

**Spatial ecology of food webs:
herbivore-parasitoid communities on the
pedunculate oak**

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Academic dissertation

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ABSTRACT

Herbivorous insects, their host plants and natural enemies form the largest and most species-rich communities on earth. But what forces structure such communities? Do they represent random collections of species, or are they assembled by given rules? To address these questions, food webs offer excellent tools. As a result of their versatile information content, such webs have become the focus of intensive research over the last few decades.

In this thesis, I study herbivore-parasitoid food webs from a new perspective: I construct multiple, quantitative food webs in a spatially explicit setting, at two different scales. Focusing on food webs consisting of specialist herbivores and their natural enemies on the pedunculate oak, *Quercus robur*, I examine consistency in food web structure across space and time, and how landscape context affects this structure. As an important methodological development, I use DNA barcoding to resolve potential cryptic species in the food webs, and to examine their effect on food web structure.

I find that DNA barcoding changes our perception of species identity for as many as a third of the individuals, by reducing misidentifications and by resolving several cryptic species. In terms of the variation detected in food web structure, I find surprising consistency in both space and

time. From a spatial perspective, landscape context leaves no detectable imprint on food web structure, while species richness declines significantly with decreasing connectivity. From a temporal perspective, food web structure remains predictable from year to year, despite considerable species turnover in local communities. The rate of such turnover varies between guilds and species within guilds.

The factors best explaining these observations are abundant and common species, which have a quantitatively dominant imprint on overall structure, and suffer the lowest turnover. By contrast, rare species with little impact on food web structure exhibit the highest turnover rates. These patterns reveal important limitations of modern metrics of quantitative food web structure. While they accurately describe the overall topology of the web and its most significant interactions, they are disproportionately affected by species with given traits, and insensitive to the specific identity of species. As rare species have been shown to be important for food web stability, metrics depicting quantitative food web structure should then not be used as the sole descriptors of communities in a changing world. To detect and resolve the versatile imprint of global environmental change, one should rather use these metrics as one tool among several.

SUMMARY

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I. Introduction

The forces that shape communities of herbivorous insects have been puzzling community ecologists for decades, and continue to do so (Holt 1977, Rosenheim 1998, Morris et al. 2004, Denno & Kaplan 2007). For long, the discussion was centered on the relative roles of top-down (predators, parasitoids and pathogens) and bottom-up (physical and chemical plant traits) forces in regulating herbivore populations (Hairston et al. 1960, Murdoch 1966, Lawton & MacNeill 1979, Hunter & Price 1992). Today, most researchers agree that no single element dominates spatially or temporally, but that the relative strength of different impacts fluctuates in space and time (Denno et al. 2005, Gripenberg & Roslin 2007, Hambäck et al. 2007, Tack et al. 2011).

To capture the relative strength of inter-specific interactions within a community, food webs offer an excellent tool. Food webs graphically visualize how individual species are not independent members of natural communities, but form parts of a large network of interactions where species affect each other either directly (by competition, predation or parasitism) or indirectly (via host plant traits or via shared natural enemies).

Food web as a concept was apparently first described by Elton in 1927 in his seminal book "Animal Ecology", which introduces much of the basis for modern ecology. However, already Darwin (1859) noted that organisms "are bound together by a web of complex relations". The first food webs constructed were interaction webs describing the species present in the community and the interactions between them as binary categories (as being present or absent). Frequently, these webs did not resolve individual species but categorized them into groups of similar taxa on either functional or taxonomical basis (e.g., Elton 1927, Lindeman 1942, Paine 1980, Sugihara et al. 1989).

One of the first enhancements of food web descriptors was to incorporate the abundance of each natural enemy (e.g., Askew 1961, Askew & Shaw 1974, 1979; Shaw & Askew 1976, Goldwasser & Roughgarden 1993, Wootton 1997, Laska & Wootton 1998). These so-called "semi-quantitative" herbivore-parasitoid food webs constructed by Askew and Shaw (Askew 1961, Askew & Shaw 1974, 1979; Shaw & Askew 1976) identified competition among parasitoids as a major force structuring the community. As the next step, Goldwasser and Roughgarden (1993) found that intermediate species (i.e. taxa in between top predators and basal species) were dominant in terms of both species richness and number of interactions. This led them to ask a question that is still under research today: which species are the most significant ones for maintaining food web structure? In this context, Wootton (1997) identified a pattern which has later been observed in several webs: that the interaction structure is dominated by a few abundant interactions along with numerous weak links. Current food web metrics are centred on describing these interaction patterns: how the interactions are spread among the component species, and how evenly energy flow is partitioned through different pathways in the web (Bersier et al. 2002, Banašek-Richter et al. 2009).

A multitude of methods and approaches can be used to quantify interactions between species. Initially, this made comparisons across different systems difficult or even impossible (Laska & Wootton 1998). As a solution, Memmott et al. (1994) published the first fully quantitative food web that measured not only the diversity and abundance of species at higher trophic level, but also of species at the lower trophic level and the frequency of individual interactions between species. This influential paper started a renaissance of food web studies.

The new generation of quantitative food webs differs from traditional, binary webs by depicting both the abundance of each species at higher and lower trophic levels, and also by the abundance of each species-specific interaction. Thereby, they pinpoint key interactions in the food web. As quantitative food webs are also built in a standardized way, they allow comparison of different food webs across different target taxa, thus helping to resolve structural differences across habitats and regions.

