Natural and human-induced dynamics in plant–animal mutualistic networks

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TABLE OF CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

„The history of evolution and biodiversity is fundamentally a history of the evolution of species interactions. Species in pure isolation simply do not make sense.“

John N. Thompson

SPECIES INTERACTIONS FORM THE BACKBONE OF ECOLOGICAL COMMUNITIES

Species interactions play an eminent role in the organization and diversification of life (Ehrlich & Raven 1964; Dawkins & Krebs 1979), because all species require one or more coevolved interactions to survive and reproduce (Thompson 2009). Often these interactions link species so strongly that they leave a long-lasting imprint in the evolutionary history of species lineages (Thompson 2005; Gómez, Verdú & Perfectti 2010). Therefore, the pervasive impact of ecological interactions on the evolution, diversification and persistence of species is evident across the entire tree of life (e.g., Farrell 1998; Dodd, Silvertown & Chase 1999; Wilf *et al.* 2005; Grant & Grant 2006; Hu *et al.* 2008; McKenna *et al.* 2009; Ramírez *et al.* 2011; Litsios *et al.* 2012; Gómez & Verdú 2012). In addition, ecological interactions form the template for a variety of processes that are essentially linked to the functioning of ecosystems and to human welfare, such as pollination and seed dispersal or biological control (Costanza *et al.* 1997; Kremen 2005). Since species interactions are so intimately linked to the organization, functioning and integrity of ecosystems, they can be considered as the backbone of ecological communities.

Importantly, ecological interactions are not a fixed species attribute but show a considerable degree of variation (Thompson 1988). One reason for this variability in interspecific interactions is that they occur between species that are themselves distributed in populations and do not necessarily have matching geographic ranges (Thompson 2005). Moreover, the spatiotemporal variability in the abundance of interacting species causes fluctuations in the availability of interaction partners. Both the geographic co-occurrence and spatiotemporal fluctuations in the abundance of species limit the degree of exclusive reciprocal coadaptation and strongly shape the variability and dynamics that ecologists observe in interspecific interactions (Thompson 2005). These spatiotemporal dynamics are central for community assembly processes, species co-existence and the coevolutionary process (Thompson 2005; Sargent & Ackerly 2008). To date, however, the mechanisms that determine the outcomes of interspecific interactions in variable biotic contexts are poorly understood.

On top of this natural variation in interspecific interactions, human land-use has a substantial and increasing impact on the earth's biosphere, and on the persistence of species and their interactions (Vitousek *et al.* 1997; Sala *et al.* 2000; Tilman *et al.* 2001; Tylianakis *et al.* 2008). Since species are embedded in large networks of interdependencies, we can expect that the population decline or extinction of one species either directly or indirectly affects populations of other species (Koh *et al.* 2004; Dunne & Williams 2009; Säterberg, Sellman & Ebenman 2013). This is impressively illustrated by the parallel disappearance of plants and herbivorous insects in fossil records at the end of the Cretaceous (Labandeira, Johnson & Wilf 2002). This example highlights that ecological interactions not only fuel the coevolution but also the coextinction of species. Importantly, ecological interactions and associated ecological functions often collapse long before ecologists encounter the last individuals of a threatened species in the wild (Janzen 1974; Anderson *et al.* 2011; Aizen, Sabatino & Tylianakis 2012; Galetti *et al.* 2013; Säterberg *et al.* 2013). This functional extinction of species, their interactions and associated ecological processes can have cascading functional consequences on the level of ecosystems (Chapin *et al.* 2000; Hooper *et al.* 2005; Cardinale *et al.* 2006; Duffy *et al.* 2007). Along these lines, recent studies provide evidence that land-use has a pervasive impact on literally all kinds of facilitative and competitive, or mutualistic and antagonistic interactions that occur within and across trophic levels (Tylianakis *et al.* 2008). However, land-use effects on different types of species interactions also show a substantial variation in their magnitude and direction (Tylianakis *et al.* 2008). The large variability in potential outcomes highlights that two of the most important challenges are to determine how biotic context alters land-use effects on species interactions and whether land-use effects on different interaction types co-vary. Answering these questions requires community-wide approaches that explicitly incorporate the complexity of interactions in highly diversified multispecific assemblages.

Pollination and seed dispersal mutualisms are key ecological interactions

Mutualistic interactions between plants and their free-living pollinators and seed dispersers are among the most visible and diverse types of interaction that can be found in terrestrial ecosystems (Thompson 2006). Owing to their ubiquity and diversity, pollination and seed dispersal mutualisms cover a wide taxonomic range and include taxa regarded as bio-indicators, such as birds and butterflies (Lawton *et al.* 1998). But more importantly, pollinators and seed dispersers provide key ecosystem services as they contribute to critical steps in the reproductive cycle of plants (Wang & Smith 2002; Kremen 2005). About 30 to 35 % of crop production and between 60 and 90 % of wild plants depend on animal pollination for successful fruit set (Klein *et al.* 2007; Kremen *et al.* 2007; Ollerton, Winfree & Tarrant 2011; Garibaldi *et al.* 2013). Similarly, seed dispersal by frugivorous animals forms the basis for plant regeneration processes and is prevalent in many terrestrial ecosystems (Janzen 1970; Howe & Smallwood 1982; Herrera 2003; Şekercioğlu, Daily & Ehrlich 2004; Şekercioğlu 2006).

Both pollination and seed dispersal are harvest-based mutualisms, which means that animals collect a certain type of rewarding resource offered by plants (Holland & DeAngelis 2010). In many cases these resources represent food items (e.g., fruit pulp, pollen, or nectar; Bascompte & Jordano 2013). The mutualistic service provided by animals, in turn, is directly linked to their foraging and movement behaviour and involves the dispersal of pollen or seeds. Since associations between plants, pollinators and seed dispersers follow similar ecological principles and are structured in the same way, they are particularly well suited for comparative studies of plant–animal mutualistic interactions (Bascompte & Jordano 2007).

Regarding the mutual benefits of plant–animal interactions one important question remains: How can we quantify in the field what is essential to these interactions—their effect on the fitness of interacting plants and animals? This question becomes even more relevant if we aim at an integrative community-wide approach to study these mutualisms. From earlier studies on pollination and seed dispersal we know that the effect of interacting species on each other's fitness is the product of two components: their interaction frequency ('*quantity component*') and the effectiveness of their interactions ('*quality component*'; Schupp 1993; Vázquez, Morris & Jordano 2005; Schupp, Jordano & Gómez 2010). The quantity component mainly depends on the abundance of interacting plants and animals. The quality component depends on the complementarity of their phenotypic traits and on animal foraging behaviour. Importantly, variation in the abundance of species typically dwarfs interspecific differences in per-interaction effects (Vázquez *et al.* 2005). Broadly speaking, this means that frequently interacting species usually contribute the most to each other's fitness, even if the effectiveness of their interactions is low (Vázquez *et al.* 2005, 2012). Therefore, interaction frequency—measured as the rate of interspecific encounter—is a practical measure of interaction strength in community-wide studies of pollination and seed dispersal mutualisms.

Interaction networks describe community-wide patterns of interspecific interactions

Ecological communities inherit a multiplicity of species, all of which interact either directly or indirectly, and all of which show substantial spatiotemporal variation in their abundance, and in the strength and outcome of their interactions (Thompson 2005). Due to the lack of an appropriate conceptual framework, early studies usually broke up interacting communities into their basic components and studied them in isolation. These studies were rich in details about the natural history of plant–animal interactions (e.g., references in Schupp 1993; Schupp *et al.* 2010). However, owing to the diffuse and largely context-dependent character of interspecific interactions, these early studies were unable to identify the major determinants of the structure of mutualistic assemblages (Herrera 1985, 1995; Ollerton 1996; Waser *et al.* 1996; Levey & Benkman 1999). In order to identify general and recurrent phenomena in what Darwin (1859) has called an '*entangled bank*', a community-wide perspective on interspecific interactions is necessary (Jordano 1987).

The recent integration of network theory into ecological research provides a straightforward conceptual framework and the tools to study species interactions at the level of entire communities (Bascompte & Jordano 2013 and references therein). In the framework of network theory we can describe the interactions between pairs of species (e.g. plants and animals) incorporating species identity and the frequency of interactions (Jordano 1987). From recent studies that used this approach we have learned a lot about the structure of mutualistic networks. These networks are very heterogeneous, they tend to be nested (i.e., specialists mainly interact with generalists), and they are built upon weak and asymmetric interactions (i.e., strong reciprocal dependence among partners is rare; Bascompte, Jordano & Olesen 2006; Bascompte & Jordano 2007; Bastolla *et al.* 2009). Moreover, recent studies that combined network analyses with phylogenetic information and with knowledge about the natural history of plant–animal interactions identified some of the evolutionary and ecological mechanisms that shape the structure of these networks (Bascompte & Jordano 2013). Thus, species abundance, phenotypic trait-matching, spatiotemporal co-occurrence, and phylogenetic history have been identified as major determinants of network structure and of species' roles in mutualistic networks (Stang, Klinkhamer & van der Meijden 2006; Rezende *et al.* 2007; Vázquez *et al.* 2007, 2009; Olesen *et al.* 2011; Encinas-Viso, Revilla & Etienne 2012). However, field-based studies that empirically demonstrate the spatiotemporal dynamics in species interactions or the disassembly of mutualistic networks after ecological perturbation are extremely rare (Vázquez & Simberloff 2003; Carnicer, Jordano & Melian 2009; Aizen *et al.* 2012; Bascompte & Jordano 2013; Rodriguez-Cabal *et al.* 2013). In addition, no study has so far quantified the collective response of coupled mutualistic networks to ecological perturbation. Here I adopt the network perspective to study natural and human-induced dynamics in mutualistic interactions between plants and their free-living pollinators and seed dispersers.

FRUGIVORE-MEDIATED COMPETITION AND FACILITATION IN PLANT COMMUNITIES

Central to pollination and seed dispersal mutualisms is a lack of strict one-to-one relationships, because many plant species share animal mutualists and vice versa (Jordano 1987). One reason for this pattern is that animals integrate a variety of plant species into their diets to meet their nutritional requirements and to cope with spatiotemporal fluctuations in the availability of different plant species (Wheelwright & Orians 1982; Waser *et al.* 1996; Whelan *et al.* 1998). Owing to the lack of strong reciprocal specificity, both pollination and seed dispersal mutualisms are assumed to be driven by indirect animal-mediated plant–plant interactions (Carlo, Aukema & Morales 2007; Sargent & Ackerly 2008). Therefore, interactions between individual plants and their mutualistic partners are to a large extent influenced by the con- and heterospecific plant neighbourhood.

In seed dispersal mutualisms, neighbourhood effects among co-occurring and simultaneously fruiting plant species can be negative if plants compete for dispersal by shared frugivores, or positive if plants facilitate each other's dispersal through joint attraction of frugivores (Snow 1965; Thompson & Willson 1979; Wheelwright 1985; Poulin *et al.* 1999; Burns 2002, 2005). Competitive plant–plant interactions are supposed to favour the evolutionary divergence of fruit phenologies, while facilitative interactions are expected to promote their convergence (Snow 1965; MacArthur & Levins 1967; Thompson & Willson 1979). This prediction is implicitly based on the assumption that frugivore-mediated plant–plant interactions are geographically invariant. However, the abundance and co-occurrence of different plant species varies geographically. This geographic variation ultimately shapes the neighbourhood context and the phenological niche overlap among locally co-occurring plant species, and consequently their interactions with frugivores. Yet, it is poorly understood to which extent competitive and facilitative interactions among plant species with similar phenological niches are controlled by geographic variation in their abundance and co-occurrence.

CONSUMER-RESOURCE DYNAMICS AND FUNCTIONAL REDUNDANCY IN PLANT–FRUGIVORE NETWORKS

A key feature of plant–animal mutualisms is that the dietary niche of animals corresponds to their '*functional niche*' within the community (Loreau 2000; Blüthgen & Klein 2011). Consequently, the extent to which animals differ in their use of plant species determines the degree of '*functional complementarity*' or '*functional redundancy*' in services provided by animal mutualists (Blüthgen & Klein 2011). Low niche differentiation among animals is predicted to increase functional redundancy and alongside the temporal stability of ecosystem services and their resilience to ecological perturbation (Naeem & Li 1997; Naeem 1998; Loreau 2000). Importantly, the dietary niche of animals is a flexible trait which results from behavioural adaptation to resource availability (Fontaine, Collin & Dajoz 2008). Optimal-foraging theory predicts an increase in the diet breadth of animals if they compete for limited resources (MacArthur & Pianka 1966). This increase in diet breadth should reduce niche differentiation and increase functional redundancy. Conversely, a decrease in diet breadth after a decline in the abundance of animal mutualists is likely to reduce functional redundancy and the stability of ecosystem services.

The degradation of old-growth forest habitats frequently involves declines in the abundance of frugivores and among them particularly of habitat specialists that rely on habitat features typical of old-growth stands (Newbold *et al.* 2013). In contrast, effects of forest fragmentation are less predictable, because a loss of habitat specialists can be compensated by habitat generalists that are able to cross habitat boundaries (Farwig, Böhning-Gaese & Bleher 2006; Breitbach *et al.* 2010; Neuschulz, Botzat & Farwig 2011; Menke, Böhning-Gaese & Schleuning 2012; Markl *et al.* 2012). Concomitant changes in the abundance of frugivores in response to the degradation and fragmentation of continuous old-growth forests likely alter consumer-resource dynamics and the functional redundancy in seed dispersal services. To date, however, optimal-foraging has not been considered as a driving force of variation in redundancy in plant–animal mutualisms after ecological perturbation.

Ecological perturbation of coupled mutualistic networks

Interactions between pairs of species are part of complex interaction networks. Since species are typically involved in diverse types of interactions with other species, different types of these networks rarely exist in isolation but form networks of interdependent networks (Olff *et al.* 2009; Fontaine *et al.* 2011; Pocock, Evans & Memmott 2012; Rodriguez-Cabal *et al.* 2013). Until recently, different types of species interaction networks have, however, mostly been studied in isolation because of the sampling effort required and because most ecologists are specialized on taxonomic subsets of species. These artificial boundaries between different network types have prevented in-depth analyses of the collective behaviour of coupled interaction networks after perturbation. A fundamental property of interdependent networks is that a perturbation in one network can have cascading effects across networks (Buldyrev *et al.* 2010; Gao *et al.* 2012). Consequently, the effects of ecological perturbation on one type of species interaction network may be mirrored and correlated with changes in coupled networks of species interactions.

Interaction networks of plants, pollinators and seed dispersers are frequently coupled through plant species that rely on animals for dispersal of both pollen and seeds. In such coupled networks, pollinators and seed dispersers form an indirect plant-mediated mutualism (Holland & DeAngelis 2010). Both benefit each other by increasing the reproductive performance and dispersal capacity of the shared food plant. We can expect that after perturbation a population decline in one of the three parties is likely to have cascading and correlated effects on the other parties (Säterberg *et al.* 2013). Given that plants represent a critical resource for both pollinators and seed dispersers, the magnitude and direction of land-use effects on both mutualisms may be bottom-up controlled by shifts in density of plant populations in degraded or fragmented habitats. Yet, these predictions have not been tested empirically.

Aims of the thesis

In the present thesis, I focussed on three main predictions about natural and human-induced dynamics in multispecific plant–animal mutualistic interactions. First, plants share animal mutualists and vice versa. These shared interactions are an important driver of indirect animal-mediated competitive and facilitative interactions between co-occurring plant species. Thus, I expected that the spatiotemporal variation in the abundance and co-occurrence of plant species is a key determinant of the outcome of these indirect plant–plant interactions. Second, in pollination and seed dispersal mutualisms the dietary niche of animals is typically linked to the function that animals perform within the community. Therefore, I expected that altered consumer-resource dynamics after ecological perturbation have a direct effect on the functional niche of animals and on the functional redundancy in pollination or seed dispersal services. Third, different types of highly diversified plant–animal interactions form large interdependent networks. To this end, I expected that the coupling of pollination and seed dispersal mutualisms by shared plant species may increase the likelihood that ecological perturbation results in cascading and correlated effects on the interaction structure of these mutualisms. Since both mutualisms are linked to the resource use of animals, I expected that shifts in the density of plant resources in secondary habitats control the magnitude and direction of land-use effects on both mutualisms.

Study area

I conducted this study in the Białowieża Forest. This forest is located at the border between Poland and Belarus and spreads over about 1,460 km². On Polish territory the Białowieża Forest covers about 625 km². Since the 14th century the Białowieża forest had been a royal hunting ground, and thus had a special protective status until the First World War (Samojlik & Jędrzejewska 2004; Bobiec 2012). Most riverine areas of the forest had, however, been cleared during the 16th and 17th centuries for the purpose of hay production (Samojlik & Jędrzejewska 2004; Bobiec 2012). Since the First World War, over 80 % of the forest has been shaped by commercial logging (Bobiec 2002a). Within the Białowieża National Park (ca. 100 km²) an area of about 60 km² is strictly protected and an area of about 45 km² has potentially never been commercially logged (Sokolowski 2004; Bobiec 2012). The old-growth forest stands in the core of the Białowieża National Park are '*a reference point, showing how humans have changed forest composition and processes elsewhere*' (Marris 2008). Therefore, the Białowieża Forest represents an '*ongoing natural experiment*' and provides a unique setting to study how the fragmentation and conversion of continuous old-growth forest ecosystems to secondary habitats alters the structure of plant–animal mutualistic communities and associated ecosystem services.

Objectives

The aim of this thesis was to investigate natural and human-induced dynamics in mutualistic interactions between plants and their free-living pollinators and seed dispersers.

In the second chapter, I studied how geographic variation in con- and heterospecific fruiting neighbourhoods alters the phenological niche of plants and how this change in context affects plant–frugivore interactions. Specifically, I tested whether variation in the abundance and phenological niche overlap among co-occurring plants shape facilitation of and competition for seed dispersal by shared frugivores.

In the third chapter, I investigated how habitat degradation and fragmentation affect the presence of forest specialist and generalist frugivores, and how these changes in the composition of frugivore assemblages alter consumer-resource dynamics and the functional niche of frugivores. In particular, I studied whether changes in frugivore densities in response to habitat degradation and fragmentation affect the specialization of frugivores on plants and the functional redundancy in seed dispersal processes.

In the fourth chapter, I aimed at a comprehensive analysis of the effects of habitat degradation and fragmentation on coupled networks of plants, pollinators and seed dispersers. First, I compared the direction and magnitude of land-use effects on the structure of both mutualisms. Then I tested whether human-induced changes in one mutualism co-varied with changes in the other coupled mutualism, and whether this co-variation could be explained by shifts in the density of plant resources in secondary habitats.

All of the studies in the present thesis have either been published or have been submitted to scientific journals. Since the essential background information is given in all studies, the chapters 2, 3 and 4 can be read independently.

CHAPTER 2

FRUGIVORE-MEDIATED COMPETITION AND FACILITATION IN PLANT COMMUNITIES

with
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(*submitted*)

SUMMARY

Co-occurring and simultaneously fruiting plant species may either compete for dispersal by shared frugivores, or enhance each other's dispersal through joint attraction of frugivores. While competitive plant–plant interactions are expected to cause the evolutionary divergence of fruit phenologies, facilitative interactions should promote their convergence. To which extent competitive and facilitative interactions among plant species with similar phenological niches are controlled by geographic variation in their abundance and co-occurrence is poorly understood. Here we test the hypotheses that when a plant species fruits in high densities, large phenological overlap with other plant species causes competition for seed dispersers owing to frugivore satiation. Conversely, we expect large phenological overlap to enhance dispersal of a plant species fruiting in low densities through attraction of frugivores by other species in their neighbourhood. We test these predictions on plant–frugivore networks quantified on 13 study sites in the last relict of old-growth forest of the European lowland (Białowieża, Poland). A null model indicated that fruit phenologies of the regional plant assemblage were more differentiated than expected by chance. In the local networks, the tendency of plants to share frugivores increased with phenological overlap. As expected, high phenological overlap with other plant species reduced the interaction strength ('*relative importance*') and the number of partners of a plant species fruiting in high densities. Conversely, plant species fruiting in low densities mainly profited from fruiting simultaneously with other plant species. Importantly, the sharing of mutualistic partners among co-fruiting plant species was also reflected in their co-occurrence. Our study highlights that in spite of the overall signal of competition in the local plant assemblages, frugivore-mediated interactions among plants may consistently promote the establishment and persistence of rare species through facilitation. In addition, our results suggest that indirect coupling of species through shared mutualistic partners is an important determinant of plant community assembly. The coupling through shared mutualists may ultimately cause the formation of associations among co-dispersed plant species and might contribute to the coexistence of species in plant–animal mutualistic communities.

INTRODUCTION

Dispersal is one of the key factors that sustain diversity in plant communities (Janzen 1970; Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Webb & Peart 2001). Dispersal of seeds by frugivorous animals is prevalent in various terrestrial ecosystems and forms the basis for regeneration of fleshy-fruited plants (Herrera 2003). By dispersing the seeds of their food plants, frugivores essentially shape the rates of recruitment (Janzen 1970; Webb & Peart 2001), the spatial mosaic of regeneration (Jordano *et al.* 2007), the gene flow between populations (Voigt *et al.* 2009), and the colonization of habitats (Nathan & Muller-Landau 2000).

Central to all plant–frugivore associations is that co-occurring and simultaneously fruiting plant species share frugivores (Herrera 1984, 1998; Jordano 1987; Fuentes 1995; Carlo, Collazo & Groom 2003; Schupp *et al.* 2010), because frugivores show a high plasticity in their foraging behaviour and in their fruit preferences (Carnicer *et al.* 2009). Owing to this lack of strong reciprocal specificity, plant–frugivore relationships are assumed to be diffuse and driven by indirect frugivore-mediated plant–plant interactions (Herrera 1985, 1995, 1998; Carlo *et al.* 2007). Consequently, rates of fruit removal from individual plants depend on their con- and heterospecific fruiting neighbourhood (Snow 1965; Carlo *et al.* 2007; Schupp *et al.* 2010; Prasad & Sukumar 2010). While the population density of a plant species determines its conspecific fruiting neighbourhood, the heterospecific fruiting neighbourhood depends on the degree of phenological differentiation among co-occurring plant species.

Co-occurring plant species that fruit simultaneously may either compete for dispersal by shared frugivores (Snow 1965; Thompson & Willson 1979; Burns 2005), or may enhance each other's dispersal through joint attraction of frugivores (Wheelwright 1985; Poulin *et al.* 1999; Burns 2002). Competitive plant–plant interactions are supposed to favour the evolutionary divergence of fruit phenologies, while facilitative interactions are expected to promote their convergence (Snow 1965; MacArthur & Levins 1967; Thompson & Willson 1979). These selective regimes should either result in maximal differentiation or synchronization of fruit phenologies (Snow 1965; Wheelwright 1985; Poulin *et al.* 1999; Burns 2005). In addition, the differentiation of fruit phenologies may vary depending on the geographic variability in the neighbourhood context of plants. Geographic variation in the neighbourhood context emerges naturally due to variation in the abundance and co-occurrence of species (Thompson 2005). This variation in neighbourhood context likely alters the phenological niche of a plant species, which may in turn shape the competitive or facilitative character of indirect frugivore-mediated plant–plant interactions. For instance, owing to frugivore satiation, large phenological overlap with other co-occurring plant species may cause competition for seed dispersers when the density of con- and heterospecific fruits is high (Thompson & Willson 1979; Rathcke & Lacey 1985; Herrera *et al.* 1994, 1998; Hampe 2008). Conversely, plant species that fruit in low densities may profit from large phenological overlap with other co-occurring plant species that attract frugivores (Herrera 1984; Whelan *et al.* 1998; Carlo 2005; Carlo *et al.* 2007). Considering the geographic variability in the neighbourhood context (Carlo *et al.* 2007), therefore, seems essential to understand the mechanisms that drive competitive and facilitative interactions among plant species with similar phenological niches.

In a two year field study, we recorded fruit removal by frugivores from 15 fleshy-fruited plant species in 13 study sites located in the last relict of old-growth forest of the European lowland (Białowieża, Poland). We combined these interaction data with estimates of the population densities and with the fruit phenologies of the plant species on the study sites. In the first step, we used a null model to test for signals of competition or facilitation in the fruit phenologies of the plant species, i.e. whether fruit phenologies were more, or less, differentiated than expected by chance (Snow 1965; Burns 2005). In the second step, we assessed whether both the variation in the abundance and phenological overlap of plant species affected their interactions with frugivores. To do so, we applied network analyses and quantified the specialization of plants (i.e. the tendency to share mutualistic partners), their interaction strength and the number of their mutualistic partners (Bascompte *et al.* 2006; Blüthgen, Menzel & Blüthgen 2006; Blüthgen *et al.* 2008). We hypothesized that (i) high phenological overlap among plant species results in low specialization of plants on frugivores and thus in a large overlap of disperser assemblages among plant species with similar phenological niches. This in turn is a precondition for indirect frugivore-mediated competitive or facilitative plant–plant interactions (Carlo *et al.* 2007). Furthermore, we expected that (ii) high phenological overlap causes competition among plants (i.e. reduces interaction strength and number of partners) when a plant species fruits in high densities. In contrast, we expected that (iii) high phenological overlap should have facilitative effects on the interaction strength and number of partners of a plant species fruiting in low densities.

Methods

Study area

We conducted this study in the Białowieża Forest, the last primary old-growth forest of the European lowland, extending across the border between Poland and Belarus. On Polish territory the forest covers an area of about 625 km². Within the Białowieża National Park (ca. 100 km²) an area of about 60 km² is strictly protected and an area of about 45 km² has potentially never been commercially logged (Sokolowski 2004). Over 80 % of the remaining forest has been shaped by commercial logging since the First World War (Bobiec *et al.* 2000; Bobiec 2002b, 2012). Moreover, most riverine areas of the forest had been cleared during the 16th and 17th centuries for the purpose of hay production (Sokolowski 2004).

Study design

The majority of fleshy-fruited plants in the study region are primarily associated with ash-alder flood plain forests (Fraxino-Alnetum community; Matuszkiewicz 2001). Thus, we established our study sites within these flood plain forests. We used maps on the distribution of ash-alder forests for the selection of study sites (Falinski 1994) and verified the suitability in the field. In 2011 and 2012, we established a total of 17 study sites that were scattered over about 400 km² covering two-thirds of the Polish part of the Białowieża Forest. These study sites were situated in old-growth and logged forest stands and covered various landscape contexts from forest interior to forest edges to forest fragments. The pair-wise distance between study sites ranged from 1.4 to 23 km (11 ± 5.8 km, mean ± SD).

Frugivore observations

From July to October in 2011 and 2012, we weekly monitored fruit ripening of the plant species on the study sites. According to the availability of fruiting individuals, we selected three ($n = 93$), two ($n = 27$) or one individual ($n = 31$) per species for the frugivore observations on each study site per year. We observed each plant species on each study site and year three times for 6 h starting at sunrise (18 h × plant species^{-1} × study site^{-1} × year^{-1}). Observation sessions were spread over the entire phenological periods of the plant species. We observed plant–frugivore interactions with binoculars from camouflaged tents simultaneously on different study sites (7 observers in 2011 and 14 observers in 2012). We recorded all frugivore species visiting the individual plants, as well as the number of frugivore individuals, duration of visits and their fruit-handling behaviour (for details see Albrecht *et al.* 2013). In total, we accumulated 2,718 h of seed disperser observations (774 h in 2011 and 1,944 h in 2012), distributed over 158 days (67 days in 2011 and 91 days in 2012). After each sampling session, we counted the fruits of the observed plant individuals. For trees, we counted the fruits on representative parts of the tree crown and then extrapolated over the whole tree crown. For the analysis, we selected data from a subset of 13 study sites on which we carried out censuses of plant population densities (see below). This subset of the data includes 2,304 h of seed disperser observations.

CENSUS OF PLANT POPULATIONS

We quantified plant population densities on 13 of the 17 study sites. To estimate plant population densities we established 20 alternating squares of 20 × 20 m size on ten study sites and, owing to logistical constraints, ten squares on three study sites. Thus, we sampled plant densities on an area of 0.8 ha on 10 sites and on an area of 0.4 ha on 3 sites, respectively. Each square was divided into four transects, each of 5 m width, in which we counted the number of individuals of each plant species. For the analyses we used the mean density per species per square as an estimate of the population density of each species on each study site (Fig. 2.1a; also see Vázquez & Simberloff 2004).

COMPILATION OF FRUIT PHENOLOGIES

We used the data on the crop size of the plant species from the frugivore observations (see above) to obtain estimates of the mean crop size of each plant species in the course of the fruiting season in each of the two study years. Similar to other studies (e.g., Burns 2005), we defined fruit phenologies as temporal changes in the availability of fruits to frugivores. During the frugivore observations we conducted on average 30 fruit censuses for each plant species. These censuses were carried out on several study sites per day at approximately 2-day intervals in both years (1.5 ± 1.4 days; mean ± SD; range: 1–8). Based on these data we constructed a matrix with I rows representing the plant species and J columns representing time intervals of equal length (here weeks), in which each cell a_{ij} gave the mean individual fruit crop of plant species i in week j. We then standardized the phenology of each species to range between 0 and 1, by dividing the fruit crop of plant species i in each week j by the maximum fruit crop of the respective species during the fruiting period (Fig. 2.1b). To achieve a high resolution of the fruit phenologies we combined the data from both years in a comprehensive phenology (Fig. 2.1b). Although this might introduce some additional uncertainty into our analyses, it should be of minor importance because the between-year variation in the timing of fruit production was low and did not vary in a consistent way across species (average difference of 5 ± 13 days in mean fruiting dates between years). However, we considered the between-year variability in absolute crop production of the plant species in our data analyses (see below).

TEST FOR COMMUNITY-WIDE PHENOLOGICAL DIFFERENTIATION

In the next step, we used this comprehensive set of fruit phenologies to test for community-wide phenological differentiation in the fruit phenologies of the regional plant assemblage. The phenology of each plant species can be split into the average fruiting time and the length of the fruiting period (Burns 2005). We calculated average fruiting times as the average week of fruit production, weighted by the relative number of fruits produced in each week. The length of the fruiting periods was defined as one weighted standard deviation σ^2 around the average fruiting time (Burns 2005).

We used a null model to test for signals of competition or facilitation in the distribution of fruit phenologies in the regional plant assemblage (MacArthur & Levins 1967; Burns 2005). Higher differentiation of fruit phenologies than expected by chance would signal competition for frugivores, whereas lower differentiation than expected by chance would indicate facilitative plant–plant interactions. First, we arranged plant species throughout the fruiting season according to their average fruiting times (Fig. 2.1). According to Burns (2005) we calculated the difference between average fruiting times, $D = \bar{x}_{i+1} - \bar{x}_i$, of two species i and i + 1 adjacent in the fruiting sequence divided by the sum of their fruiting periods, $H = \sigma^2\left(\bar{x}_{i+1}\right) + \sigma^2\left(\bar{x}_i\right)$, to quantify their phenological differentiation D/H (MacArthur & Levins 1967; Burns 2005). We calculated the index D/H for all adjacent species pairs in the temporal sequence, and used the variance of these values to quantify the community-level differentiation of fruit phenologies (Burns 2005).

To determine whether the fruit phenologies are more differentiated than expected by chance, we compared the observed variance in the index D/H to expected variance values generated in Monte Carlo simulations. Following Burns (2005) we started simulations by choosing 13 random numbers from within the observed range of average fruiting times. To reduce type I error rates we preserved the length of the original phenology by keeping the positions of the fruiting periods of the first and of the last species fixed (Burns 2005). The fruiting periods of the 13 remaining species were then assigned to the random numbers according to the observed species sequence. Then the index D/H was calculated for all adjacent species pairs and the variance in these values was calculated. The procedure was iterated 10,000 times. The fraction of iterations generating variance values less than the observed value was multiplied by two to obtain two-tailed type I error rates (i.e., *P*-values).

Local fruit densities and phenological differentiation

The main prediction of our study was that between-population variability of conspecific and heterospecific neighbourhood densities determines the effect of phenological differentiation on plant–frugivore interactions. To capture this variability we quantified the conspecific fruit density of a plant species in the local plant assemblages (Fig. 2.1c), as well as its phenological differentiation from other plant species in the local assemblages (Fig. 2.1d).

To quantify the fruit density of plant species *i* on each study site (mean density of fruits per hectare on each study site in each year), we multiplied the number of individuals of plant species *i* on the study sites by the mean crop size of the respective plant species in a given year (Fig. 2.1a,c). Therefore, the fruit densities of a plant species could vary between both study years depending on the average fruit crop of a species in a given year. Thus, we assume that all plant individuals in a population produced fruits in a given year. Although this approach may overestimate the total fruit density within populations, our conclusions should not be affected, since this bias should be consistent across plant species.

To quantify the phenological differentiation of the plant species in the local plant assemblages, we constructed local '*realized*' phenologies of the plants based on the regional set of fruit phenologies (Fig. 2.1b,d; see Supplementary Methods 2.1 in Appendix). For each study site in each year, we created a subset of phenologies for those plant species that produced fruits on the respective study site in the respective year. The regional set of fruit phenologies was based on the standardized fruiting intensities of each plant species (see above; range: 0–1). Thus, we multiplied these standardized phenologies with the mean fruit density of each plant species on a given study site in the respective study year to get an estimate of the mean fruit density a_{ij} for each plant species *i* in each week *j* and on each study site in each year.

