monophagous (Novotny et al. 2010) and thus are reflecting changes in plant communities directly, whereas parasitoids of leaf miners are likely to be less host specific (Lewis et al. 2002), and therefore unlikely

to be responding as closely to changes in vegetation. This can be seen in the fact that the food webs presented here show high host-specificity indicating highly specialised parasitoids, when in fact the species studied are known to be generalists (Shaw, pers comm..), but will likely be parasitising other species outside of the study area.

The remaining species rich grasslands throughout Europe often exist as small isolated fragments and the areas available in reserves on which to restore grassland are also small, so understanding impacts on these scales is still relevant to habitat management (Oster et al. 2009). Furthermore, despite the potential drawbacks of the small experimental scale, the landscape context is the same for all treatments, which is important as landscape heterogeneity is an important factor driving the structure of food webs (Fabian *et al.* 2013).

4.5 Conclusion

The restoration of native grassland onto degraded landscapes has become a priority in many countries (Walker et al. 2004; Torok et al. 2011; Littlewood, Stewart & Woodcock 2012). Insect parasitism is a critical component of herbivore population regulation, hence the study of parasitism and parasitoid community composition in restored grasslands is important in itself from conservation and management perspectives (Rossetti *et al.* 2013). Our results indicate that certain food webs may be robust to different types of restoration methods. However, further work is needed to compare multiple network responses to restoration, since different types of networks have been shown not to respond uniformly (Pocock, Evans & Memmott 2012).

Chapter 5

Grassland restoration using low-intensity seasonal grazing leads to changes in soil ecosystem functioning

Abstract

- Restoration studies rarely include the consideration of management impacts on below ground fauna and ecosystem functioning, despite the fact that these processes can be critical for the outcomes above ground.
- Grazing strategies implemented to restore lowland calcareous grassland can have a variety of impacts on below ground fauna via mechanisms such as compaction of the soil, changes to root plant structure and nutrient addition via animal dung.
- In this chapter I investigate whether seasonal grazing impacts soil feeding activity by invertebrates.
- I show that whilst overall density of key soil invertebrates and averaged soil feeding activity is unchanged, the vertical profile of soil ecosystem functioning is unique under each grazing regime.
- This finding has implications for the choice of seasonal grazing activities since the vertical profile of soil feeding activity may impact on above ground processes.

5 Grassland restoration using low-intensity seasonal grazing leads to changes in soil ecosystem functioning

5.1 Introduction

Temperate grassland is one of the most endangered habitats in the world, having suffered greater losses and with less area under preservation than tropical forests (Hoekstra *et al.* 2005). Since it is now widely recognised that the maintenance of existing ecosystems alone is insufficient to stem the global decline in biodiversity and ecosystem services a concerted effort to restore target habitats, such as temperate grassland, will be essential if there is to be any hope of reversing current trends (CBD 2012). Consequently, restoring temperate grassland is a widespread management practise and research focus across Europe (Barbaro, Dutoit & Cozic 2001), North America (Fuhlendorf et al. 2002; Rowe 2010) and parts of Asia (Huang et al. 2013; Wan, Pan & Bai 2013).

In Europe, temperate calcareous grassland is one of the most bio-diverse habitats, containing a rich flora and invertebrate fauna (Prendergast et al. 1993; Partel & Zobel 1999; Poschlod & WallisDeVries 2002; WallisDeVries, Poschlod & Willems 2002). Over the past one hundred years the area of land covered by semi-natural or unimproved calcareous grassland has decreased dramatically, as has the average area of remaining fragments (Polus et al. 2007). This has been largely due to changes in agricultural practices, with the shift from traditional pastoral techniques, which created and maintained calcareous grassland, to high intensity grazing and large-scale arable farming (Hodgson et al. 2005). This loss of grassland in Europe has contributed to sharp declines in many of our charismatic invertebrate fauna such as butterflies (Polus et al. 2007) and

bumblebees (Carvell et al. 2006) and the vital pollination services they provide (Biesmeijer et al. 2006). Finding cost-effective ways of re-establishing native grassland onto degraded landscapes is thus an important area of research (Walker et al. 2004; Torok et al. 2011; Littlewood, Stewart & Woodcock 2012).

The reintroduction of low-intensity grazing is considered to be the most natural and effective method for the restoration and management of grasslands (Gibson & Brown 1991; Walker et al. 2004; Klimek et al. 2007; Maccherini & Santi 2012). Consequently, in the UK light, seasonal grazing is now a widely used management practise for grassland restoration (Roach 1995; Walker et al. 2004; Whyte 2012). However, despite continued interest in the development of effective grassland restoration methods and the setting of ambitious grassland restoration targets by government agencies (Bullock et al. 2011) the soil community is often overlooked in research, despite its importance for restoration outcomes.