The first quantitative food webs generated for insects and their parasitoids were used to examine general features of food webs in different habitats: e.g., the ratio between the number of interacting species and the number of interactions, the diet breadth (or degree of specialization) of the species involved and the partitioning of the webs into individual compartments (Memlott et al. 1994, Müller et al. 1999, Rott & Godfray 2000, Lewis et al. 2002). Moreover, they were also used to assess the potential for apparent competition (Müller et al. 1999, Rott & Godfray 2000, Valladares et al. 2001, Lewis et al. 2002, Hirao & Murakami 2008), tropical insect diversity (Godfray et al. 1999), and the impact of alien species on native community structure (Schönrogge & Crawley 2000, Henneman & Memlott 2001). Later studies have increasingly concentrated on external factors effecting food web structure, such as habitat degradation (Tylianakis et al. 2007), organic versus conventional farming (Macfadyen et al. 2009), host resource quality (Bukovinszky et al. 2008) and habitat restoration (Albrecht et al. 2007, Henson et al. 2009).

HABITAT FRAGMENTATION AND SHRINKING BIODIVERSITY

So far, only few studies have investigated the effects of habitat fragmentation on food web structure (but see Valladares et al. 2006, Cagnolo et al. 2009). Such habitat modification is one of the leading threats to biodiversity worldwide (Hanski 2005). As a result of human land use, landscapes are broken into smaller pieces of remaining habitat, surrounded by a matrix of transformed environments. How different species adapt to this new landscape, or whether they are able to adapt in the first place, depends on species-specific traits (for a review, see Henle et al. 2004) such as their dispersal abilities (Roslin & Koivunen 2001, Ekroos et al. 2010), degree of specialization (Steffan-Dewenter 2003, Cagnolo et al. 2009), trophic level (Dupont & Overgaard Nielsen 2006, Helm et al. 2006, Krauss et al.

2010), population size (Fenoglio et al. 2010) and reproductive potential (Öckinger et al. 2010).

While many empirical studies have examined how species' traits affect their response to habitat fragmentation, few authors have addressed these effects at a food web level. Cagnolo et al. (2009) were among the first to take such an approach. Comparing communities of plants, leaf-miners and parasitoid wasps in multiple habitat fragments of varying size, these authors found area-related species loss to be highest among specialist parasitoids. Findings by Holzschuh et al. (2010) support these results: working on trap-nesting bees, wasps and parasitoids in agricultural landscapes, they reported that specialist parasitoids were more sensitive to intensive habitat use than were generalists. Fallow strips on field margins were found to increase habitat connectivity and thus to increase the ratio of parasitized brood cells. Together, these studies confirm the earlier finding that specialized species are more sensitive to habitat fragmentation than are generalists, and that this may be especially true at the higher trophic level. The effect of habitat fragmentation on food web structure may then depend on species-specific traits.

DIVERSITY HIDDEN IN CRYPTIC SPECIES

Correct species identification is the cornerstone of any food web study. To make valid conclusions and to derive new hypotheses concerning community structure, it is essential to gain an accurate and correct picture of the species present in the focal community. In itself, this statement may sound trivial, but has proven to be more complex and challenging than one might expect (see Bridge et al. 2003, Scott & Hallam 2003, Smith et al. 2006, Metcalf et al. 2007).

Cryptic species are species that are closely related and impossible or difficult to identify using morphological characters alone (according to Bickford et al. 2007). Recently, an increasing number of studies have described cryptic species within natural communities, sometimes in surprisingly large numbers (Smith et al. 2008, Janzen et al. 2009). Yet only a single study has exploited DNA-based molecular tools for species identification in a food web context: van Veen et al. (2003) resolved cryptic taxa among a specific species complex of parasitoid wasps, but left the rest of the parasitoid species unchecked. Even this limited application of molecular species criteria to a subcompartment of the food web changed the impression of overall food web

structure, identifying the need for more thorough assessment of a similar kind.

INDIRECT INTERACTIONS IN FOOD WEBS

As quantitative food webs have gained ground, many studies have used the interaction structure uncovered to infer a large potential for indirect interactions as a force structuring natural communities (Rott & Godfray 2000, van Veen et al. 2006, Hirao & Murakami 2008). Apparent competition is defined as indirect competition between two species, as mediated through shared natural enemies (Williamson 1957, Holt 1977). Under such a scenario, the enemies of the more common species “spill over” and thus also attack alternative, less abundant species resulting in patterns much akin to the imprints of “regular” competition (Holt 1977). Partly as a result of abundant indirect interactions uncovered in quantitative food webs, apparent competition has been predicted to be an important process structuring natural communities (e.g., Müller et al. 1999, Lewis et al. 2002, Morris et al. 2004, Nakamura & Kimura 2009, DeCesare et al. 2010). However, very few studies have experimentally tested these predictions (Morris et al. 2004, Tack et al. 2011), leaving ample scope for critical evaluation.

2. Objectives

Given the state of the art in food web studies, my contribution was aimed at adding a novel perspective: where most studies have examined only a few webs at single locations, I explored general patterns across multiple food webs at several locations. Moreover, as a methodological development, I used extensive DNA barcoding to examine the impact of cryptic species on our perception of food web structure. More specifically, I asked:

Are there cryptic species within our study system, and how will the resolution of these species change quantitative descriptors of food web structure (I)?

- How much does species richness and food web structure vary in space? Is this variation related to habitat fragmentation (II)?
- How much does species richness and food web structure vary in time (III), and what features affect such variation?
- How are patterns at the level of the overall food web structure rooted in species-specific responses to landscape composition (II, III)?

- What is the role of apparent competition in structuring local communities in space and time (III)?

3. Study system: Oaks on islands

To gain a realistic impression of how habitat fragmentation affects food web structure, it is essential to work with a system that can be thoroughly described from a spatial perspective and accurately sampled from an entomological point of view. For this reason, we chose to work on monophagous herbivores, leaf-miners (Lepidoptera: Coleophoridae, Gracillaridae, Heliozelidae, Nepticulidae, Tischeridae and Tortricidae; and Hymenoptera: Tenthredinidae) and gallwasps (Hymenoptera: Cynipidae) feeding on the pedunculate oak (*Quercus robur*, Fagaceae), the only naturally-occurring oak species in Finland (Govaerts & Frodin 1998; See Box 1 for details on the insects). This study system allowed us to establish accurate host-parasitoid interactions by rearing of hosts (*see footnote in the end of section three), and also to make direct comparisons among parasitoid guilds differing in their degree of host specialization.