To quantify the phenological differentiation of plant species *i* in the local plant communities we used the Kullback-Leibler divergence d_i as a measure of relative entropy in its standardized form (Blüthgen *et al.* 2006). This index was originally suggested by Blüthgen *et al.* (2006) to measure the specialization of species, in the sense of '*niche differentiation*', in ecological interaction networks. Here we adopted this index to quantify the niche differentiation of a plant species in the phenological context (for more details see Supplementary Methods 2.2 in Appendix). If p'_{ij} is the proportion of the number of fruits (a_{ij}) of plant species *i* in time interval *j* in relation to the respective row total (A_i), then $p'_{ij} = a_{ij}/A_i$ and $\sum_{j=1}^{J} p'_{ij} = 1$. Furthermore, if q_j is the proportion of all fruits in time interval *j* in relation to the total number of fruits in the local plant assemblage across the entire season (*m*, i.e., the matrix total), then $q_j = A_j/m$ and $\sum_{j=1}^{J} q_j = 1$. The Kullback-Leibler divergence for plant species *i* is then denoted as:

$$d_i = \sum_{j=1}^{J} p'_{ij} \ln\left(\frac{p'_{ij}}{q_j}\right) \qquad \text{eqn. 2.1}$$

In the phenological context the Kullback-Leibler divergence thus compares the temporal distribution of the fruits of plant species *i* (p'_{ij}) in the course of the fruiting season relative to the overall fruit availability in the whole plant assemblage (q_j) in each time interval *j*. The standardized form d'_i ranges from 0 for a plant species that produces fruits in synchrony with other species (i.e., high phenological overlap) to 1 for a plant species that produces fruits when no other plant species produce fruits (i.e., high phenological differentiation, similar to species level specialization; Blüthgen *et al.* 2006). Thus, d'_i quantifies the deviation of the actual temporal distribution of fruits of plant species *i* from a null model which assumes that the fruits are distributed in proportion to the overall fruit availability in the local plant assemblage (*sensu* Blüthgen *et al.* 2006), that is, without phenological differentiation among the plant species.

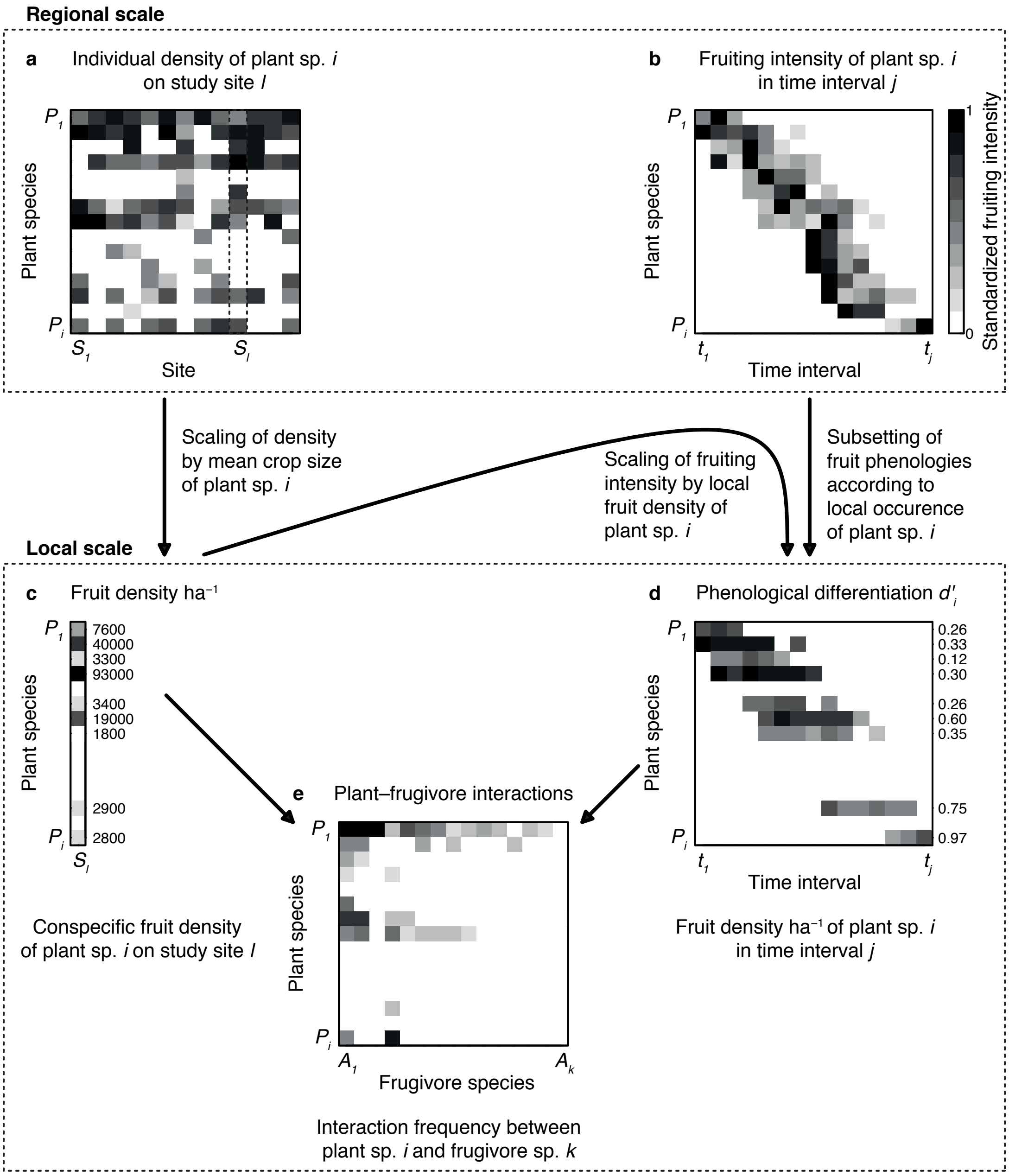

Figure 2.1. An approach to quantify how conspecific fruit densities and phenological differentiation of plant species generate observed interaction patterns in local plant–frugivore networks. (**a**) Plant densities of the regional plant assemblage on the study sites. (**b**) Comprehensive set of fruit phenologies incorporating the temporal distribution of fruiting intensities of the regional plant assemblage. (**c**) Conspecific fruit densities of each plant species in a local plant assemblage. (**d**) Realized phenology of the co-occurring plant species in a local plant assemblage. (**e**) Interactions between the local plant assemblage and the local frugivore assemblage.

Network analyses

For each study site, we constructed a quantitative interaction matrix based on the frequency of interactions between plants and frugivores (Fig. 2.1e). Across the 13 study sites and both years we quantified a total of 20 interaction matrices. In contrast to previous network studies (Schleuning *et al.* 2011; Menke *et al.* 2012; Albrecht *et al.* 2013), here we defined the interaction frequency as the number of fruits that frugivores removed from a plant species. Thus, our estimates of interaction frequency reflect the quantity component of seed dispersal (Schupp *et al.* 2010). To do so we estimated the mean number of fruits that frugivore species *k* removed from plant species *i* per visit based on the frugivore

Table 2.1. Summary of linear mixed effects models. Shown are the effects of conspecific fruit densities [fruits ha^{-1}], phenological differentiation [d'_{phen}], and their interaction on (**a**) the specialization of the plants on frugivores [d'_{web}], on (**b**) the interaction strength of the plants, and on (**c**) the number of frugivore species visiting plants.

Source of variance	Estimate	SE	*z*-value	*P*-value
(**a**) *Response: Plant specialization*				
Conspecific fruit density	−0.0082	0.021	−0.385	0.70
Phenological differentiation	**0.060**	**0.021**	**2.93**	**0.0034**
Conspecific fruit density × Phenological differentiation	−0.0045	0.020	−0.226	0.82
(**b**) *Response: Interaction strength*				
Conspecific fruit density	**0.53**	**0.15**	**3.47**	**0.00052**
Phenological differentiation	−0.13	0.15	−0.831	0.41
Conspecific fruit density × Phenological differentiation	**0.29**	**0.13**	**2.13**	**0.033**
(**c**) *Response: Number of frugivore species*				
Conspecific fruit density	**0.13**	**0.063**	**2.12**	**0.034**
Phenological differentiation	0.021	0.060	0.356	0.72
Conspecific fruit density × Phenological differentiation	**0.11**	**0.053**	**2.12**	**0.034**

Notes: Given are parameter estimates and corresponding standard errors (SE). Significant effects at a level of $P < 0.05$ are highlighted in boldface type.

observations (Farwig *et al.* 2006; Albrecht, Neuschulz & Farwig 2012). We then multiplied the number of visits of frugivore species *k* on plant species *i* by the mean number of fruits that frugivore species *k* removed from the plant species *i* per visit. The total interaction frequency of a frugivore species was defined as the number of fruits removed from all plant species within a network, whereas the interaction frequency from the plants' perspective was defined as the total number of fruits removed from a plant species. The standardized sampling effort per plant species across the study sites allowed us to draw specific conclusions from the plants' perspective in terms of fruit removal rates and potential consequences for seed dispersal.

To test our hypotheses we used a combination of three measures: (i) the specialization of the plant species, (ii) their interaction strength, and (iii) the number of their partners. In analogy to phenological differentiation above, we calculated the standardized Kullback-Leibler divergence (d'_i) for each plant species *i* to quantify the degree of complementary specialization among plants in the networks (Blüthgen *et al.* 2006). In the context of interaction networks, a value of 0 indicates highest possible generalization and 1 indicates highest possible specialization of plants on frugivores. Therefore, d' quantifies the tendency of plants to share frugivores with other plants, that is, the degree of '*niche exclusiveness*' in mutualistic interactions (Blüthgen 2010).

To determine the '*relative importance*' of a plant species in the networks, we used the interaction strength of plants (Bascompte *et al.* 2006; Vázquez *et al.* 2007), a measure of the ecological impact of a species. Interaction strength differs conceptually from the niche property d' because it directly reflects the interaction counts (Blüthgen 2010). We defined the interaction strength of a plant species in a given network as the interaction frequency of plant species *i* divided by the total number of interactions in the network (i.e., the proportion of interactions that plant species *i* has in the network). Finally, the number of partners was simply given by the number of frugivore species that visited plant species *i* (i.e., plant degree; Bascompte *et al.* 2006).

Statistical analyses

We used linear mixed-effects models to analyze the variation in the specialization of plants on frugivores, the interaction strength of plants, and the number of frugivore species. In these analyses, we treated conspecific fruit density, phenological differentiation and their interaction as fixed continuous predictors. Conspecific fruit density and phenological differentiation were only weakly correlated ($r = 0.17$), which suggested no collinearity between these predictors. As not all plant species occurred on every study site and in each study year (i.e., site, year and plant species were not full factorial), we fitted site (13 sites), year (2 years) and plant species (15 plant species) as separate random grouping factors. The model for plant specialization was fitted with a Gaussian error distribution and an identity link function. For the interaction strength of plants we fitted a model with binomial error distribution and a logit link function. In this model we analyzed the interaction strength (response variable) as the interaction frequency A_i of plant species *i* versus the summed interaction frequency of the remaining plant species in a network ($m - A_i$). Since the residuals of this model were overdispersed ($\chi^2 = 9652.09$, ratio = 79.77, $df = 121$, $P < 0.001$), we fitted an additional observation-level random effect to account for this extra variation (Hinde 1982; Williams 1982; Breslow 1984; Bates *et al.* 2013). The number of partners of plants represented a count variable, but was not strongly skewed. Thus, we fitted a model with poisson error distribution and a square-root link function for the number of partners. We found no overdispersion in the residuals of this model ($\chi^2 = 76.1$, ratio = 0.62, $df = 121$, $P = 0.99$). We standardized the predictor variables to zero mean and unit variance to allow for a comparison of effect sizes. We used the estimates of the three models to predict under which conditions the plant species in a local assemblage tended to compete for frugivores or tended to enhance each other's interactions with frugivores. All statistical analyses were performed in *R* (R Development Core Team 2013) using the package *lme4* for mixed model analyses (Bates *et al.* 2013), and the package *bipartite* for calculation of species level specialization *d'* (Dormann *et al.* 2009).

RESULTS

The null model analysis indicated that the fruit phenologies in the regional plant assemblage were more differentiated than expected by chance, suggesting competition for frugivores ($P < 0.01$; Fig. 2.1b). Overall, the 20 analyzed plant–frugivore networks describe a total of 5,748 visits of 33 frugivore species (29 bird and 4 mammal species) on the 15 plant species. During these visits the frugivores removed an estimated number of 15,766 fruits from the focal plants. The fruit density of the plant species in the local networks had no effect on the specialization of plants on frugivores (Table 2.1). However, as expected, those plant species with a high phenological overlap shared most of their frugivores with other plant species, whereas frugivore assemblages became more exclusive as phenological differentiation increased (Table 2.1; Fig. 2.2a).

Conspecific fruit densities and phenological differentiation interactively determined the interaction strength of a plant species in the local networks and the number of attracted frugivore species (Table 2.1; Fig. 2.2b,c). Those plant species that fruited in high densities had the highest interaction strength and attracted the

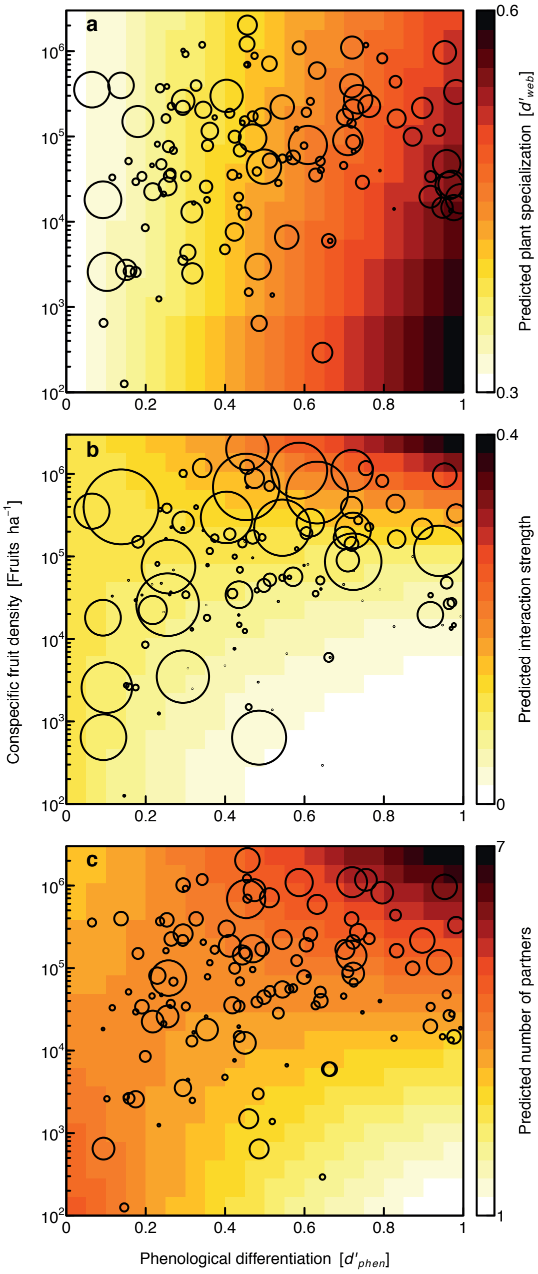

Figure 2.2. Predicted effects of phenological differentiation and conspecific fruit densities on plant–frugivore interactions. Effects of phenological differentiation [d'_{phen}] and conspecific fruit densities [fruits ha^{-1}] on (**a**) the specialization of plants on frugivores [d'_{web}], on (**b**) the interaction strength of plants, and on (**c**) the number of frugivore species visiting plants. The circles depict the position of the raw data ($n = 128$) in relation to the two explanatory variables and the area of the circles corresponds to the raw value of the respective response variables. The trend surfaces show the model predicted effects of conspecific fruit densities and phenological differentiation on the three interaction characteristics of the plants.

largest number of frugivore species when no other plant species produced fruits (i.e., when their phenological differentiation was high; Fig. 2.2b,c). However, the interaction strength and the number of frugivore species decreased as soon as these species fruited in synchrony with other species. In contrast, plant species fruiting in low densities had the highest interaction strength and attracted a larger number of frugivore species when they fruited simultaneously with other species (Fig. 2.2b,c). Interestingly, the models predicted that these locally rare species (with a conspecific fruit density of 100 to 1,000 fruits per hectare) were unlikely to attract any frugivores at times when no other plant species produce fruits (Fig. 2.2b,c).

Discussion

We found evidence that overall, fruit phenologies in the regional plant assemblage were more differentiated than expected by chance. At the local scale, low phenological differentiation among plant species involved a large overlap of frugivore assemblages, which indicates a high potential for frugivore-mediated competition among co-occurring plant species. In accordance with this, the interactions of abundant plants were enhanced when no other plant species fruited at the same time. In contrast, however, interactions of rare plants were enhanced when they fruited simultaneously with other plant species.

Phenological differentiation and plant specialization on frugivores

The temporal differentiation of fruit phenologies is thought to be a consequence of competition for frugivores between plants (Snow 1965; Thompson & Willson 1979). The null model analysis indicated that fruit phenologies were significantly more differentiated than expected by chance, which suggests that phenological patterns of fruit production in the studied plant assemblage are likely to be a result of competition for frugivores. These results contrast with earlier studies that reported random patterns of fruit production (Wheelwright 1985; Smith-Ramírez, Armesto & Figueroa 1998; Burns 2005), and add to those studies that reported non-random patterns in fruit production (Poulin *et al.* 1999; Thies & Kalko 2004).

The sharing of frugivores is a prerequisite for frugivore-mediated competition or facilitation between locally co-occurring plant populations (Snow 1965; Carlo & Aukema 2005). In fact, we found that plant species whose fruit phenologies overlapped were indirectly coupled through shared frugivores. The overlap of frugivore assemblages among co-occurring and simultaneously fruiting plant species is in line with theoretical expectations (Vázquez *et al.* 2009), and can be attributed to the low degree of reciprocal specialization in plant–frugivore associations (Jordano 1987; Fuentes 1995). In the majority of the local plant–frugivore assemblages co-fruiting plant species were coupled through the most generalized frugivore species (i.e., *Sylvia atricapilla*, *Turdus merula* and *Erithacus rubecula*; Albrecht *et al.* 2013). In temperate regions, these highly generalized frugivores are likely to be the main drivers of indirect frugivore-mediated interactions between co-occurring and co-fruiting plant species.

Effects of conspecific fruit densities and phenological differentiation on plant–frugivore interactions

Our results showed that the interaction strength of a plant species as well as the number of its frugivore partners depended on both its conspecific fruit density and on the degree of phenological differentiation from other fruiting species. Plant species that occurred in high fruit densities had a low interaction strength and low numbers of frugivore species when their phenology overlapped with other fruiting species. Thus, our results suggest that highly abundant co-fruiting plant species are likely to compete for frugivores. Conversely, the positive effects of phenological overlap on the interaction strength and number of partners of plant species occurring in low densities indicate facilitative neighbourhood effects on interactions of these rare species.

The negative effects of high phenological overlap among plant species fruiting in high conspecific densities may be explained by frugivore satiation (Herrera *et al.* 1994; Hampe 2008). Frugivore satiation has already been suggested as a main driver of mast fruiting strategies in animal-dispersed plant species, because mast-fruiting should minimize seed loss due to predation by specialized seed eaters (Herrera *et al.* 1998). At the same time, high conspecific fruit densities may reduce fruit removal by legitimate seed dispersers through a dispersion of frugivores into the local fruiting neighbourhood. This would limit the availability of frugivores to individual plants (Thompson & Willson 1979).

The high interaction strength of plant species fruiting in high densities but lacking heterospecific co-fruiting neighbours may be partially explained by the spatial distribution of fleshy-fruited plants in the Białowieża forest. In this region fleshy-fruited plants are mainly associated with ash-alder floodplain forests, which show a patchy distribution in the landscape since they require special edaphic conditions (Falinski 1994). Thus, fruit resources are highly aggregated, and monospecific fruit patches of high density may act as foci for frugivores (Carlo & Morales 2008). Previous studies could show that frugivores track the availability of fruit resources over large spatial and temporal scales (e.g., Tellería, Ramirez & Pérez-Tris 2008). The high interaction strength of plant species fruiting in high densities may thus increase with phenological differentiation (Fig. 2.2b,c), because frugivores are likely to concentrate on these plant species as soon as other species in the local fruiting neighbourhood become scarce (Prasad & Sukumar 2010).

The most captivating aspect of our study is the prediction that, despite the overall signal of competition among the dominant species in the local plant assemblages, plant species that fruit in low conspecific densities may actually benefit from their co-fruiting heterospecific neighbours. This is also supported by similar patterns in the absolute rates of fruit removal from plants (Supplementary Methods 2.3 in Appendix). These results lend support to the hypothesis that an attractive fruiting neighbourhood may facilitate the dispersal of less attractive plant species (Carlo *et al.* 2007 and references therein). Importantly, species that occur in low densities are likely to be dispersal-limited (Carlo *et al.* 2007). Thus, our results suggest that the low dispersal capacity of rare plants is enhanced by the local presence of other plant species that attract frugivores.

Potential consequences for network structure and seed dispersal

We found contrasting effects of phenological differentiation on rare and abundant plant species. Large phenological overlap resulted in competitive plant–plant interactions in plant species that fruited in high densities, but resulted in facilitative interactions in species that fruited in low densities. These results have important implications for the structure of plant–animal mutualistic networks and for frugivore-mediated seed dispersal. A commonly observed pattern in mutualistic networks is that specialists mainly tend to interact with generalists (Bastolla *et al.* 2009). This nested structure is supposed to reduce interspecific competition and to enhance the number of coexisting species (Bascompte *et al.* 2006; Bastolla *et al.* 2009; but see James, Pitchford & Plank 2012). Importantly, simulations predict that a nested network emerges naturally, if new species enter a community where they have minimal competitive load (Bastolla *et al.* 2009; Encinas-Viso *et al.* 2012). Similarly, Olesen *et al.* (2008) found for arctic plant–pollinator networks that plant species entering the community as the season progresses tend to interact with the most connected pollinator species. Our study adds to these findings, because our results suggest that phenological coupling of plant species may facilitate the establishment and persistence of rare species. This may also explain why rare animal-dispersed plant species preferentially co-occur with widespread species (Lázaro, Mark & Olesen 2005). Literally speaking, rare species may be '*passengers*' that profit from the presence of abundant species which drive the movement of frugivores through the landscape (*sensu* drivers and passengers; Peterson, Allen & Holling 1998; Carlo *et al.* 2007).

The fruiting neighbourhood may not only affect the seed dispersal quantity of rare plant species, but also the directionality of seed dispersal (Carlo *et al.* 2007; Schupp *et al.* 2010). First, an increase in absolute fruit removal is likely to enhance the quantity of seed dispersal and recruitment, if frugivores move seeds to suitable microhabitats. Second, a diverse frugivore assemblage may increase the quality of dispersal, if frugivores differ in their movement behaviour or in their use of microhabitats (Carlo 2005; Carlo & Aukema 2005; Morales & Carlo 2006; Jordano *et al.* 2007). Third, the co-dispersal of different plant species that fruit simultaneously is likely to result in directional seed dispersal patterns between co-fruiting plant species, and might contribute to the formation of species associations (Wenny 2001; Clark *et al.* 2004; Carlo & Aukema 2005). Thus, our results imply that the co-occurrence of plant species across populations may be correlated with the similarity of the phenological niche of the plant species, which is supported by our data (Procrustes analysis: $r = 0.71$, $P < 0.05$; Supplementary Methods 2.4 in Appendix).

Limitations

In the present study, the local plant–frugivore networks provide a summary of several snapshots of frugivore activity across the phenological period of the plant species. Likewise, we simplified the between-population variability in the temporal distribution of fruit production of plants. We acknowledge that this approach disregards the variability that may be observed within a plant species during the course of its fruiting season (Carlo *et al.* 2007). Future studies will certainly profit from an explicit consideration of this temporal variation (Carlo *et al.* 2007; Carnicer *et al.* 2009; Morales *et al.* 2013). However, using relatively simple models, we were able to confirm the predictions of our study, and we are confident that our approach provides valuable insights into the effects of variation in neighbourhood context on indirect frugivore-mediated plant–plant interactions.

Conclusions

Our study highlights that phenological differentiation has contrasting effects on interactions between rare and abundant plants and their frugivores, and that the density of fruit resources mediates these effects. High phenological overlap had negative effects on interactions between frugivores and plants fruiting in high densities, but enhanced the interactions of rare plants. These results suggest that indirect interactions among plants that share seed dispersers may consistently promote the establishment and persistence of rare species through facilitation. Importantly, the sharing of mutualistic partners among co-fruiting plant species was also reflected in their co-occurrence. This suggests that indirect coupling of species through shared mutualistic partners is an important determinant of plant community assembly processes. The indirect coupling through shared mutualists may drive the formation of associations among co-dispersed plant species and might contribute to species coexistence in plant–animal mutualistic communities.

CHAPTER 3

CONSUMER-RESOURCE DYNAMICS AND FUNCTIONAL REDUNDANCY IN PLANT–FRUGIVORE NETWORKS

with
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SUMMARY

Seed dispersal by frugivores is the basis for regeneration of fleshy-fruited plants in forest ecosystems. Previous studies have reported a decrease of forest specialist frugivores due to logging and forest edges. Forest generalists appear less sensitive and may even increase at forest edges. Such changes in the abundance of frugivores may have consequences for consumer/resource ratios and competition in plant–frugivore networks. Optimal-foraging theory predicts an increase in dietary specialization of animals at low consumer/resource ratios due to reduced competition. A decrease of forest specialists in logged forests should cause decreased consumer/resource ratios, increased dietary specialization and reduced redundancy, whereas an increased abundance of forest generalists at edges may compensate for a loss of specialists. In Europe's last old-growth lowland forest (Białowieża, Eastern Poland) we recorded fruit removal by frugivores from fleshy-fruited plant species in the interior and at edges of logged and old-growth forests for two consecutive years. The abundance of forest generalists increased at forest edges whereas specialists were unaffected. Conversely, logging resulted in a decrease in abundance of forest specialists but had no effect on the abundance of generalists. Accordingly, consumer/resource ratios increased from interior to edges and were reduced in the interior of logged forests compared to the interior of old-growth forests. As predicted by optimal-foraging theory, a decrease in consumer/resource ratios coincided with increased dietary specialization, and a loss of redundancy in the interior of logged forests. Despite low dietary specialization redundancy was reduced at forest edges as forest generalists dominated plant–frugivore interactions. These results show that a shift in frugivore assemblages at forest edges and increased dietary specialization of frugivores in the interior of logged forests involved a loss of redundancy compared with continuous old-growth forests. This suggests that seed dispersal services in secondary forest habitats depend on an impoverished subset of dispersal vectors and may suffer reduced adaptive potential to changing environmental conditions. Thus, our study highlights the value of old-growth forests for the conservation of frugivore-mediated seed dispersal processes.

INTRODUCTION

The mutualism between fleshy-fruited plants and frugivores is an important process in forest ecosystems (Howe & Smallwood 1982). Fleshy-fruited plants depend on seed dispersal by animals to escape from increased seedling mortality near mother plants, to reach adequate microhabitats for regeneration and to ensure gene flow among populations (Janzen 1970; Nathan & Muller-Landau 2000; Schupp *et al.* 2010).

Old-growth forests comprise only 0.2 % of all extant European forests (Hannah, Carr & Landerani 1995; Bengtsson *et al.* 2000). Recent work has shown that frugivores, particularly forest specialists, are threatened by the conversion of old-growth forest ecosystems into secondary habitats (Newbold *et al.* 2013). Studies from both temperate and tropical forests have reported that logging and fragmentation can result in a decrease of forest specialist frugivores and in reduced fruit removal (Moran *et al.* 2004; Kirika, Farwig & Böhning-Gaese 2008; Albrecht *et al.* 2012). On the other hand, a loss of habitat specialists may be compensated or even over-compensated by less sensitive habitat generalists that are capable of passing habitat boundaries to exploit fruit resources (Farwig *et al.* 2006; Breitbach *et al.* 2010; Neuschulz *et al.* 2011). Such compositional changes in the abundance of frugivore assemblages may have consequences for consumer-resource dynamics (Fontaine *et al.* 2008), competition for resources and the stability of seed dispersal services of entire plant–frugivore associations. Understanding the mechanisms that influence these dynamics requires a network perspective on plant–frugivore interactions.

In recent years mutualistic plant–animal interactions have been increasingly analyzed using a network approach. Such networks represent the interactions between several plants and animals on the level of species assemblages, incorporating species identity and the frequency of pair-wise interactions (Jordano 1987). Conceptually, the stability of an interaction network with a given number of species is expected to increase with the number of links and with the evenness in the strength of these links (MacArthur 1955). This suggests that low specialization, that is, low niche differentiation, may contribute to the stability of food webs and mutualistic networks (MacArthur 1955; James *et al.* 2012).

In plant–animal mutualisms the dietary niche of animals is often closely linked to the function that animals perform within the community (Holland & DeAngelis 2010; Blüthgen & Klein 2011). This is emphasised in the term '*functional niche*' (Loreau *et al.* 2001). The extent to which animal species differ in their use of plant resources (i.e., niche differentiation) therefore determines the degree of '*functional complementarity*' and '*functional redundancy*' in plant–animal interactions (Blüthgen & Klein 2011). A low level of niche differentiation implies functional redundancy, suggesting a higher temporal stability or persistence of the function if some interactions disappear (MacArthur 1955; James *et al.* 2012). Further, a low level of niche differentiation should be favoured in a situation of high inter-specific competition due to resource limitation, i.e. at high consumer/resource ratios (MacArthur & Pianka 1966). Competition may strongly constrain plant–animal mutualisms (Blüthgen *et al.* 2007; Benadi *et al.* 2012), which suggests an equilibrium between the redundancy in biotic processes maintained by animals and individual dietary specialization of animals. Plants profit most from high dietary generalization of frugivores, as the number of dispersal vectors increases, while frugivore individuals have to adapt their foraging behaviour in response to the spatio-temporal availability of fruit resources and the density of competitors.

A recent empirical network study on plant–herbivore and host–parasitoid networks reported that diet breadth of consumers and resource availability determine the sensitivity of species interactions to ecosystem perturbation (Valladares, Cagnolo & Salvo 2012). However, this implies that the dietary specialization of animals is a fixed species attribute. According to optimal-foraging theory, the diet breadth of animals is a flexible trait and expected to decrease in response to reduced competition at low consumer/resource ratios (MacArthur & Pianka 1966). In line with this, an experimental study has shown that the specialization of pollinators on plants increases at low consumer/resource ratios (Fontaine *et al.* 2008). Fontaine *et al.* (2008) predicted that perturbation of ecosystems is likely to alter consumer/resource ratios, which in turn may affect the diet breadth and the functional niche of animal mutualists. In support of this hypothesis, Aizen *et al.* (2012) showed for plant–pollinator networks that once the most vulnerable species have become extinct, the remaining common and most generalised species begin to specialise and shift from the core to the periphery of the network. Likewise, altered consumer-resource dynamics in degraded forest habitats may influence the foraging behaviour of frugivores. A decrease in the diet breadth of frugivores at low frugivore densities may reduce redundancy, that is, the number of dispersal vectors. Up to now optimal-foraging has not been considered as a driving force of changes in redundancy in plant–animal mutualisms following ecosystem perturbation.

Here we present a study on the effects of logging and anthropogenic forest edges on consumer/resource ratios, dietary specialization and redundancy in plant–frugivore networks in an old-growth European forest. For two consecutive years we recorded fruit removal by frugivores from fleshy-fruited plants in the interior and at edges of logged and old-growth forests in Europe's best preserved old-growth lowland forest (Białowieża, Eastern Poland). Based on the results of previous studies, we expected (i) a decrease in the abundance of forest specialist frugivores in logged forests and at forest edges and an increase in the abundance of forest generalists at edges (Farwig *et al.* 2006; Kirika *et al.* 2008; Neuschulz *et al.* 2011; Menke *et al.* 2012). This compositional change in frugivore abundance should result in (ii) reduced consumer/resource ratios, that is, reduced competition, in the interior of logged forests, but a compensation or even over-compensation and increased competition at forest edges. According to optimal-foraging theory we expected that (iii) frugivore specialization on plants increases when competition for resources is reduced, that is, at low consumer/resource ratios (Fontaine *et al.* 2008), and that an increase in dietary specialization causes a decrease in redundancy (MacArthur 1955). Thus, we expected a reduction of redundancy in the interior of logged forests, but no change or even an increase in redundancy at forest edges.

Methods

Study area

Our study was conducted in Białowieża Forest, the last European primary old-growth lowland forest, extending over the border between Poland and Belarus. On Polish territory the forest covers an area of about 625 km². Within the Białowieża National Park (ca. 100 km²) an area of about 60 km² is strictly protected and an area of about 45 km² has potentially never been commercially logged (Falinski 1986; Sokolowski 2004). Over 80 % of the remaining forest has been shaped by commercial logging since the First World War (Bobiec *et al.* 2000; Bobiec 2002b). Moreover, most riverine areas of the forest had been cleared during the 16th and 17th centuries for the purpose of hay production, which led to the creation of numerous forest-grassland transitions along rivers (Sokolowski 2004). The core of the Białowieża National Park is an exceptional and rare reference site for studying the impact of anthropogenic habitat degradation on ecological processes in temperate forest ecosystems (Falinski 1986; Bobiec *et al.* 2000; Bobiec 2002b; Tomiałojć & Wesołowski 2004; but see Niklasson *et al.* 2010).