The soil fauna in grasslands is dominated by nematodes (Yeates et al. 1997). Changes in above ground plant species communities caused by management practices such as grazing, have been shown to cause shifts in below ground nematode communities (Eisenhauer et al. 2011). Conversely, as the most abundant soil herbivores, nematodes have the ability to affect above-ground plant composition by reducing primary productivity (Ingham & Detling 1990) and by altering the competition between plant species (Verschoor et al. 2002) and functional groups (Wurst et al. 2008) through selective root grazing pressure. This can ultimately influence the process of plant succession (Brown et al. 1987) and therefore species composition of a restored grassland, demonstrating the reciprocal link between aboveground and belowground processes.

Since the soil surface represents an interface between two very different environments, soil conditions are not likely to be uniform, but rather change across a gradient with increasing depth. In a grazed ecosystem the upper surface of soil will receive direct nutrient addition from animal dung and decomposing litter, which is then pulled down into the soil by invertebrates and plant root activities (Hättenschwiler & Gasser, 2005). This often leads to the vertical stratification of soil nutrient properties (Jobbágy & Jackson 2000; Franzluebbers 2002). Properties such as moisture and climate may also be stratified through the soil profile due to differing above-ground vegetation structure affecting rainfall infiltration, soil temperature, gaseous exchange with the atmosphere and soil structure (Russell 1971; Franzluebbers 2002). These abiotic properties are known to have impacts on the ecosystem functioning of soil (McCalla, Blackburn & Merrill 1984; Houlbrooke & Laurenson 2013; Schrama et al. 2013) and for this reason we may expect to see a depth gradient for many soil ecosystem processes.

In this context, this study set out to address current gaps in our understanding of how commonly used grassland restoration practices affect the soil nematode fauna and the profile of soil ecosystem functioning with depth.

5.2 Materials and Methods

5.2.1 Site Description

The study was carried out on a long-term calcareous grassland restoration experiment running at Upper Seeds, Wytham Woods, Oxfordshire (51°76'96.22"N, −01° 33'05.25"W). This experiment, established in 1985, investigates the effect of grazing season on the restoration of calcareous grassland though natural succession. It is set in a 10 ha field which was cultivated mostly for cereals between 1960 and 1981. In 1981 a final crop of winter wheat was sown, after which the site was abandoned before harvest (Gibson, Watt & Brown 1987).

5.2.2 Experimental Design

The design of the experiment consists of two Latin squares, each containing nine 30 x 30 metre plots fenced off from deer grazing. Three grazing regimes designed to elucidate the effects of the different grazing periods on long-term restoration goals (ungrazed control, short spring grazing and short autumn grazing) are replicated six times across these paddocks. Spring grazing is applied using three ewes in each paddock for ten days in late April, and autumn grazing has used the same stocking density for fourteen days in late September. An annual grazing density of 0.5 Livestock Units (LSU, 1 LSU=9 Lowland ewes (Nix 2003)) per hectare is recommended for lowland grassland (Crofts & Jefferson 1994). The stocking density in this experiment is 0.74 LSU, which is comparable with recommendations. The timing of treatments were chosen to represent the periods of maximum plant growth in spring and autumn (Gibson et al. 1987), as the season of grazing is known to be an important factor for consideration when managing grassland for conservation (Duffey 1974; Bullock et al. 2001).

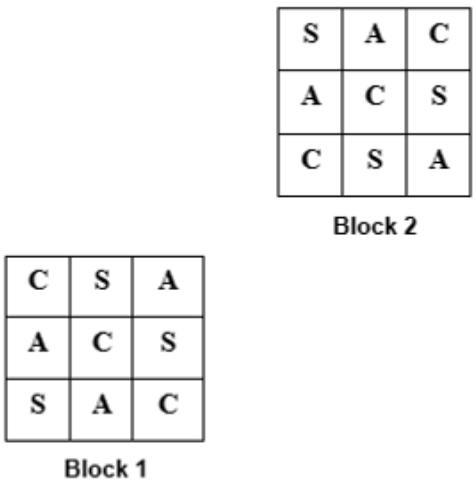


Figure 20. Experimental design of the three grazing treatments: autumn (A), spring (S) and ungrazed control (C) in Upper Seeds Field, Wytham Woods, Oxfordshire.

5.2.3 Data collection

Data were collected between the 9th and 30th of November 2011. This survey period was chosen as autumn represents a peak for soil activity (Anderson 1988; Jamieson et al. 1998). At the time of data collection, grazing had ceased. The spring-grazed treatments had last been grazed 6 months prior to this study in April 2011 and the autumn-grazed treatment had been grazed one year prior to data collection in September 2010.

5.2.4 Nematode density

Three soil cores, 5 cm wide by 8 cm deep, were taken at random locations in each plot. From these cores 25 g of soil was placed in a Baermann funnel from which nematodes were extracted over a 24 hour period (van Bezooijen 2006). Extracted nematodes were stored in Propylene glycol before being counted using a microscope. Nematode density per plot was calculated as the average density from the three cores in each paddock.

5.2.5 Environmental Measurements

Soil moisture and temperature were measured at three random locations within each plot with a hand held 12 cm TDR probe (HydroSense, Campbell Scientific Ltd., Shepshed, U.K.) and averaged per plot.