The study area is located in the archipelago of south-western Finland (see Fig. 1 for an illustration of the study area). These surroundings offer an ideal setting to study the effects of fragmentation: First, the area spans from the densest oak stands in Finland (on the mainland) towards patches separated by progressively increasing distances (the archipelago). Second, this area encompasses the island of Wattkast, where intensive oak-herbivore research has continued for almost a decade (e.g., Roslin et al. 2006, Gripenberg & Roslin 2008, Tack et al. 2011). In this subarea, the locations of all 1868 oak trees have been accurately recorded (Gripenberg & Roslin 2005). By comparing patterns at two spatial scales (across different landscapes across the archipelago, and across individual trees differing in spatial connectivity within the island of Wattkast), I was then able to verify the effects of fragmentation on food web structure from two complementary perspectives.

(*Note: The food webs studied in this thesis are not food webs in the strict sense, but association webs between hosts and their natural enemies: without dissecting galls or mines it is not possible to separate primary parasitoids from hyperparasitoids, or inquiline parasitoids from the galler parasitoids.)

BOX 1. LEAF-MINERS, GALLWASPS AND THEIR NATURAL ENEMIES

This thesis is based on data on the specialist herbivores and their natural enemies of the pedunculate oak *Quercus robur* L. 1753. Among the herbivores, I focus on leaf-miners and gall wasps.

LEAF-MINERS (Lepidoptera: Coleophoridae, Gracillariidae, Heliozelidae, Nepticulidae, Tischeridae, Tortricidae; and Hymenoptera: Tenthredinidae; Panels 2, 6-11) feed on plant tissues within the leaf, protected from predators and weather conditions. The larvae of this guild usually form transparent blotches or tunnels visible on the leaf surface, with a characteristic, species- or genus-specific morphology. In this study, eleven taxa of leaf-miners were examined. One species of leaf-folder, *Ancylus mitterbacheriana* (Lepidoptera: Tortricidae) was also included. The larva of this species lives inside a leaf-fold mounted by silk.

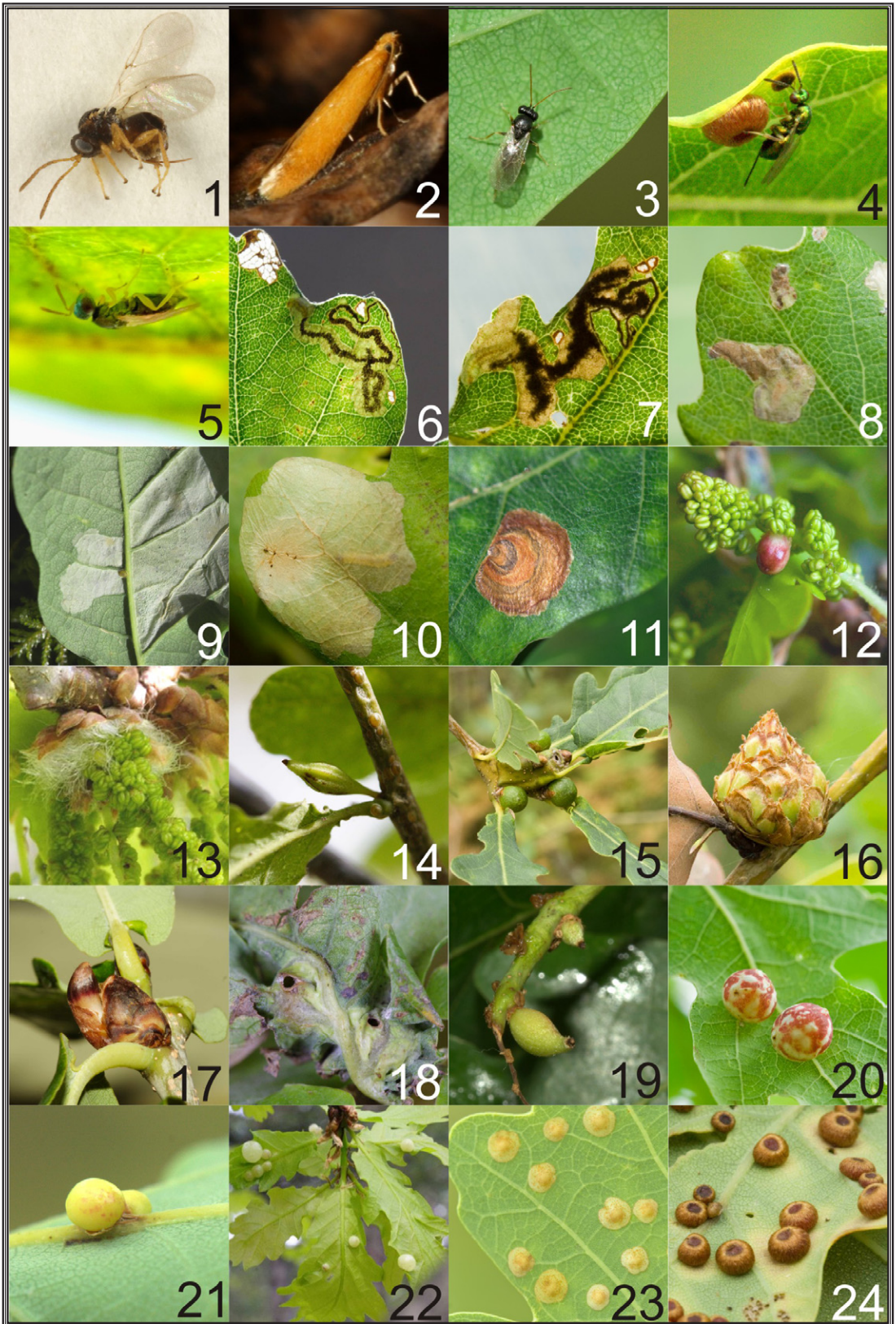
GALL WASPS (Hymenoptera: Cynipidae; Panels 1, 12-24) are a species-rich group of insects with ca. 1300 species described worldwide. Most of their species diversity is found in the northern hemisphere (Stone et al. 2002, van Noort et al. 2007). The vast majority of Cynipid species is specialized on oaks of the genus *Quercus*, but some species are encountered also on southern beech (*Nothofagus*), rose (*Rosa*), Acacia and various herbs. The majority of gall wasp species have two alternating generations, an asexual and a sexual one. These generations have substantially different gall morphologies, and are easily identified under field conditions (Askew 1984).