STUDY DESIGN

In the study region the majority of fleshy-fruited plants are primarily associated with ash-alder flood plain forests (*Fraxinus excelsior* and *Alnus glutinosa*, Fraxino-Alnetum community; Matuszkiewicz 2001). Thus, we established our study sites within these flood plain forests. We used maps on the distribution of ash-alder forests for the selection of study sites (Falinski 1994) and verified the suitability in the field. The two-factorial design of our study included a total of 10 study sites. We established our study sites in the interior ($n = 3$) and at edges ($n = 2$) of logged forests outside the National Park (stand age: ~50 years) and in the interior ($n = 2$) and at edges ($n = 3$) of old-growth forests within the National Park (stand age: ~100–150 years). We refer to forest edges as transitional zones between closed forest and historically-managed riverine meadows. The pair-wise distance between study sites ranged from 1.3 to 18 km (9.1 ± 5.3 km, mean ± SD throughout).

FRUGIVORE OBSERVATIONS

We conducted field sampling on all study sites in 2011 and in 2012, due to logistical constraints, in eight of these study sites (for details see Supplementary Table 3.2 in Appendix). From July to October 2011 and 2012 we weekly monitored fruit ripening of fleshy-fruited plants on the study sites and searched for plant species bearing ripe fruits in a radius of 500 m around the centre of each study site. According to availability of fruiting plants we selected three individuals ($n = 72$), two individuals ($n = 15$) or one individual ($n = 14$) per species for the frugivore observations on each site and in each year. The number of fruit producing plant species per study site was lower in 2011 (4.3 ± 1.9) than in 2012 (7.3 ± 1.4; Supplementary Table 3.3 in Appendix), but did not differ between forest interior and edges or logged and old-growth forests (Supplementary Table 3.3 in Appendix). To document frugivore visits on plants, we observed each plant species on each study site and year three times for a period of six hours starting from sunrise (18 hours × plant species^{-1} × study site^{-1} × year^{-1}).

We observed plant–frugivore interactions equipped with binoculars from camouflage tents simultaneously on different study sites (seven observers and 14 observers in 2011 and 2012, respectively). We recorded all frugivore species visiting the individual plants, as well as the number of frugivore individuals, the duration of frugivore visits and fruit handling behaviour. We distinguished between swallowing, crushing, pecking and dropping of fruits. If a group of conspecific frugivores visited a plant and individual behaviour could not be observed simultaneously, we focussed on the individual being most visible. If the behaviour of different species could not be observed simultaneously, we focussed on the rarer species. We were able to observe fruit handling in 78 % of all frugivore visits. Of these, we observed swallowing of fruits in 92 %, crushing in 4 %, pecking in 4 % and dropping of fruits in 3 % of visits. Proportions do not add to 100 % as single visitors handled fruits in various ways: some fruits were swallowed, crushed or pecked, while others were dropped during the same visit. As fruit handling could only be observed in 78 % of visits, we used the data on fruit handling in a first step to determine which frugivore species act as seed dispersers on each plant species (i.e. frugivores swallowing, crushing, or pecking on fruits of the respective plant species). In a second step, we defined interaction frequency as the number of visits of the identified seed dispersers on a plant species, independent of their fruit handling (visits hereafter). We classified frugivores into forest specialists and generalists (Supplementary Table 3.4 in Appendix; Jędrzejewska & Jędrzejewski 1998a, b; Svensson, Mullarney & Zetterström 2009). Forest specialists reproduce exclusively in forest habitats, whereas forest generalists also reproduce in non-forest habitats.

We estimated the crop size of the observed plant individuals by counting their fruits on the day of observation. In the case of trees, we counted the fruits at representative parts of the tree crown and then extrapolated over the whole tree crown. We estimated the crop size three times for each focal plant species, i.e. during each of the three observation sessions, and calculated the mean crop size for each plant species on each study site and in each year. Then we calculated the total fruit crop (fruit abundance hereafter) within each network by summing the crop size of each plant species in the respective networks. In 2011 we additionally monitored fruit abundance on the study sites along 250 m transects (for details see Supplementary Methods 3.1 in Appendix). Fruit abundance along transects correlated positively with fruit abundance in the networks in 2011 ($r = 0.91$, $t = 6.49$, $df = 8$, $P < 0.001$). Therefore, we used the fruit abundance based on total fruit crop in the networks for all further analyses.

Network analysis

For each study site we constructed two quantitative interaction matrices (for each year separately) based on the frequency of interactions between plants and frugivores except for the two study sites that were sampled in 2011 only (Supplementary Table 3.2 in Appendix). In 2011 three focal plants with very low crop size received no visits and were excluded from the network analysis. The total frequency of a frugivore species was defined as the number of visits on all plant species within a network, whereas the visitation rate from the plants' perspective was given by the total number of frugivore visits on a plant species. Thus, we used the marginal totals of the interaction matrices for calculation of the total interaction frequencies (Blüthgen *et al.* 2007). Standardisation of our study design to the same sampling effort per plant species on each study site allowed us to quantify network structure from the plants' perspective. Hence, our study design allows for conclusions about potential consequences for frugivore-mediated seed dispersal processes.

To test our hypotheses we used a combination of four measures: (i) the consumer/resource ratio, (ii) the specialization of frugivores on plants (iii) the evenness in the contribution of frugivores to interaction frequencies per plant species and (iv) redundancy, that is, the effective number of frugivore species per plant species. To estimate the consumer/resource ratio CR_q in the networks, we first divided the number of frugivore visits on each plant species i in a given network by the crop size of the respective plant species as:

$$cr_i = \frac{A_i}{F_i} \qquad \text{eqn. 3.1}$$

where A_i is the sum of interactions of plant species i and F_i is the number of fruits of plant species i (Supplementary Methods 3.2 in Appendix). To summarise the consumer/resource ratio CR_q for each network q, we calculated the mean consumer/resource ratio per plant species weighted by interaction strength of plants as:

$$CR_q = e^{\sum_{i=1}^{I} \frac{A_i}{m} \ln(cr_i)} \qquad \text{eqn. 3.2}$$

where A_i is sum of interactions of plant species i and m is the sum of interactions in the network. Consumer/resource ratios were ln(x) transformed before calculation of the mean for each network q, because consumer/resource ratios showed a strongly skewed distribution (Supplementary Fig. 3.1 in Appendix).

To quantify the degree of complementary specialization among frugivores within each network, we compared the observed frequency distribution of interactions with an expected probability distribution that assumes that all species interact with their partners in proportion to their observed frequency totals (Blüthgen *et al.* 2006, 2007). We calculated the deviation from the expected probability distribution as the standardized Kullback-Leibler distance d' for each frugivore species j (Blüthgen *et al.* 2006). Then, we estimated for each network the mean specialization of frugivores $\langle d'_j \rangle$ where each frugivore was weighted by its total interactions in the respective network. The index d' ranges from 0 to 1, where 0 indicates highest possible generalization and 1 indicates highest possible specialization of frugivores on plants. By definition d' is a conservative index of specialization, since it is relatively insensitive to asymmetric specialization, which may occur if a frugivore species specialises on a commonly used resource (Blüthgen 2010). Thus, d' not only considers the diversity of plants used by frugivores but also whether plant resources are used by other frugivores and quantifies the degree of exclusiveness in the resource niches of frugivores (i.e., resource partitioning).

We quantified redundancy S_q in the networks based on Shannon-entropy. In contrast to the niche property d'_j of frugivores, our measure of redundancy S_q reflects the plants' perspective and is based on relative interaction frequencies. Since S_q is based on Shannon-entropy it can be partitioned into independent evenness and richness components in a multiplicative manner (Supplementary Methods 3.3 in Appendix; Tuomisto 2012), where the evenness component E_q quantifies the equitability of interaction frequencies among frugivores per plant species. Here we use E_q for inference about the extent to which changes in redundancy are attributable to changes in the relative contribution of frugivores to interaction frequencies. To quantify evenness E_q and redundancy S_q we first calculated the Shannon entropy H_i for each plant species i as:

$$H_i = -\sum_{j=1}^{J} \frac{a_{ij}}{A_i} \ln \frac{a_{ij}}{A_i} \qquad \text{eqn. 3.3}$$

where a_{ij} is the number of visits of frugivore species j on plant species i and A_i is the sum of interactions of plant species i (Blüthgen *et al.* 2008). The exponential form e^{H_i} (Jost 2006) expresses the '*effective*' number of frugivore species on plant species i, that is, the number of frugivore species if all were equally common. The evenness in the interaction frequencies of frugivore species' on plant species *i* is given by:

$$E_i = \frac{e^{H_i}}{J_i} \quad \text{eqn. 3.4}$$

where J_i is the number of frugivore species on plant species *i* (for derivation and justification see Hill 1973). To summarize the redundancy for each network *q*, we calculated redundancy S_q, the mean effective number of dispersal vectors per plant species weighted by interaction strength of plants as:

$$S_q = \sum_{i=1}^{I} \frac{A_i}{m} e^{H_i} \quad \text{eqn. 3.5}$$

where A_i is the sum of interactions of plant species *i* and *m* is the sum of interactions in the network. Likewise, evenness E_q, the mean equitability in the contribution of frugivores to interaction frequencies per plant species, was calculated as:

$$E_q = \sum_{i=1}^{I} \frac{A_i}{m} E_i \quad \text{eqn. 3.6}$$

DATA ANALYSIS

We first tested for a relationship between habitat specialization of frugivores (forest generalist and specialist, respectively; Supplementary Table 3.4 in Appendix) and habitat types (location: edge vs. interior; logging: logged vs. old-growth) using a quantitative fourth-corner analysis (Dray & Legendre 2008). The fourth corner analysis requires (i) a site × species community matrix containing the abundance of each frugivore species on each study site, (ii) a trait matrix containing the habitat specialization of each frugivore species and (iii) a habitat matrix containing information on the location (interior vs. edge) and logging activities (logged vs. old-growth) of each study site (Dray & Legendre 2008). To construct the site × species matrix we first calculated the mean abundance of each frugivore species across the plant species for each study site and in each year (i.e., the mean visitation rate of each frugivore species in each of the 18 networks during 18 hours). Then we calculated the mean abundance of each frugivore species across the two study years for each study site (i.e., the mean abundance of each frugivore species across the two networks per study site). The significance of the relationship between habitat specialization and habitat type was tested with a χ^2-statistic and a permutation test (9,999 iterations). We chose permutation model 1 which permutes the abundances for each species independently and tests the null hypothesis that species are randomly distributed among the habitats (Legendre, Galzin & Harmelin-Vivien 1997; Dray & Legendre 2008).

Secondly, we analyzed the variation in the dependent variables of (i) consumer/resource ratio CR_q, (ii) evenness E_q, (iii) frugivore specialization $\langle d'_j \rangle$ and (iv) redundancy S_q with linear mixed effects models. In these analyses, we treated location (edge vs. interior), logging (logged vs. old-growth) and their interaction as fixed factors. As the data were recorded in two years on the same sites we included site as a random grouping factor and year as a conditional random factor on site. According to the specification of the random terms the fixed factors were tested against the residual variation among sites to avoid pseudo-replication. Since mean visitation rates on plants in the networks increased with fruit abundance (Pearson correlation on ln(*x*) transformed variables: $r = 0.58$, $t = 2.85$, $df = 16$, $P = 0.012$), we included fruit abundance as a continuous covariate in the models to account for differences in resource quantity across study sites and years. As fruit abundance and network size were highly correlated (Pearson correlation on ln(*x*) transformed variables: $r = 0.69$, $t = 3.76$, $df = 16$, $P = 0.0017$), we did not include network size as an additional predictor in the analyses. However, by including fruit abundance in the analysis we implicitly consider differences in network size across study sites. As our study design is unbalanced, the effects of location and logging are not orthogonal, that is, effects are not independent. To account for this uncertainty we used Type III Sums of Squares to estimate the effects of the explanatory variables. Fruit abundance was ln(*x*) transformed prior to statistical analysis. We also tested for an effect of second order interactions between year and the main factors location and logging. However, we found no significant interactions with year (Supplementary Table 3.5 in Appendix). As the sample size in our study is low, we report results of the simpler models only (Table 3.1).

Finally, we conducted an exploratory path analysis to separate direct and indirect effects of consumer/resource ratios on frugivore specialization, evenness and redundancy. Based on our hypothesis we constructed an *a priori* path model which included the direct effects of consumer/resource ratio on frugivore specialization, evenness and redundancy as well as its indirect effects on evenness and redundancy via frugivore specialization (Fig. 3.3). We further included the covariance between

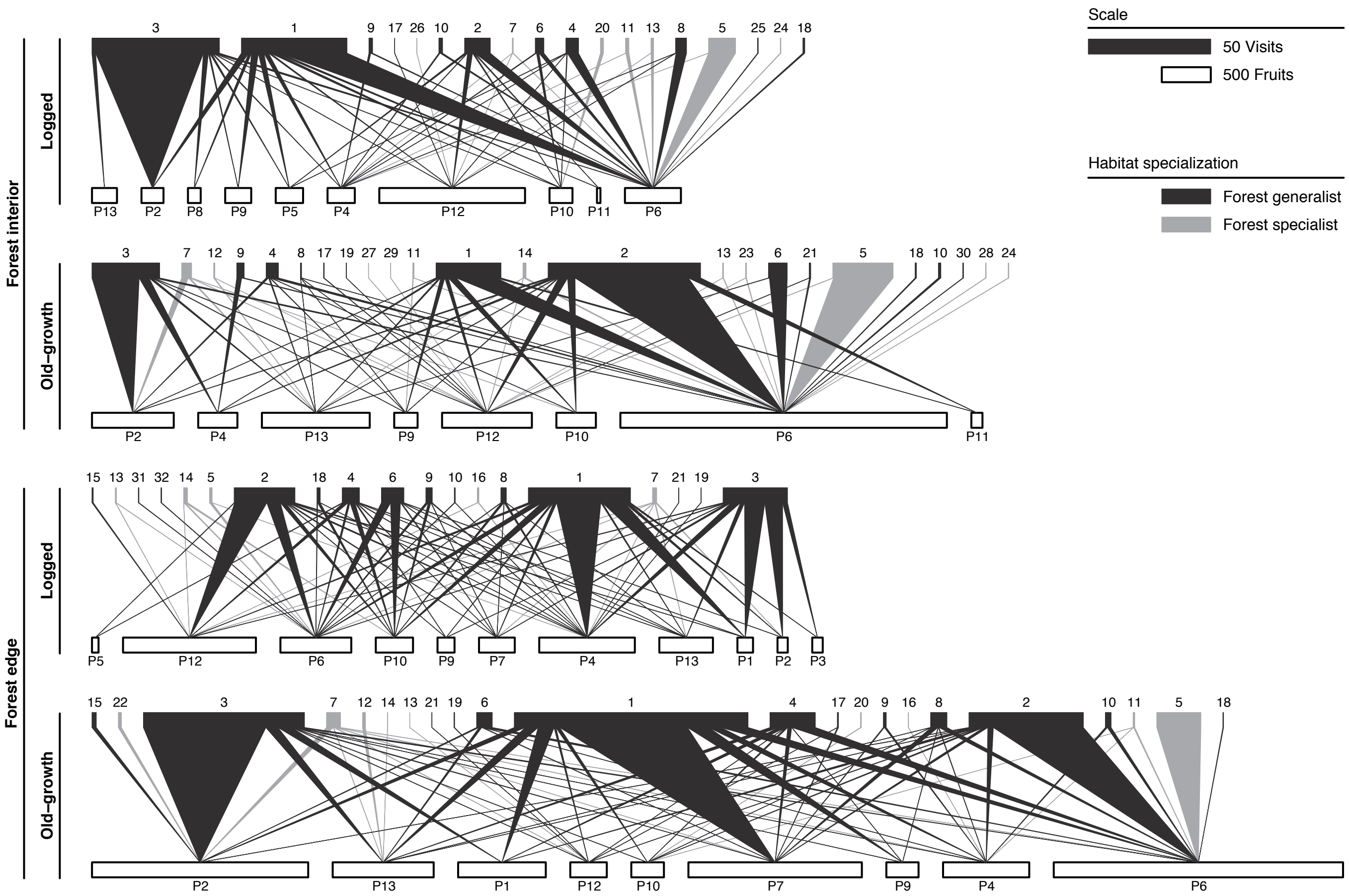

Figure 3.1. Plant–frugivore networks in the interior and at edges of logged and old-growth ash-alder forests in Białowieża, Eastern Poland. Lower bars represent fruit abundance of plants and upper bars frugivore visitation rates drawn at different scales. Linkage width represents interaction frequency. As a summary, networks are based on the mean frugivore visitation rates on plants and the mean crop size of plants across years and sites for each habitat type. Labels depict plants and frugivores, respectively. For species names see Supplementary Table 3.4 in Appendix.

evenness and redundancy into the model. As the sample size in our study is low we used the data from all 18 networks for the path analysis. However, the significance of the path coefficients was assessed using conservative z-tests with adjusted sample size ($n = 10$, i.e., the number of study sites).

We are aware that our study design is spatially confounded as the distribution of the remaining old-growth stands is limited to a single relict of preserved forest within the Białowieża National Park being surrounded by logged forest. Therefore, we assessed the extent to which the species turnover in the frugivore assemblages among study sites was related to the spatial and environmental components in our study design. To do so, we used a PCNM analysis (Principal Coordinates of Neighbourhood Matrix) combined with a multivariate redundancy analysis (RDA) and partitioned the variance in the species turnover that was explained by environmental and spatial components in the study design (Supplementary Methods 3.4 in Appendix). All analyses were conducted in *R* version 2.14.0 (R Development Core Team 2013), using the packages *bipartite* (network analysis; Dormann *et al.* 2009), *ade4* (fourthcorner analysis; Dray & Dufour 2007), *nlme* (Pinheiro *et al.* 2013) and *sem* (path analysis; Fox, Nie & Byrnes 2013).

Results

During 1,818 observation hours (774 hours in 2011 and 1,044 hours in 2012) we recorded 4,377 visits (1,583 visits in 2011 and 2,794 visits in 2012) of 32 frugivore species (29 bird and three mammal species) on 13 plant species (Fig. 3.1, Supplementary Table 3.4 in Appendix). Three bird species were the most frequent visitors, that is, *Sylvia atricapilla* (1,763 visits), *Turdus merula* (851), and *Erithacus rubecula* (742). Three understorey woody species received the most visits per 18 hours, that is,

Table 3.1. Summary of linear mixed effects models. Shown are mixed models (Typ III SS) testing the effect of fruit abundance, location (forest interior vs. edge), logging (logged vs. old-growth), and location × logging on (**a**) consumer/resource ratio CR_q, (**b**) frugivore specialization $\langle d'_j \rangle$, (c) evenness E_q and (d) redundancy S_q of the plant–frugivore networks (n = 18) quantified in Białowieża Forest, Eastern Poland.

Source of Variance	Df_{num},Df_{den}	F	P
(**a**) *Consumer/resource ratio*			
Fruit abundance	1,6	**32.0**	**0.0013**
Location	1,6	2.56	0.16
Logging	1,6	**8.93**	**0.024**
Year	1,6	1.71	0.24
Location × logging	1,6	**10.2**	**0.019**
(**b**) *Frugivore specialization*			
Fruit abundance	1,6	**12.9**	**0.011**
Location	1,6	1.81	0.23
Logging	1,6	21.1	0.0037
Year	1,6	1.91	0.22
Location × logging	1,6	**16.0**	**0.0072**
(**c**) *Evenness*			
Fruit abundance	1,6	**33.7**	**0.0011**
Location	1,6	**11.5**	0.015
Logging	1,6	1.67	0.24
Year	1,6	0.0845	0.78
Location × logging	1,6	3.25	0.12
(**d**) *Redundancy*			
Fruit abundance	1,6	**11.1**	**0.016**
Location	1,6	**7.53**	**0.034**
Logging	1,6	**15.7**	**0.0074**
Year	1,6	5.58	0.056
Location × logging	1,6	**9.50**	**0.022**

Notes: Fruit abundance was ln(x) transformed prior to statistical analysis. Significant predictors at a level of $P < 0.05$ are given in boldface type. Df_{num} and Df_{den} give numerator and denominator degrees of freedom, respectively.

Prunus padus (137 ± 105 visits), *Rhamnus cathartica* (119 ± 154) and *Euonymus europaeus* (62 ± 48).

The abundance of forest specialists did not differ between forest edges and the interior (χ^2 = 6.35, P = 0.29), while forest generalists were more abundant at forest edges than in the interior (χ^2 = 169.4, P = 0.0044). Conversely, forest specialists were less abundant in logged forests than in old-growth forests (χ^2 = 20.0, P = 0.035), whereas generalists were unaffected by logging (χ^2 = 99.1, P = 0.20). Accordingly, the consumer/resource ratio in the networks increased from the forest interior to forest edges and was reduced in the interior of logged forests compared to the interior of old-growth forests (Table 3.1, Fig. 3.2a). Frugivore specialization

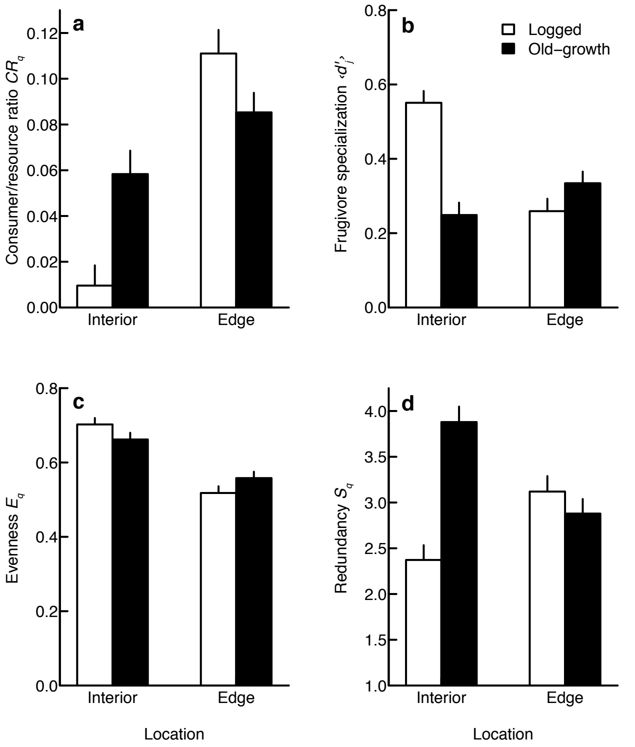

Figure 3.2. The effects of logging and fragmentation on consumer/resource ratios and network structure. (**a**) Consumer/resource ratio CR_q [visits fruit^{-1} 18 h^{-1}], (**b**) frugivore specialization $\langle d'_j \rangle$, (**c**) evenness E_q and (**d**) redundancy S_q of plant–frugivore networks in the interior and at edges of logged and old-growth ash-alder forests in Białowieża, Eastern Poland. Given are least square means controlling for fruit abundance and corresponding standard errors. For statistical analyses see Table 3.1. For details on calculation of network metrics see Methods.

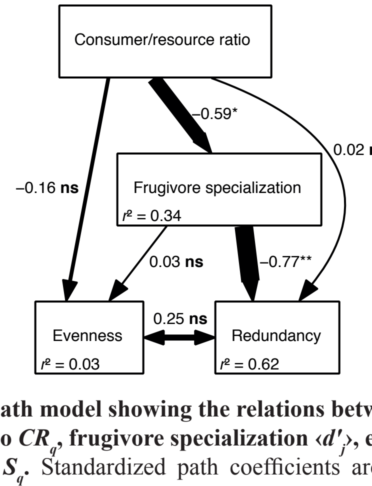

Figure 3.3. Path model showing the relations between consumer/resource ratio CR_q, frugivore specialization $\langle d'_j \rangle$, evenness E_q and redundancy S_q. Standardized path coefficients are given next to path arrows with significances depicted by ns $P > 0.1$, *$P < 0.05$ and **$P < 0.01$. Explained variance for endogenous variables is denoted by r^2 and double-headed arrows indicate covariance. All arrow widths are proportional to path coefficients. Note that data from all 18 networks were used for the path analysis. The significance of the path coefficients was assessed using z-tests with adjusted sample size (n = 10, i.e., the number of study sites).

on plants increased in the interior of logged forests, compared to the interior of old-growth forests and forest edges (Table 3.1, Fig. 3.2b). Evenness was higher in the forest interior than at forest edges and did not vary with logging (Table 3.1, Fig. 3.2c). Redundancy was higher in the interior of old-growth forests compared to the interior of logged forests and forest edges (Table 3.1, Fig. 3.2d).

The path analysis indicated an indirect positive effect of increased consumer/resource ratios on redundancy via decreased frugivore specialization and a weak indirect negative effect via reduced evenness (Fig. 3.3). The negative effect via reduced evenness partly counteracted the positive effect via reduced frugivore specialization at forest edges (Figs. 3.2c,d).

Discussion

The increased abundance of forest generalist frugivores at forest edges caused an increase in consumer/resource ratios while a loss of forest specialist frugivores in the interior of logged forests resulted in reduced consumer/resource ratios, compared with the interior of old-growth forests (Fig. 3.2a). In accordance with optimal-foraging theory, a decrease in consumer/resource ratios went along with increased frugivore specialization and a loss of redundancy (Fig. 3.3). However, despite low dietary specialization redundancy was reduced at forest edges as evenness was lower compared to interiors (i.e., few frugivore species dominated interactions, Figs. 3.2c,d). A shift in the frugivore assemblages at forest edges and increased dietary specialization in the interior of logged forests thus involved a clear loss of redundancy compared to continuous old-growth forests.

Frugivore community composition and consumer/resource ratios

Previous studies have reported a decrease of forest specialists due to logging and forest edges, whereas forest generalists seem less sensitive and may even increase at forest edges (Farwig *et al.* 2006; Kirika *et al.* 2008; Neuschulz *et al.* 2011; Menke *et al.* 2012). In accordance with these studies, changes in the composition of frugivore assemblages were not random, but related to the habitat specialization of frugivores. Forest generalists, but not specialists, were more abundant at forest edges than in forest interiors. Conversely, forest specialists, but not generalists, were more abundant in old-growth forests than in logged forests. Frugivores are known to track the distribution of fruit resources in the landscape (Tellería *et al.* 2008), and habitat generalists may be particularly attracted to forest edges, due to widely visible fruit resources (e.g., Menke *et al.* 2012). The higher visibility of fruit resources may thus have caused the strong increase of frugivore densities at forest margins. Yet, the strong increase of forest generalists at forest edges compared to the forest interior resulted in reduced evenness in the frugivore assemblages as forest generalists dominated the assemblage of seed dispersers (Fig. 3.2c). Apart from the habitat specialization, the dominance of a subset of frugivores at high densities may also derive from differences in the efficiency of frugivores to track fruit resources (Tellería *et al.* 2008), and from differences in the overall specialization on fruits in relation to other food types (e.g., invertebrates; Carnicer *et al.* 2009). The reduced abundance of forest specialists in logged forests is consistent with a study from Białowieża Forest that reported reduced bird abundance in logged forests compared to old-growth stands in the National Park (Jędrzejewska & Jędrzejewski 1998a). The higher abundance of forest specialists in the old-growth parts of the forest is likely a result of the high habitat quality of the old-growth stands featuring multi-storey vegetation layers, standing dead wood, snags and uprooted trees which provide irreplaceable habitat for a variety of bird species (Tomiałojć & Wesołowski 2004). The compositional changes in the frugivore assemblages entailed increased consumer/resource ratios at forest edges and reduced consumer/resource ratios in the interior of logged forests compared to the interior of old-growth forests. Thus, our results support the hypothesis that anthropogenic perturbation of ecosystems can result in a shift of consumer/resource ratios in mutualistic networks (Fontaine *et al.* 2008).

Consumer/resource ratio, dietary specialization and redundancy

The path analysis showed that an increase in consumer/resource ratios went along with a decrease in dietary specialization of frugivores which is in line with optimal-foraging theory (MacArthur & Pianka 1966), and with previous experimental results from plant–pollinator systems (Fontaine *et al.* 2008). This suggests that frugivores adapted their foraging behaviour in response to local changes in competition for fruit resources (see Supplementary Methods 3.2 in Appendix). In contrast to Fontaine *et al.* (2008), we measured the mean dietary specialization on the level of frugivore assemblages but did not consider changes within single species. Hence, we cannot disentangle the extent to which the observed change in mean dietary specialization of frugivores was related to species turnover among sites or to changes in the foraging behaviour of frugivores. However, as the most common frugivores also tended to be most abundant in the local networks (e.g. three birds, *S. atricapilla*, *T. merula* and *E. rubecula* together accounted for 77 % of all visits, Fig. 3.1), compositional changes should be of minor importance compared to species level changes in dietary specialization. Further, although changes in consumer/resource ratios explained a considerable proportion of the variation in dietary specialization of frugivores (34 %), our results also suggest that other factors beyond the density of frugivores and fruits influenced individual foraging decisions. For instance, the selection of fruit resources may be influenced by differences in the nutritional quality and the relative abundance of fruiting plants (Herrera 1984). The path analysis also showed a strong negative relationship between redundancy and the specialization of frugivores on plants. This supports the prediction that increased niche overlap among species results in increased redundancy in biotic processes (MacArthur 1955; Loreau *et al.* 2001). However, the path analysis also suggests a weak negative effect of consumer/resource ratios on redundancy via reduced evenness (i.e., a subset of frugivores dominated interactions; Fig. 3.3). This effect partly counteracted the positive effect of increased consumer/resource ratios on redundancy via reduced dietary specialization at forest edges (Figs. 3.2c,d). To conclude, the shift in the dominance structure of frugivore assemblages at forest edges and increased dietary specialization of frugivores in the interior of logged forests coincided with a clear loss of redundancy compared to continuous old-growth forests.

In contrast to our findings, recent studies from tropical forests suggest no effect of logging and even a positive effect of forest edges on generalization and stability of plant–frugivore associations (Schleuning *et al.* 2011; Menke *et al.* 2012). Plant–frugivore associations are generally more diverse and less specialised in tropical than in temperate ecosystems and a large proportion of birds feeds exclusively on fruits in the tropics (Kissling, Böhning-Gaese & Jetz 2009; Schleuning *et al.* 2012). The differences in the response of temperate and tropical plant–frugivore associations to forest degradation may derive from higher diversity and lower specialization in tropical systems. Our results support the hypothesis that temperate plant–frugivore associations may be more prone to species loss than those in the tropics (Schleuning *et al.* 2012).

POTENTIAL CONSEQUENCES FOR SEED DISPERSAL PROCESSES

We found a clear loss of redundancy in plant–frugivore associations in secondary forest habitats compared to continuous old-growth forests. From the plants' perspective, the loss of dispersal vectors both in the interior of logged forests and at forest edges may entail reduced adaptive potential and a higher vulnerability of seed dispersal services to changing environmental conditions compared to continuous old-growth forests. In fact, some uncertainty remains in our conclusions since we lack information on the relative contribution of frugivores to plant recruitment. However, we observed swallowing of fruits in 92 % of frugivore visits and this is likely to result in dispersal of seeds (Herrera *et al.* 1994). In addition, Vázquez *et al.* (2005) have shown that the number of visits is more important for seed dispersal rates than the number of fruits dispersed per visit. This suggests visitation rates are an adequate surrogate for seed dispersal services. Certainly, frugivore species differ in their effect on plant recruitment (Schupp *et al.* 2010). However, in this case a loss of dispersal vectors may be even more severe, as different frugivore species often act complementary, because frugivore species may differ in their use of microhabitats or in their home-range sizes (Jordano *et al.* 2007; McConkey & Brockelman 2011). An impoverished set of dispersal vectors might thus also have consequences for the spatial variability in patterns of plant recruitment and the genetic structure of plants (Bleher & Böhning-Gaese 2001; Voigt *et al.* 2009).

LIMITATIONS

So far empirical network data based on field surveys have always been constructed from incomplete samples (e.g., Aizen *et al.* 2012). Despite a major sampling effort in our study, we certainly did not observe all possible interactions. However, here we deliberately standardized our sampling effort across study sites to make inferences from our comparison valid. Furthermore, plant species richness, total interaction frequencies, variability in interaction frequencies and network size neither differed between forest interior and edges nor between logged and old-growth forest (Supplementary Table 3.3 in Appendix). Accordingly, none of the reported patterns can be attributed to any habitat related sampling artefact. Finally, our results were consistent between both study years, though the networks were larger in 2012 than in 2011 (Supplementary Table 3.3 in Appendix). This suggests our results are robust and not confounded by under-sampled interactions.

Although we used a replicated study design, our study is limited to a single relict of old-growth forest and the generality of our conclusions is not known.

Still, after accounting for the spatial component in the study design, the environmental component significantly influenced the frugivore composition in the networks (Supplementary Table 3.1 in Appendix). Thus, we are confident that the observed patterns are not merely a spatial artefact. Given that the Białowieża Forest is the best preserved example of old-growth lowland forest in Europe (Bengtsson *et al.* 2000; Bobiec *et al.* 2000), we believe that our results provide valuable insights into the dynamics of plant–animal mutualistic networks after ecosystem perturbation.

CONCLUSIONS

Within the limitations of our study we provide evidence that compositional changes in frugivore assemblages alter consumer-resource dynamics, the dietary specialization of animal mutualists on plants, and redundancy in plant–frugivore interactions. The loss of dispersal vectors both in logged forests and at forest edges may impose consequences for seed dispersal of fleshy-fruited plants, as (i) it is likely to reduce the adaptive potential under changing environmental conditions and as (ii) it might affect the spatial variability in plant recruitment. Future studies should aim at linking changes in the structure of plant–frugivore networks to spatial patterns of plant recruitment. Overall, our findings from this unique temperate plant–frugivore association strongly imply a high level of plant dependence on a small set of frugivores and higher vulnerability of frugivore-mediated seed dispersal processes than in some tropical ecosystems. Our study highlights the value of old-growth forests for the conservation of frugivore-mediated seed dispersal processes.