5.2.6 Vegetation structure

Sward height was assessed using the drop-disc method. This method involves letting a standardised disc of 30 cm diameter and 200g weight with a central slot slide down a metre rule and recording the height where it come to rest (Holmes 1974). There are many methods for measuring vegetation height, but this method is considered the best in studies involving assessment of vertebrate herbivory (Stewart, Bourn & Thomas 2001). Three measurements of vegetation height were taken at six locations within each plot and the overall average maximum height was calculated per plot using a pole with the point from the ground to maximum vegetation touch point measured.

5.2.7 Soil Feeding Activity (Bait Lamina)

The ecosystem functioning of soil fauna was assessed using bait lamina sticks (Terra Protecta GmbH, Berlin, Germany) (von Torne 1990), which is a method that has been used successfully in grassland (Filzek et al. 2004; Hamel et al. 2007) and forests (Rombke et al. 2006; Simpson et al. 2012) to assess the activity of the soil fauna and to demonstrate the effects of different types of management on soil fauna feeding activity (Reinecke et al. 2008).

Bait lamina sticks are PVC sticks of dimension 200 mm × 6 mm × 1 mm, with 16 biconical apertures of 1.5 mm in diameter, spaced 5 mm apart on the lower 10 cm of the stick. These apertures are filled with bait made of powdered cellulose, bran flakes and activated carbon (70:27:3), mixed with distilled water. The paste is squeezed into the holes by hand and left to dry at room temperature. Each aperture is then checked as being filled completely by holding the sticks against a light source after the bait had dried.

Twelve bait-lamina sticks were placed randomly in each plot for three weeks. Three weeks had been determined as the appropriate period from a previous trial. The sticks were inserted vertically into the soil, the uppermost hole at the soil surface interface and the bottommost hole at 7.5 cm depth. At the end of the recording period bait lamina sticks were collected from the field, wrapped in transparent film and held against a light to examine for evidence of bait consumption. Holes were recorded as either 0 (no evidence of bait consumption) or 1 (evidence of bait consumption), which was determined by whether light was visible through the bait.

5.2.8 Statistical Analysis

5.2.8.1 Nematode density and environmental conditions

Linear models were used to investigate the effects of grazing treatments on nematode density, soil temperature, soil moisture and vegetation height, with block included as a fixed effect. Block was modelled as a fixed effect as it was part of the experimental design and could not be removed as a random effect due to the experimental set-up containing only two blocks. P-values of fixed effects were obtained by likelihood-ratio tests of the full model with the explanatory variable included versus excluded. The residual plots of

the minimum adequate model were then visually inspected to check that the requirements for homoscedasticity and normality had been met.

5.2.8.2 Soil fauna feeding activity

Feeding activity was calculated as the proportion of holes perforated per bait lamina stick, averaged across the 12 bait lamina sticks placed in each plot. Generalized linear models with binomial error structures were used to investigate the relationship between feeding activity and the explanatory variables of grazing treatment, soil temperature, vegetation height, nematode density and block.

Soil moisture was excluded from the model as it was highly correlated with temperature. Vegetation height was log transformed to normalise the data. Analyses began with the maximal model, with all explanatory factors and interactions included, from which non-significant effects were removed until a minimum adequate model was obtained. The model selection procedure was carried out as described above.

5.2.8.3 Feeding activity with depth

Feeding activity with depth (a binary variable of 0 (not eaten) and 1 (eaten) for each hole in each stick) was modelled using a generalized additive mixed model (GAMM) with binomial errors. Grazing treatment, soil temperature, log(vegetation height), nematode density and block were modelled as fixed effects with plot as a random effect to account for the grouping of 12 bait lamina sticks per plot. Depth was modelled using a cubic regression spline smoother due to the nonlinear relationship between feeding activity and depth. In the full model, all interactions were included and non-significant interactions

dropped until the minimal adequate model was found. Alternative models were compared using AIC values (including a model with one general smoother for depth vs. smoothers by grazing treatment). The optimal model with the lowest AIC value was selected.

Analyses were carried out using R packages lme4 and mcgv (Wood 2011; Bates, Maechler & Bolker 2013).

5.3 Results

5.3.1 Environmental conditions

Soil moisture content varied between 32% and 50 % and was the only environmental variable measured which showed no significant variation between grazing treatments (df=16, F=0.29, p=0.75). Soil temperature varied from 10.1^{o}C to 11^{o}C and was significantly higher in autumn grazed treatments compared to ungrazed controls ($F_{2,16}$=10.37, p=0.002) (Figure 21).

5.3.2 Nematode density

Nematode density varied from 52 individuals to 130 individuals per 25 grams, with grazing treatment having a significant effect on nematode density (Figure 21, $F_{2,16}$=10.24, p=0.002).

5.3.3 Vegetation structure

Maximum vegetation height differed significantly among treatments, varying from 109 cm in control treatments to 30 cm in the short turf created by spring grazed treatments (Figure 21, $F_{2,16}$= 4.33, p=0.034).