THE NATURAL ENEMIES (Panels 3-5) of leaf-miners and gall wasps consist of parasitoid (Hymenoptera, Ichneumonoidea, Chalcidoidea) and inquiline (Hymenoptera, Cynipidae) wasps.

The parasitoid wasps are divided in two guilds: parasitoids of gall wasps exclusively attack gall wasps on oak, whereas a significant fraction of the leaf-miner parasitoids also attack miners on host plants other than oak (Askew 1980, Hayward & Stone 2005).

Inquiline wasps are specialist parasites of gall wasps which are closely related to their host species. Currently all inquilines are classified into a single tribe Synergini (Cynipidae), but based on molecular phylogenetic data, it seems more likely that inquilinism has evolved several times from gall-inducing ancestors (Ronquist 1994, van Noort et al. 2007). Inquilines feed on gall tissue and nearly always kill the host, either directly or indirectly, by consuming the resources of the developing gall wasp larva (Ronquist 1994).

Organisms studied in this thesis: panels 1-5 adults of 1. Gall wasp (*Andricus callidoma* sexual generation female), 2. Leaf-mining moth (*Tischeria ekebladella*), 3. Inquiline wasp (*Synergus* sp.), 4. Galler parasitoid (*Torymus* sp.), 5. Leaf-miner parasitoid (Eulophidae). **Panels 6-11 leaf-miners** 6. *Stigmella* sp., 7. *Ectoedemia albifasciella*, 8. *Profenusa pygmaea*, 9. *Phyllonorycter* sp., 10. *Tischeria ekebladella*, 11. *Tischeria dodonaea*. **Panels 12-24 gall wasps** 12. *Andricus quadrilineatus* asexual generation, 13. *Andricus callidoma* sexual generation, 14. *Andricus callidoma* asexual generation, 15. *Andricus inflator* sexual generation (inflation with emergence hole) and asexual generation (pea-shaped gall), 16. *Andricus fecundatrix* asexual generation, 17. *Andricus curvator* asexual generation, 18. *Andricus curvator* sexual generation, 19. *Andricus seminationis* asexual generation, 20. *Cynips longiventris* asexual generation, 21. *Neuroterus anthracinus* asexual generation, 22. *Neuroterus quercusbaccarum* sexual generation, 23. *Neuroterus quercusbaccarum* asexual generation, 24. *Neuroterus numismalis* asexual generation. Photos by R. Kaartinen.