CHAPTER 4

ECOLOGICAL PERTURBATION OF COUPLED MUTUALISTIC NETWORKS

with
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SUMMARY

Networks of species interactions promote biodiversity and provide important ecosystem services. These networks have traditionally been studied in isolation, but species are commonly involved in multiple, diverse types of interaction. Therefore, whether different types of species interaction networks coupled through shared species show idiosyncratic or correlated responses to habitat degradation is unresolved. Here we study the collective response of coupled mutualistic networks of plants and their pollinators and seed dispersers to the degradation of Europe's last relict of old-growth lowland forest (Białowieża, Poland). We show that logging of old-growth forests has correlated effects on the number of partners and interactions of plants in both mutualisms and that these effects are mediated by shifts in plant densities on logged sites. These results suggest bottom-up controlled effects of habitat degradation on plant–animal mutualistic networks and predict that the conversion of primary old-growth forests to secondary habitats may cause a parallel loss of multiple animal-mediated ecosystem services.

INTRODUCTION

All species are directly or indirectly involved in mutualistic and antagonistic interactions, which together form complex interaction networks (Thompson 2005, 2009). These networks of species interactions structure ecological communities (Bascompte & Jordano 2007) and maintain processes that are essentially linked to the functioning of ecosystems (Kremen 2005). Recent studies provide evidence that the structure of such networks is altered by habitat degradation (Tylianakis, Tscharntke & Lewis 2007) and that rare and specialized interactions are the first to disappear after habitat reduction (Aizen *et al.* 2012). However, to date, most studies have focussed on only a single type of interaction (e.g., pollination) even though species are commonly involved in multiple, diverse types of interaction (Thompson 2005; Pocock *et al.* 2012). A key question is hence whether habitat degradation has correlated effects on multiple interaction networks each providing different ecosystem services, such as pollination and seed dispersal (Kremen 2005; Pocock *et al.* 2012). For example, a correlated response to habitat degradation could arise through the sharing of plant resources among different interaction networks (Fontaine *et al.* 2011; Pocock *et al.* 2012; Rodriguez-Cabal *et al.* 2013). Simulations suggest that extinction of plants can cause correlated co-extinctions in different interaction networks when these are coupled through shared plant resources (Pocock *et al.* 2012). This implies that plants are critical nodes of coupled interaction networks (Pocock *et al.* 2012; Rodriguez-Cabal *et al.* 2013) and that plants may mediate a correlated response of such coupled networks to habitat degradation.

Here we empirically test this prediction on coupled mutualistic networks of ten keystone plant species, their pollinators and their seed dispersers. In these networks pollinators and seed dispersers form an indirect plant-mediated mutualism (Holland & DeAngelis 2010), because both benefit each other by increasing the reproductive output and dispersal capacity of the shared food plant. We study these coupled mutualistic networks in Europe's last relict of old-growth lowland forest (Białowieża, Poland; Marris 2008), and find strong evidence that plants mediate a correlated response of both their pollinators and their seed dispersers to the degradation of this forest ecosystem. Thus, habitat degradation may critically endanger the integrity of ecosystems through a parallel loss of multiple animal-mediated ecosystem services.

RESULTS

OVERALL EFFECTS OF LOGGING AND FRAGMENTATION

We quantified the interactions between the focal plants and their animal mutualists in the last European relict of old-growth lowland forest in Białowieża, eastern Poland (Marris 2008). During the last century, this unique ecosystem has been fragmented, and over 80 % of the Polish part of the forest (625 km²) has been converted to secondary forests owing to commercial logging (Bobiec 2002a). Currently, only 45 km² of the forest still feature natural dynamics typical of old-growth forests. In this setting, we established 17 study sites scattered over 400 km², situated in both logged and old-growth forests and covering various landscape contexts ranging from forest interior to edges to small forest remnants. In a two-year field survey on these sites, we quantified the mutualistic interactions of the focal plant species with both their pollinators and their seed dispersers. We documented 5,784 interactions with 294 pollinator species (mainly from the orders Diptera, Hymenoptera, Coleoptera and Lepidoptera) and 5,935 interactions with 34 seed disperser species (30 avian and 4 mammalian species; Fig. 4.1). Rarefaction analyses indicated that our sampling identified the functionally most important species (Supplementary Methods 4.1; Supplementary Fig. 4.1 in Appendix). Based on this dataset, we quantified the number of partners (number of distinct links) and the interaction frequency (rate of interactions) of the plants for both mutualistic relationships. Both the number of partners and interaction frequency are major determinants of a species' impact in an interaction network (Vázquez *et al.* 2005; James *et al.* 2012). The number of partners is essential for species persistence (James *et al.* 2012), and the interaction frequency is highly correlated with the effect of interacting species on each other's reproductive performance (Vázquez *et al.* 2005, 2012; Schupp *et al.* 2010).

Model selection suggested that changes in both the number of partners and interactions of plants in both mutualisms were consistently associated with logging of old-growth forests (Fig. 4.1; Table 4.1; Supplementary Table 4.1 in Appendix). Forest fragmentation was of minor importance (Table 4.1), which may be explained by the moderate degree of fragmentation and the diverse mosaic of forest and open landscape in our study area. This adds to previous findings that predict moderate habitat fragmentation to be of lesser importance

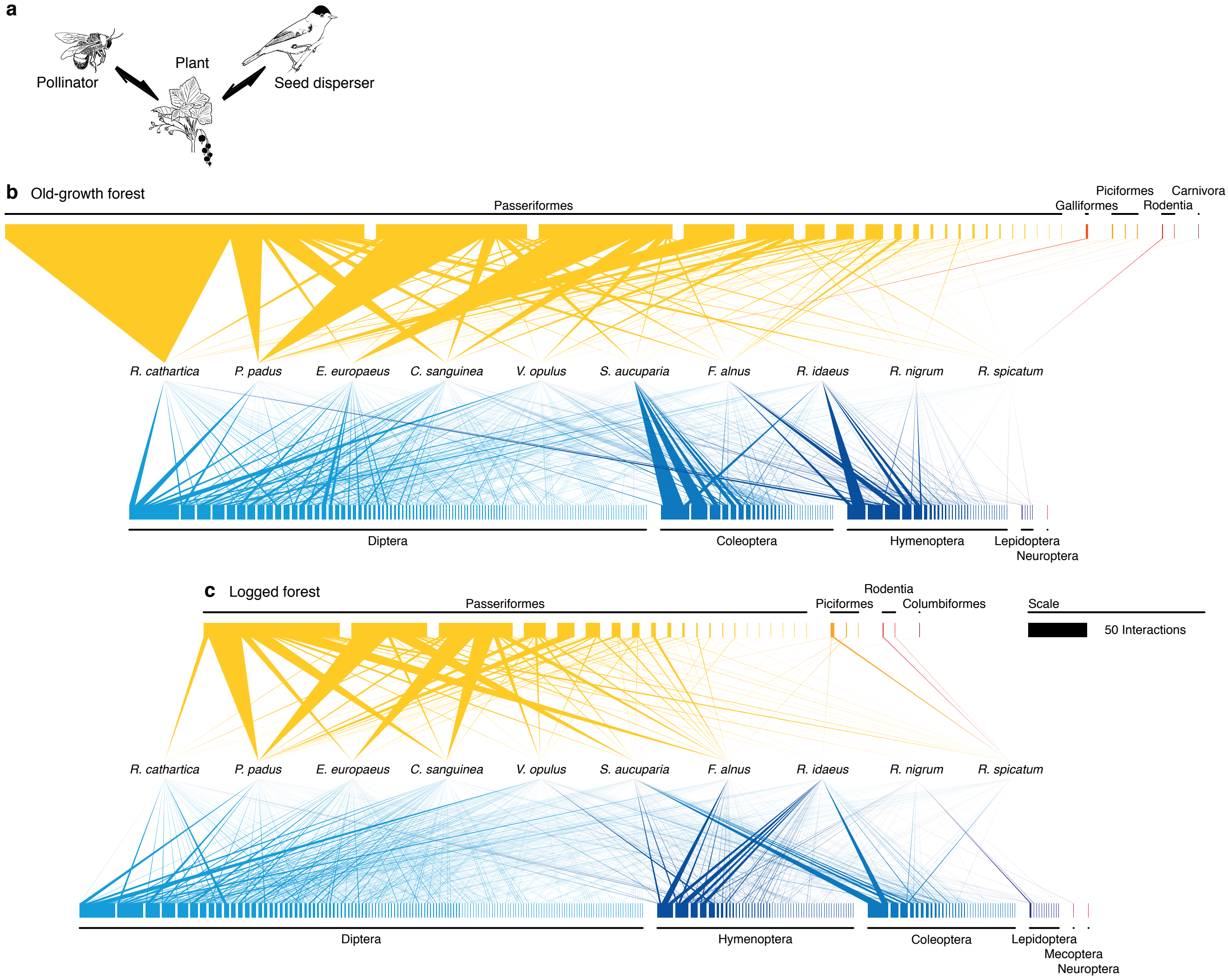


Figure 4.1. Coupled mutualist networks of plants and their pollinators and seed dispersers in old-growth forest and logged forest in Białowieża (Poland). (**a**) A simple association of a plant, a pollinator, and a seed disperser. (**b**, **c**) The quantified networks in old-growth forest (**b**) and logged forest (**c**). The ten focal plant species are in the centre of each depicted network, pollinators are at the bottom, and seed dispersers are at the top. Each bar depicts an animal species, and its width represents its mean abundance across the two study years. The widths of the base of the lines connecting plants with their pollinators and seed dispersers depict pair-wise interaction frequencies. See Supplementary Table 4.6 in Appendix for full species names.

Table 4.1. Summary of model selection. Most parsimonious linear mixed-effects models showing the effects of resources and logging on the number of partners and interaction frequency of plants in the plant–pollinator and plant–seed disperser mutualisms and the relative importance of the predictors (AIC_c weight).

Source of variance	Estimate‡	Lower CI‡	Upper CI‡	*P*-value‡	AIC_c weight¶
*Response: Number of partners**					
Resource units*†	0.19	0.13	0.24	< 0.0001	1.000
Mutualism	1.0	0.67	1.3	< 0.0001	1.000
Logging	−0.24	−0.40	−0.084	0.0022	0.979
Mutualism × Logging	0.36	0.16	0.57	0.00040	0.971
Location	–		–	–	0.137
Mutualism × Location	–		–	–	0.021
*Response: Interaction frequency**					
Resource units*†	0.47	0.38	0.55	< 0.0001	1.000
Mutualism	2.7	2.2	3.3	< 0.0001	1.000
Logging	−0.37	−0.62	−0.12	0.0032	0.901
Mutualism × Logging	0.39	0.072	0.71	0.019	0.767
Location	–		–	–	0.205
Mutualism × Location	–		–	–	0.077

Notes: The models included an offset to account for differences in sampling intensity in the plant–pollinator mutualism between the two study years (2011: 60 min × plant species^{-1} × study site^{-1}; 2012: 45 min × plant species^{-1} × study site^{-1}; coded for pollinators: 1 in 2011 and 0.75 in 2012; seed dispersers: 1 in both years). This offset was kept fixed during the model selection procedure (i.e., was retained in all component models; see Supplementary Table 4.1 in Appendix for model set). All component models included study site, year and plant species as random grouping factors. The sample size in the analyses was *n* = 322.

* Transformed to its natural logarithm.

† Flowers or fruits per sampled plant individual.

‡ Parameter estimates, 95 % confidence intervals (CIs), and *P*-values based on bootstrap with 10,000 simulations.

¶ Summed AIC_c weights that measure the relative importance of a predictor over all models, with 0 indicating low importance and 1 indicating high importance.

than typically observed levels of habitat degradation (Tscharntke & Brandl 2004; Markl *et al.* 2012).

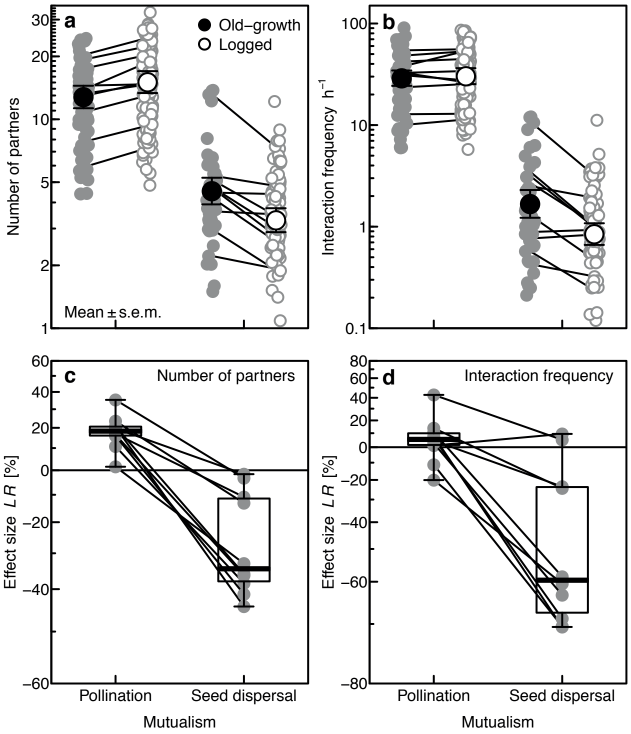


Figure 4.2. Effects of logging on the number of partners and interactions of plants in the plant–pollinator and plant–seed disperser mutualisms. The number of partners (**a**) and the interaction frequency (**b**) of plants in both mutualisms (plant–pollinator, plant–seed disperser) in old-growth forest (closed circles) and logged forest (open circles). Grey circles depict model predicted data (*n* = 322), lines represent the predicted mean response of each of the ten focal plant species, and black circles indicate the predicted mean response on the level of the plant assemblage (mean ± s.e.m.). The log response ratios *LR* in (**c**, **d**) estimate the '*effect size*' of logging. *LR* measures the proportional difference between the mean value of the response variable *y* in old-growth forest and the mean value of *y* in logged forest. *LR* < 0 indicates a negative effect of logging on (**c**) the number of partners and (**d**) interaction frequency of plants in both mutualisms. The lines in (**c**, **d**) connect the responses of both mutualisms for each plant species.

We used the predictions derived from the most parsimonious models (Table 4.1) and calculated for each plant species *i* the proportional difference in the number of partners and interactions for each mutualism *j* between the mean of old-growth forest and logged forest as the log response ratio $LR_{ij} = \ln\left(\bar{y}_{ij[Logged]} / \bar{y}_{ij[Old-growth]}\right)$ (Methods; Hedges, Gurevitch & Curtis 1999). This unitless metric allows us to test for a significant change in the number of partners and interactions with logging when averaged across all plant species. Logging, averaged across all plant species, had contrasting effects on the number of partners and interactions of plants in the two mutualisms (Fig. 4.2a,b; Table 4.1). Logging caused an average increase of 18 % in the number of partners in plant–pollinator associations (*t*-test, $t = 7.03$, $n = 10$, $P < 0.001$; Fig. 4.2c), and a decrease of 27 % in the number of partners in plant–seed disperser associations (*t*-test, $t = -4.64$, $n = 10$, $P < 0.01$; Fig.

4.2c). Logging had no consistent effect on interaction frequencies of plants with pollinators (average change of 4.7 %; *t*-test, $t = 0.961$, $n = 10$, $P > 0.05$; Fig. 4.2d), but reduced interaction frequencies with seed dispersers by 50 % (*t*-test, $t = -4.11$, $n = 10$, $P < 0.01$; Fig. 4.2d). The increased number of pollinator species in logged forest may derive from local disturbance regimes associated with logging that increase the availability of open habitats and alternative resources (Winfree, Bartomeus & Cariveau 2011). Conversely, the substantial loss of partners and interactions in the plant–seed disperser associations can at least partly be attributed to a loss of forest specialists that rely on old-growth forests (Albrecht *et al.* 2013). A previous study has shown that the loss of forest specialists in logged forests reduces the redundancy in these plant–seed disperser associations (Albrecht *et al.* 2013). These changes in interaction structure are likely to limit the dispersal and recruitment ability of fleshy-fruited plants in secondary forest habitats (Jordano *et al.* 2007; Schupp *et al.* 2010). Thus, our study supports previous concerns on the high vulnerability of animal-mediated seed dispersal to habitat degradation (Şekercioğlu *et al.* 2004; Markl *et al.* 2012).

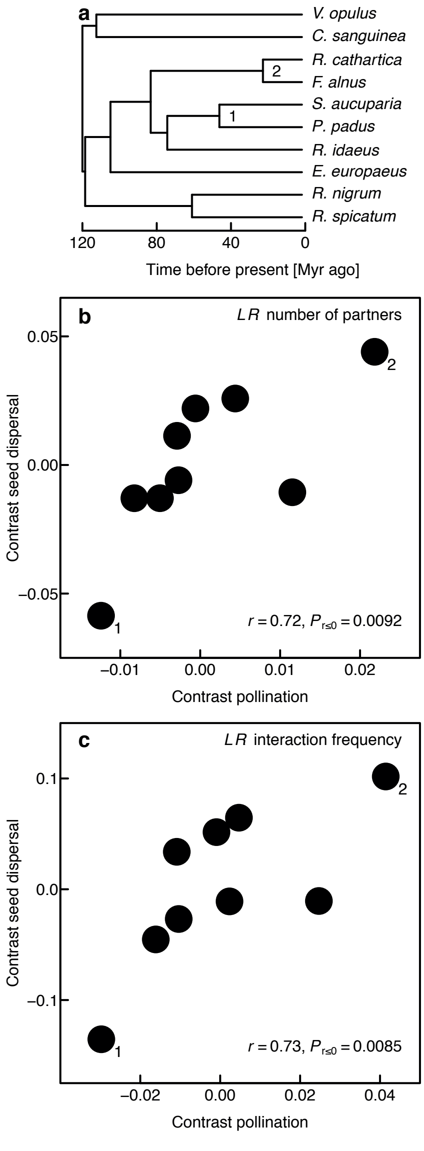


Figure 4.3. Correlations between the responses of pollinators and seed dispersers to logging. Phylogenetic relationships of the focal plant species (**a**) with branch lengths given in million years (Myr). Correlations between phylogenetic independent contrasts (PICs; $n = 9$) of the log response ratios *LR* of (**b**) the number of partners and (**c**) the interaction frequency of plants in the plant–pollinator and plant–seed disperser mutualisms. Highlighted are the contrasts (nodes 1 and 2 in the phylogeny) of two closely related species pairs (1: *P. padus* and *S. aucuparia*; 2: *F. alnus* and *R. cathartica*).

Correlated loss of interactions

In the next step, we used the log response ratios (LR_{ij}) to test whether effects of logging on interactions of plant species with their pollinators and their seed dispersers were correlated. From previous work we know that phylogenetically related species tend to interact with a similar set of mutualistic partners, because ecological interactions are evolutionarily conserved (Rezende *et al.* 2007; Gómez *et al.* 2010). Thus, we can expect that, owing to shared mutualistic partners, interactions of closely related plant species should be affected more similarly by perturbation than interactions of distantly related species (Rezende *et al.* 2007). To account for this effect of phylogenetic relatedness, we

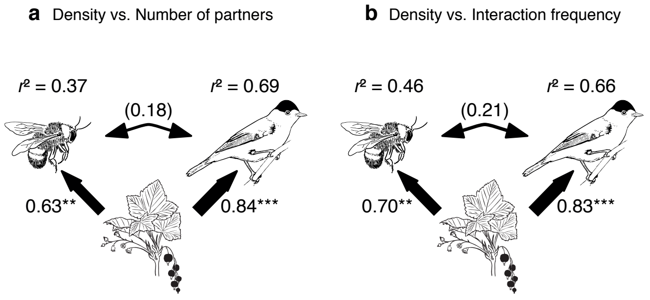


Figure 4.4. Summary of path analyses testing for bottom-up control in the responses of pollinators and seed dispersers to logging. Path models are based on phylogenetic independent contrasts (PICs; $n = 9$) and show the effects of the log response ratio (LR_{ij}) in plant density between old-growth forest and logged forest on the log response ratio in number of partners (**a**) and interaction frequencies (**b**) of plants in the plant–pollinator and plant–seed disperser mutualism. Shown are results for the predicted data from most parsimonious linear mixed-effects models (Table 4.1). Standardized path coefficients are given next to path arrows. Arrow widths are proportional to path coefficients. Residual covariance is denoted by double-headed arrows. Proportion of explained variance (r^2) is denoted above each mutualism. Significance of path coefficients is depicted by $^{**}P < 0.01$; $^{***}P < 0.001$. Both path models fit the data (**a**) $\chi^2 = 1.5$, $df = 2$, $P = 0.47$, (**b**) $\chi^2 = 2.19$, $df = 2$, $P = 0.33$.

used correlations based on phylogenetic independent contrasts (Methods; Pagel 1999). After accounting for phylogenetic relationships among plant species, we found a strong and significant correlation between the responses of both mutualisms to logging (Pearson's correlation forced through origin, number of partners: $r = 0.72$, one-tailed $P < 0.01$; interaction frequency: $r = 0.73$, one-tailed $P < 0.01$, $n = 9$ in both cases; Fig. 4.3b,c). The correlated response of both mutualisms to logging was also supported by non-phylogenetic correlations, by raw data and by randomization tests (Supplementary Table 4.2; Supplementary Figs. 4.3 and 4.4 in Appendix). This suggests that independently of the similarities in interactions due to the shared ancestry of plants, stronger changes in one mutualism were correlated with changes in the other mutualism because both are '*biologically coupled*' through the reproductive cycle of the plants. Perhaps the most striking aspect of these results is that we found this correlation despite the apparently contrasting effects of logging on pollinators and seed dispersers. Previous studies that used single plant species as model organisms also have found contrasting effects of habitat degradation on pollinators and seed dispersers (Breitbach *et al.* 2012). These studies concluded that different functional groups of animals respond idiosyncratically to land-use change. However, our study revealed hidden effects of land-use changes on the structure of ecological communities. Such effects will most likely remain undetected in studies that do not simultaneously quantify different types of species interactions on the level of entire communities.

Bottom-up control

Previous studies highlight the importance of shifts in the density of plant resources in degraded habitats as determinants of the direction and magnitude of land-use effects on mutualistic plant–animal interactions (Ghazoul 2005; Tylianakis *et al.* 2008; Schupp *et al.* 2010; Winfree *et al.* 2011). Although pollinators and seed dispersers differ in their specialization on food plants (Blüthgen *et al.* 2007), both may respond similarly to changes in the densities of the plants (Holland & DeAngelis 2010; Rodriguez-Cabal *et al.* 2013; Säterberg *et al.* 2013). Accordingly, path analyses revealed that shifts in plant population densities between old-growth forest and logged forest largely explained the magnitude of the effects of logging on interactions of plants with their pollinators and seed dispersers (Fig. 4.4): plant species that showed a disproportionate increase or decrease in their density in logged forest also experienced a disproportionate gain or loss of partners and interactions in both mutualistic relationships. These results suggest that effects of habitat degradation on mutualistic plant–animal interactions are bottom-up controlled by shifts in the density of food plants that occur following habitat degradation (Holland & DeAngelis 2010). This does not necessarily mean that shifts in species interactions follow the exact trajectories of shifts in the population density of plants, as is evident from our results (Fig. 4.2c,d). Our results rather suggest that shifts in the population density of plant resources are likely to amplify the magnitude of the effects of habitat degradation on species interactions.

Discussion

Our study provides one of very few empirical examples of coupled, interdependent networks (Ideker *et al.* 2001; Olff *et al.* 2009; Buldyrev *et al.* 2010; Brummitt, D'Souza & Leicht 2012; Gao *et al.* 2012; Pocock *et al.* 2012). Together with the existing examples, our study highlights that complex systems, be it infrastructural (Buldyrev *et al.* 2010), biological (Ideker *et al.* 2001) or climate systems (Gao *et al.* 2012), do not exist in isolation but form parallel, interdependent networks that respond collectively to perturbation. Our study demonstrates that strong interdependence among coupled networks can cause predictable transmission of perturbations across these networks. This suggests that it may be essential to consider this interdependence, if we aim to identify properties that account for the structural and functional stability of complex networks.

The ecological implications of our study are twofold. First, our results demonstrate that a consideration of the biotic context (Tylianakis *et al.* 2008) of mutualistic associations (e.g., shifts in resource densities) improves predictions of the effects of land-use changes on species interactions. Second, we find that habitat degradation induces a correlated shift in the interaction structure of the studied plant species and their animal mutualists. These results suggest that effects of habitat degradation on multiple interdependent plant–animal mutualistic networks are predictable. In principle, our findings may also be valid for other trophic interactions directly or indirectly linked to plant resources (e.g., plant–herbivore or plant–herbivore–parasitoid webs; Holland & DeAngelis 2010; Pocock *et al.* 2012). Since old-growth forests comprise only 0.2 % of all extant European forests (Hannah *et al.* 1995) and are globally declining, our findings signal an alarm, as they predict that the conversion of primary old-growth forest ecosystems to secondary habitats may involve a parallel loss of multiple animal-mediated ecosystem services.

Methods

Study area

We conducted our field campaign in the Białowieża Forest, the best-preserved European old-growth lowland forest, extending across the border between Poland and Belarus (Bobiec *et al.* 2000; Bobiec 2002b). On Polish territory, the forest covers an area of about 625 km². Within the Białowieża National Park (ca. 105 km²), an area of about 60 km² is strictly protected and an area of about 45 km² features natural vegetation dynamics typical for old-growth forests without recent human influence (Falinski 1986; Sokolowski 2004). Over 80 % of the remaining forest has been shaped by commercial logging since the First World War (Bobiec *et al.* 2000; Bobiec 2002b). Moreover, most riverine areas of the forest had been cleared during the 16th and 17th centuries for hay production, which resulted in a mosaic of meadows along rivers and in the vicinity of villages (Sokolowski 2004). The core of the Białowieża National Park is an exceptional and unique reference site for studying the impact of anthropogenic habitat degradation on ecological processes in temperate forest ecosystems (Falinski 1986; Bobiec *et al.* 2000; Bobiec 2002b; Sokolowski 2004).

Study species and design

We focussed our study on woody, fleshy-fruited plant species that depend on animal pollination and seed dispersal (see below). Since the focal plant species of our study are mainly associated with ash–alder floodplain forests (Fraxino–Alnetum community; Matuszkiewicz 2001), we chose our study sites within this plant association. In 2011, we established ten study sites in the interior (*n* = 3) and at edges (*n* = 2) of logged forest (stand age: ~50 years) and in the interior (*n* = 2) and at edges (*n* = 3) of old-growth forest within the national park (stand age: ~100–150 years). In 2012, we established additional study sites at edges (*n* = 3) and in fragments (*n* = 4; size ~1 ha) of logged forest to extend the fragmentation gradient. Study sites in the forest interior were located at least 500 m from forest edges, and forest edge sites were located at transitional zones between closed forest and riverine meadows. Forest fragment sites were located in small ash–alder forest remnants entirely surrounded by meadows (for details on characteristics of the study sites, see Supplementary Table 4.3 in Appendix). Thus, our study was conducted on a total of 17 sites scattered over about 400 km² covering two-thirds of the Polish part of the Białowieża Forest. The pair-wise distance between study sites ranged from 1.4 to 23 km (11 ± 5.8 km, mean ± SD).

We searched for fleshy-fruited plant species in a radius of 500 m around the centre of each study site and identified 16 plant species. For the analyses, we selected the subset of plant species that occurred in both logged and old-growth forest habitats as well as in both continuous (interior) and fragmented (edge and fragment) forest habitats. Thus, the dataset included ten understorey, woody, fleshy-fruited plant species from nine genera and five families (five tree and five shrub species, respectively; Supplementary Table 4.4; Supplementary Table 4.5 in Appendix). These plant species are common throughout Europe (Ellenberg 2011). In ash–alder flood plain forests, these plant species occur in high densities and thus represent critical keystone species for flower-visiting insects and frugivorous birds and mammals.

Sampling of pollinator assemblages

From May to June in 2011 and 2012, we monitored the flowering of the focal plant species on the study sites weekly (Supplementary Table 4.5 in Appendix). According to the availability of flowering individuals, we selected three (*n* = 78), two (*n* = 74) or one individual (*n* = 35) per species for the pollinator observations per study site and year. To document pollinator visits on flowers, we observed each species on each study site twice for 30 min in 2011 and three times for 15 min in 2012 (2011: 60 min × plant species^{-1} × study site^{-1}; 2012: 45 min × plant species^{-1} × study site^{-1}). Flower-visiting insects were sampled between 9:00 and 17:30 during good weather conditions and simultaneously at different study sites (3 observers in 2011 and 2 observers in 2012). Because of potential temporal differences in pollinator activity, we varied the time of day in which sampling took place across sites and across the sessions for each species per site. We conducted one session in the morning (9:30–12:30), one in the early afternoon (12:30–15:30) and one in the late afternoon (15:30–17:30). During each sampling session, all insect visitors that contacted floral sexual organs were caught with a sweep net and killed in ethyl acetate in a test tube. In the case of larger plant individuals (i.e., trees or large shrubs), we restricted our sampling to a subset of flowers. Hence, for large plant individuals, the sampling sessions represent a random snapshot of simultaneous flower visitor activity on plants. In the subsequent analyses, we accounted for the uncertainties associated with our sampling protocol (see below). In the first study year, we sorted all caught insects, identified them to the lowest taxonomic level possible, and prepared a collection of reference specimens (with the help of two experts:

B. Jauker (Apidae) and F. Jauker (Syrphidae), Justus Liebig University Gießen, IFZ - Department of Animal Ecology). In the second year, we extended this reference collection and used it for identification of caught insects. We identified 76 % of all flower visitors to the species level, 88 % to the genus level and 95 % to the family level (for simplicity, we refer to all morphospecies as species). All flower visitors were assumed to be potential pollinators (hereafter referred to as pollinators). In total, we accumulated 157 h of pollinator observations (66 h in 2011 and 91 h in 2012), distributed over 81 days (34 days in 2011 and 47 days in 2012). After each sampling session, we counted the number of observed flowers as well as the total flower burden of each observed plant individual. In the case of trees, we counted the flowers on representative parts of the tree and extrapolated over the whole crown. For analyses, we calculated the mean flower burden across the observed individuals of each plant species on each study site per year. Total flower burden and number of observed flowers were highly correlated (Pearson's $r = 0.81$, $n = 187$, $P < 0.001$). The results of subsequent analyses (see below) were similar for both measures; thus, we only report results of the analyses based on the number of observed flowers.

SAMPLING OF SEED DISPERSER ASSEMBLAGES

From July to October in 2011 and 2012, we monitored fruit ripening of the plant species on the study sites weekly (Supplementary Table 4.5 in Appendix). According to the availability of fruiting individuals, we selected three ($n = 91$), two ($n = 24$) or one individual ($n = 21$) per species for the frugivore observations on each study site per year. We observed each species on each study site and year three times for 6 h starting at sunrise (18 h × plant species^{-1} × study site^{-1} × year^{-1}). We observed plant–frugivore interactions with binoculars from camouflaged tents simultaneously at different study sites (7 observers in 2011 and 14 observers in 2012). We recorded all frugivore species visiting the individual plants, as well as the number of frugivore individuals, duration of visits and their fruit-handling behaviour (for details, see Albrecht *et al.* 2013). In total, we accumulated 2,430 h of seed disperser observations (702 h in 2011 and 1,728 h in 2012), distributed over 158 days (67 days in 2011 and 91 days in 2012). After each sampling session, we counted the fruits of the observed plant individuals. For trees, we counted the fruits on representative parts of the tree crown and then extrapolated over the whole tree crown. For analyses, we calculated the mean number of fruits across the observed individuals for each plant species on each study site per year.

SAMPLING OF PLANT POPULATION DENSITIES

We recorded the abundance of fleshy-fruited plant species on 13 of the 17 study sites (Supplementary Table 4.3 in Appendix). To do so, we established 20 alternating squares on 10 of the study sites and, owing to logistical constraints, 10 squares on 3 of the sites, each 20 × 20 m (covering a total area of 0.8 or 0.4 ha, respectively, on each study site). In each square, we counted the number of individuals of each focal plant species. Because all of the focal plant species were perennials, we assumed that their population abundance would not change significantly between years. Thus, although we studied interactions with pollinators and seed dispersers in two consecutive seasons (2011 and 2012), we estimated plant abundances only in the second season (2012). We used the mean density per species per square as an estimate of absolute population density.

STATISTICAL ANALYSIS

We used linear mixed-effects models to analyze the variation in the number of partners and interaction frequency of plants in the plant–pollinator and plant–seed disperser mutualisms. In these analyses, we treated fragmentation (interior, edge, fragment), logging (logged, old-growth) and mutualism (plant–pollinator, plant–seed disperser) as fixed factors. We refined comparisons of fragmentation using orthogonal contrasts to compare between continuous and fragmented forest (interior vs. edge and fragment) and among fragmented forests (edge vs. fragment). Since our design is not full factorial with respect to logging and fragmentation, we only included interactions of logging × mutualism and fragmentation × mutualism but not the logging × fragmentation interaction. Furthermore, our study design was not full factorial with respect to site, year and plant species (i.e., not all plant species occurred on every study site and not all study sites were sampled in both years). Therefore, we fitted site, year and plant species as separate random grouping factors. We nested mutualism within plant species, corresponding to a full factorial design. To account for any potential effects of differences in sampling intensity of pollinator assemblages in 2011 and 2012 (60 min vs. 45 min), we used the relative sampling duration (sampling intensity) as an offset (Crawley 2007; O'Hara & Kotze 2010) in the models (coded for pollinators: 1 in 2011 and 0.75 in 2012; seed dispersers: 1 in both years). Furthermore, we included the abundance of resource units (flowers or fruits) as a continuous covariate in the models to account for variation in resource abundance across focal plants. Number of partners, interaction frequency and number of resource units were transformed to their natural logarithm prior to statistical analyses. Based on the above-described global models, we generated a set of component models. This model set contained 25 component models for all possible combinations of predictor variables plus a model including only the intercept (the offset was kept fixed). To find the most parsimonious model, these models were compared according to small sample unbiased Akaike's information criterion (AIC$_c$; Supplementary Table 4.1 in Appendix). To obtain a measure of the relative importance of the main predictors, we calculated the Akaike weight for each model and summed these weights for each predictor over all models including the respective variable (Johnson & Omland 2004). Significance of the fixed effects in the most parsimonious models was assessed using a bootstrap procedure with 10,000 simulations as implemented in the *R* package *lme4* (Bolker *et al.* 2009; Bates *et al.* 2013).