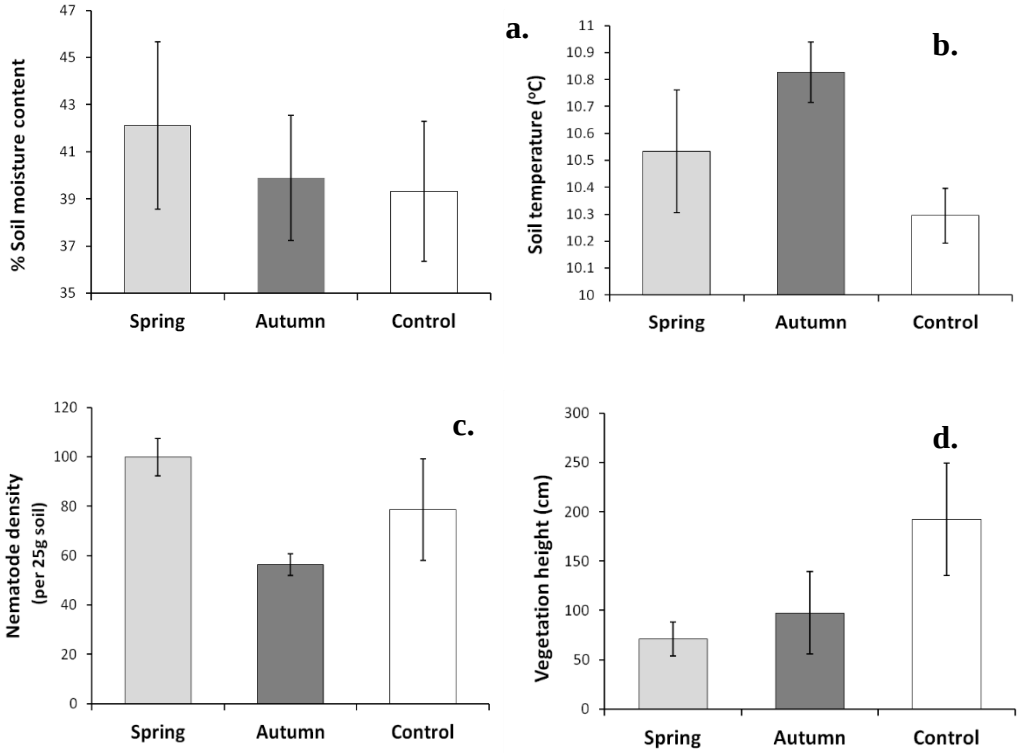


Figure 21. Mean soil moisture content (a), soil temperature (b), nematode density (c) and vegetation height (d) under the three different grazing treatments: spring grazed, autumn grazed and ungrazed control in the Upper Seeds experiment, Oxfordshire. Error bars show standard error of the mean (s.e.m.).

5.3.4 Soil feeding activity

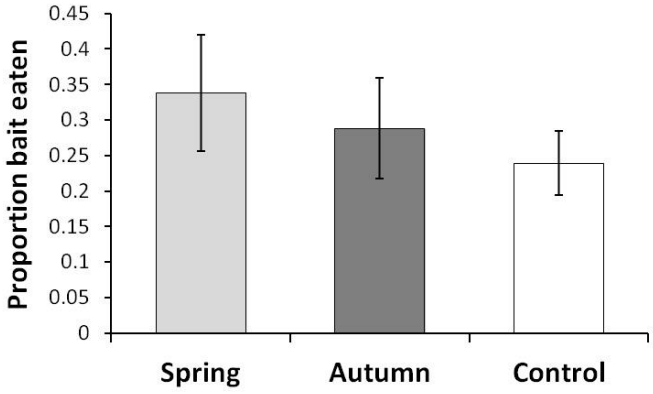


Figure 22. Soil faunal feeding activity, measured as proportion of bait eaten, in relation to grazing treatment in the Upper Seeds experiment, Oxfordshire. Error bars show standard error of the mean.

Soil trophic activity as measured using the proportion of bait eaten was highly variable between individual bait lamina sticks, covering the full range of activity from 0% to100%. No significant effect of grazing treatment on overall soil trophic activity could be detected (Figure 22).

Investigations into any effect of nematode density, soil temperature, grazing treatments or any interactions between these variables on overall feeding activity found no significant relationships (Table 19).

Table 19. Generalised linear model of soil feeding activity as a function of nematode density, grazing treatment, vegetation height and soil temperature in the Upper Seeds experiment, Oxfordshire

Explanatory variable	Degrees of freedom	Deviance	P
Nematode Density	12	0.016	0.90
Log (Vegetation Height)	13	0.008	0.93
Grazing Treatment	15	0.120	0.94
Soil Temperature	16	0.085	0.77
Block	17	0.020	0.89

5.3.5 Feeding activity with soil depth

Soil faunal activity was greatest in the top 2 cm of soil. The change in the rate of soil feeding with depth differed significantly between grazing treatments with spring grazed treatments having a noticeably more uniform depth profile (Figure 23, Table 20).