2006

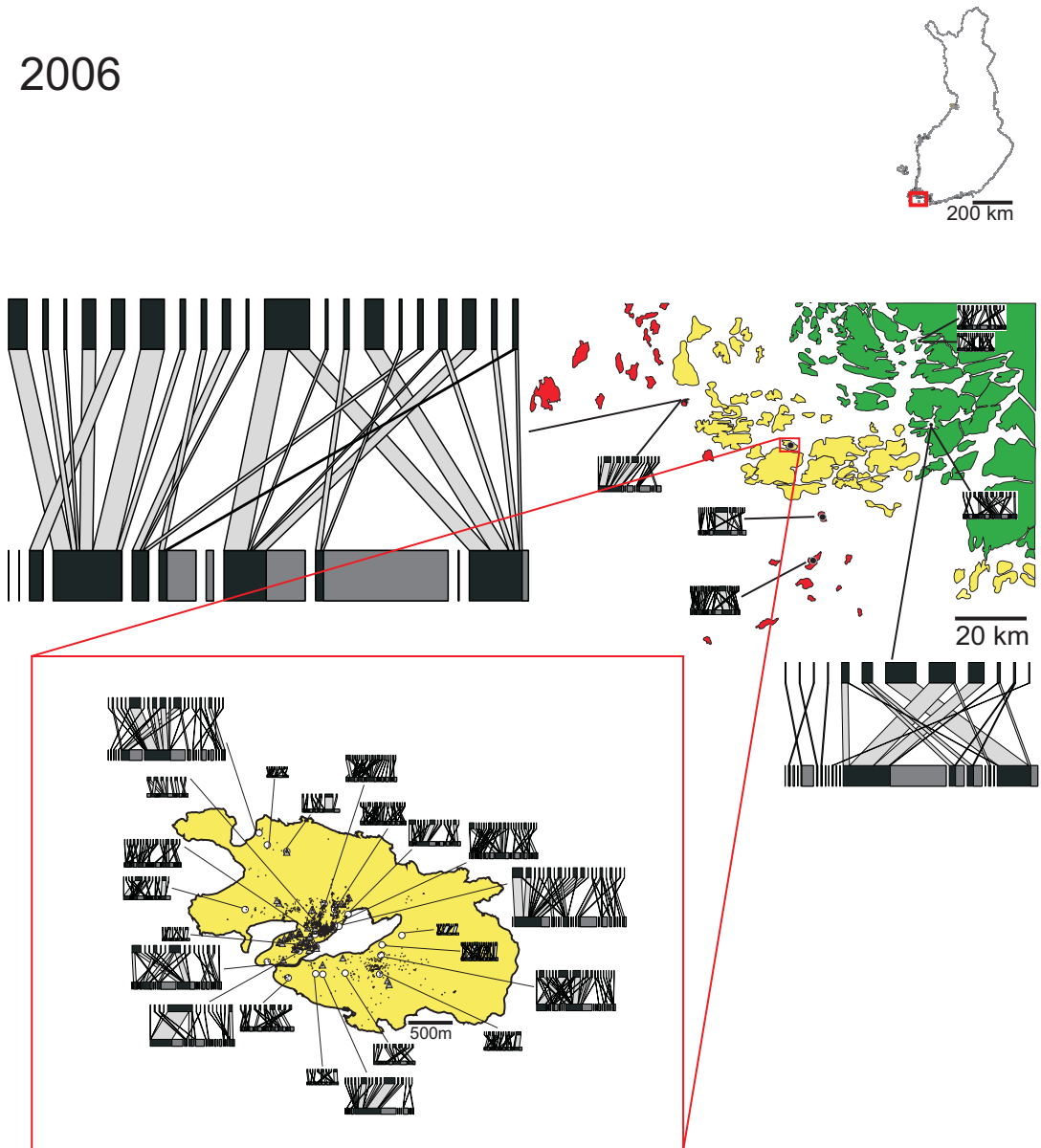
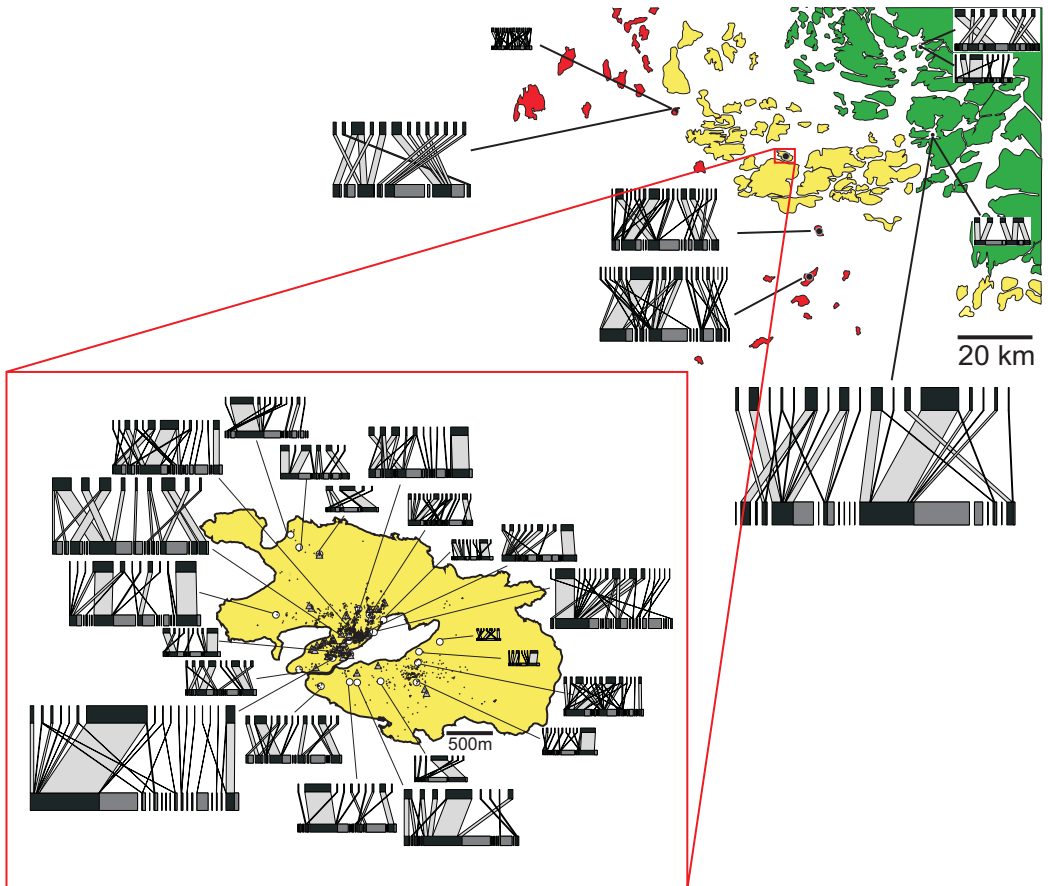


Fig. 1. Empirical materials collected for this study during 2006–2007. The sampling sites were partitioned among different “fragmentation zones”, as indicated by colours (for details, see II). Within the island of Wattkast (enlarged area) black dots show the location all of 1868 naturally-occurring oak trees, of which 22 large trees (white circles) and 52 young trees (grey triangles) were sampled. For the trees used to analyze fragmentation impacts on food web structure, we show a quantitative representation of the local food web. In a web, each bar at the lower level represents a host species and each bar at the upper level a parasitoid or inquiline species. Inside the host bars, the black part indicates parasitized host individuals and the grey part unparasitized ones. Lines between hosts and parasitoids describe trophic interactions, with the width of the line proportional to the frequency of the interaction. Host species detected at a site but not involved in trophic interactions (i.e. not yielding a single parasite) can be distinguished as blocks from which no line emanates. The width of each web has been scaled to reflect the total number of individuals recorded in the field. Note that due to technical reasons individual species are shown in a different order in different webs.

2007



4. Methods

This thesis is primarily based on two methodological developments: on molecular-based species identification (I) and on the construction of quantitative food webs for tens of sites in a spatially explicit context (II, III). While the details are given in individual chapters, I will here summarize the methodological solutions chosen and their novel aspects, to show how my thesis contributes to the methodological development of the subject field.

DNA BARCODING

To establish the identity of parasitoid species in food webs, I based my identifications of the target species not only on morphology, but also on DNA characters. By DNA barcoding the natural enemies (22 species of Chalcidoid parasitoids (Hymenoptera) and an inquiline wasp genus *Synergus* (Cynipidae)), I was able to scan morphologically distinguishable species for cryptic taxa, and to clean the web of misidentifications (see Box 2 for details for cryptic speciation and DNA barcoding). Through

this approach, I was thereby able to verify that the nodes of the web corresponded to accurately-identified, ecologically-relevant species.