The decision to use log-transformed response variables may influence the results of our analyses (O'Hara & Kotze 2010). Thus, we compared both models to alternative generalized models assuming a Poisson distribution for the number of partners (discrete counts of species), and a Gamma distribution for the interaction frequency (continuous rate of interaction per hour; Supplementary Methods 4.2 in Appendix). The results of the generalized models confirmed those of the models based on the log-transformed response variables. However, since the models based on the log-transformed response variables had substantially higher prediction accuracy and a slightly higher precision than the generalized models (Supplementary Fig. 4.2 in Appendix), we report results of the models based on the log-transformed data.

The most parsimonious models suggested that logging, but not fragmentation, explained changes in the interaction structure of plants with their pollinators and seed dispersers (Table 4.1 and Supplementary Table 4.1 in Appendix). Thus, we used these models to predict the number of partners and interactions of the plants in both mutualistic relationships in logged and old-growth forest (at the level of observations). We conditioned these predictions on the specified random effects (Bates *et al.* 2013). Furthermore, to account for any potential effects of differences in sampling intensity of pollinator assemblages between study years, we explicitly incorporated these differences into the predictions (i.e., by setting the sampling effort in both years to the same relative intensity of 1). For comparison, we ran all subsequent analyses based on the predicted data and based on the raw data. The estimated effects based on the raw data were equal or stronger compared to those based on the predicted data (Supplementary Fig. 4.3; Supplementary Table 4.2 in Appendix), suggesting that the estimates based on the predicted data are conservative. In the main text we report the results based on the more conservative model predictions that explicitly integrate potential effects of sampling intensity.

Based on these predictions we calculated for each plant species *i* the mean number of partners and interactions in old-growth forest and logged forest in the pollination and seed dispersal mutualisms. In the next step, we used the mean values of the number of partners and interactions of plant species *i* in mutualism *j* to calculate the log response ratio between old-growth forest and logged forest as $LR_{ij} = \ln\left(\bar{y}_{ij[Logged]}/\bar{y}_{ij[Old-growth]}\right)$ (Hedges *et al.* 1999). Log response ratios are the most adequate metric for our purpose because they estimate a proportional difference between habitats that can be readily compared between plant species, and because they have sampling properties that are known to be normal and that are robust to bias from small sample sizes (Hedges *et al.* 1999). To facilitate the interpretation of the results, we transformed the axes of the log response ratios in Fig. 4.2 to an index of percentage change $[\%] = -\left(1-e^{LR}\right)\times 100$ (Hedges *et al.* 1999). However, statistical analyses were performed using untransformed log response ratios. We used the log response ratios for a prediction of the expected change in number of partners and interaction frequencies across the studied plant species due to logging, and used *t*-tests to evaluate the null hypothesis of no change between old-growth forest and logged forest. Furthermore, we used more conservative binomial tests to test whether the raw effect directions were consistent across the ten plant species. The results of the binomial tests were consistent with those of the *t*-tests.

TEST FOR CORRELATED RESPONSE OF BOTH MUTUALISMS

We used correlations to test whether the responses of both mutualisms to logging (LR_{ij}) were correlated across the focal plant species. Since pollinators and seed dispersers form an indirect plant-mediated mutualism (Holland & DeAngelis 2010), we can expect a positive correlation between the effects of logging on interactions in both mutualisms (Säterberg *et al.* 2013) and used one-tailed statistical tests in all subsequent analyses. Since the ten studied plant species are part of a hierarchically structured phylogeny, we calculated correlations using phylogenetic independent contrasts (PICs; Felsenstein 1985; Pagel 1999). We extracted the appropriate information from a dated phylogeny of a large European flora (Fig. 4.3a; Durka & Michalski 2012). Phylogenetic correlations were computed through the origin (Garland, Harvey & Ives 1992). We used generalized least squares (GLS) to estimate the strength of the phylogenetic signal (Pagel's λ; Pagel 1999; Freckleton, Harvey & Pagel 2002). Since the likelihood profiles of the estimates were flat, we used the special cases with λ set to zero (a star phylogeny) and with λ set to 1 (Brownian motion; Freckleton *et al.* 2002). Since the sample size for two plant species (*Rubus idaeus* and *Cornus sanguinea*; Supplementary Table 4.5 in Appendix) was limited, we performed GLS analyses with and without weighting of the log response ratios of plant species by their variance, giving greater weight to plant species with higher '*certainty*'. Weighted and unweighted analyses led to identical conclusions. Finally, we used a permutation test to assess whether the observed correlations were larger than expected from a null distribution (assuming no relationship between the responses of both mutualisms). In this test, we randomized the log response ratios in one mutualism among the tips of the phylogeny (999 permutations), recalculated PICs and correlation coefficients, and compared the resulting null distribution with the observed correlation coefficients. Observed correlations were significantly larger than expected from the null distribution (Supplementary Fig. 4.4 in Appendix).

Test for bottom-up control

We used path analyses to test whether effects of logging on both mutualisms were bottom-up controlled by specific shifts in plant densities between old-growth forest and logged forest. First, we calculated the log response ratio *LR* of plant population densities between old-growth forest and logged forest, and calculated PICs (similar to the responses of both mutualisms). Since we only had vegetation data from 13 of the 17 study sites, we repeated the above-described analytical procedures only including these 13 sites and recalculated log response ratios for both mutualisms. The results based on the full and reduced datasets were qualitatively and quantitatively similar. Then we constructed *a priori* path models to test for bottom-up control based on the PICs (Fig. 4.4). These models included the correlations of the PICs of the *LR* plant density on the PICs of the *LR* in number of partners and *LR* in interaction frequencies in both mutualisms (plant–pollinator or plant–seed disperser). We also included the covariance between both mutualisms. We calculated correlations in the path models through the origin (Garland *et al.* 1992). Model fit was assessed with a χ^2-test. Path analyses based on model predicted data and raw data led to the same conclusion that the correlated effects of logging on both mutualisms were mediated by shifts in the density of plant populations on logged sites (Fig. 4.4; Supplementary Fig. 4.5 in Appendix).

Spatial autocorrelation

We are aware that our study design is limited to a single relict of preserved primary old-growth forest within the Białowieża National Park, which is surrounded by logged forest. Therefore, we tested for spatial dependency (Moran's *I* similarity) in the residuals of the two most parsimonious models. For both models, Moran's *I* similarities were close to zero and did not decrease with increasing distance (0—24 km) of discrete distance classes (2 km), which indicated a random spatial pattern (Supplementary Fig. 4.6 in Appendix).

Statistical software

All analyses were conducted in *R* (R Development Core Team 2013) using the packages *lme4* (Bates *et al.* 2013) and *glmmADMB* (Skaug *et al.* 2013) for analyzing mixed-effects models, *MuMIn* (Barton 2013) for model selection, packages *ape* (Paradis & Claude 2004) and *nlme* (Pinheiro *et al.* 2013) for phylogenetic analyses and package *lavaan* (Rosseel 2012) for path analyses. Networks were plotted with a customized version of the function plotweb from the package *bipartite* (Dormann *et al.* 2009).

CHAPTER 5
SYNTHESIS

Species interactions are an integral part of ecological communities. Collectively, these interactions form complex and highly dynamic networks. The structure of these networks varies due to geographic and temporal variation in the abundance and co-occurrence of interacting species and due to species gains and losses after ecological perturbation. In this thesis, I studied the outcomes of these natural and human-induced dynamics in highly diversified mutualistic networks of plants, pollinators and seed dispersers.

FRUGIVORE-MEDIATED COMPETITION AND FACILITATION IN PLANT COMMUNITIES

In the second chapter, I studied how geographic variation in the abundance and co-occurrence of plant species, and concomitant variation in phenological niche overlap among plants shape indirect frugivore-mediated interactions in plant communities. I aimed to portray a comprehensive picture of the mechanisms that structure indirect facilitative and competitive interactions among plant species sharing seed dispersers. First, I used a null model to test for signals of competition or facilitation among plants with overlapping fruit phenologies. Then I analyzed how geographic variation in the abundance, co-occurrence and phenological overlap of plants affect their specialization on frugivores, their interaction strength and their number of partners in the local networks. Finally, I tested whether, owing to dispersal by shared frugivores, plants with similar phenological niches show similar patterns of geographic co-occurrence.

I found that fruit phenologies were more differentiated than expected by a null model. In the local plant assemblages, the tendency of plants to share frugivores increased with their phenological overlap. These results suggest that shared frugivores may cause indirect competitive interactions among co-fruiting plant species. However, the effects of these indirect plant–plant interactions on the importance of plants in the local assemblages were more complex. Both the interaction strength and the number of partners of plants were interactively determined by variation in their abundance and in the phenological overlap with other co-occurring species. Large phenological overlap among plant species caused a reduction in interaction strength and in the number of partners of abundant plants. In contrast, large phenological overlap enhanced the interaction strength and number of partners of rare plants. On the one hand, these results suggest that, owing to frugivore satiation, abundant plant species mainly competed for dispersal by shared frugivores. On the other hand, the findings show that rare species profited from the attraction of frugivores by other fruiting species in their neighbourhood. These results imply that rare plant species, which are often dispersal-limited, are likely to be co-dispersed with other more abundant plant species that attract frugivores. These results suggest that indirect interactions among plants that share seed dispersers may promote the establishment and persistence of rare species through facilitation. Thus, indirect coupling of species through shared mutualistic partners may be an important determinant of the structure of mutualistic networks. Finally, I found that phenological niche similarity among plant species strongly correlated with their spatial co-occurrence. This suggests that shared frugivores co-disperse simultaneously fruiting plant species in a non-random and directed way to similar habitats. In spite of the overall signal of competition among the central species in the local plant assemblages, co-dispersal by shared frugivores may, thus, cause the formation of plant associations and strongly determine the assembly of plant communities.

CONSUMER-RESOURCE DYNAMICS AND FUNCTIONAL REDUNDANCY IN PLANT–FRUGIVORE NETWORKS

In the third chapter, I studied consumer-resource dynamics in plant–frugivore networks in response to logging and fragmentation of old-growth forests and the effects of these dynamics on the dietary specialization of frugivores and on the functional redundancy in seed dispersal services. First, I used a trait-based approach to study the responses of forest specialist and generalist frugivores to logging and fragmentation. Then I combined network and path analyses to disentangle how changes in the abundance and composition of frugivore assemblages alter competition for fruit resources, the specialization of frugivores on plants, and redundancy in seed dispersal services.

I found that logging involved a reduction in the abundance of forest specialist frugivores, while fragmentation coincided with an increase in the abundance of forest generalists. The reduction in the abundance of forest specialist frugivores in the interior of logged forests involved an increase in dietary specialization of the remaining frugivores and a reduction in functional redundancy. Conversely, the dietary specialization of frugivores decreased at forest edges due to higher densities of forest generalists. This reduction in the dietary specialization of frugivores at forest edges did, however, not enhance functional redundancy, as few generalist frugivores dominated the frugivore assemblages. Therefore, both logging and fragmentation of old-growth forests entailed a reduction in the functional redundancy in frugivore-mediated seed dispersal. These findings suggest that dynamics in the foraging behaviour of frugivores after changes in their population densities affect the structure and potentially the functioning of seed dispersal mutualisms. First, the loss of redundancy in degraded forest habitats may weaken the adaptive potential of frugivore-mediated seed dispersal to changing environmental conditions. Second, the reduction in the number of dispersal vectors may also affect seed shadows and ultimately patterns of plant regeneration in degraded habitats. Thus, my study highlights that the conversion of old-growth forests to secondary habitats may not only entail the loss of rare species, but may also have cascading effects on the structure, functioning and integrity of the communities in which these species are embedded.

Ecological perturbation of coupled mutualistic networks

In the fourth chapter, I studied the collective response of coupled mutualistic networks of plants, pollinators and seed dispersers to logging and fragmentation of continuous old-growth forests. In the first step, I used an information theoretic model selection procedure to estimate the relative importance of the effects of logging and fragmentation on the structure of these coupled networks. Then I combined a meta-analytical approach, with phylogenetic information and path analyses to disentangle the complex factors that were simultaneously operating.

I found that logging of old-growth forests had a strong effect on the interactions of plants with their pollinators and seed dispersers. Unexpectedly, the effect of fragmentation on the structure of these coupled mutualistic networks appeared to be minor, which may be explained by the moderate degree of fragmentation and complex landscape mosaic in the study area. This suggests that the interaction structure of mutualistic communities may be partly preserved in habitat fragments that mimic the structure of primary habitats. On average, logging caused a slight increase in the number of partners and interactions of plants in the pollination mutualism, and a substantial loss of partners and interactions in the seed dispersal mutualism. The gain of pollinators on logged sites may derive from the increased availability of open habitats and alternative resources. In contrast, the marked loss of partners and interactions in the seed dispersal mutualism in logged forest may in part originate from the loss of forest specialists shown in the third chapter. The consistent erosion of plant–seed disperser interactions in logged forests stresses the vulnerability of animal-mediated seed dispersal processes to ecological perturbation. Despite these apparently contrasting responses of both mutualisms, I found that the effects of logging on interactions of plants with their pollinators and seed dispersers were correlated. This means that plant species that were disproportionally affected in one mutualism were also disproportionally affected in the other mutualism. This correlated response of both mutualisms to logging was indirectly mediated by shifts in the density of plant species in secondary forests. Together these results suggest that effects of habitat degradation on coupled mutualistic networks are non-idiosyncratic and bottom-up controlled by the density of plant resources.

Conclusion

All presented studies show that plant–animal mutualistic networks are highly dynamic systems that respond collectively to changing biotic context and human-induced perturbation. The shifts in facilitative and competitive interactions among plants sharing mutualistic partners show that biotic context is a strong determinant of the outcome of interspecific interactions. The use of network analyses, thereby, allowed me to identify some of the mechanisms that shape species interactions and their outcomes. For example, my studies show that a change in the population density of one species suffices to trigger cascading effects on the interactions and populations of other species. This finding highlights that species interactions may have a pervasive effect on the assembly and disassembly of ecological communities. Even more importantly, I could show that these community-wide dynamics were in all cases linked to consumer-resource relationships which are key determinants of plant–animal mutualisms. Thus, changes in the foraging behaviour of animals in response to variation in the density of plant resources and competitors affected the structure of mutualistic communities. This underscores that despite the evolutionary conservatism in ecological interactions, biotic context determines to which extent these coevolved interactions are realized. The fact that the sharing of mutualistic partners among plant species was reflected in their co-occurrence demonstrates that the above-mentioned dynamics in ecological networks may also determine community assembly processes and species co-existence.

Importantly, the comparison of several types of species interactions revealed how biotic context in its various forms can shape land-use effects on species interactions. I found that the mutualism between plants and seed dispersers was more susceptible to habitat degradation than the mutualism between plants and their pollinators. This finding highlights that a high degree of generalization, such as in the seed dispersal mutualism, does not necessarily buffer ecological communities against the loss of species. This becomes even more important if a few species have a disproportionate effect on a given target function and if species are particularly vulnerable to ecological perturbation, such as habitat specialists or large-bodied frugivores. Furthermore, I observed that shifts in the abundance of plant resources in degraded habitats can amplify land-use effects on plant–animal mutualistic interactions. Importantly, changes in the density of plant resources explained about 40 to 70 percent of the variation in land-use effects on interactions between plants and their pollinators and seed dispersers. This demonstrates that a consideration of biotic context (e.g. in the form of resources) may considerably improve predictions of the magnitude of land-use effects on species interactions. Thereby, the correlated responses of pollinators and seed dispersers to the shifts in plant population densities in degraded habitats highlight that these dynamics are not restricted to single types of interaction, but potentially operate at the level of ecosystems. Studies that only focus on subsets of species or interaction types may be unable to identify the consequences of human land-use that have been shown here. In principle, the results of the presented studies may also be valid for other types of mutualistic and antagonistic interactions that are based on consumer-resource relationships. Altogether, the results of my thesis suggest that natural and human-induced dynamics in plant–animal mutualistic networks follow similar principles. In the worst case these dynamics might have cascading effects on the functioning and integrity of ecosystems through a parallel loss of multiple animal-mediated ecosystem services after habitat degradation.

CHAPTER 6

PERSPECTIVES

PROMISING AVENUES FOR FUTURE RESEARCH

The present study has certainly raised more questions than it could answer. In this last chapter, I would like to focus on some of these open questions to highlight promising avenues for future research.

Throughout this thesis I have, apart from the frequency of interactions between pairs of species, not considered differences in the effectiveness of these interactions. In addition, I have not quantified the ultimate effects of species interactions on plant reproductive output and regeneration (Wang & Smith 2002). To date, this lack of information in the '*seed dispersal loop*' is common to all studies of plant–animal mutualistic networks. Owing to this lack of information predictions about potential consequences for plant regeneration and community assembly often remain speculative. Future studies have to evaluate these predictions based on data that go beyond the mere presence and frequency of interactions (Carlo & Yang 2011). For instance, we could ask to which extent species perform particular functions such as long-distance dispersal of pollen or seeds, or how much they contribute to plant regeneration in specific microhabitats (Godínez-Alvarez & Jordano 2007; Díaz *et al.* 2013). One method to incorporate such information is the weighting of interactions with additional information. For example, the interaction frequency can be weighted by fruit handling efficiency of frugivores (Schupp *et al.* 2010), the frequency of their movements to specific microhabitats, and subsequent plant regeneration rates in these microhabitats (Jordano & Schupp 2000; Jordano *et al.* 2007). This information could then be incorporated into population projection matrices (Godínez-Alvarez & Jordano 2007). These projection matrices could in turn be used to make predictions about long-term consequences of a loss of seed dispersers for plant population dynamics, which could then be tested in field studies.

The field of interdependent networks is a newly emerging and very active field of research. Recent theoretical advances highlight the importance of studying several types of species interactions simultaneously (Thébault & Fontaine 2010; Fontaine *et al.* 2011; Mougi & Kondoh 2012; Sauve, Fontaine & Thébault 2013). For instance, early simulation studies suggested that species-rich communities are inherently unstable (May 1972). This view has recently been challenged by simulation studies showing that the diversity of interaction types promotes the stability of species-rich communities (Mougi & Kondoh 2012). However, there are only a few empirical examples of interdependent ecological networks. Augmenting existing datasets with other types of interactions (e.g., herbivory or parasitism) is a promising avenue for future research and may change our perception of species interaction networks (Fontaine *et al.* 2011). For instance, in the studied pollination and seed dispersal mutualisms plants can be considered as '*foundation species*', because they have a disproportionate and predictable effect on community structure and ecosystem processes through interactions with other species (Whitham *et al.* 2006, 2008; Bangert *et al.* 2008). The associated communities and ecosystem processes, thus, represent the '*extended phenotype*' of these foundation species (Whitham *et al.* 2003). Importantly, this extended phenotype has a genetic basis and is heritable (Whitham *et al.* 2006, 2008), which implies that we can study coupled interaction networks within an evolutionary framework. Thus, network analyses could be combined with phylogenetic information and with details about the natural history of plants to explore the ecological and evolutionary mechanisms that structure coupled mutualistic and antagonistic networks. To date, we know that coevolution shapes species traits in mutualistic networks by speeding up the overall rate of evolution, and by favouring trait complementarity among interacting species and trait convergence in species of the same trophic level (Guimarães, Jordano & Thompson 2011). It would be highly interesting to study, whether these coevolutionary dynamics also spread across coupled species interaction networks, and whether these cascades result in the correlated evolution of traits that are associated with different interaction types (Strauss 1997; Thompson 2005). For example, by using phylogenetic comparative analyses it could be tested whether correlated evolution of mutualism and antagonism related traits is a recurrent phenomenon in flowering plants (Herrera 2000; Herrera *et al.* 2002; Gómez 2005; Rey *et al.* 2006; Valdivia & Niemeyer 2007; Abdala-Roberts *et al.* 2009). Moreover, we may ask whether the '*ecological role*' of plant species in different types of species interaction networks is correlated. Then, we could determine the ecological correlates (e.g., abundance or traits) of the plants' roles in these networks (Bascompte & Jordano 2013). Finally, it would be interesting to see whether the same phenotypic traits drive different types of interaction, and whether these traits are phylogenetically conserved (Díaz *et al.* 2013). The answers to these questions likely contribute to our understanding of how networks of interacting species shape evolution and coevolution in species-rich communities, and how human-induced perturbation of ecological communities may alter coevolutionary trajectories and ecosystem integrity.

DEUTSCHE ZUSAMMENFASSUNG

Interaktionen zwischen Arten sind ein essentieller Bestandteil ökologischer Lebensgemeinschaften, weil sie eng mit der Koevolution von Arten sowie mit der Organisation und der Funktionalität von Ökosystemen verbunden sind. Zusammengenommen bilden diese Interaktionen zwischen Arten komplexe und sehr dynamische Beziehungsgeflechte, sogenannte Interaktionsnetzwerke. Die Struktur dieser Netzwerke ändert sich aufgrund der räumlichen und zeitlichen Variabilität im gemeinsamen Vorkommen interagierender Arten und aufgrund der Zu- oder Abnahme einzelner Arten durch die Fragmentierung oder Degradierung natürlicher Lebensräume. Im letzten Urwaldrelikt des Europäischen Tieflands in Białowieża, Ostpolen, untersuchte ich natürliche und menschlich bedingte Dynamiken in hoch diversen mutualistischen Netzwerken aus Pflanzen und deren bestäubenden und samenausbreitenden Tieren. Diese mutualistischen Interaktionen sind von großer Bedeutung, da die Blüten und Früchte vieler Pflanzenarten wichtige Ressourcen für verschiedenste Tierarten darstellen, die ihrerseits entscheidend zur Regeneration von Pflanzengemeinschaften beitragen.

ZENTRALE ERGEBNISSE

Im Rahmen meiner Studien konnte ich zeigen, dass räumliche und zeitliche Variation im Vorkommen verschiedener Pflanzenarten auch deren phänologische Nischen beeinflusst. Die phänologische Nische wiederum bestimmte, inwiefern zeitgleich fruchtende Pflanzenarten um samenausbreitende Tiere konkurrieren oder sich gegenseitig in ihrer Ausbreitungsfähigkeit fördern. So wurden häufige Pflanzenarten seltener von Samenausbreitern besucht, wenn sie zeitgleich mit anderen Arten fruchteten. Seltene Pflanzenarten hingegen profitierten von der Präsenz anderer fruchtender Arten. Zudem waren Pflanzenarten mit einem ähnlichen Spektrum an samenausbreitenden Tierarten auch stark räumlich miteinander assoziiert. Diese Ergebnisse deuten an, dass ökologische Interaktionen sowohl die Organisation ökologischer Gemeinschaften als auch die Koexistenz von Arten beeinflussen. Desweiteren konnte ich zeigen, dass Veränderungen im Nahrungssuchverhalten der Samenausbreiter als Reaktion auf die Verfügbarkeit von Fruchtressourcen und Nahrungskonkurrenz durch andere Tiere einen starken Effekt auf die Struktur der Gemeinschaften hatten. So hatte beispielsweise verminderte Konkurrenz durch den Verlust von Waldspezialisten in genutzten Waldgebieten eine erhöhte Spezialisierung und eine Abnahme der Redundanz in den Beziehungen zwischen Pflanzen und deren Samenausbreitern zur Folge. Dies könnte das Anpassungspotential dieser Gemeinschaften gegenüber Umweltveränderungen einschränken.

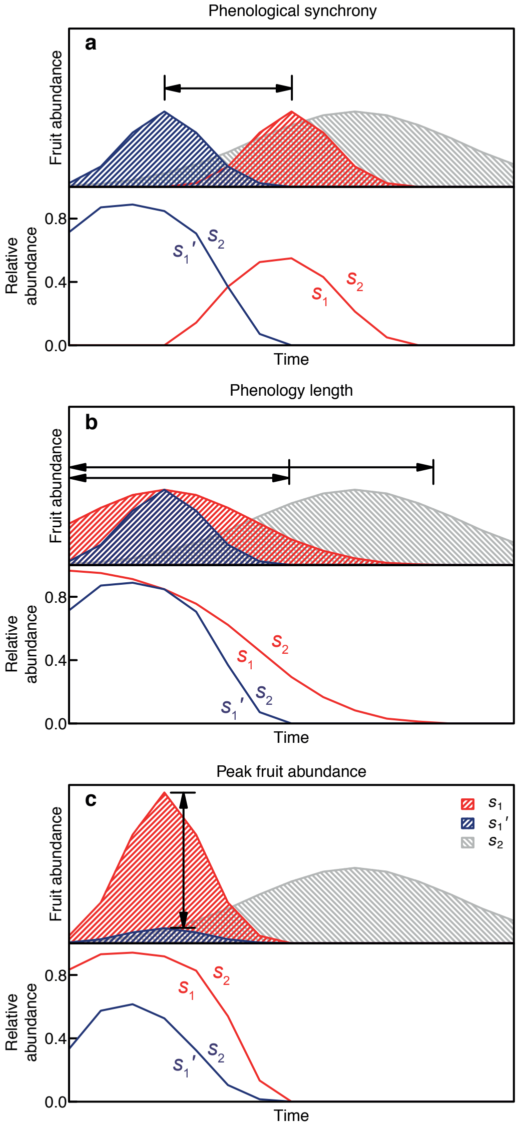
Ein Vergleich der mutualistischen Beziehungen zwischen Pflanzen und ihren Bestäubern und Samenausbreitern zeigte, auf welche Weise der biotische Kontext Landnutzungseffekte auf ökologische Gemeinschaften beeinflussen kann. So reagierte der Mutualismus zwischen Pflanzen und Samenausbreitern empfindlicher auf die Degradation des untersuchten Urwaldgebietes als der Mutualismus zwischen Pflanzen und Bestäubern. Dieses Ergebnis verdeutlicht, dass ein hohes Maß an Generalisierung, wie etwa im Mutualismus zwischen Pflanzen und Samenausbreitern, nicht notwendigerweise einen stabilen Puffer gegenüber einem Verlust von Arten bildet. Dies gilt insbesondere, wenn wenige Arten einen überproportionalen Effekt innerhalb einer Gemeinschaft haben, oder wenn bestimmte Arten besonders sensibel auf menschliche Störung reagieren. Darüber hinaus zeigen meine Studien, dass forstliche Nutzung von Urwaldgebieten korrelierte Effekte auf die Interaktionen der Pflanzen in beiden mutualistischen Beziehungen hatte: Pflanzenarten, die in genutzten Wäldern viele Samenausbreiter verloren, waren auch von einem Verlust an Bestäubern betroffen. Die Stärke dieser Landnutzungseffekte konnte anhand von Verschiebungen in der Häufigkeit einzelner Pflanzenarten in genutzten Waldgebieten mit einer Bestimmtheit von 40 bis 70% vorhergesagt werden. Das bedeutet, dass eine Änderung in der Populationsdichte einer einzigen Art ausreicht, um in einer Art Domino-Effekt die Interaktionen sowie die Populationen anderer Arten zu beeinflussen. Diese Ergebnisse legen nahe, dass die Effekte von Landnutzung auf ökologische Gemeinschaften teilweise durch die Verfügbarkeit von pflanzlichen Nahrungsressourcen in genutzten Lebensräumen getrieben sind. Da natürliche und menschlich bedingte Dynamiken in mutualistischen Gemeinschaften ähnlichen Prinzipien zu folgen scheinen, könnte eine Berücksichtigung der Verfügbarkeit von Ressourcen in genutzten Lebensräumen genauere Vorhersagen über die Stärke von Landnutzungseffekten auf ökologische Gemeinschaften ermöglichen. Insgesamt deuten diese Ergebnisse an, dass Landnutzungseffekte auf Interaktionen zwischen Arten weitreichende Konsequenzen für die Funktionalität ganzer Ökosysteme haben könnten, da sie potentiell zu einem parallelen Verlust verschiedener ökosystemarer Dienstleistungen, wie etwa Bestäubung oder Samenausbreitung, führen können.

APPENDIX CHAPTER 2

Supplementary methods 2.1
Properties of the phenological niche

The ecological niche can either be considered as reflecting species' requirements (Grinellian niche) or species' impacts in an ecosystem (Eltonian niche; Devictor *et al.* 2010). Since the phenological niche of a plant species will affect its relative abundance in the course of the fruiting season, fruit phenologies should, thus, be directly related to the foraging behaviour of frugivores and along with this to a plant's impact in an interaction network (Herrera 1984, 1998; Vázquez *et al.* 2007, 2009). Thus, we can expect that the fruit phenologies are related to the impact of plants in plant–frugivore networks (Devictor *et al.* 2010). In addition, here we refer to the realized rather than the fundamental phenological niche of plants (Devictor *et al.* 2010), because we explicitly incorporate the spatial variability of the biotic environment into our analyses (i.e., the between population variability in the co-occurrence and population density of the plant species).

Which niche properties are important in the context of fruit phenologies? For a community consisting of S species the species' phenologies can be arranged in a matrix with I rows representing the plant species and J columns representing time intervals of equal length, in which each cell a_{ij} gives the mean individual fruit crop of plant species i in week j. If we consider a simple community of $S = 2$ species, the fruit phenology of species s_1 in relation to that of s_2 can be described by three distinct properties: The first two properties are the phenological synchrony between species s_1 and s_2 (Burns 2005) and the length of the fruit phenology of species s_1 in the course of the fruiting season (Supplementary Fig. 2.1a,b; González-Castro *et al.* 2012). These two properties determine the relative temporal position of s_1 in the fruiting sequence and the overlap between species s_1 and s_2. Importantly, in mutualistic networks, a large overlap in species' phenologies (e.g., among plants) is expected to result in a large proportion of shared interactions (Vázquez *et al.* 2009). Moreover, the length of the fruiting season reflects the temporal persistence of a particular fruiting plant species in the course of the fruiting season and is positively correlated with centrality of a plant species in plant–frugivore networks (González-Castro *et al.* 2012). The third property is the relative fruit abundance of species s_1 (Supplementary Fig. 2.1c). The relative fruit abundance varies in the course of the fruiting season, if the fruits of species s_1 or the other species in the community ripen or become depleted. Here we approximate the relative fruit abundance, for illustrative and analytical purposes (see below), as the proportion of all fruits of species s_i (A_i) in relation to the matrix total m (i.e., $q_i = A_i/m$). Importantly, the dominance of a species in a community (e.g., in terms of population density) causes a sharp transition in the temporal distribution of relative fruit abundances,



Supplementary Figure 2.1. Three properties that qualify the phenological niche of species s_1 (red, scenario s_1; darkblue, scenario s_1') in the context of a second species s_2 (grey). Shown are scenarios with (**a**) varying phenological synchrony between species s_1 and species s_2, (**b**) varying phenology length of s_2, and (**c**) varying peak fruit abundance of species s_1. The lower panels in (**a**–**c**) show the relative abundances of species s_1 and species s_2 in the course of the fruiting season for two scenarios for species s_1 (s_1, red; and s_1', darkblue). Note that all else being equal (**a**) phenological asynchrony, (**b**) short, non-overlapping phenologies, and (**c**) the dominance of a species (e.g., in terms of population density) cause sharp transitions in the temporal distribution of relative fruit abundances.

whereas even species abundances result in time periods without clearly differentiated patterns of relative fruit abundance (Supplementary Fig. 2.1c). Frugivores, in turn, are likely to concentrate their foraging activities on the most abundant fruiting plant species to reduce energetic costs, while they may use rare plant species more opportunistically to complement their diet (Herrera 1984, 1998; Whelan *et al.* 1998). The relative abundance of a species at a certain time of the fruiting season should hence be related to the interaction frequency in mutualistic networks (Vázquez *et al.* 2007; Encinas-Viso *et al.* 2012). According to this rationale species s_1 may represent a peripheral resource compared to species s_2 if it accounts for a small proportion of the overall fruit availability (Supplementary Fig. 2.1c). Conversely, the fruits of species s_2 may represent peripheral resources if plant species s_1 is dominant during its fruiting period and fruiting patterns of s_1 and s_2 will be more differentiated (Supplementary Fig. 2.1c). In conclusion, this means that the relative abundance of a fruiting plant species can offset its degree of niche differentiation.

Supplementary methods 2.2

Standardized Kullback-Leibler divergence as a measure of phenological niche differentiation

For the reasons outlined above, a suitable measure of niche differentiation should not only be sensitive to '*phenological overlap*' per se but should also reflect the between-population variability in the relative abundances of different fruiting plant species. The necessity to incorporate relative species abundances into indices of niche overlap in consumer-resource relationships has already been highlighted by Hurlbert (1978) and has been taken on by Blüthgen *et al.* (2006, 2008). However, none of the traditional niche overlap indices fulfils this requirement (Hurlbert 1978; Blüthgen *et al.* 2006, 2008). Recently novel indices based on the Kullback-Leibler divergence have been introduced to measure the specialization of species in ecological interaction networks (Blüthgen *et al.* 2006). These indices measure specialization as the deviation of observed interactions between pairs of species from a null expectation assuming that species interact with other species in proportion to their relative abundance (Blüthgen *et al.* 2006). However, in its essence the metric proposed by Blüthgen *et al.* (2006) characterises the niche overlap between species in a community and may in principle reflect species' differentiation in any niche dimension.