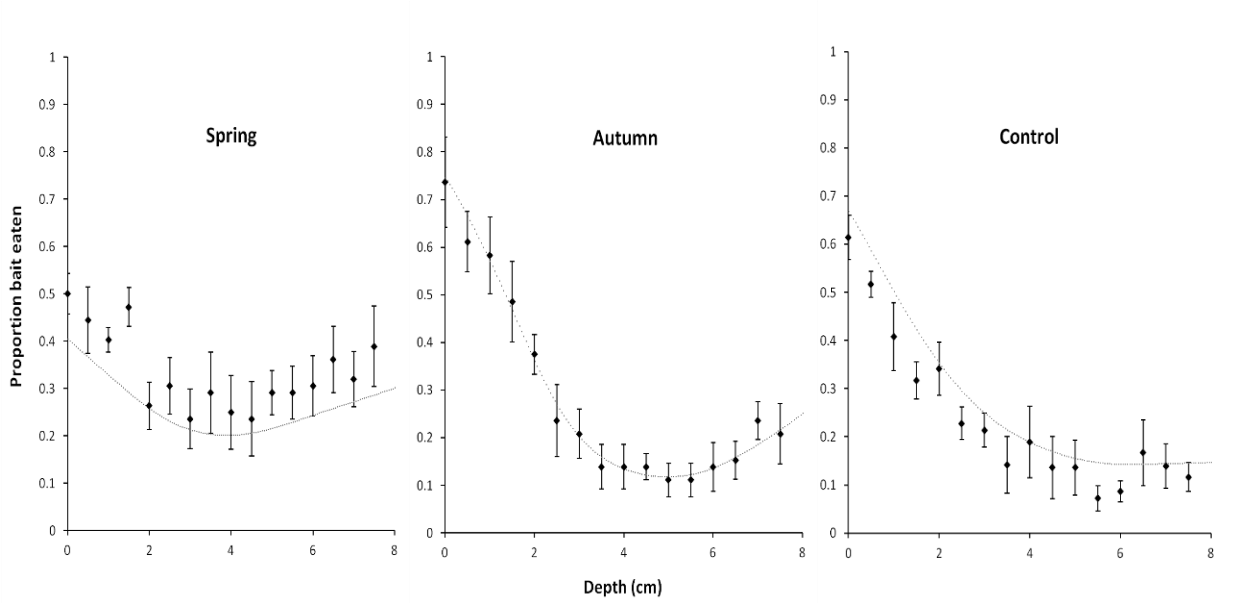


Figure 23. Soil feeding activity in relation to depth across the three grazing treatments: (a) spring grazed, (b) autumn grazed and (c) ungrazed control the Upper Seeds experiment, Oxfordshire.

Table 20. Generalised additive mixed model (gamm) for soil feeding activity with depth in relation to grazing treatment

Explanatory variable	Degrees of freedom	Chi-Square	P
Spring Depth Smoother	2.930	23.07	<0.001
Autumn Depth Smoother	3.704	187.09	<0.001
Control Depth Smoother	2.844	134.67	<0.001

N.B. Depth was modelled with cubic regression spline smoothers. Note that the degrees of freedom and p values for smoothers are estimates. The higher the degrees of freedom the more non-linear the smoother (df=1 indicates a linear smoother)

5.4 Discussion

It is well known that the season of grazing used during grassland restoration has an impact on the nature of the restored plant community (Bullock et al. 2001). This study now adds to this the knowledge that the season of grazing can also affect soil ecosystem functioning.

My most notable finding is the fact that altered seasons of grazing treatment do not lead to an overall change in soil feeding activity, but do lead to a significantly different soil feeding profile with depth (Figure 23, Table 21). This is a novel result, which needs further investigation as to its causes and implications, but here we discuss some possibilities for this finding.

Spring grazing can be more effective at preventing encroachment by woody shrubs and dominant grasses such as *Arrhenatherum* species than autumn grazing because the turf layer is reduced at the beginning of the peak growing season. In autumn grazed sites, stock tend to avoid areas of over-mature turf which has developed over the summer, enabling grasses to set seeds which may then be enhanced by the additional nutrients animal dung provides (Gibson & Brown 1992; Dostálek & Frantík 2012). This difference in above ground vegetation structure caused by the different grazing treatments may account for the different soil functioning profiles.

Since autumn grazed treatments retain more deep-rooted shrubs than spring grazed treatments, as indicated by vegetation height in this study (Figure 21.d.) we may expect the soil layer beneath autumn grazed treatments to be more vertically stratified owing to a greater depth of root activity. The structure of soil has been found to affect the soil feeding activity as measured by the bait lamina (Gongalsky et al. 2004) and so the

difference in below ground feeding structure may be representing the difference in above ground vegetation structure.