REPLICATE FOOD WEBS

To understand the extent of spatial variation in food web structure, I adopted a novel approach by constructing multiple food webs in a spatially variable setting. By combining materials collected at two different scales, I was able to verify my findings from two different perspectives: At a landscape level, I was able to place each local food web in the context of its connectivity to other webs in the same habitat. At a regional scale, I compared three zones with differently-spaced oak stands. This approach is further outlined in Fig. 1.

5. Key results: Spatial and temporal variation in food web structure

The most important finding of this thesis was that the structure of local food webs remains predictable in both space and time - despite ample turnover in the specific set of species present at any given site in any given year. Individual species and feeding guilds react differently to spatial setting and differ in their temporal persistence, highlighting the role of species-specific ecological traits. Indirect interactions seemed to play a minor role in structuring local community dynamics. Finally, while DNA barcoding assigned many insects to new species, these changes caused relatively minor changes in the structure of the overall food web. Below, I will discuss each of these key findings in turn.

DNA BARCODING CHANGES THE IDENTITY OF A THIRD OF THE INDIVIDUALS

Barcoding species at the higher trophic level changed our perception of the species composition of the food webs (**I**). Overall, the species identity of over a third of the individuals changed, either due to misidentifications being corrected or cryptic species being revealed. Among the inquilines, most individuals were in fact attributed to new taxa.

The large difference in species identity between morphologically and DNA-based webs shows the high resolution offered by DNA markers, and their potential for changing our perception of what species really are. Since this study is

one of the first to use systematic barcoding as a tool for species identification of a relatively large and species-rich food web (but see Janzen et al. 2009), one can only guess at the extent of changes barcoding may bring to other systems, especially in poorly-known regions such as the tropics (Bickford et al. 2007).

...WITHOUT CHANGING THE STRUCTURE OF THE FOOD WEB

Surprisingly, the added resolution offered by barcoding did not translate into major changes in food web structure (**I**). This result was most likely due to the fact that the cryptic taxa resolved were relatively few in number (four out of 30 sequenced species) and - most importantly - to the fact that these species were relatively rare and not involved in quantitatively dominant interactions. Nonetheless, the directions of the observed changes were consistent with a priori predictions: web metrics suggested higher specialization of parasitoid species in molecularly-informed than morphologically-based webs.

FOOD WEB STRUCTURE IS CONSISTENT ACROSS SPACE

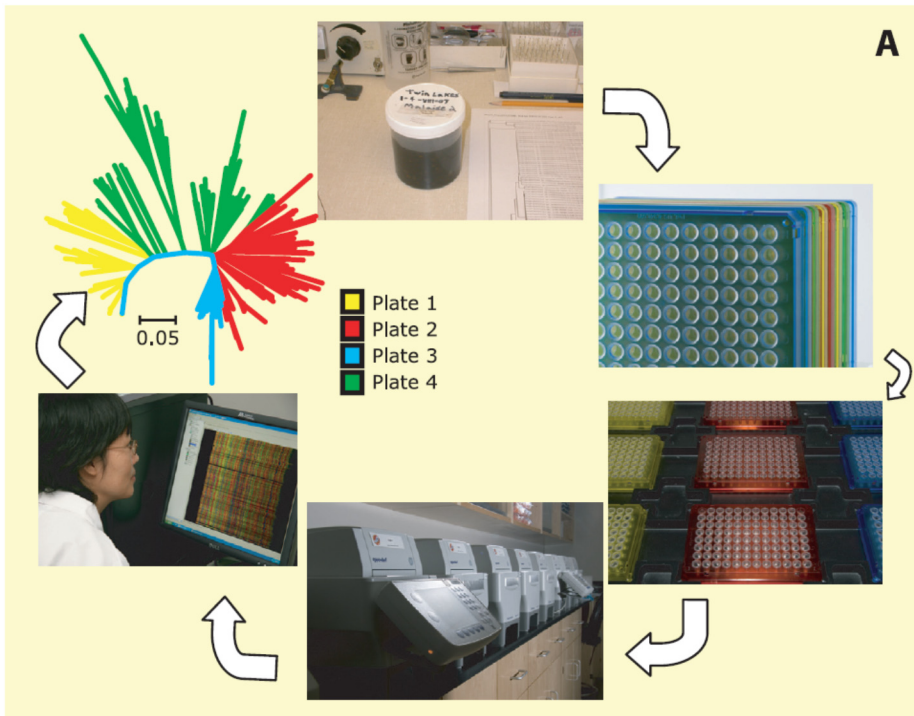
The structure of the local food webs remained surprisingly stable over the study area, both at a regional and a landscape level (**II**). Despite substantial differences in species composition among sites, measures of interaction structure were not detectably related to spatial setting (**II**). This consistency concerned both qualitative and quantitative measures.

Few previous studies have reported - or even assessed - consistency in food web structure among multiple local webs: many studies have focused on single food webs (e.g., Rott & Godfray 2000, Hirao & Murakami 2008). In one of the studies comparing multiple webs, Tylianakis et al. (2007) found a pattern exactly opposite to that uncovered in our study: Surveying a gradient of increasing habitat modification, these authors detected remarkable changes in food web structure among habitats, but not in species composition. As suggested in **II**, these discrepancies in results may relate to a general association between connectance and stability. That poorly-connected webs may remain unaltered in the face of habitat fragmentation offers hope-inspiring news to species conservation, but also comes with a caveat: if stability varies between systems, the exact impact of habitat modification may be hard to predict a priori.

BOX 2. DNA BARCODING AND CRYPTIC SPECIES DIVERSITY

DNA barcoding is based on the idea that a single, short fragment of mitochondrial DNA may be used to identify any species on the globe (Hebert et al. 2003). This is the key objective of International Barcode of Life project, or iBOL (<http://ibol.org/>). To date, the iBOL database consists of over a million specimens, and up to 75 000 barcoded species.