Here we propose the use of the Kullback-Leibler divergence in its standardized form (Blüthgen *et al.* 2006) to quantify the niche differentiation of plant species in the phenological context. To outline the method we adopt the notation of Blüthgen *et al.* (2006). Consider a matrix of I rows and J columns, in which each cell gives the average number of fruits of plant species i in each time interval j. If p'_{ij} is the proportion of the number of fruits (a_{ij}) of plant species i in time interval j in relation to the respective row total (A_i), then $p'_{ij} = a_{ij}/A_i$ and $\sum_{j=1}^{J} p'_{ij} = 1$. Furthermore, if q_j is the proportion of all fruits in time interval j in relation to the total number of fruits in the local plant assemblage across the entire season (m, i.e., the matrix total), then $q_j = A_j/m$ and $\sum_{j=1}^{J} q_j = 1$. The Kullback-Leibler divergence for plant species i is then denoted as:

$$d_i = \sum_{j=1}^{J} p'_{ij} \ln\left(\frac{p'_{ij}}{q_j}\right) \qquad \text{eqn. 2.2}$$

In the phenological context the Kullback-Leibler divergence thus compares the temporal distribution of the fruits of plant species i (p'_{ij}) in the course of the fruiting season J relative to the overall fruit availability in the whole plant assemblage (q_j) in each time interval j. Blüthgen *et al.* (2006) suggest a standardization of the measure by the theoretical minimum and maximum d_i for a particular matrix configuration:

$$d'_i = \frac{\left(d_i - d_{\min}\right)}{\left(d_{\max} - d_{\min}\right)} \qquad \text{eqn. 2.3}$$

where the theoretical maximum is $d_{\max} = \ln\left(m/A_i\right)$ and the theoretical minimum is zero if all $p'_{ij} = q_j$ (Blüthgen *et al.* 2006). In practice, Blüthgen *et al.* (2006) propose a more constrained variant to approximate $d_{\min}$ by using a heuristic search algorithm. The standardized form d'_i ranges from 0 to 1, and quantifies the deviation of the actual temporal distribution of fruits of plant species i from a null model which assumes that the fruits are distributed in proportion to the overall fruit availability in the local plant assemblage, that is without phenological differentiation among the plant species.

Both the theoretical minimum and maximum have important properties that have to be mentioned here, as they have an effect on the estimates of niche differentiation d'. If q_i is the proportion of all fruits of species i (A_i) in relation to the matrix total m, then $q_i = A_i/m$. From this equation it is clear that $d_{\max}$ converges towards zero as q_i approaches 1, since A_i approaches m:

$$\lim_{q_i \to 1} d_{\max}\left(q_i\right) = \ln\left(\frac{1}{q_i}\right) = \ln\left(\frac{m}{A_i}\right) = 0 \qquad \text{eqn. 2.4}$$

Furthermore, if p'_{ji} is the proportion of the number of fruits (a_{ij}) of plant species i in time interval j in relation to the respective column total (A_j), then $p'_{ji} = a_{ji}/A_j$. If plant species i does not produce fruits in all time intervals J, then the sum of all p'_{ji} of plant species i will always be smaller than the number of time intervals J (i.e., $\sum_{j=1}^{J} p'_{ji} << J$). Therefore, d'_i will converge towards 1, if and only if plant species i is superabundant (i.e., $q_i \approx 1$), and the fruit phenology does not cover the entire season (i.e., $\sum_{j=1}^{J} p'_{ji} << J$).

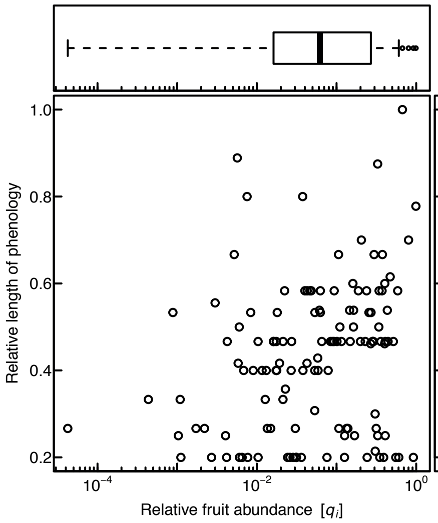
Regarding the theoretical minimum (zero) where all $p'_{ij} = q_j$, it is important to note that d_i converges towards zero if the sum of all p'_{ji} of plant species i approaches the number of time intervals J of the entire fruiting season:

$$\lim_{\sum_{j=1}^{J} p'_{ji} \to J} d_i\left(\sum_{j=1}^{J} p'_{ji}\right) = 0 \qquad \text{eqn. 2.5}$$

Thus, d'_i will converge towards 0, if plant species i is superabundant (i.e., $q_i \approx 1$), and dominant in all time intervals J (i.e., $\sum_{j=1}^{J} p'_{ij} \approx J$). This property inflates the monotonic increase of d'_i if plant species i becomes superabundant. This was, however, not the case in the empirical fruit phenologies (Supplementary Fig. 2.2).

SIMULATION STUDY

To assess whether the niche metric d' has desirable properties for our purpose and within the empirical range of the data, we simulated plant phenologies for a simple two species assemblage in which we varied the phenological synchrony between s_1 and s_2, the phenology length of s_1, and the relative fruit abundance (q_1) of s_1 (Supplementary Fig. 2.3). Since the metric d' compares the proportional abundance of plant species i to the marginal distribution of the phenology matrix (equation 2.2), phenologies for a simple two species assemblage suffice for our simulations. The phenologies in our study represented the average number of ripe fruits counted on a plant species in weekly time intervals. In the simulation we set the length of the fruiting season to 15 weeks, which corresponded to the time span of the empirical fruiting season. We simulated phenologies by sampling '*successes*' from a multinomial distribution with $J = 15$ classes representing the J weeks of the phenology, in which the fruits of a plant species could be encountered.

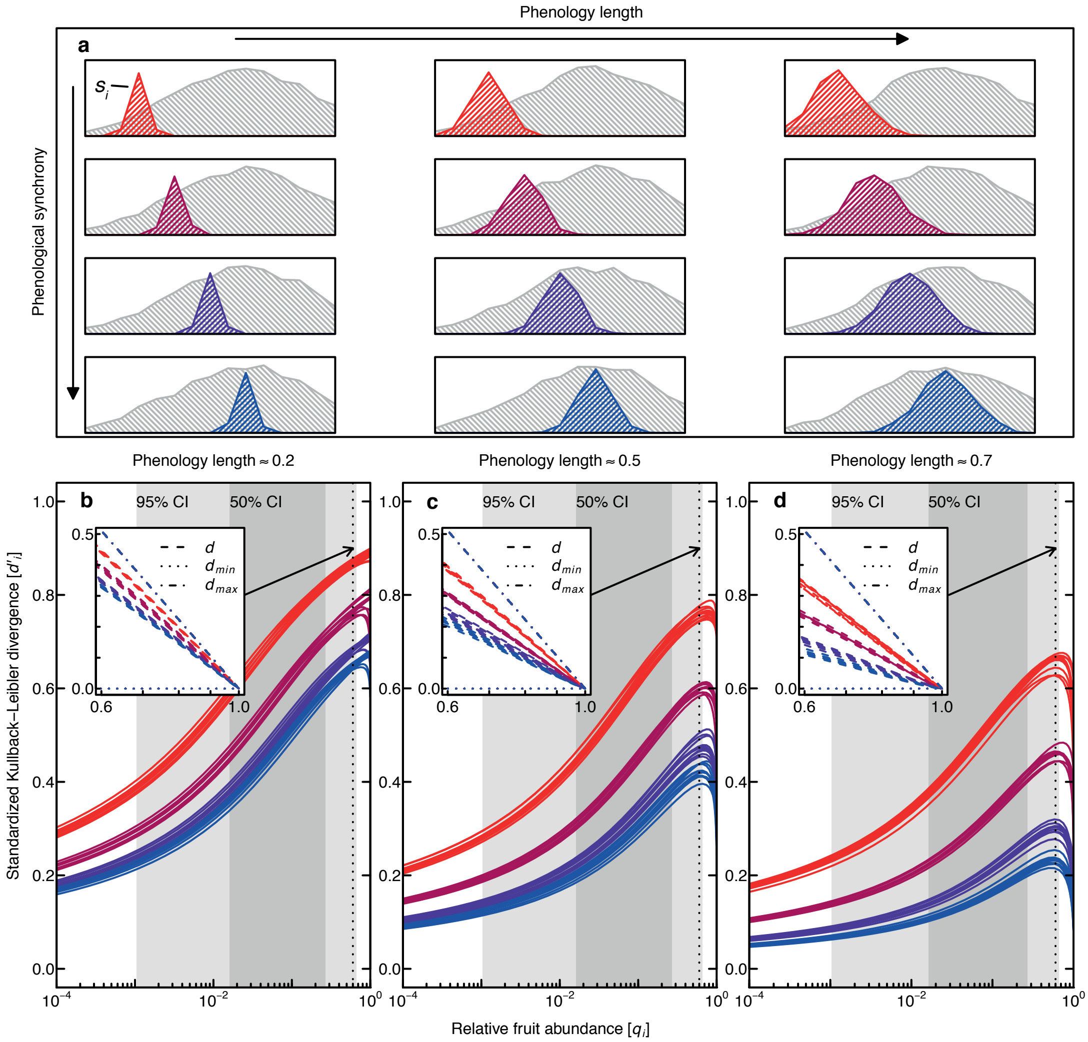


Supplementary Figure 2.2. Range of the empirical data for relative fruit abundance and relative length of the phenology of the focal plants in the data set (*n* = 128).

The likelihood of sampling a success in week j was given by the probability density function of a normal distribution $f(j, \mu, \sigma^2)$ with mean μ and standard deviation σ^2. In order to obtain similar peak fruit densities [i.e., $\max(p_{1j}) \approx \max(p_{2j})$] for different standard deviations in the simulation, the number of trials in the multinomial sampling process was given by $1{,}000 / \sigma^2$. For instance, we sampled a total of 1,000 fruits for a normal distribution with $\sigma^2 = 1$ and 500 fruits for a distribution with $\sigma^2 = 2$. We set the mean fruiting weak μ for species s_1 to 4, 6, 8 and 10, whereas μ for species s_2 was kept fixed at a value of 10. The standard deviation σ^2 for species s_1 was set to 0.5, 1 and 1.5, which corresponded to the empirical relative phenology lengths of approximately 0.2, 0.5, and 0.7 in our dataset (Supplementary Fig. 2.2). The standard deviation for species s_2 was set to $\sigma^2 = 4$ so that its phenology covered the entire fruiting season. For each parameter combination we simulated 10 fruiting seasons. To obtain a continuum of relative fruit abundances q_1 for species s_1 (for definition see above), we multiplied the fruit phenology of species s_1 with a sequence of values ranging from 100 to 10^8. The fruit phenology of species s_2 was multiplied by a fixed value of 10^4.

RESULTS OF THE SIMULATION STUDY

The simulations highlight three important properties of the niche metric d'. All else being equal, the phenological differentiation of species s_1 from species s_2 increases as (1) the phenological synchrony between s_1 and s_2 decreases, (2) the relative length of the fruit phenology of species s_1 decreases, and (3) the relative



Supplementary Figure 2.3. Results of the simulation study showing the behaviour of the standardized Kullback-Leibler divergence *d′* as a measure of phenological niche differentiation. (**a**) Examples of simulated phenologies with varying phenological synchrony, and phenology length of species s_i in relation to the overall length of the fruiting season against a background phenology of a second species. (**b**–**d**) Standardized Kullback-Leibler divergence d'_i as a function of relative peak fruit abundance of species s_i for 10 simulated phenologies for each parameter set. In (**b**–**d**) the colours of the lines correspond to the different parameter sets of phenological synchrony shown in (**a**). Note that the phenological differentiation (d'_i) of species s_i from the remaining species $S\backslash s_i$ increases as (1) the phenological synchrony between s_i and $S\backslash s_i$ decreases, as (2) the phenology length of species s_i decreases, or as (3) the relative fruit abundance of species s_i approaches 1, that is, as the dominance of species s_i in the plant community increases. The shades of grey in (**b**–**d**) give the 50 % and 95 % confidence regions of the empirical data. The insets in (**b**–**d**) show the behaviour of d, d_{min} and d_{max}, at the upper limit of the relative abundance of species s_i, that is, if species s_i becomes extremely dominant.

fruit abundance of species s_1 approaches 1, that is, as the dominance of species s_1 increases. As expected, the relationship between the relative fruit abundance and *d′* of species s_1 is only monotonic up to a certain threshold of relative abundance *q*, if the fruiting phenology of species s_1 covers a large fraction of the fruiting season (Supplementary Fig. 2.3c). However, the majority of the empirical data of the relative fruit abundance and relative length of the fruit phenologies of the sampled plant species is within the range in which *d′* shows a monotonic increase (Supplementary Fig. 2.3b–d). Thus, we conclude that within the range of our empirical data *d′* has desirable properties to describe the phenological differentiation of the studied plant species.

Supplementary methods 2.3

Neighbourhood effects on absolute rates of fruit removal from plants

To test for effects of conspecific fruit densities and

Supplementary Table 2.1. Summary of linear mixed effects model. Shown are the effects of conspecific fruit densities [fruits ha^{-1}], phenological differentiation [d'_{phen}], and their interaction on the rate of fruit removal by frugivores from plants.

Source of variance	Estimate	SE	*z*-value	*P*-value
Response: Fruit removal rate				
Conspecific fruit density	**0.46**	**0.14**	**3.25**	**0.0012**
Phenological differentiation	−0.044	0.14	−0.325	0.74
Conspecific fruit density × Phenological differentiation	**0.28**	**0.12**	**2.42**	**0.015**

Notes: Given are standardized parameter estimates and corresponding standard errors (SE). Significant effects at a level of $P < 0.05$ are highlighted in boldface type.

phenological differentiation on absolute rates of fruit removal from plants we used linear mixed-effects models similar to those employed in the main text (see section on Statistical analysis in main document; Bates *et al.* 2013). In these analyses, we treated conspecific fruit density, phenological differentiation and their interaction as fixed continuous predictors. We fitted site, year and plant species as separate random grouping factors. For the number of fruits removed from the plants we fitted a model with poisson error distribution and a log link function. Since the residuals of this model were overdispersed ($\chi^2 = 10953.84$, ratio = 90.53, $df = 121$, $P < 0.001$), we fitted an additional observation-level random effect to account for this extra variation (Hinde 1982; Williams 1982; Breslow 1984; Bates *et al.* 2013). We standardized the predictor variables to zero mean and unit variance to allow for a comparison of effect sizes. The results obtained from this model were similar to the results for the interaction strength of plants (Supplementary Table 2.1, Table 2.1 in main text). The results for the absolute fruit removal indicate that low phenological differentiation reduced fruit removal from plants at high conspecific densities, but enhanced fruit removal at low conspecific densities.

SUPPLEMENTARY METHODS 2.4

CORRELATION BETWEEN THE CO-OCCURRENCE AND THE PHENOLOGICAL NICHE SIMILARITY OF THE PLANT SPECIES

Co-dispersal of different plant species that fruit simultaneously, as well as directional seed dispersal patterns between co-fruiting plant species, might contribute to the formation of species associations (Wenny 2001; Clark *et al.* 2004; Carlo & Aukema 2005). This implies that the co-occurrence of plant species at the landscape scale may be correlated with the similarity of the phenological niche of the plant species. To test for this correlation we performed a procrustes analysis. Previous work suggests that Procrustes analysis can outperform the Mantel test in determining the concordance between matrices (Jackson 1995; Peres-Neto & Jackson 2001).

QUANTIFICATION OF SPECIES CO-OCCURRENCE AND PHENOLOGICAL SIMILARITY

In our case the analysis required a species × site community matrix and a week × species phenology matrix. In the first step, we created the species × site matrix, in which each cell contained the population density of each plant species i on each study site l (see Methods section: Census of plant population densities in main text). These population densities were then standardized by the total plant density on each study site (i.e., corresponding to relative species densities). In the next step, we used the comprehensive set of standardized fruit phenologies (see Methods section: Compilation of the regional set of fruit phenologies in main text), in which each cell gave the mean individual fruit crop of plant species i in week j. The phenology of each species was standardized to range between 0 and 1, by dividing the fruit crop of plant species i in each week by the maximum fruit crop of the respective species during the fruiting period. Similar to population densities, these fruiting intensities were then standardized by the total fruit crop in each week (i.e., corresponding to relative species densities). We then created for each matrix a distance matrix based on Bray-Curtis distances.

PROCRUSTES CORRELATION BETWEEN PHENOLOGICAL AND CO-OCCURRENCE DISTANCE MATRICES

On these distance matrices we performed orthogonal, least-squares Procrustes analyses. The Procrustes algorithm minimizes the sums-of-squares distances between corresponding observations between two matrices by translating, reflecting, rotating and scaling one matrix to fit the other (Jackson 1995; Peres-Neto & Jackson 2001). The approach thus maps the positions of plant species in the phenology on superimposed co-occurrences across the study sites. The goodness-of-fit of the superimposition is measured with the $m_{12}{}^2$ statistic, because it is symmetric and varies from 0 to 1, with smaller values indicating a better fit (Jackson 1995; Peres-Neto & Jackson 2001). The correlation between the two matrices can then be expressed as $r = \sqrt{(1 - m_{12}^2)}$ (Peres-Neto & Jackson 2001). Significance of the statistic was determined using a permutation test (9,999 permutations; Jackson 1995; Peres-Neto &

Jackson 2001). Statistical analyses were done in *R* (R Development Core Team 2013), using the package *vegan* for Procrustes analysis (Oksanen *et al.* 2011).

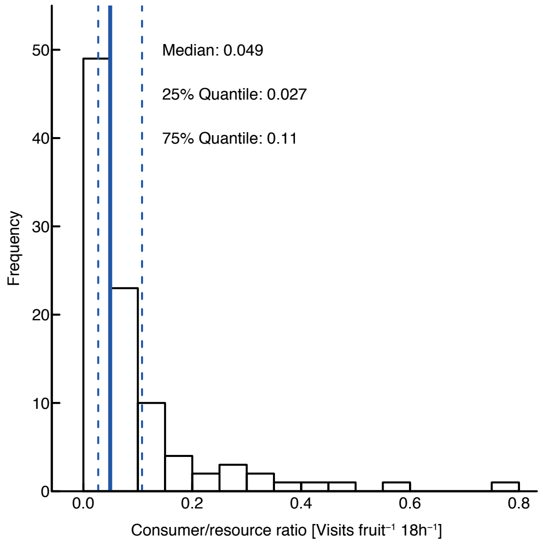
The procrustes analysis indicated that the similarity of fruit phenologies was strongly correlated with the co-occurrence of the plant species ($r = 0.71$, $P < 0.05$). This strong and non-random correlation indicates that simultaneous fruit production is likely to result in the co-dispersal of plant species by shared frugivores.

APPENDIX CHAPTER 3

Supplementary methods 3.1

Monitoring of fruit abundance along transects in 2011

From July to October 2011 we monitored overall fruit abundance on all study sites. On each study site we established one transect of 250 m length and 20 m width covering a total area of 0.5 ha. On some study sites ash-alder forests were continuously flooded and accessibility was limited. Thus, we established transects on all study sites along pre-existing trails. As the temporal turnover in fruit ripening of plants was low, we repeated transect walks twice during the study period (from the 1st to 5th August, 2011 and from 1st to 5th September, 2011). During the transect walks all fleshy-fruited plants bearing ripe fruits were identified within each transect. For each plant the presence and number of ripe fruits were estimated on a logarithmic scale and the number of fruits available per transect walk and plot was calculated. For each study site we calculated the mean fruit abundance by averaging across the two transect walks.



Supplementary Figure 3.1. Distribution of observed consumer/ resource ratios [visits fruit^{-1} 18 h^{-1}] of all observed focal plants (*n* = 98). The vertical lines represent the median (solid line) and the 25 % and 75 % quartiles (dashed lines).

Supplementary methods 3.2

Estimation of consumer/resource ratios and inference about competition

Measuring competition for resources is not trivial. Here we used the consumer/resource ratio as a rather simple surrogate for the degree of competition for fruit resources. This measure has to be interpreted with caution since we have no information on the absolute effect of consumer/resource ratios on the fitness of the consumers (i.e., reproductive success). However, the mean consumer/resource ratios in the different forest types can be interpreted relative to the distribution of the consumer/resource ratios of all observed focal plants (*n* = 98). At least, a comparison of consumer/resource ratios in a given habitat type with the overall distribution provides an indication of how much the consumer/resource ratio deviates from what is expected from the overall sample. In order to draw inferences about competition from consumer/resource ratios we first calculated the consumer/resource ratio for each focal plant and determined the median and the 25 % and 75 % quartiles of the distribution (Supplementary Fig. 3.1). Next we compared the observed distribution of consumer/resource ratios with the mean consumer/resource ratios in the different habitat types (Fig. 3.2a and Supplementary Fig. 3.1). In the interior of old-growth forests the consumer/resource ratio (0.058 ± 0.010; mean ± SE) equalled the median consumer/resource ratio of all observed focal plants (median = 0.049; 25 % quartile: 0.027; 75 % quartile: 0.11). In contrast, the consumer/resource ratios were lower (0.0096 ± 0.0089) in the interior of logged forests and were higher (logged: 0.11 ± 0.010; old-growth: 0.085 ± 0.0086) at forest edges than the median consumer/resource ratio of all observed focal plants. This suggests a higher pressure on the available fruit resources at forest edges (i.e. increased competition) and a reduced pressure on fruit resources in the interior of logged forests (i.e. reduced competition) compared to the interior of old-growth forests.

Supplementary methods 3.3

Partitioning of diversity into independent richness and evenness components

A recent review by Tuomisto (2012) has shown that Shannon diversity can be partitioned into independent richness and evenness components in a multiplicative manner (equation 3.7). This approach is mathematically related to the partitioning of diversity into alpha and beta components (Jost 2007) According to the above mentioned concept multiplicative partitioning of diversity into richness and evenness components can be written as:

$$e^{H_i} = E_i \times J_i \qquad \text{eqn. 3.7}$$

where e^{H_i} is the exponent of the Shannon-index, E_i is the evenness component and J_i is the richness component in the spectrum of frugivores on plant species *i*. Following the correct definition of evenness (Hill 1973):

$$E_i = \frac{e^{H_i}}{J_i} \qquad \text{eqn. 3.8}$$

equation 3.7 can also be rewritten as follows:

$$e^H = \frac{e^H}{J_i} \times J_i \qquad \text{eqn. 3.9}$$

Note that the evenness and richness components measure two different phenomena, that is, (1) the equitability in the interaction frequency of species and (2) the number of involved species (Tuomisto 2012). Further, evenness is replication invariant, that is, does not change when a dataset is replicated such that each of its species gives rise to n new species of the same absolute abundance as the original one (Hill 1973). Given that both of these measures quantify different phenomena they can vary independently of each other and multiplied express the '*effective*' number of species if all were equally common (Tuomisto 2012).

In the following we show that this framework easily can be generalised to be used with species interaction networks. To measure the effective number of dispersal vectors per plant species S_q we calculated the mean across the plants in a given network where each plant was weighted by its interaction strength as:

$$S_q = \sum_{i=1}^{I} \frac{A_i}{m} e^{H_i} \qquad \text{eqn. 3.10}$$

where A_i is the sum of interactions of plant species *i* and *m* is the sum of interactions in the network. Likewise the evenness and richness components can be calculated. Finally, equation 3.7 can be generalised to the network context as follows:

$$\sum_{i=1}^{I} \frac{A_i}{m} e^{H_i} = \sum_{i=1}^{I} \frac{A_i}{m} \frac{e^{H_i}}{J_i} \times \sum_{i=1}^{I} \frac{A_i}{m} J_i \qquad \text{eqn. 3.11}$$

Since equation 3.7 holds for all plant species *I* in a network and diversity as well as its components for each plant species *i* are scaled by the same constants (i.e. the interaction strength of plant species *i*) the assumptions of equation 3.7 also hold for equation 3.11.

SUPPLEMENTARY METHODS 3.4

PARTITIONING OF ENVIRONMENTAL AND SPATIAL EFFECTS ON COMPOSITION OF FRUGIVORE ASSEMBLAGES

We used a PCNM analysis (Principal Coordinates of Neighbourhood Matrix; Dray, Legendre & Peres-Neto 2006) combined with a multivariate redundancy analysis (RDA) to partition the variance in the species turnover of the frugivore assemblages among study sites that was explained by environmental and spatial components. In our case the analysis required (i) a site × species community matrix, (ii) a table containing spatial eigenvectors retained from PCNM analysis and (iii) a table containing the environmental variables.

COMMUNITY DATA

For the multivariate redundancy analysis (RDA) we constructed a site × species matrix. To do so we first calculated the mean abundance of each frugivore species across the plant species for each study site and year (i.e., the mean visitation rate of each frugivore species in each of the 18 networks during 18 hours). Then we calculated the mean abundance of each frugivore species across the two study years for each study site (i.e., the mean abundance of each frugivore species across the two networks per study site). We applied a Hellinger transformation to the abundance data prior to analysis (Legendre & Gallagher 2001). Hellinger transformation makes abundance data containing many zeros suitable for analysis by linear methods such as redundancy analysis (Legendre 2007).

SPATIAL VARIABLES

We derived the spatial variables by using principal coordinates of neighbourhood matrices (PCNM), a method well suited for the detection of spatial trends across a wide range of scales (Borcard & Legendre 2002; Borcard *et al.* 2004; Dray *et al.* 2006). The GPS coordinates of the centre of each study site were used to construct a Euclidean distance matrix. This matrix was truncated at the smallest distance that keeps all sites connected in a single network (9.8 km in our case). The distances above the truncation threshold were given an arbitrary value of four times the threshold. Then, we used a principal coordinates analysis (PCoA) to retain the eigenvectors associated with positive eigenvalues as spatial variables (PCNM variables; Borcard & Legendre 2002; Borcard *et al.* 2004). We used a forward selection procedure based on redundancy analysis (RDA) to retain the spatial eigenvectors that explain most of the variation in the species turnover among the study sites. The

Supplementary Table 3.1. Partitioning of variation in the composition of frugivore assemblages in the local networks that was explained by environmental and spatial components.

Source of Variance	$Df_{\mathrm{num}}, Df_{\mathrm{den}}$	r^2_{adj}	F	P
Environment + spatially structured environment	**4,5**	**0.31**	**2.04**	**0.019**
Space + spatially structured environment	1,8	0.14	2.44	0.10
Environment + space + spatially structured environment	**5,4**	**0.50**	**2.79**	**0.0047**
Environment	**4,4**	**0.36**	**2.44**	**0.017**
Space	1,4	0.18	2.81	0.079
Spatially structured environment	–	−0.040	–	–
Residual	–	0.50		

Notes: The spatially structured environment fraction is not testable in a separate model. The negative variance component for spatially structured environment indicates that environmental and spatial components are not completely uncorrelated, that is, they are not orthogonal. Df_{num} and Df_{den} give numerator and denominator degrees of freedom, respectively. Significant predictors at a level of $P < 0.05$ are given in boldface type.

forward selection was based on a double-stop criterion (Blanchet, Legendre & Borcard 2008). The procedure began with performing a global test (RDA) with all spatial eigenvectors. Afterwards, α-values ($P < 0.1$ based on pseudo F-values after 9,999 permutations) and coefficients of determination (r^2) of global tests were used as stopping criteria in the forward selection of variables. The spatial eigenvectors that fulfilled both stopping criteria were identified as the significant spatial variables influencing the variation in the species turnover among the study sites.

ENVIRONMENTAL VARIABLES

The environmental table contained the two main factors location and logging. The main factors were represented by dummy variables coded by 0 and 1. The interaction between the main factors was included as the product of the two dummy variables. Moreover, we included fruit abundance (ln(x) transformed, mean across the two years for each study site) as a continuous predictor into the environmental table.

PARTITIONING OF ENVIRONMENTAL AND SPATIAL COMPONENTS

In the last step we used multivariate redundancy analysis to partition the variation in the species turnover among the study sites with respect to the environmental and spatial components (Borcard, Legendre & Drapeau 1992). For inference we used adjusted r^2 values as unbiased estimators of explained variation (Peres-Neto *et al.* 2006). We assessed the significance of the joint and independent environmental and spatial components using pseudo F-tests based on 9,999 permutations. All analyses were conducted in *R* version 2.14.0 (R Development Core Team 2013), using the packages *vegan* (Oksanen *et al.* 2011) and *packfor* (Dray, Legendre & Blanchet 2011).

VARIATION IN SPECIES TURNOVER EXPLAINED BY ENVIRONMENTAL AND SPATIAL COMPONENTS

The forward selection procedure identified one spatial eigenvector (PCNM4: $r^2 = 0.05$; $P = 0.095$) as predictor of species turnover. The partitioning of environmental and spatial effects showed that the spatial component in our study design explained 18 % of the variation in species turnover among study sites ($F_{1,4} = 2.81$, $P = 0.079$; Supplementary Table 3.1). After accounting for the spatial component the environmental component significantly explained 36 % of the variation in the species turnover among study sites ($F_{4,4} = 2.44$, $P = 0.017$; Supplementary Table 3.1). Thus, we are confident that the observed patterns are not merely a spatial artefact.

Supplementary Table 3.2. Geographical coordinates and characteristics of the 18 plant–frugivore networks quantified in Białowieża forest, Eastern Poland in the years 2011 and 2012.

Site	Latitude	Longitude	Logging	Location	Fruit abundance		Number of plant species		Number of frugivore species		Number of interaction links		Total number of interactions		CV Interaction frequencies	
					2011	2012	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
1	52.702392	23.653490	Logged	Interior	3820	4494	3	8	5	11	6	31	16	192	120.2	142.3
2	52.704851	23.622394	Logged	Interior	2303	2016	4	9	7	15	8	39	52	306	154.7	159.9
3	52.670400	23.685470	Logged	Interior	973	–	2	–	6	–	7	–	33	–	79.10	–
4	52.742117	23.834359	Old-growth	Interior	2000	6262	3	6	11	19	17	40	51	397	141.4	247.5
5	52.789228	23.846072	Old-growth	Interior	4852	5568	5	6	9	13	20	30	110	239	157.8	165.9
6	52.716240	23.815790	Logged	Edge	2809	3075	6	8	9	12	24	28	207	260	151.6	253.9
7	52.734361	23.789260	Logged	Edge	5915	3209	5	8	14	11	27	42	336	156	264.7	128.4
8	52.730727	23.822149	Old-growth	Edge	494	2464	2	5	7	9	9	17	44	111	125.0	102.8
9	52.799012	23.824978	Old-growth	Edge	9794	13739	8	8	11	16	29	51	510	1133	236.9	230.4
10	52.779600	23.857875	Old-growth	Edge	4250	–	5	–	12	–	25	–	224	–	149.2	–

Notes: CV, coefficient of variation.

Supplementary Table 3.3. Summary of linear mixed effects models. Shown are mixed models (Typ III SS) testing the effect of location (forest interior vs. edge), logging (logged vs. old-growth), year and second order interactions on (**a**) fruiting plant richness, (**b**) network size, (**c**) total number of interactions and (**d**) coefficient of variation (CV) of interaction frequencies in the 18 plant–frugivore networks quantified in Białowieża Forest, Eastern Poland in 2011 and 2012.

Source of Variance	Df_{num},Df_{den}	*F*	*P*
(**a**) *Fruiting plant richness*			
Location	1,6	1.07	0.34
Logging	1,6	0.141	0.72
Year	1,5	**9.75**	**0.026**
Location × logging	1,6	0.087	0.78
Year × location	1,5	2.86	0.15
Year × logging	1,5	4.95	0.077
(**b**) *Network size*			
Location	1,6	0.469	0.52
Logging	1,6	1.34	0.29
Year	1,5	**14.5**	**0.013**
Location × logging	1,6	1.14	0.33
Year × location	1,5	4.68	0.083
Year × logging	1,5	0.612	0.47
(**c**) *Total number of interactions*			
Location	1,6	2.74	0.15
Logging	1,6	0.521	0.5
Year	1,5	**14.9**	**0.012**
Location × logging	1,6	0.349	0.58
Year × location	1,5	**7.31**	0.043
Year × logging	1,5	0.116	0.75
(**d**) *CV of interaction frequency*			
Location	1,6	0.16	0.7
Logging	1,6	0.553	0.49
Year	1,5	1.24	0.32
Location × logging	1,6	1.86	0.22
Year × location	1,5	1.03	0.36
Year × logging	1,5	0.116	0.75

Notes: Network size and total number of interactions were ln(*x*) transformed prior to statistical analysis. Significant predictors at a level of $P < 0.05$ are given in boldface type.

Supplementary Table 3.4. List of codes for frugivore and plant species. Mammals are marked with an asterisk. Frugivores were classified into forest specialists and generalists (Jędrzejewska & Jędrzejewski 1998a, b; Svensson *et al.* 2009). Forest specialists reproduce exclusively in forest habitats, whereas generalists also reproduce in non-forest habitats.