Both autumn-grazed and control grazed treatments are able to develop a humus layer of leaf litter owing to the greater amount of vegetation compared to the short turf of spring grazed treatments. This enhanced humus layer may account for the greater feeding activity in the upper 2 cm of soil since there is greater organic material for soil fauna to break down (Figure 23) and the absence of this in the spring grazed treatments creates the uniform spring grazed feeding profile. The greater stratification of the autumn grazed and control treatments compared to the spring grazed treatment could therefore be representing a stratification of organic carbon in the soil layer, which has been hypothesised as a good indication of a "healthy" soil profile by Franzluebbers (2002).

An alternative hypothesis for the difference in soil functioning profile could be the impact of soil compaction caused by grazing animals. The smooth decline in feeding activity with depth shown in the control plots which have been ungrazed for 30 years (Figure 23) mirror the pattern consistently found in other European bait lamina studies (von Torne 1990; Simpson et al. 2012), suggesting that this is the "normal" soil activity feeding profile. The spring grazed activity profile is much more homogenised, with the spring grazed treatment showing similar activity at all depths. Gongalsky et al. 2004 found that the depth distribution of bait lamina feeding activity was linked to soil texture, noting that a homogenous vertical soil structural profile resulted in bait lamina activity that did not vary with depth. The spring treatments had been grazed six months prior to the commencement of this study compared to one year since the autumn treatments had been grazed. The resulting spring soil activity profile may therefore be indicative of a uniform

soil structure caused by compaction during the most recent grazing event, though soil structure was not measured. This could indicate that grazing substantially impacts the ecosystem functioning by disturbing the natural depth profile of the soil, which appears to recover a typical structure within a year, as evidenced by the similar soil profile between autumn grazed and ungrazed treatments (Figure 23).

Previous studies have shown that vertebrate grazing can alter soil structure, often leading to substantial reductions in ecological function (Eldridge & Whitford 2009). In the current study there was no alteration in overall soil ecosystem functioning, but there was evidence that grazing may have altered the vertical distribution of soil ecosystem functioning. Whether the change in soil ecosystem functioning with depth is caused by compaction of the soil due to grazing could be tested with further studies looking at soil ecosystem functioning profile with depth both before and after a grazing event and with different levels of stocking density, to see if greater stocking densities lead to greater disturbance to the soil profile.

A final point to consider is whether alterations to the soil faunal community and environmental conditions caused by the different grazing treatments lead to the different soil feeding profiles. The season of grazing affected soil nematode densities and soil temperature, though there was no direct link evident between nematode densities, temperature and feeding activity, as measured through bait lamina sticks.

Nematode density was highly variable, which is unsurprising since nematode density is known to vary greatly over small spatial scales (Ferris, Mullens & Foord 1990; Robertson & Freckman 1995). Despite this variability, overall nematode density was found to be

greater under spring grazed plots than autumn grazed plots. The distribution of soil organisms is primarily driven by abiotic soil conditions (Birkhofer et al. 2012). However, soil moisture was uniform across treatments and temperature only varied by 1^{o}C. This leaves the cause of the higher nematode density under spring grazed treatments unexplained. It may have been caused by a factor which was not the focus of this study, such as the overall species diversity of vegetation which is known to affect nematode communities (Eisenhauer et al. 2011). In addition, previous studies have demonstrated that the relationship between the abundance of soil invertebrates and soil feeding activity is likely to be complicated (Birkhofer et al. 2011), with some groups of species facilitating others through bio-perturbation. These authors caution against drawing simplistic relationships between belowground fauna and feeding activity.

The relationships between both soil moisture and temperature and feeding activity have generally been shown to be strongly positive (Simpson et al. 2012), however this was not observed in this study. Since previous studies (Simpson et al. 2012) which found a positive relationship between feeding activity and soil moisture had lower overall moisture levels than this study, it may be that past a certain level, soil moisture ceases to be a limiting factor. The variation in temperature across treatments in this study was significant, but temperatures varied by only 1 ^{o}C, possibly insufficient to cause a detectable difference in activity of soil biota (Papatheodorou, Argyropoulou & Stamou 2004). Future investigations into changes in soil temperature, moisture and faunal composition with depth under different grazing regimes could begin to tease apart the relative contribution of these factors to the changes in soil feeding activity with depth found in this study.

Understanding how management treatments may affect the spatial patterning of soil biotic activity is important as this can impact the above ground community structure (Ettema & Wardle 2002). Importantly, in the restoration of grassland communities it must be remembered that below ground conditions can even affect above-ground plant-pollinator networks (de la Peña et al. 2012). Similarly, above ground communities can affect below ground food webs, demonstrating that plant and soil communities are mutually dependent (Wardle et al. 2004) and should both be taken into account during restoration.