By barcoding, one may surpass many problems associated with morphological species identification. Theoretically, the method allows one to find the limits of phenotypic and genotypic plasticity within species, to identify all life-stages and both genders of a species, to detect cryptic species and finally, to identify small-sized species showing little morphological variation (Valentini et al. 2009). Despite the many advantages, this method does come with certain limitations. It has thus provoked some debate regarding whether it will ever be able to replace “traditional” taxonomical work (Quicke 2004, Will & Rubinoff 2004, Ebach & Holdrege 2005, Meyer & Paulay 2005, Schindler & Miller 2005). Most importantly, mitochondrial genes may not always represent independently evolving lineages, due to e.g., lineage-sorting, hybridization and introgression (Funk & Omland 2003, Hurst & Jiggins 2005, Knowles & Carstens 2007, Lohse 2009). One way to overcome possible misinterpretations is to combine the sequencing of the barcoding locus COI (located in the mitochondrial genome) with the sequencing of a nuclear gene. For specific details on the molecular methods used in this thesis, see chapter I.



The barcoding process: DNA extraction from insect specimens (top & top-right), replication of DNA by polymerase chain reaction (PCR; lower right), sequencing of the barcode region (bottom), sequence alignment and the construction of phylogenetical trees (lower left), and finally examining of phylogenies (where different taxa are shown as different colours; top left). After Smith et al. 2009 (reprint permission from John Wiley & Sons, Inc.).

...AND TIME

Consistency in food web structure concerned not only patterns in space, but also patterns in time: within individual food webs, interaction structure was highly consistent from one year to the next (**III**). This consistency included both food web structure and species richness.

A handful of other studies have also examined temporal stability in food web structure, and report patterns similar to those detected by us. Most of these studies restrict themselves to noticing that the web structure remained “unchanged”, without further examining the causes (Müller et al. 1999, Lewis et al. 2002, Albrecht et al. 2007). A notable exception is offered by Laliberté & Tylianakis (2010), who found significant spatial and temporal variability in food web structure, and looked for causes among factors such as host and parasitoid body size and abundance. They found the most variable food webs in complex habitats, presumably because it may be difficult for parasitoids to find their hosts in these habitats.

That food web structure may indeed be rather predictable, as suggested by my study, offers hope that the interaction structure within natural communities may be more stable than the composition of species per se. Nonetheless, this finding also offers cause for concern with respect to the appropriate use of quantitative metrics of food web structure as measures of community change (see below).

SPECIES RICHNESS VARIES IN SPACE

Species richness increased significantly with habitat connectivity (**II**): within the landscape of Wattkast, the total number of species, and the number of host species, was higher on less-isolated trees. This pattern concerned insect communities on both small and large trees. On the large trees, the number of parasitoid species increased with connectivity (**II**).

The relationship between species richness and landscape context is, in itself, consistent with classical patterns of both island biogeography and metapopulation theory (MacArthur & Wilson 1967, Laurence 2008). At a species-specific level, the incidence of species is predicted to be higher on better-connected patches, as a result of an increasing colonization pressure (Hanski 1999). At a community level, similar processes acting in multiple species will increase overall species diversity in well-connected communities (Hanski & Gyllenberg 1997). That such effects

are likely to be accentuated at higher trophic levels is suggested by the trophic rank hypothesis (Holt et al. 1999). Hence, the patterns detected are well-supported by general ecological theory.

SPECIES-SPECIFIC INCIDENCE VARIES ACROSS THE LANDSCAPE

Patterns in species richness across food webs reflect differences in how individual species perceive the landscape (**II**). Overall, species-specific incidence increased with tree connectivity, but finer incidence patterns varied significantly among feeding guilds: while the parasitoids of gall wasps showed the strongest response to connectivity, the incidence of many leaf-miner parasitoids seemed to be more or less independent of the surrounding landscape setting.

Idiosyncratic responses in different taxa may reflect differences in host range among parasitoid guilds: while galler parasitoids are exclusively specialized on oak-inhabiting gall wasps, many leaf-miner parasitoids are generalists which are able to attack leaf-miners on host trees other than the oak. Therefore, the parasitoids of leaf-miners may simply not perceive the landscape as equally fragmented as the gallers do.

...AND IN TIME

Despite overall consistency in food web structure (**II**, **III**), there was ample temporal turnover in species composition. From one year to the next, a mean 44% of species in the first year went extinct from a local community, while an average 31% of species in the second year had newly colonized the site (**III**). Hence, the specific members of local communities differed substantially in time, a pattern consistent with that observed in other tree-living insects (Fagan et al. 2006, Sobek et al. 2009).

...AND IS DETERMINED BY SPECIES-SPECIFIC TRAITS

Species turnover differed among feeding guilds, but there were no clear differences between trophic levels (**III**). This finding runs contrary to the trophic rank hypothesis, which posits that extinctions are more likely at higher trophic levels, since predatory species are confined to prey presence (Holt et al. 1999).

Rather than being linked to trophic rank, turnover rates seem reflective of guild-specific differences in ecological specialization: gallers and their parasitoids in our system had higher extinction probabilities than did leaf-miners

and miner parasitoids. Galls have a special morphology (hairs, thick and hard walls; see Box 1 for variable gall morphology) which calls for special adaptations among the parasitoids attacking them (Bailey et al. 2009). Also, differences within species in population sizes significantly contributed to extinction probability: the smaller the population, the higher the extinction probability (III). Here, different feeding guilds are likely to undergo different fluctuations in population size: gall wasps are characterized by particularly large variations in their population density, occasionally reaching very low local densities (Schönrogge & Crawley 2000). Overall, how ecological communities respond to the surrounding landscape may then depend on the ecological traits and population dynamics of their member species.