Code	Scientific name	Vernacular name	Habitat specialization
Frugivores			
1	*Sylvia atricapilla*	Eurasian Blackcap	Generalist
2	*Turdus merula*	Common Blackbird	Generalist
3	*Erithacus rubecula*	European Robin	Generalist
4	*Turdus philomelos*	Song Thrush	Generalist
5	*Coccothraustes coccothraustes*	Hawfinch	Specialist
6	*Parus major*	Great tit	Generalist
7	*Sylvia borin*	Garden Warbler	Generalist
8	*Poecile palustris*	Marsh Tit	Specialist
9	*Sitta europaea*	Eurasian Nuthatch	Generalist
10	*Muscicapa striata*	Spotted Flycatcher	Generalist
11	*Fringilla coelebs*	Common Chaffinch	Generalist
12	*Dendrocopos major*	Great Spotted Woodpecker	Generalist
13	*Luscinia luscinia*	Thrush Nightingale	Specialist
14	*Garrulus glandarius*	Eurasian Jay	Specialist
15	*Ficedula hypoleuca*	European Pied Flycatcher	Specialist
16	*Tetrastes bonasia*	Hazel Grouse	Specialist
17	*Poecile montanus*	Willow Tit	Generalist
18	*Dendrocopos medius*	Middle Spotted Woodpecker	Specialist
19	*Phylloscopus trochilus*	Willow Warbler	Generalist
20	*Pyrrhula pyrrhula*	Eurasian Bullfinch	Generalist
21	*Apodemus flavicollis**	Yellow-necked Mouse	Specialist
22	*Ficedula parva*	Red-breasted Flycatcher	Specialist
23	*Dendrocopos leucotos*	White-backed Woodpecker	Specialist
24	*Oriolus oriolus*	Eurasian Golden Oriole	Specialist
25	*Turdus pilaris*	Fieldfare	Generalist
26	*Columba palumbus*	Common Wood Pigeon	Generalist
27	*Dryocopus martius*	Black Woodpecker	Specialist
28	*Martes martes**	European Pine Marten	Specialist
29	*Periparus ater*	Coal Tit	Specialist
30	*Sciurus vulgaris**	Eurasian Red Squirrel	Specialist
31	*Turdus iliacus*	Redwing	Generalist
32	*Turdus viscivorus*	Mistle Thrush	Generalist
Plants			
P1	*Cornus sanguinea*	Common Dogwood	–
P2	*Euonymus europaeus*	European Spindle	–
P3	*Euonymus verrucosus*	Spindletree	–
P4	*Frangula alnus*	Glossy Buckthorn	–
P5	*Lonicera xylosteum*	Common honeysuckle	–
P6	*Prunus padus*	Hackberry	–
P7	*Rhamnus cathartica*	Common Buckthorn	–
P8	*Ribes alpinum*	Alpine Currant	–
P9	*Ribes nigrum*	Black Currant	–
P10	*Ribes spicatum*	Red Currant	–
P11	*Rubus idaeus*	Red Raspberry	–
P12	*Sorbus aucuparia*	Rowan	–
P13	*Viburnum opulus*	Guelder Rose	–

Supplementary Table 3.5. Summary of linear mixed effects models. Shown are mixed models (Typ III SS) testing the effect of fruit abundance location (forest interior vs. edge), logging (logged vs. old-growth), year and second order interactions between the main factors and year on (**a**) consumer/resource ratio CR_q, (**b**) frugivore specialization ‹d'_j›, (**c**) evenness E_q, and (**d**) redundancy S_q of the 18 plant–frugivore networks quantified in Białowieża Forest, Eastern Poland in 2011 and 2012.

Source of Variance	Df_{num},Df_{den}	F	P	$r_{adj\ full}$	$r_{adj\ reduced}$
(**a**) *Consumer/resource ratio*					
Fruit abundance	1,4	28.7	0.0058	(−) **0.94**	(−) **0.92**
Location	1,6	1.20	0.32	0.41	0.55
Logging	1,6	7.94	0.031	(−) **0.75**	(−) **0.77**
Year	1,4	4.21	0.11	0.72	0.47
Location × logging	1,6	9.97	0.020	(+) **0.79**	(+) **0.79**
Year × location	1,4	6.45	0.064	0.79	-
Year × logging	1,4	0.757	0.43	0.40	-
(**b**) *Frugivore specialization*					
Fruit abundance	1,4	8.92	0.041	(+) **0.83**	(+) **0.83**
Location	1,6	0.008	0.93	0.040	0.48
Logging	1,6	9.30	0.023	(+) **0.78**	(+) **0.88**
Year	1,4	2.36	0.20	0.61	0.49
Location × logging	1,6	8.97	0.024	(−) **0.77**	(−) **0.85**
Year × location	1,4	1.93	0.24	0.57	-
Year × logging	1,4	0.197	0.68	0.22	-
(**c**) *Evenness*					
Fruit abundance	1,4	27.0	0.0066	(−) **0.93**	(−) **0.92**
Location	1,6	12.9	0.011	(−) **0.83**	(−) **0.81**
Logging	1,6	0.0785	0.79	0.11	0.47
Year	1,4	2.89	0.16	0.65	0.12
Location × logging	1,6	2.85	0.14	0.57	0.59
Year × location	1,4	3.71	0.13	0.69	-
Year × logging	1,4	0.596	0.48	0.36	-
(**d**) *Redundancy*					
Fruit abundance	1,4	8.81	0.041	(−) **0.83**	(−) **0.81**
Location	1,6	2.53	0.16	(−) **0.54**	(−) **0.75**
Logging	1,6	8.73	0.026	(−) **0.77**	(−) **0.85**
Year	1,4	2.36	0.20	0.61	0.69
Location × logging	1,6	6.85	0.040	(+) **0.73**	(+) **0.78**
Year × location	1,4	0.410	0.56	0.30	-
Year × logging	1,4	0.0942	0.77	0.15	-

Notes: Fruit abundance was ln(x) transformed prior to statistical analysis. Given are adjusted effect sizes radj according to the formula given in Rosenthal and Rosnow (1985) as the square-root of the ratio: $r^2 = df_{num} \times F / \left(df_{num} \times F + df_{den}\right)$. For comparison significant effects at a level of $P < 0.05$ and effect directions from the full and the reduced model are given in boldface type. Note that inclusion of the second order interactions between year and the two main factors does not affect our main conclusions qualitatively (effect direction) and that interaction terms including year were not significant in any of the models.

APPENDIX CHAPTER 4

Supplementary methods 4.1
Missing interactions

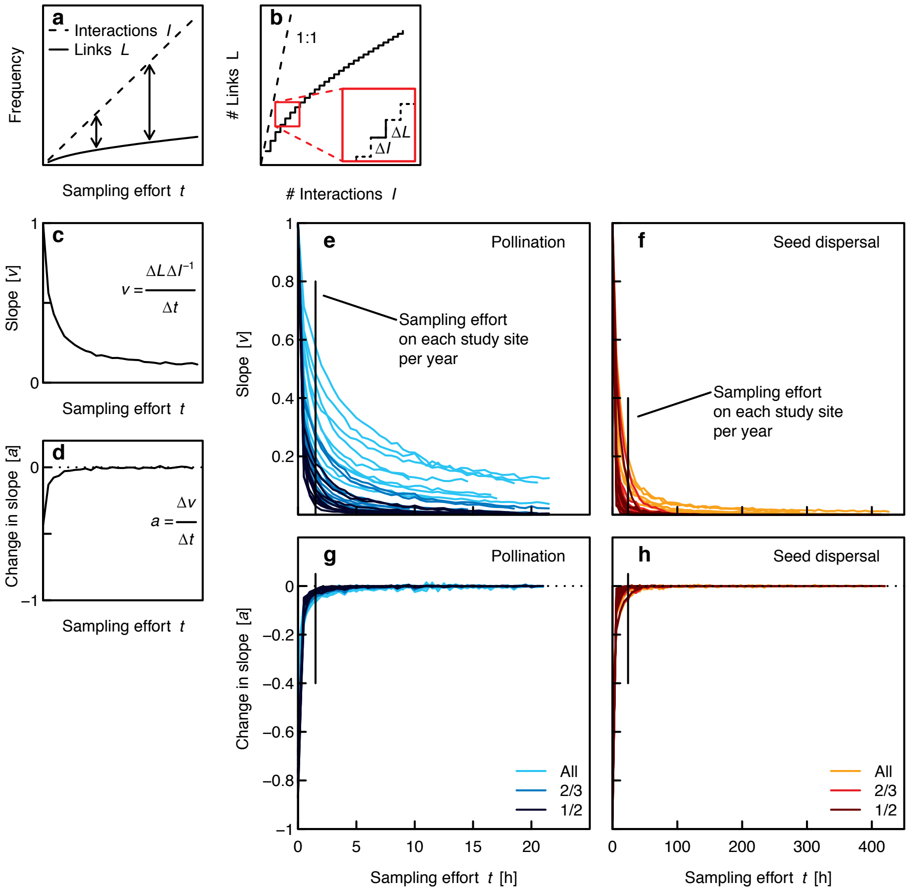
Networks of species interactions vary in space and in time (Carnicer *et al.* 2009; Dupont *et al.* 2009; Laliberté & Tylianakis 2010; Fründ, Dormann & Tscharntke 2011; Gagic *et al.* 2012; Plein *et al.* 2013). Hence, inherent to all empirical network studies is the lack of detection of some interactions even with intense sampling effort (Bascompte *et al.* 2006; Rezende *et al.* 2007; Thébault & Fontaine 2010; Aizen *et al.* 2012). During recent years, several approaches have been adopted to estimate and deal with these sampling-derived uncertainties (Jordano 1987; Gibson *et al.* 2011; Olesen *et al.* 2011; Chacoff *et al.* 2012; Devoto *et al.* 2012; Bartomeus 2013), namely standardized sampling designs and rarefaction techniques.

Here we used a standardized sampling design in the form of timed observations (Gibson *et al.* 2011) to allow valid comparisons among plant species, between both mutualisms (plant–pollinator and plant–seed disperser) and between habitats. Compared to transect sampling methods, where plants are observed for time periods relative to their abundance, timed observations allocate equal sampling effort per plant species (Gibson *et al.* 2011). Although timed observations have a lower resolution per unit time, they have a higher resolution per observation because rare interactions are more likely to be observed (Gibson *et al.* 2011). Hence, timed observations are best suited to achieve a high resolution for each focal plant species and to allow for valid comparisons among the focal plant species, which was the aim in our study.

Nonetheless, information about ‘sampling completeness’ surely enhances the predictive value of any field study. Rarefaction curves have been one important step forward in the estimation of the number of undetected interactions in network studies (Jordano 1987; Olesen *et al.* 2011; Chacoff *et al.* 2012; Devoto *et al.* 2012). However, so far it remains elusive whether rarefaction curves for interactions can be interpreted in the same way as for species (Aizen *et al.* 2012). Consequently, the use of rarefaction curves has been criticized with the main argument that asymptotic diversity estimators (e.g., the *Chao* estimator) may actually overestimate the total number of possible distinct interactions (see supplemental material of Aizen *et al.* 2012). For instance, rarefaction analyses have suggested that previous plant–pollinator network studies only detected about 55 % of all possible interactions after several years of sampling (e.g., Chacoff *et al.* 2012, 55 %; Devoto *et al.* 2012, 57 %). Thus, conventional rarefaction techniques may be misleading.

Here, we suggest an alternative rarefaction-based approach to estimate the ‘*completeness*’ of sampled interactions. Central to any sampling process is that the number of interactions I (i.e., the total number of observed plant–animal interactions) will increase constantly with increasing sampling effort t, whereas the number of distinct links L (i.e., the number of distinct pair-wise interactions) saturates at some point (Supplementary Fig. 4.1a). Likewise, the relationship between the number of interactions I and the number of links L in a given sample saturates during the sampling process (Supplementary Fig. 4.1b). This means that at a high sampling effort, a further increase in sampled interactions does not lead to a substantial increase in sampled links. The slope of the relationship between I and L hence gives the velocity v of sampling a new link in a sample of interactions for a given sampling interval Δt. We can calculate the slope for each successive sampling interval as $v = \Delta L \Delta I^{-1} / \Delta t = \left[L(t_{i+1}) - L(t_i)\right] / \left[I(t_{i+1}) - I(t_i)\right] / (t_{i+1} - t_i)$ with $0 \leq v \leq 1$ (Supplementary Fig. 4.1c). If the slope v equals 1, then every new sampled interaction represents a new link. Conversely, a slope of 0 means that an increase in sampled interactions does not lead to an increase in links. Importantly, this slope has direct relevance because the most frequent links are likely to be sampled first and at the same time are functionally most important (Jordano & Schupp 2000; Vázquez *et al.* 2005, 2012; Schupp *et al.* 2010). In contrast, rarer links are only infrequently sampled, as they are more variable in space and time and perhaps more facultative. Furthermore, the change in slope v as *a* function of sampling effort t gives the acceleration a (deceleration if $a < 0$) in the accumulation of links for a given sampling interval Δt (Supplementary Fig. 4.1d). We can calculate this change in slope for each successive sampling interval as $a = \Delta v / \Delta t = \left[v(t_{i+1}) - v(t_i)\right] / (t_{i+1} - t_i)$, with $-1 \leq a \leq 1$. If the change a in the slope equals –1 the velocity of accumulation of links is decelerating. Conversely, if a equals 0, the velocity remains constant (Supplementary Fig. 4.1c,d). In the following, we used this approach to estimate the sampling completeness in our study.

Since we used timed observations of focal plant species (Gibson *et al.* 2011), we calculated separate rarefaction curves for each of the ten plant species and both mutualisms (Supplementary Fig. 4.1e–h). To calculate rarefaction curves, we accumulated the number of interactions I and the number of links L from 1,000 random permutations of the data (i.e., sub-sampling



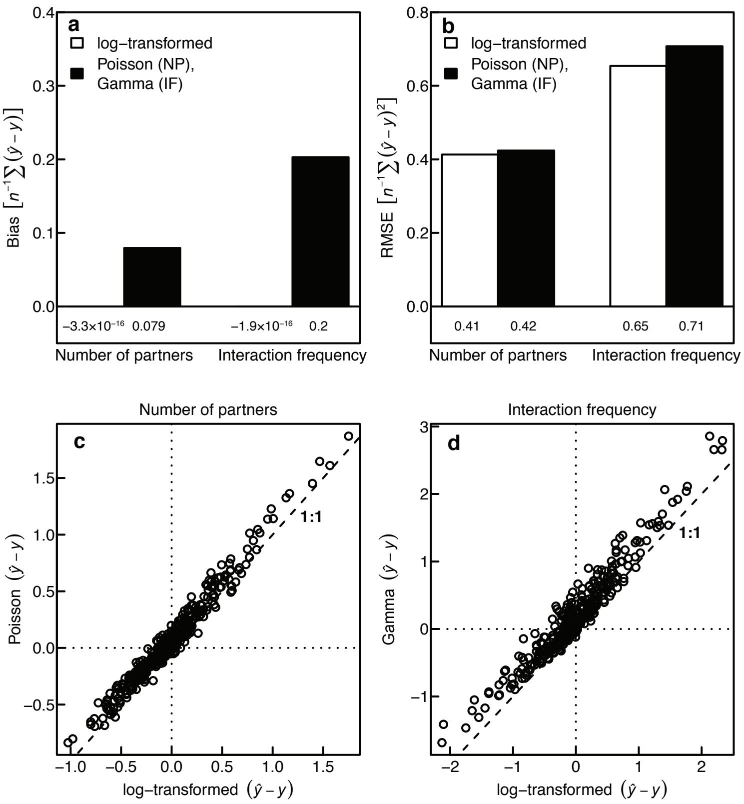
Supplementary Figure 4.1. Schematic representation and results of the rarefaction analysis used to assess the '*sampling completeness*' of the study. (**a**) With increasing sampling effort t, the number of interactions I increases constantly, whereas the number of distinct links L saturates. (**b**) We used the slope of the relationship between I and L to gain (**c**) the velocity v of sampling a new link in a sample of interactions for each sampling interval Δt. If the slope v is 1 or 0, each sampled interaction represents a new or an already sampled link, respectively. (**d**) The change in the slope for each sampling interval Δt gives the acceleration a in the accumulation of links. If the change a in the slope is negative or zero, the velocity of accumulation of links is decelerating or constant, respectively. The resulting rarefaction curves are shown for (**e**, **g**) the plant–pollinator mutualism and (**f**, **h**) the plant–seed disperser mutualism. In (**e**–**h**), mean rarefaction curves averaged across 1,000 permutations are plotted for each of the ten plant species; different colour hues indicate different subsets of animal mutualists (All: complete dataset; 2/3 and 1/2: the most frequent animal mutualists that account for 66 % and 50 % of all interactions, respectively). The vertical lines in (**e**–**h**) depict the actual sampling effort for each plant species on each study site per year (total effort pollinators: 157 h over 81 days of sampling; total effort seed dispersers: 2,430 h over 158 days of sampling).

without replacement). In the next step, we calculated ΔI and ΔL for each successive sample across the 1,000 runs for each plant species and mutualism and averaged these values across the runs of each plant species. Finally, we obtained the slope v and the change a in the slope of the relationship between interactions and links for each plant species as $v = \Delta L \Delta I^{-1} / \Delta t$ and $a = \Delta v / \Delta t$ (Supplementary Fig. 4.1e–h). Furthermore, to assess whether our sampling protocol sufficed in identifying the '*functionally most important*' animal species, we adopted a recently developed approach (Hegland *et al.* 2010). Following this approach, we considered an animal species to be functionally important when it has many interactions with other species, as the species with high interaction frequencies usually contribute most to the reproductive performance of their interaction partners (Jordano & Schupp 2000; Vázquez *et al.* 2005, 2012; Schupp *et al.* 2010). In addition, such core species ('*super generalists*' *sensu* Guimarães *et al.* 2011) are predicted to have the strongest impact on the organization and dynamics of mutualistic networks on ecological and evolutionary time scales (Bascompte & Jordano 2007; Guimarães *et al.* 2011). For both mutualisms, we ranked the animal species according to the total interaction frequency with all plant species and built two subsets of those most frequent species that together accounted for at least 66 % and 50 % of all sampled interactions. Then we calculated, based on these subsets, v_{sub} and

a_{sub} for each plant species as $v_{sub} = \Delta L_{sub} \Delta I^{-1} / \Delta t$ and $a_{sub} = \Delta v_{sub} / \Delta t$.

In the plant–pollinator mutualism, the slope *v* rapidly dropped during the first hours of sampling (Supplementary Fig. 4.1e). Consequently, the deceleration of the velocity of accumulation of links was most pronounced during the first sampling sessions (Supplementary Fig. 4.1g). When we considered all pollinator taxa, our sampling protocol reached a saturation of 0.43 new distinct links per sampled interaction (Supplementary Fig. 4.1e). Twenty-five of the 294 pollinator species accounted for 66 % of all 5,784 recorded interactions. For this subset of functionally important species, we reached a saturation of 0.21 new distinct links per sampled interaction (Supplementary Fig. 4.1e). Thirteen of these species accounted for 50 % of all recorded interactions. For this subset of core species, we reached a saturation of 0.13 new distinct links per sampled interaction (Supplementary Fig. 4.1e). It has to be mentioned that this is a conservative estimate because we pooled the samples from both years and the turnover of interactions in plant pollinator networks between years is known to be huge (Petanidou *et al.* 2008; Dupont *et al.* 2009). The results are consistent with a recent study that has shown that the functionally most important species of flower visitors on plants can be identified with relatively little sampling, particularly when using timed observations (Hegland *et al.* 2010; Gibson *et al.* 2011). The sampling effort for the plant–seed disperser mutualism in our study was intense, and rarefaction curves suggested that the accumulation of links dropped more rapidly compared to the plant–pollinator mutualism (Supplementary Fig. 4.1f). As for the plant–pollinator mutualism, the change in the slope was most pronounced during the first sampling sessions, i.e. rapidly decelerating (Supplementary Fig. 4.1h). When we considered all seed disperser taxa, our sampling protocol reached a saturation of 0.11 new distinct links per sampled interaction (Supplementary Fig. 4.1f). Three of the 34 seed disperser species accounted for 66 % of all 5,935 recorded interactions. When we used this subset of the functionally most important species, we reached a saturation of 0.055 new distinct links per sampled interaction (Supplementary Fig. 4.1f). Two of these species accounted for more than 50 % of all interactions. For these core species, we reached a saturation of 0.039 new distinct links per sampled interaction (Supplementary Fig. 4.1f).

Therefore, we can conclude that within the limitations of a realistic field study, our sampling identified the functionally most important animal taxa in both mutualisms (Supplementary Fig. 4.1e,f). Furthermore, the rapid deceleration of the accumulation of links during the first sampling sessions suggested that our sampling was as complete as reasonably possible because a substantial increase in the resolution of the samples would have required an unrealistic increase in sampling effort (Supplementary Fig. 4.1g,h). This does not mean that we could not have sampled some of the rarer links if we had been able to increase our sampling effort. However, to account for these sampling-derived uncertainties and to allow for valid comparisons between habitats, we used a standardized sampling protocol. Consequently, we are certain that our finding of a correlated effect of habitat degradation on these coupled mutualistic networks is real and not just an artefact of our sampling.

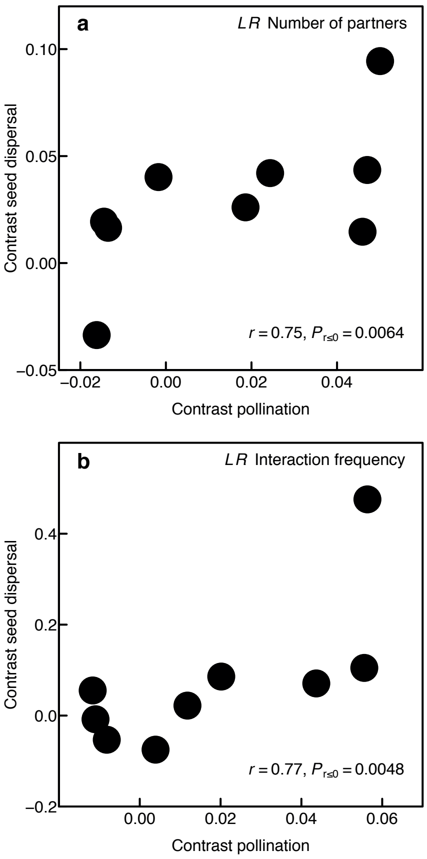


Supplementary Figure 4.2. Comparison of estimated mean biases and root mean-squared error from linear mixed-effects models on log-transformed response variables and generalized linear mixed-effects models assuming that the response variables follow a Poisson (number of partners) or Gamma (interaction frequency) distribution. Comparison of estimated mean biases (**a**) and root mean-squared error (**b**) from linear mixed-effects models (log-transformed response variables) and from generalized linear mixed-effects models for number of partners (NP) and interaction frequency (IF). Values are provided under each histogram. Relationships between the estimated biases at the observations (**c**, **d**) from the linear mixed-effects models (log-transformed response variables) and from generalized linear mixed-effects models assuming a Poisson (number of partners) or Gamma (interaction frequency) distribution. Note that the models based on log-transformed response variables had substantially higher prediction accuracy (i.e., less bias) and slightly higher precision (i.e., less error) than the models assuming a Poisson or Gamma distribution.

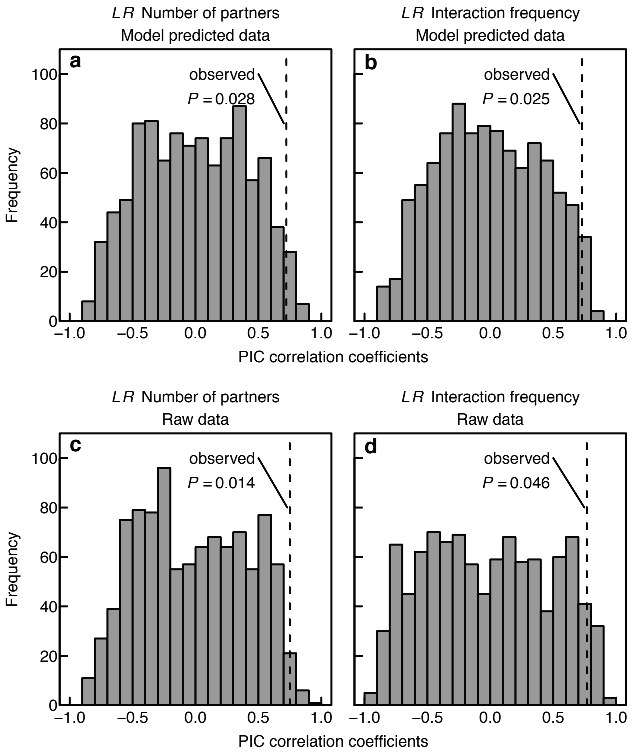
SUPPLEMENTARY METHODS 4.2
ASSESSMENT OF MODEL FIT

The two response variables, number of partners and interaction frequency, analyzed here do not follow a normal distribution. The decision to use log-transformed response variables in the linear mixed-effects models may influence the results of our analyses, if the models perform poorly (O'Hara & Kotze 2010). This is however unlikely when the mean counts are large and the dispersion θ of the distribution is small (a larger θ indicates smaller dispersion), as was the case in our study (number of partners: mean = 9.52, $\theta = 4.42$; interaction frequency: mean = 19.00, $\theta = 26.10$; compare to results of O'Hara & Kotze [2010]). However, we refitted these models as generalized linear mixed-effects models. For the number of partners we assumed a Poisson distribution, as this variable describes discrete counts of species. We detected no overdispersion in the residuals of the Poisson model ($\chi^2 = 293.5$, ratio = 0.94, $df = 313$, $P = 0.78$). For the interaction frequency we assumed a Gamma distribution (continuous rate of interaction h^{-1}).

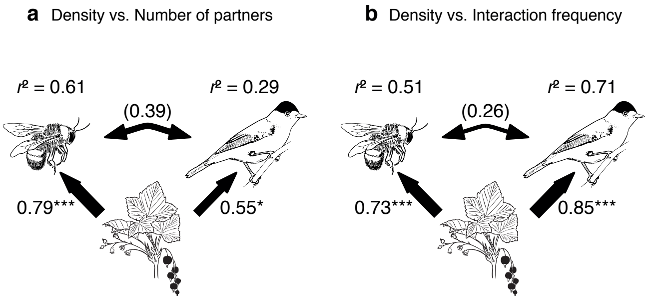
The results of the Poisson/Gamma models confirmed those of the models based on the log-transformed response variables. Then we compared the models (O'Hara & Kotze 2010) according to their mean prediction bias (accuracy), $Bias = 1/n \times \sum \hat{y} - y$, and according to their root-mean-squared error (precision), $RMSE = 1/n \times \sum (\hat{y} - y)^2$, where $\hat{y}$ is the estimated value of the response, y is the observed value, and n is the sample size (Supplementary Fig. 4.2). The models based on the log-transformed response variables had substantially higher prediction accuracy and a slightly higher precision in explaining the observed data compared to the Poisson/Gamma models. Thus, we report results of the models based on the log-transformed data in the main text.



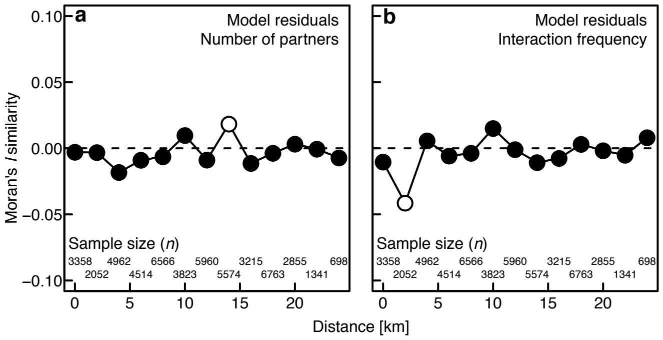
Supplementary Figure 4.3. Phylogenetic correlations between the responses of pollinators and seed dispersers to logging based on the raw data. Correlations between phylogenetic independent contrasts (PICs; $n = 9$) of the log response ratios LR of (**a**) the number of partners and (**b**) the interaction frequency of plants in the plant–pollinator and plant–seed disperser mutualisms.



Supplementary Figure 4.4. Results of the permutation analysis testing for a correlation between the responses of pollinators and seed dispersers to logging. Correlations between phylogenetic independent contrasts of the log response ratios LR of (**a**, **c**) the number of partners and (**b**, **d**) the interaction frequency of plants in the plant–pollinator and plant–seed disperser mutualisms based on the model predicted data (**a**, **b**) and based on the raw data (**c**, **d**). In the permutation analysis, the log response ratios (LR_{ij}) in one mutualism were randomized among the tips of the phylogeny, while those of the other were kept fixed. Phylogenetic independent contrasts (PICs) and correlation coefficients were recalculated for each permutation (n = 999) to generate a null distribution of the expected correlation coefficients. Note that the observed correlations were significantly larger than expected from the null distribution in all cases.



Supplementary Figure 4.5. Summary of path analyses testing for bottom-up control in the responses of pollinators and seed dispersers to logging based on the raw data. Path models are based on phylogenetic independent contrasts (PICs; *n* = 9) and show the effects of the log response ratio (LR_{ij}) in plant density between old-growth forest and logged forest on the log response ratio in number of partners (**a**) and interaction frequencies (**b**) of plants in the plant–pollinator and plant–seed disperser mutualism. Shown are results for the PICs based on raw data. Standardized path coefficients are given next to path arrows. Arrow widths are proportional to path coefficients. Residual covariance is denoted by double-headed arrows. Proportion of explained variance (r^2) is denoted above each mutualism. Significance of path coefficients is depicted by **P* < 0.05; ****P* < 0.001. Both path models fit the data (**a**) χ^2 = 3.18, *df* = 2, *P* = 0.20, (**b**) χ^2 = 1.45, *df* = 2, *P* = 0.48.



Supplementary Figure 4.6. Spatial autocorrelation in the residuals of most parsimonious linear mixed-effects models of (a) number of partners and (b) interaction frequency. Note that Moran's *I* similarity in the residuals of both models was close to 0 (Moran's *I* values are always < |0.05|) and did not decrease with increasing distance of discrete distance classes (2 km), which indicates a random spatial pattern. Open circles depict distance classes in which Moran's *I* similarity differed significantly from 0 at *α* = 0.05. Sample size (*n*) is given below each distance class.

Supplementary Table 4.1. Summary of model selection.

Variables	*df*	logLik	AIC_c	Delta	AIC_c Weight
Response: Number of partners					
M, R, L, M×L	**10**	**−208.8**	**438.3**	**0.00**	**0.839**
M, F, R, L, M×L	12	−208.7	442.3	4.02	0.112
M, F, R, L, M×F, M×L	14	−208.2	445.8	7.47	0.020
M, R	8	−214.8	446.1	7.78	0.017
M, R, L	9	−214.7	448.0	9.64	0.007
M, F, R	10	−214.6	449.9	11.6	0.003
M, F, R, M×F	12	−213.4	451.9	13.6	0.001
M, F, R, L	11	−214.5	451.9	13.6	0.001
M, F, R, L, M×F	13	−213.4	453.9	15.6	0.000
R	7	−228.4	471.2	32.9	0.000
R, L	8	−228.3	473.1	34.7	0.000
F, R	9	−228.2	475.0	36.7	0.000
F, R, L	10	−228.1	477.0	38.7	0.000
M, L, M×L	9	−230.0	478.6	40.3	0.000
M, F, L, M×L	11	−229.7	482.3	44.0	0.000
M, F, L, M×F, M×L	13	−229.1	485.4	47.1	0.000
M	7	−239.3	493.0	54.7	0.000
M, L	8	−238.7	493.9	55.6	0.000
M, F	9	−238.7	496.1	57.8	0.000
M, F, M×F	11	−236.7	496.3	58.0	0.000
M, F, L	10	−238.4	497.5	59.2	0.000
M, F, L, M×F	12	−236.4	497.7	59.4	0.000
Null model	6	−252.4	517.0	78.7	0.000
L	7	−251.8	517.9	79.6	0.000
F	8	−251.7	519.9	81.6	0.000
F, L	9	−251.4	521.4	83.1	0.000
Response: Interaction frequency					
M, R, L, M×L	**10**	**−359.0**	**738.6**	**0.00**	**0.598**
M, R, L	9	−361.7	742.0	3.35	0.112
M, F, R, L, M×L	12	−358.6	742.2	3.60	0.099
M, R	8	−363.0	742.5	3.92	0.084
M, F, R, L, M×F, M×L	14	−356.8	742.9	4.29	0.070
M, F, R, L	11	−361.4	745.7	7.04	0.018
M, F, R	10	−362.9	746.5	7.87	0.012
M, F, R, L, M×F	13	−360.7	748.5	9.86	0.004
M, F, R, M×F	12	−362.2	749.5	10.9	0.003
R, L	8	−380.7	777.8	39.2	0.000
R	7	−382.0	778.4	39.8	0.000
F, R, L	10	−380.5	781.6	43.0	0.000
F, R	9	−381.9	782.5	43.8	0.000
M, L, M×L	9	−406.1	830.7	92.1	0.000
M, F, L, M×L	11	−405.9	834.7	96.1	0.000
M, F, L, M×F, M×L	13	−404.7	836.5	97.9	0.000
M, L	8	−411.6	839.7	101	0.000
M	7	−413.1	840.6	102	0.000
M, F, L	10	−411.5	843.8	105	0.000
M, F	9	−412.8	844.3	106	0.000

Notes: List of the component models included in the model set of linear mixed-effects models for the number of partners and interactions of plants in the pollination and seed dispersal mutualisms. R, Resource units; M, mutualism; L, Logging; F, fragmentation; ×, interaction. The null model included the sampling intensity as an offset (even though this variable is not listed in the table) because the offset was kept fixed during the model selection procedure to account for any potential effects of sampling intensity between years. A value of $\Delta\text{AIC}_c < 2$ indicates substantial support for a model (Burnham & Anderson 2002).