With the recognition that the preservation of existing ecosystems alone is insufficient to stem the global decline in biodiversity and ecosystem services, slowing or halting continued species losses through the restoration of already degraded habitats will be essential (CBD 2012). This has led to an ambitious target being proposed at Rio+20 to achieve a "land degradation neutral world" by 2030 (UN 2012). To meet this target the international community will need to work together to coordinate conservation, restoration and sustainable land-use in order to preserve biodiversity and the provision of ecosystem services (Aronson & Alexander, 2013). In addition to reducing biodiversity losses, the restoration of degraded lands is acknowledged as a way to mitigate against climate change (CBD 2012), meaning that restoration practises based on informed science are of greater importance than ever. Bait lamina studies, such as this, are increasingly showing that management, soil conditions, climate and soil fauna are important drivers of overall soil activity. This paper adds the fact that depth profile changes in soil feeding activity caused by grassland restoration are an important factor to consider and given the current global push towards widespread grassland restoration we advocate further investigations in this area to build on these initial findings.

Chapter 6

General discussion

6.1 How does environmental change affect invertebrate community structure and ecosystem function?

Global environmental change continues to threaten the future persistence of biodiversity and many ecosystem services on which humans are dependent (Kremen 2005), yet there is still no consensus on how ecological communities will respond to the wide range of pressures environmental change brings (Walther et al. 2002). More studies are needed, particularly on invertebrates which are functionally extremely important (Klein et al. 2007; Kremen & Chaplin-Kramer 2007). Experimental studies in real world environments are particularly important as they allow the assessment of responses to change to be determined without having to wait for those changes to occur in the environment (Lawton & Kinne 2000).

This thesis contributes to studies on the effects of different forms of environmental change on invertebrate communities and ecosystem functioning. In particular I address aspects of changes in invertebrate community structure and function that have previously been understudied, including habitat fragmentation and alterations to rainfall regimes which may be a consequence of climate change. I also assess the amelioration of environmental change effects on ecological communities by studying the effects of habitat restoration.

The work in this thesis has addressed four main questions relating to the effects of environmental change on invertebrate communities. First, is a community and ecosystem approach beneficial to our understanding of environmental change on natural

communities? Second, do the impacts of environmental change affect different trophic levels to different extents? If so, do these change at different levels result in changes to food web structure and ecosystem function? Third, how does habitat restoration affect community structure and functioning? And finally, can our understanding of environmental changes be enhanced by considering the below ground environment and its ecosystem processes? I have discussed my results in detail in each chapter. To conclude this thesis I consider the four questions above and discuss the particular contribution of this thesis to answering them. Following this I discuss main themes arising from my research and suggest potential areas for future research.

6.1.1 Is a community and ecosystem approach beneficial to our understanding of environmental change on natural communities?

In chapter 3 I show that although species richness and abundance is not affected by experimental alterations to climate change, the phenological matching between hosts and parasitoids can be. This finding was only apparent due to the implementation of a community approach, adding to the growing body of research highlighting that the effect of climate change on species interactions should be incorporated into ecological research (Gilman et al. 2010; Stewart et al. 2015). Similarly, environmental change in the form of habitat degradation and fragmentation may lead to shifts in ecological communities that are not immediately apparent from individualistic species responses. For example, anthropogenic habitat modification in Ecuador altered patterns of trophic interactions among species while leaving the identities and relative abundance of component species little changed (Tylianakis et al. 2007). Such results suggest that ecologists and

conservation biologists interested in understanding the consequences of global change for ecological communities may need to move beyond conventional metrics such as abundance of individual species and the species richness and diversity of communities, to consider also emergent, community level outcomes.

6.1.2 Do the impacts of environmental change affect different trophic levels to different extents? If so, do these change at different levels result in changes to food web structure and ecosystem function?

In chapter 2 I showed that landscape level fragmentation effects such as fragment area, isolation and edge effects can impact on different trophic levels to different extents, but that this does not necessarily translate into overall alterations to the ecosystem function of parasitism. In contrast to Tscharntke et al. (2002), who found that lower trophic level insect herbivores showed greater similarity in community structure in habitats in a fragmented landscape than insects at higher trophic levels, I found that lower trophic levels were responding to fragmentation whilst the highest trophic level showed no response.

However, in the study presented in chapter 2, the highest trophic level was represented by a single species, the parasitoid *Melittobia australica*. Since species traits can affect their responses to fragmentation (Ney-Nifle & Mangel 2000; Steffan-Dewenter & Tscharntke 2000), it may be that the particular species traits of the sole parasitoid species in this study had a greater effect than its trophic level. It is hypothesised that species which show a greater number of links in a food web to other species are more resistant to

perturbations in the environment due to the availability of alternative links if a species interaction is lost (Beismiejer et al, 2006). *Melittobia australica* is a highly generalist parasitoid and thus might be expected to be relatively insensitive to fragmentation.

In chapter 3 I show that alterations to rainfall regimes have the potential to alter host-parasitoid synchrony, but that this perturbation to the system does not result in food web changes at the scale studied. Other studies have similarly shown that predator-prey and plant-pollinator interactions can be de-coupled by climate change (Parmesan 2006). However, it is cautioned that both individual species traits and methods of study can affect outcomes of climate research (Parmesan 2007). In chapter 3 I show a snapshot of the impact of rainfall regime on one generation of insects. Phenological responses to climate change are likely to cause individual evolutionary responses within species which may affect interactions between species over time (Lavergne et al. 2010). Hence if this study had been continued over a longer time scale, the small shift in phenology could have resulted in a de-coupling of the interaction and a consequent food web structural change, but over the time-scale studied no such effect took place.