APPARENT COMPETITION REVISITED

While linked by high parasitoid overlap, eight species pairs examined revealed no imprints of apparent competition (III): changes in the relative population growth rate of the more abundant species affected neither the abundance nor parasitism rate of the less common species.

This observation adds a further warning against uncritical inferences from patterns in food web structure. Quantitative food webs represent snapshots of interactions between species in time and space. How these interactions translate into realized population and community dynamics may be hard to deduce from food web structure alone (Tack et al. 2011).

6. Conclusions

In this thesis, I apply novel methods to accurately identify the species present in species-rich food webs (I), and demonstrate striking consistency in the structure of local food webs across space and time (II, III). While landscape context did not affect food web structure, it created variation in the specific set of species present at any one site - a pattern reflecting differential responses in different community members (II, III). Apparent competition seemed to leave little imprint on food web dynamics (III). These are novel results, raising the question whether or not these findings may be generalized to other systems.

While our study is the first to directly examine the effect of connectivity on the structure of

local quantitative food webs (but see Valladares et al. 2006, Cagnolo et al. 2009), multiple considerations do suggest that the results may be applicable to other taxa. Most prominently, several other studies have acknowledged the importance of species abundance (Gaston 1994, Henle et al. 2004, Fenoglio et al. 2010) and other species-specific traits (Roland & Taylor 1997, Roslin & Koivunen 2001, Carvalheiro et al. 2010) in determining community traits, suggesting that the patterns detected may apply more broadly. Yet, little is known with respect to how species-specific traits transfer to predictable patterns at the ecosystem level (Tylianakis 2009). What may be the most general finding is then that responses vary with the system.

In our system, the host larvae are characterized by certain features which affect their parasitoids: the hosts are small-sized, specialist herbivores, the larvae of which live sedentarily within galls and leaf-mines. These features may create differences in community dynamics as compared to other systems:

First, sedentary, concealed larvae cannot escape parasitism, and they thus need to create “armour”. Gall wasps in particular have evolved a huge variety of defensive gall structures - e.g., scales, hairs, false larval chambers and toughness. Such structures will clearly demand specialization from their parasitoids and consequently constrain their use of alternative hosts (Bailey et al. 2009). The structure of leaf-mines is less specialized, as also reflected in a higher proportion of generalist species among their parasitoids (Askew & Shaw 1974, Askew 1980, Noyes 2001). These patterns suggest how host morphology may cause system-specific differences in the specificity of host-parasitoid interactions.

Second, small host size restricts the body size of parasitoids: a small host species can only offer adequate resources for a small parasitoid. Considerable size variation is known from parasitoids, also within species according to the specific host species or its size (Godfray 1994). Parasitoid body size in turn has been shown to affect longevity and dispersal ability, and even to affect food web attributes in terms of species turnover and temporal stability (Laliberté & Tylianakis 2010). According to this rationale, larger parasitoids are likely to search for hosts over a larger area than small parasitoids do, both because larger species are able to disperse further and live longer. Future comparisons among study systems will reveal to what extent parasitoid body size affects food web dynamics.

Finally, specialist parasitoids are more vulnerable to extinction (e.g., Henle et al. 2004), because of their population demography or interaction structure to other species (Allesina & Bodini 2004, Jonsson et al. 2006). Generalist species may be more flexible in terms of host switching. Hence, differences in host-specificity among systems may affect their relative stability in time and space.

Together, these features will likely contribute to generating particular population and community dynamics in our study system. Yet importantly, all study systems will likely show their specific quirks in species- and guild-specific ecology. The overall message is then that spatiotemporal patterns in the dynamics of a given community can only be understood on the basis of the ecology of its member species.

7. Future perspectives

In this thesis, I present the results of one of the broadest studies of quantitative food webs conducted so far. The new initiative of comparing food webs replicated in space will likely help us better understand the structure and function of natural communities (see Albrecht et al. 2007, Tylianakis et al. 2007, Henson et al. 2009, Macfadyen et al. 2009, Laliberté & Tylianakis 2010, Novotny et al. 2010). While my thesis resolves the impact of some factors on food web structure in changing landscapes, it also suggests some avenues for further research. Below, I will identify some promising directions.

First, given the rapid development of molecular tools, DNA-based species identification has the potential to transfer the whole field of food web research: by allowing the detection of cryptic species and the catching of misidentified individuals, it allows us to verify the basic structure of the food webs examined with a completely new resolution. When transferred to regions hosting large numbers of poorly known species, this technique will likely change our perception of how food webs are structured overall. Added molecular technologies, such as identifying host-parasitoid associations on the basis of host DNA from adult parasitoid gut contents (Rougerie et al. 2010) may eventually allow us to short-cut the most labour-intensive phase of food web construction, i.e. the rearing of large numbers of host insects.

Second, recent studies of quantitative food webs have increasingly concentrated on the role of certain attributes in modifying food

web structure, and on applied questions such as climate change, habitat restoration or the effect of invasive species on native ones (Heleno et al. 2008, Henson et al. 2009, Carvalheiro et al. 2010, Holzschuh et al. 2010, Memmott et al. 2010). So far lacking are large-scale studies exploring the role of food web structure on ecosystem services, such as pest control, nutrient recycling, or pollination (Fontaine et al. 2006, Slade et al. 2007, Bukovinszky et al. 2008, van Veen et al. 2008, Macfadyen et al. 2009; see Memmott 2009 for further discussion).

Third, additional metrics of food web structure will be needed to depict realized changes in natural communities. While traditional metrics of species richness have proven insufficient in detecting all changes (Tylianakis et al. 2007), our findings reveal that relying on current food web metrics alone will not detect all realized changes in community composition. As also noted by Tylianakis and colleagues (2010), most food web metrics do not take into account the specific identity of the component species or the interactions among them.

Together, these fascinating developments within the still-emerging field of food web studies have the potential to transform our understanding of how natural communities are structured and of the forces shaping them.

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