Supplementary table 4.1. (continued).

Variables	*df*	logLik	AIC$_c$	Delta	AIC$_c$ Weight
M, F, L, M×F	12	−410.8	846.6	108	0.000
M, F, M×F	11	−412.2	847.2	109	0.000
L	7	−430.0	874.4	136	0.000
Null model	6	−431.5	875.3	137	0.000
F, L	9	−429.9	878.4	140	0.000
F	8	−431.2	878.8	140	0.000

Notes: List of the component models included in the model set of linear mixed-effects models for the number of partners and interactions of plants in the pollination and seed dispersal mutualisms. R, Resource units; M, mutualism; L, Logging; F, fragmentation; ×, interaction. The null model included the sampling intensity as an offset (even though this variable is not listed in the table) because the offset was kept fixed during the model selection procedure to account for any potential effects of sampling intensity between years. A value of $\Delta AIC_c < 2$ indicates substantial support for a model (Burnham & Anderson 2002).

Supplementary Table 4.2. Summary of generalized least squares analysis testing for a correlated response of pollinators and seed dispersers to logging.

Variable*	λ	Log Likelihood	GLS regression slope (95 % Confidence interval)	*t*-value	$P[t \leq 0]$
1.) Model derived predictions					
a) unweighted					
Number of partners	0	1.73	1.42 (−0.38, 3.22)	1.55	0.080
	1	2.02	2.04 (0.69, 3.4)	2.95	0.0092
Interaction frequency	0	−5.90	1.73 (−0.34, 3.8)	1.63	0.070
	1	−5.48	2.38 (0.83, 3.93)	3.01	0.0085
b) weighted†					
Number of partners	0	1.94	1.41 (0.14, 2.69)	2.18	0.031
	1	2.33	1.81 (0.9, 2.72)	3.90	0.0023
Interaction frequency	0	−6.11	1.79 (0.08, 3.5)	2.05	0.037
	1	−5.62	2.2 (0.95, 3.45)	3.45	0.0043
2.) Raw data					
a) unweighted					
Number of partners	0	−1.70	0.77 (0.23, 1.32)	2.78	0.012
	1	−2.21	1.06 (0.41, 1.71)	3.20	0.0063
Interaction frequency	0	−9.85	2.16 (0.76, 3.57)	3.02	0.0083
	1	−13.0	4.13 (1.73, 6.52)	3.38	0.0048
b) weighted†					
Number of partners	0	−2.54	0.76 (0.32, 1.2)	3.37	0.0049
	1	−3.18	1.05 (0.53, 1.56)	3.97	0.0020
Interaction frequency	0	−9.78	2.29 (1.15, 3.42)	3.95	0.0021
	1	−12.4	4.03 (2.26, 5.8)	4.46	0.0011

Notes: Slope of the regressions of the plant-species-specific (n = 10) log response ratios (LR_{ij}) of seed dispersers plotted against the log response ratios of pollinators from generalized least squares (GLS). The correlations were calculated based on predicted data (from most parsimonious linear mixed-effects models, see Supplementary Table 4.1) and based on raw data. We fixed the parameter λ to 0 and 1, where 0 indicates a star phylogeny (i.e., no phylogenetic signal) and 1 indicates strong phylogenetic signal, assuming Brownian motion along the phylogeny. In addition, we performed GLS analyses with and without weighting of the log response ratios of plant species by their variance, giving greater weight to plant species with higher '*certainty*'. The log likelihood values of the respective correlations as estimates of the model fit and one-tailed *P*-values are shown.

* Regression equations were in all cases $LR_{i[Dispersal]} \sim a \times LR_{i[Pollination]} + b$, where LR_i is the log response ratio of pollinators and seed dispersers for plant species i, a is the regression slope and b is the intercept.

† Formulas of variance weights (w) for plant species i were $w_i = 1/\mathrm{var}\left(y_{i[Pollination]}\right) + 1/\mathrm{var}\left(y_{i[Dispersal]}\right)$, where y is number of partners or interaction frequency, respectively.

Supplementary Table 4.3. Summary of the geographic coordinates and the characteristics of the 17 study sites on which pollinator and seed disperser assemblages were sampled during the field campaigns in 2011 and 2012 in the Białowieża Forest, eastern Poland.

Site	Latitude	Longitude	Forest	Fragmentation	Proportion forest cover [500 m]	Plant density [individuals/100 m^2]*
1	52.742522	23.833125	Old-growth	Interior	1.00	2.17
2	52.789420	23.844638	Old-growth	Interior	1.00	–
3	52.779399	23.858086	Old-growth	Edge	0.90	–
4	52.730643	23.822146	Old-growth	Edge	0.88	1.17
5	52.798711	23.826023	Old-growth	Edge	0.82	1.30
6	52.703070	23.653528	Logged	Interior	0.85	0.69
7	52.670146	23.685385	Logged	Interior	0.97	–
8	52.704294	23.622402	Logged	Interior	1.00	2.45
9	52.717234	23.816766	Logged	Edge	0.37	0.57
10	52.733813	23.789229	Logged	Edge	0.95	2.16
11	52.688673	23.877749	Logged	Edge	0.72	2.02
12	52.855240	23.839993	Logged	Edge	0.54	–
13	52.854070	23.729802	Logged	Edge	0.46	1.08
14	52.845312	23.809758	Logged	Fragment	0.30	6.58
15	52.832209	23.772104	Logged	Fragment	0.19	3.22
16	52.691722	23.840740	Logged	Fragment	0.06	1.54
17	52.872765	23.722445	Logged	Fragment	0.14	3.35

Notes: * Mean density of focal plants from sampling of plant population densities. Sites with no value could not be sampled owing to logistical constraints.

Supplementary Table 4.4. Summary of the number of plant, pollinator and seed disperser species and the total number of interactions sampled on each study site in each year.

Site	Forest	Pollination						Seed dispersal					
		Plant species sampled		Pollinator species		Total interactions		Plant species sampled		Frugivore species		Total interactions	
		2011	2012	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
1	Old-growth	5	6	46	52	99	239	3	6	11	19	51	397
2	Old-growth	7	8	54	65	233	222	5	6	9	13	110	239
3	Old-growth	7	–	66	–	305	–	5	–	12	–	224	–
4	Old-growth	4	7	21	58	43	226	2	5	7	9	44	111
5	Old-growth	8	10	59	83	328	330	7	8	11	16	510	1133
6	Logged	5	7	35	64	184	196	2	6	5	11	15	160
7	Logged	6	–	54	–	174	–	2	–	6	–	33	–
8	Logged	8	9	58	73	206	277	3	8	7	15	52	300
9	Logged	8	10	46	82	191	316	5	6	9	12	207	254
10	Logged	8	9	59	68	258	242	5	8	14	11	336	156
11	Logged	–	8	–	65	–	217	–	6	–	12	–	132
12	Logged	–	6	–	58	–	241	–	3	–	8	–	105
13	Logged	–	8	–	86	–	377	–	7	–	10	–	314
14	Logged	–	9	–	68	–	252	–	7	–	12	–	260
15	Logged	–	7	–	57	–	161	–	5	–	9	–	135
16	Logged	–	8	–	59	–	216	–	7	–	10	–	471
17	Logged	–	9	–	76	–	251	–	8	–	10	–	186

Supplementary Table 4.5. Summary of sampling of pollinator (P) and seed disperser (SD) assemblages on the ten plant species across the 17 study sites and the two study years.

		Plant species																			
		RhCa		PrPa		EuEu		CoSa		ViOp		SoAu		FrAl		RuId		RiNi		RiSp	
Site	Forest	P	SD	P	SD	P	SD	P	SD	P	SD	P	SD	P	SD	P	SD	P	SD	P	SD
1	Old-growth			2	1					2	2	2	2			1	1	2	2	2	1
2	Old-growth			2	1	2	2			2	2	2	2	2	1	1		2	2	2	1
3	Old-growth		1	1				1	1	1	1	1	1	1	1			1		1	
4	Old-growth	1		2	1							2	2	1	2	1		2	1	2	1
5	Old-growth	2	2	2	1	2	2	2	2	2	2	2	2	1		1		2	2	2	2
6	Logged			2	1	2						2	2	2	2	1	1	2	1	1	1
7	Logged			1				1				1	1	1	1			1		1	
8	Logged	1		2	1	2	1	2		2	2	2	2	1	2	1	1	2	1	2	1
9	Logged	2	1	2	1	2	1	2	2	2	2	2	1	2	2	1		2	1	1	
10	Logged	2	2	2	1	2	1			2	2	2	2	2	2	1		2	2	2	1
11	Logged			1	1	1				1		1	1	1	1	1	1	1	1	1	1
12	Logged									1		1		1	1	1	1	1		1	1
13	Logged	1	1	1	1	1	1			1	1	1	1	1	1	1		1	1		
14	Logged	1	1	1	1	1	1			1	1	1	1	1	1	1		1		1	1
15	Logged			1	1					1		1	1	1	1	1		1	1	1	1
16	Logged			1	1	1	1			1	1	1	1	1	1	1		1	1	1	1
17	Logged	1	1	1	1	1	1			1	1	1	1	1	1	1		1	1	1	1

Notes: If the entry is 1, then the assemblage on a given plant on a given site was sampled in one year; if an entry is 2, then an assemblage was sampled in both years. Sites 3 and 7 were sampled only in 2011, whereas sites 11 to 17 were sampled only in 2012. Plant species codes: RhCa, *Rhamnus cathartica*; PrPa, *Prunus padus*; EuEu, *Euonymus europaeus*; CoSa, *Cornus sanguinea*; ViOp, *Viburnum opulus*; SoAu, *Sorbus aucuparia*; FrAl, *Frangula alnus*; RuId, *Rubus idaeus*; RiNi, *Ribes nigrum*; RiSp, *Ribes spicatum*

Supplementary Table 4.6. Complete list of plant, seed disperser and pollinator species.

Species code	Order	Family	Genus	Species
Plants				
P1	Celastrales	Celastraceae	*Euonymus*	*europaeus*
P2	Cornales	Cornaceae	*Cornus*	*sanguinea*
P3	Dipsacales	Adoxaceae	*Viburnum*	*opulus*
P4	Rhamnales	Rhamnaceae	*Frangula*	*alnus*
P5	Rhamnales	Rhamnaceae	*Rhamnus*	*cathartica*
P6	Rosales	Rosaceae	*Prunus*	*padus*
P7	Rosales	Rosaceae	*Rubus*	*idaeus*
P8	Rosales	Rosaceae	*Sorbus*	*aucuparia*
P9	Saxifragales	Grossulariaceae	*Ribes*	*nigrum*
P10	Saxifragales	Grossulariaceae	*Ribes*	*spicatum*
Seed dispersers				
F1	Carnivora	Mustelidae	*Martes*	*martes*
F2	Columbiformes	Columbidae	*Columba*	*palumbus*
F3	Galliformes	Phasianidae	*Tetrastes*	*bonasia*
F4	Passeriformes	Acrocephalidae	*Hippolais*	*icterina*
F5	Passeriformes	Corvidae	*Garrulus*	*glandarius*
F6	Passeriformes	Fringillidae	*Coccothraustes*	*coccothraustes*
F7	Passeriformes	Fringillidae	*Fringilla*	*coelebs*
F8	Passeriformes	Fringillidae	*Pyrrhula*	*pyrrhula*
F9	Passeriformes	Muscicapidae	*Erithacus*	*rubecula*
F10	Passeriformes	Muscicapidae	*Ficedula*	*hypoleuca*
F11	Passeriformes	Muscicapidae	*Ficedula*	*parva*
F12	Passeriformes	Muscicapidae	*Luscinia*	*luscinia*
F13	Passeriformes	Muscicapidae	*Muscicapa*	*striata*
F14	Passeriformes	Oriolidae	*Oriolus*	*oriolus*
F15	Passeriformes	Paridae	*Parus*	*major*
F16	Passeriformes	Paridae	*Periparus*	*ater*
F17	Passeriformes	Paridae	*Poecile*	*montanus*
F18	Passeriformes	Paridae	*Poecile*	*palustris*
F19	Passeriformes	Phylloscopidae	*Phylloscopus*	*trochilus*
F20	Passeriformes	Sittidae	*Sitta*	*europaea*
F21	Passeriformes	Sylviidae	*Sylvia*	*atricapilla*
F22	Passeriformes	Sylviidae	*Sylvia*	*borin*
F23	Passeriformes	Turdidae	*Turdus*	*iliacus*
F24	Passeriformes	Turdidae	*Turdus*	*merula*
F25	Passeriformes	Turdidae	*Turdus*	*philomelos*
F26	Passeriformes	Turdidae	*Turdus*	*pilaris*
F27	Passeriformes	Turdidae	*Turdus*	*viscivorus*
F28	Piciformes	Picidae	*Dendrocopos*	*major*
F29	Piciformes	Picidae	*Dendrocopos*	*leucotos*
F30	Piciformes	Picidae	*Dendrocopos*	*medius*
F31	Piciformes	Picidae	*Dryocopus*	*martius*
F32	Rodentia	Gliridae	*Muscardinus*	*avellanarius*
F33	Rodentia	Muridae	*Apodemus*	*flavicollis*
F34	Rodentia	Sciuridae	*Sciurus*	*vulgaris*
Pollinators				
M1	Coleoptera	Byturidae	*Byturus*	*ochraceus*
M2	Coleoptera	Byturidae	*Byturus*	*tomentosus*
M3	Coleoptera	Cantharidae	*Cantharis*	*nigricans*
M4	Coleoptera	Cantharidae	*Cantharis*	*pelucida*
M5	Coleoptera	Cantharidae	*Mathodes*	*minimus*

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M6	Coleoptera	Cerambycidae	*Acmaeops*	*collaris*
M7	Coleoptera	Cerambycidae	*Grammoptera*	*ruficornis*
M8	Coleoptera	Cerambycidae	*Leptura*	*virens*
M9	Coleoptera	Cerambycidae	*Leptura*	–
M10	Coleoptera	Cerambycidae	*Leptura*	–
M11	Coleoptera	Cerambycidae	*Leptura*	–
M12	Coleoptera	Cerambycidae	*Molorchus*	*minor*
M13	Coleoptera	Cerambycidae	*Molorchus*	*umbellatarum*
M14	Coleoptera	Cerambycidae	*Obreum*	*brunneum*
M15	Coleoptera	Cerambycidae	*Rhagium*	*mordax*
M16	Coleoptera	Cerambycidae	*Stenurella*	*melanura*
M17	Coleoptera	Cerambycidae	*Strangalia*	*attenuata*
M18	Coleoptera	Cerambycidae	–	–
M19	Coleoptera	Cerambycidae	–	–
M20	Coleoptera	Cleridae	*Trichodes*	*apiarius*
M21	Coleoptera	Coccinellidae	*Coccinella*	*septempunctata*
M22	Coleoptera	Coccinellidae	*Propylea*	*quattuordecimpunctata*
M23	Coleoptera	Dasytidae	*Aplocnemus*	*nigricornis*
M24	Coleoptera	Dasytidae	*Dasytes*	*plumbeus*
M25	Coleoptera	Dasytidae	–	–
M26	Coleoptera	Dermestidae	*Anthrenus*	*scrophulariae*
M27	Coleoptera	Dermestidae	*Attagenus*	–
M28	Coleoptera	Dermestidae	*Trogoderma*	*granarium*
M29	Coleoptera	Dermestidae	–	–
M30	Coleoptera	Dermestidae	–	–
M31	Coleoptera	Dermestidae	–	–
M32	Coleoptera	Dermestidae	–	–
M33	Coleoptera	Melyridae	*Malachius*	*bipustulatus*
M34	Coleoptera	Mordellidae	*Cyrtanaspis*	*phalerata*
M35	Coleoptera	Mordellidae	*Mordellistena*	*abdominalis*
M36	Coleoptera	Mordellidae	*Mordellistena*	–
M37	Coleoptera	Nitidulidae	*Epuraea*	*depressa*
M38	Coleoptera	Nitidulidae	*Nitidula*	–
M39	Coleoptera	Nitidulidae	*Pocadius*	*ferrugineus*
M40	Coleoptera	Oedemeridae	*Ischnomera*	*caerula*
M41	Coleoptera	Oedemeridae	*Oedemera*	*lurida*
M42	Coleoptera	Pyrochroidae	*Pyrochroa*	*coccinea*
M43	Coleoptera	Scarabaeidae	*Cetonia*	*aurata*
M44	Coleoptera	Scarabaeidae	*Gnorimus*	*nobilis*
M45	Coleoptera	Scarabaeidae	*Phyllopertha*	*horticola*
M46	Coleoptera	Scarabaeidae	*Protaetia*	*cuprea*
M47	Coleoptera	Scarabaeidae	*Tropinota*	*hirta*
M48	Coleoptera	–	–	–
M49	Coleoptera	–	–	–
M50	Diptera	Anthomyiidae	–	–
M51	Diptera	Bibionidae	*Bibio*	–
M52	Diptera	Bibionidae	*Dilophus*	–
M53	Diptera	Calliphoridae	*Calliphora*	*ecythrocephala*
M54	Diptera	Calliphoridae	*Cynomya*	*mortuorum*
M55	Diptera	Calliphoridae	*Cynomya*	–
M56	Diptera	Calliphoridae	*Lucilia*	–
M57	Diptera	Calliphoridae	*Melinda*	*caerulea*

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M58	Diptera	Calliphoridae	*Melinda*	–
M59	Diptera	Calliphoridae	–	–
M60	Diptera	Conopidae	*Sicus*	–
M61	Diptera	Dolichopodidae	–	–
M62	Diptera	Dolichopodidae	–	–
M63	Diptera	Empididae	*Empis*	*opaca*
M64	Diptera	Empididae	*Empis*	*tesselata*
M65	Diptera	Empididae	*Empis*	–
M66	Diptera	Empididae	*Rhamphomyia*	–
M67	Diptera	Empididae	*Xanthempis*	*digramma*
M68	Diptera	Empididae	*Xanthempis*	–
M69	Diptera	Empididae	–	–
M70	Diptera	Muscidae	*Graphomyia*	*maculata*
M71	Diptera	Muscidae	*Mesembrina*	–
M72	Diptera	Muscidae	*Mesembrina*	–
M73	Diptera	Muscidae	*Musca*	–
M74	Diptera	Muscidae	*Mydea*	–
M75	Diptera	Muscidae	*Neomyia*	–
M76	Diptera	Muscidae	*Neomyia*	–
M77	Diptera	Muscidae	*Neomyia*	–
M78	Diptera	Muscidae	*Polietes*	–
M79	Diptera	Muscidae	–	–
M80	Diptera	Rhinophoridae	–	–
M81	Diptera	Sarcophagidae	*Sarcophaga*	*carnaria*
M82	Diptera	Sarcophagidae	*Sarcophaga*	–
M83	Diptera	Sarcophagidae	*Sarcophaga*	–
M84	Diptera	Sarcophagidae	*Sarcophaga*	–
M85	Diptera	Sarcophagidae	–	–
M86	Diptera	Sciomyzidae	–	–
M87	Diptera	Sepsidae	–	–
M88	Diptera	Sepsidae	–	–
M89	Diptera	Stratiomyidae	–	–
M90	Diptera	Syrphidae	*Anasimyia*	*interpunctata*
M91	Diptera	Syrphidae	*Baccha*	*elongata*
M92	Diptera	Syrphidae	*Blera*	*fallax*
M93	Diptera	Syrphidae	*Brachyopa*	*bicolor*
M94	Diptera	Syrphidae	*Brachyopa*	*insensilis*
M95	Diptera	Syrphidae	*Brachyopa*	*panzeri*
M96	Diptera	Syrphidae	*Brachyopa*	*plena*
M97	Diptera	Syrphidae	*Brachyopa*	*scutellaris*
M98	Diptera	Syrphidae	*Brachyopa*	*testacea*
M99	Diptera	Syrphidae	*Brachyopa*	*vitata*
M100	Diptera	Syrphidae	*Brachypalpoides*	*lentus*
M101	Diptera	Syrphidae	*Brachypalpus*	*laphriformis*
M102	Diptera	Syrphidae	*Ceriona*	*canopsoides*
M103	Diptera	Syrphidae	*Chalcosyrphus*	*nemorum*
M104	Diptera	Syrphidae	*Cheilosia*	*carbonaria*
M105	Diptera	Syrphidae	*Cheilosia*	*impressa*
M106	Diptera	Syrphidae	*Cheilosia*	*nebulosa*
M107	Diptera	Syrphidae	*Cheilosia*	*variabilis_melanopa*
M108	Diptera	Syrphidae	*Cheilosia*	–
M109	Diptera	Syrphidae	*Cheilosia*	–

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M110	Diptera	Syrphidae	*Chrysogaster*	–
M111	Diptera	Syrphidae	*Chrysotoxum*	*cautum*
M112	Diptera	Syrphidae	*Chrysotoxum*	*fasciolatum*
M113	Diptera	Syrphidae	*Criorhina*	*asilica*
M114	Diptera	Syrphidae	*Criorhina*	*berberina*
M115	Diptera	Syrphidae	*Criorhina*	*floccosa*
M116	Diptera	Syrphidae	*Criorhina*	*ranunculi*
M117	Diptera	Syrphidae	*Dasysyrphus*	*albostriatus*
M118	Diptera	Syrphidae	*Dasysyrphus*	*pauxillus*
M119	Diptera	Syrphidae	*Dasysyrphus*	*pinastri*
M120	Diptera	Syrphidae	*Dasysyrphus*	*tricinctus*
M121	Diptera	Syrphidae	*Dasysyrphus*	*venustus*
M122	Diptera	Syrphidae	*Didea*	*alneti*
M123	Diptera	Syrphidae	*Epistrophe*	*eligans*
M124	Diptera	Syrphidae	*Epistrophe*	*euchroma*
M125	Diptera	Syrphidae	*Epistrophe*	*nitridicollis.flava*
M126	Diptera	Syrphidae	*Epistrophe*	*obscuripes*
M127	Diptera	Syrphidae	*Episyrphus*	*balteatus*
M128	Diptera	Syrphidae	*Eristalis*	*abusivus*
M129	Diptera	Syrphidae	*Eristalis*	*cryptarum*
M130	Diptera	Syrphidae	*Eristalis*	*intricaria*
M131	Diptera	Syrphidae	*Eristalis*	*lineata*
M132	Diptera	Syrphidae	*Eristalis*	*pertinax*
M133	Diptera	Syrphidae	*Eristalis*	*pseudorupium*
M134	Diptera	Syrphidae	*Eristalis*	*rupium*
M135	Diptera	Syrphidae	*Eristalis*	*tenax*
M136	Diptera	Syrphidae	*Eumerus*	–
M137	Diptera	Syrphidae	*Eupeodes*	*lapponicus*
M138	Diptera	Syrphidae	*Eupeodes*	*nitens*
M139	Diptera	Syrphidae	*Eupeodes*	*nielseni.*
M140	Diptera	Syrphidae	*Ferdinandea*	*cuprea*
M141	Diptera	Syrphidae	*Hammerschmidtia*	*ferruginea*
M142	Diptera	Syrphidae	*Helophilus*	*hybridus*
M143	Diptera	Syrphidae	*Helophilus*	*pendulus*
M144	Diptera	Syrphidae	*Helophilus*	*trivittatus*
M145	Diptera	Syrphidae	*Heringia*	–
M146	Diptera	Syrphidae	*Leucozona*	*lucorum*
M147	Diptera	Syrphidae	*Mallotta*	*megilliformes*
M148	Diptera	Syrphidae	*Mallotta*	*tricolor*
M149	Diptera	Syrphidae	*Melangyna*	*barbifrons*
M150	Diptera	Syrphidae	*Melangyna*	*cincta*
M151	Diptera	Syrphidae	*Melangyna*	*cingulata*
M152	Diptera	Syrphidae	*Melangyna*	*quadimaculata*
M153	Diptera	Syrphidae	*Melangyna*	*triangulifera*
M154	Diptera	Syrphidae	*Melanogaster*	–
M155	Diptera	Syrphidae	*Melanogaster*	–
M156	Diptera	Syrphidae	*Melanostoma*	*mellinum*
M157	Diptera	Syrphidae	*Melanostoma*	–
M158	Diptera	Syrphidae	*Meligramma*	–
M159	Diptera	Syrphidae	*Myathropa*	*florea*
M160	Diptera	Syrphidae	*Neoascia*	*meticulosa*
M161	Diptera	Syrphidae	*Orthonevra*	*brevicornis*

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M162	Diptera	Syrphidae	*Orthonevra*	*intermedia*
M163	Diptera	Syrphidae	*Parasyrphus*	*annulatus*
M164	Diptera	Syrphidae	*Parasyrphus*	*lineolus*
M165	Diptera	Syrphidae	*Parasyrphus*	*nigritarsis*
M166	Diptera	Syrphidae	*Parhelophilus*	*frutetorum*
M167	Diptera	Syrphidae	*Parhelophilus*	*versicolor*
M168	Diptera	Syrphidae	*Pipiza*	*luteitarsis*
M169	Diptera	Syrphidae	*Pipiza*	*noctiluca*
M170	Diptera	Syrphidae	*Pipiza*	*quadimaculata*
M171	Diptera	Syrphidae	*Pipiza*	–
M172	Diptera	Syrphidae	*Pipizella*	–
M173	Diptera	Syrphidae	*Platycheirus*	*kittilaensis*
M174	Diptera	Syrphidae	*Pocota*	*personata*
M175	Diptera	Syrphidae	*Psilota*	*anthacina*
M176	Diptera	Syrphidae	*Psilota*	*atra*
M177	Diptera	Syrphidae	*Psilota*	*inupta*
M178	Diptera	Syrphidae	*Ringhia*	*campestris*
M179	Diptera	Syrphidae	*Sericomyia*	*lappona*
M180	Diptera	Syrphidae	*Sericomyia*	*silentis*
M181	Diptera	Syrphidae	*Spaziogaster*	*ambulans*
M182	Diptera	Syrphidae	*Sphaerophoria*	*ruepelli*
M183	Diptera	Syrphidae	*Sphaerophoria*	*scripta*
M184	Diptera	Syrphidae	*Sphegina*	*sibirica*
M185	Diptera	Syrphidae	*Sphegina*	–
M186	Diptera	Syrphidae	*Syrphus*	*vitripennis*
M187	Diptera	Syrphidae	*Temnostoma*	*apiforme*
M188	Diptera	Syrphidae	*Temnostoma*	*bombylans*
M189	Diptera	Syrphidae	*Temnostoma*	*vespiforma*
M190	Diptera	Syrphidae	*Trichopsomyia*	*joratensis*
M191	Diptera	Syrphidae	*Volucella*	*bombylans*
M192	Diptera	Syrphidae	*Xanthandrus*	*comtus*
M193	Diptera	Syrphidae	*Xylota*	*coeruleiventris*
M194	Diptera	Syrphidae	*Xylota*	*florum*
M195	Diptera	Syrphidae	*Xylota*	*jakutorum*
M196	Diptera	Syrphidae	*Xylota*	*meigeniana*
M197	Diptera	Syrphidae	*Xylota*	*segnis*
M198	Diptera	Syrphidae	*Xylota*	*sylvarum*
M199	Diptera	Syrphidae	–	–
M200	Diptera	Syrphidae	–	–
M201	Diptera	Syrphidae	–	–
M202	Diptera	Syrphidae	–	–
M203	Diptera	Syrphidae	–	–
M204	Diptera	Syrphidae	–	–
M205	Diptera	Syrphidae	–	–
M206	Diptera	Syrphidae	–	–
M207	Diptera	Syrphidae	–	–
M208	Diptera	Syrphidae	–	–
M209	Diptera	Syrphidae	–	–
M210	Diptera	Syrphidae	–	–
M211	Diptera	Tabanidae	*Chrysops*	*caecutiens*
M212	Diptera	Tachinidae	*Echinomyia*	*fera*
M213	Diptera	Tachinidae	*Exorista*	*rustica*

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M214	Diptera	Tachinidae	*Exorista*	–
M215	Diptera	Tachinidae	–	–
M216	Diptera	–	–	–
M217	Diptera	–	–	–
M218	Hymenoptera	Andrenidae	*Andrena*	*cineraria*
M219	Hymenoptera	Andrenidae	*Andrena*	*flavipes*
M220	Hymenoptera	Andrenidae	*Andrena*	*fulva*
M221	Hymenoptera	Andrenidae	*Andrena*	*haemorrhoa*
M222	Hymenoptera	Andrenidae	*Andrena*	*helvola*
M223	Hymenoptera	Andrenidae	*Andrena*	*jacobi*
M224	Hymenoptera	Andrenidae	*Andrena*	*nigroaenea*
M225	Hymenoptera	Andrenidae	*Andrena*	*nitida*
M226	Hymenoptera	Andrenidae	*Andrena*	*vaga*
M227	Hymenoptera	Andrenidae	*Andrena*	*varians*
M228	Hymenoptera	Andrenidae	*Andrena*	–
M229	Hymenoptera	Andrenidae	*Andrena*	–
M230	Hymenoptera	Andrenidae	*Andrena*	–
M231	Hymenoptera	Andrenidae	*Andrena*	–
M232	Hymenoptera	Andrenidae	*Andrena*	–
M233	Hymenoptera	Andrenidae	*Andrena*	–
M234	Hymenoptera	Andrenidae	*Andrena*	–
M235	Hymenoptera	Apidae	*Anthophora*	*plumipes*
M236	Hymenoptera	Apidae	*Apis*	*mellifera*
M237	Hymenoptera	Apidae	*Bombus*	*horturum*
M238	Hymenoptera	Apidae	*Bombus*	*humilis*
M239	Hymenoptera	Apidae	*Bombus*	*hypnorum*
M240	Hymenoptera	Apidae	*Bombus*	*jonellus*
M241	Hymenoptera	Apidae	*Bombus*	*lapidarius*
M242	Hymenoptera	Apidae	*Bombus*	*pascuorum*
M243	Hymenoptera	Apidae	*Bombus*	*pratorum*
M244	Hymenoptera	Apidae	*Bombus*	*sylvarum*
M245	Hymenoptera	Apidae	*Bombus*	*terrestris agg.*
M246	Hymenoptera	Apidae	*Hylaeus*	*communis*
M247	Hymenoptera	Apidae	*Lasioglossum*	*majus*
M248	Hymenoptera	Apidae	*Nomada*	*panzeri*
M249	Hymenoptera	Apidae	*Nomada*	–
M250	Hymenoptera	Apidae	*Psithyrus*	*campestris*
M251	Hymenoptera	Apidae	*Psithyrus*	*sylvestris*
M252	Hymenoptera	Apidae	*Psithyrus*	–
M253	Hymenoptera	Apidae	–	–
M254	Hymenoptera	Colletidae	*Hylaeus*	*gracilicornis*
M255	Hymenoptera	Cynipidae	–	–
M256	Hymenoptera	Eumenidae	–	–
M257	Hymenoptera	Halictidae	*Halictus*	–
M258	Hymenoptera	Halictidae	*Lasioglossum*	*calceatum*
M259	Hymenoptera	Halictidae	*Lasioglossum*	*pauxillum*
M260	Hymenoptera	Ichneumonidae	*Diplazon*	–
M261	Hymenoptera	Ichneumonidae	–	–
M262	Hymenoptera	Sphecidae	–	–
M263	Hymenoptera	Tenthredinidae	–	–
M264	Hymenoptera	Vespidae	*Dolichovespula*	*adulterina*
M265	Hymenoptera	Vespidae	*Dolichovespula*	*saxonica*

Supplementary Table 4.6. (continued).

Species code	Order	Family	Genus	Species
M266	Hymenoptera	Vespidae	*Dolichovespula*	*sylvestris*
M267	Hymenoptera	Vespidae	*Eumenes*	–
M268	Hymenoptera	Vespidae	*Polistes*	*gallicus*
M269	Hymenoptera	Vespidae	*Vespa*	*crabro*
M270	Hymenoptera	Vespidae	*Vespula*	*austriaca*
M271	Hymenoptera	Vespidae	*Vespula*	*vulgaris*
M272	Hymenoptera	Vespidae	–	–
M273	Hymenoptera	Vespidae	–	–
M274	Hymenoptera	Vespidae	–	–
M275	Hymenoptera	–	–	–
M276	Hymenoptera	–	–	–
M277	Hymenoptera	–	–	–
M278	Lepidoptera	Geometridae	*Epirrhoe*	*alternata*
M279	Lepidoptera	Hesperiidae	*Carterocephalus*	*palaemon*
M280	Lepidoptera	Lycaenidae	*Lycaena*	*helle*
M281	Lepidoptera	Lycaenidae	*Lycaena*	*tityrus*
M282	Lepidoptera	Nymphalidae	*Inachis*	*io*
M283	Lepidoptera	Nymphalidae	*Araschnia*	*levana*
M284	Lepidoptera	Nymphalidae	*Melitaea*	–
M285	Lepidoptera	Pieridae	*Pieris*	*napi*
M286	Lepidoptera	–	–	–
M287	Lepidoptera	–	–	–
M288	Lepidoptera	–	–	–
M289	Lepidoptera	–	–	–
M290	Lepidoptera	–	–	–
M291	Lepidoptera	–	–	–
M292	Mecoptera	Panorpidae	*Panorpa*	*communis*
M293	Neuroptera	Chrysopidae	*Chrysopa*	–
M294	Neuroptera	Chrysopidae	–	–

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Erklärung

Hier mit versichere ich, dass ich meine Dissertation mit dem Titel

„Natural and human-induced dynamics in
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Unterschrift (Jörg Albrecht)

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