In chapter 4 I show that the application of different grazing regimes in grassland can impact trophic level community compositions differentially, but that these changes in individual species do not alter host-parasitoid food webs at the patch scale. It is likely that this was the result of species responding to the environment at different spatial scales (Roland & Taylor 1997).

In summary my research found that communities did respond to the environmental changes studied differently across trophic levels; however these responses were likely due to individual species responses and not trophic level responses.

These changes in communities across trophic levels did not result in food web structural changes in the systems studied. This is likely due to the small time-scale and size of the studies, which is a limitation in the application of quantitative food web analysis which often needs very large and highly resolved interaction data in order to truly reveal community structure accurately (Ings et al. 2009).

6.1.3 How does habitat restoration affect community structure and functioning?

In chapter 4 I show that the community structure of leaf-miners and their parasitoids in a lowland calcareous grassland restoration experiment show remarkably consistent food web structure under different grazing regimes. Despite this consistency in food web structure, the individual host leaf miner species are responding to the changes in grazing management whilst their hosts are not. This again highlights the difficulties of carrying out experiments at the necessary spatial scale for all organisms involved. Restoration is dominated by local scale efforts (Hobbs and Norton 1996) but needs a landscape scale approach (Bestelmeyer et al. 2003).

However, despite these caveats relating to spatial scale, the findings in chapter 4 are in agreement with other food web studies which show consistency in food web structure in environments undergoing restoration (Forup et al. 2008b; Henson, Craze & Memmott

2009). The fact that restoration projects by their nature involve purposeful manipulations of the environment means that future restoration projects on larger scales could offer the unique opportunity to carry out food web and functional experiments that would otherwise not be feasible (Ehrenfeld & Toth 1997). So whilst in this thesis I cannot definitively say whether restoration science benefits from a food web approach, I can conclude that the research area of quantitative food web ecology could benefit from using restoration programmes to explore fundamental questions in the assembly of food webs.

6.1.4 Can our understanding of environmental changes be enhanced by considering the below ground environment and its ecosystem processes?

The inclusion of below ground processes in studies of environmental changes, such as those undergone during restoration, can be of great benefit to our understanding of ecosystem processes (Kardol & Wardle 2010). In chapter 5 I show that different grazing regimes result in unique vertical soil ecosystem function profiles, which was previously unknown. Further work is needed to discover how these changes in soil ecosystem processes translate into changes in above ground processes.

6.1.5 Themes arising

Whilst a food web and community approach has been shown to be useful in the study of environmental change (e.g. Tylianakis et al. 2007), the findings in this thesis were dominated by individual species responses which did not result in changes in species richness or overall food web changes. This implies that the food web approach has its

limitations in small-scale studies and may benefit from the addition of information relating to individual species traits, such as in the growing field of functional trait analysis (McGill et al. 2006).

Functional trait analysis looks at a variety of life-history traits such as dispersal potential, fecundity, mobility, longevity etc. in correlation with the contribution of species to ecosystem functioning (Hillebrand & Matthiessen 2009). This may be a more effective way of assessing ecosystem responses to environmental change than species composition or trophic group analysis (Petchey & Gaston 2006), since traits can be used to predict extinction risk or vulnerability of declining species (Díaz et al. 2013).

6.1.6 Future directions for research

I have shown that long-term and small scale experiments can be very useful in elucidating the mechanisms by which interactions between species and below ground ecosystem functioning may be altered by environmental change. However, such studies could be improved by being conducted on a realistic scale, taking greater account of how far the study species moves. Landscape scale is an important factor to include because it may be the surrounding landscape rather than the focal study area that is crucial in determining responses, and if we simply focus on the study area we will not get the complete picture.

Species traits are also an important area to incorporate into future research. Research aiming to identify the particular type of functional traits which are most responsible for community response to environmental change is a growing area of research (de Bello *et*

al. 2010) and if incorporated into a food web approach (Reiss et al. 2009) could lead to a more complete understanding of ecosystem responses.

6.2 Conclusions

This thesis investigated impacts of environmental change on invertebrate community structure and ecosystem function. The results showed that species can display individualistic responses to environmental change which do not always translate into changes in food web structure or ecosystem function. These results have extended our knowledge on the effects of environmental change and restoration on ecological communities. For example, I have shown that consideration of the below ground environment may be important. My results have also highlighted areas where current research is limited. Studying the wider landscape context and carrying out manipulation experiments over greater scales could provide more representative insights into community responses to environmental change. Finally, an increased focus on species traits could help us to better understand why different species respond to environmental changes to different extents. Such approaches should allow ecologists to move beyond the idiosyncratic responses observed for individual species in particular circumstances, and help build a more general and mechanistic understanding of how ecological communities respond to environmental change.

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