Biodiversity – from genes to species to communities –
and ecosystem services under global change: bees, pollination and
urbanization

Dissertation

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To caffeine, my best friend

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General Introduction

Global change pressures on pollinators: urbanization

Animal-mediated pollination is an essential ecological process, which ensures the reproduction of the majority of angiosperms (87.5 % based on Ollerton et al. 2011), including crops, and thus also providing products and food for humans and animals (e.g. Klein et al. 2007; Kremen et al. 2007). The economic contribution of pollinators to crop production is remarkable, with an estimate of €20 billion in Europe and €210-510 billion worldwide (Gallai et al. 2009; Lautenbach et al. 2012). Among the main insect pollinators, namely the Coleoptera, Diptera, Lepidoptera and Hymenoptera (Kevan and Baker 1983), bees are of particular importance, contributing on average over €3,000 ha^{-1} to the production of insect-pollinated crops (Kleijn et al. 2015). However, several recent reports have highlighted declines of insect pollinators that could have major ecological and economic consequences (reviewed in Potts et al. 2010; Potts et al. 2016b).

Pollinator declines have been attributed to a variety of global change pressures (Brown and Paxton 2009; Potts et al. 2010; González-Varo et al. 2013; Potts et al. 2016a) and mirror those for biodiversity decline (Pereira et al. 2012). They include (i) habitat loss, fragmentation and degradation; (e.g. Garibaldi et al. 2011; Winfree et al. 2011); (ii) agricultural intensification (e.g. Kremen et al. 2002); (iii) climate change (e.g. Hegland et al. 2009); (iv) spread of pathogens (e.g. Cameron et al. 2011) and (v) invasive alien species (e.g. Moroń et al. 2009) (Fig. 1). These are among the main identified causes for shifts in pollinator community composition, including a decrease in pollinator species richness and abundance (e.g. Biesmeijer et al. 2006; Bartomeus et al. 2013).

Habitat loss, resulting from the conversion of semi-natural to human dominated habitats, is widely considered the most universal and high impact factor driving pollinator declines (Brown and Paxton 2009; González-Varo et al. 2013). Two of the main drivers of habitat loss, with overall negative effects on pollinator biodiversity, are agricultural development and urbanization (McKinney 2002, Tscharntke et al. 2005, Vanbergen and Pollinator Initiative 2013). However, compared to agricultural systems (and semi-natural habitats), pollinators in urban areas remain relatively under-studied (Winfree et al. 2011). This is not surprising given that approximately 38% of earth ice-free land mass is used for agricultural purposes (Foley et al. 2005) and only 8% is urbanized/suburbanized (Ellis et al. 2010). Nonetheless, cities are growing rapidly worldwide (United Nations 2005; Seto et al. 2012) and the lack of extensive research in urban ecosystems does not allow comparisons of pollinator responses and provision of the ecosystem service of pollination between rural and urban areas and across the rural-urban transition (chapters I & II).
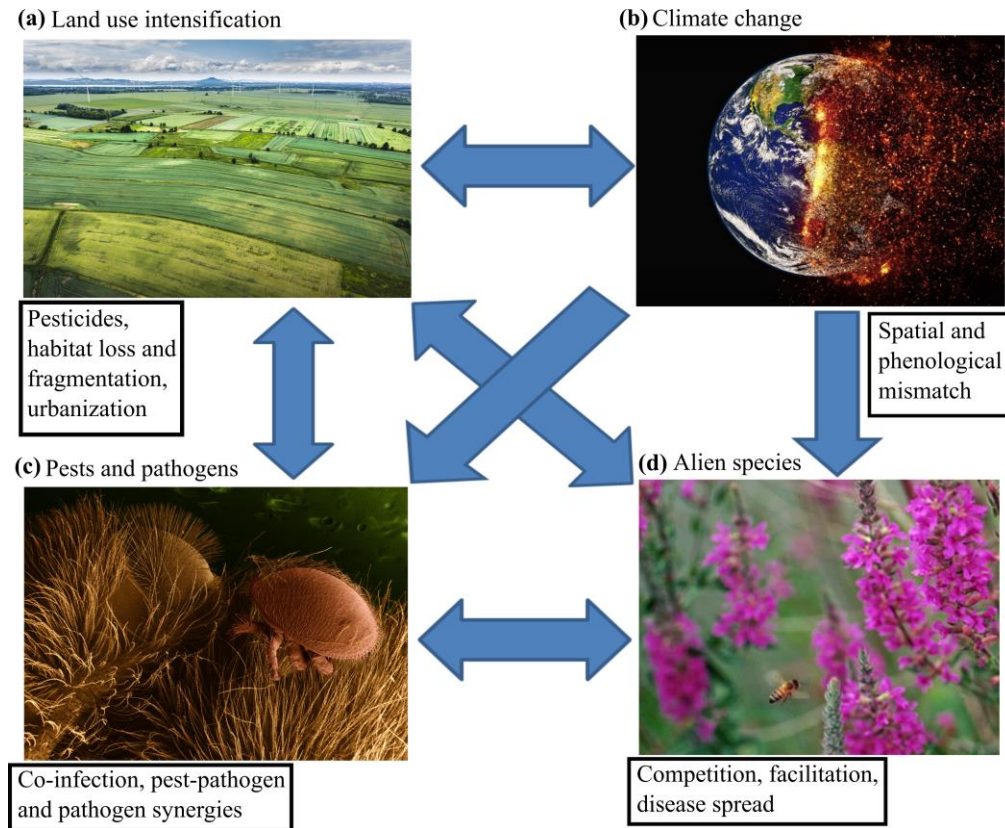
Figure 1. Global change pressures (a-d) and their interactions (arrows), as they affect pollinators. Adapted from Vanbergen and Pollinator Initiative (2013).

Impacts of urbanization combine both the rapid destruction of natural habitats and their slow degradation. Urbanization can directly affect species fitness (Bonier et al. 2007), alter competition and predation dynamics (Cook and Saccheri 2013; Turrini et al. 2016), and challenge the persistence of most species, including essential ecosystem service providers like insect pollinators (McKinney 2008; Bates et al. 2011). Paradoxically, though, several studies have shown that anthropogenic habitats, including both urban and agricultural areas, can have neutral or even positive effects on pollinator diversity (Cane et al. 2006; Carré et al. 2009; Winfree et al. 2011; Baldock et al. 2015) and pollination (Cussans et al. 2010; Verboven et al. 2014). Urban habitats can contain remarkably high pollinator species richness. For example, half of the German bee fauna has been recorded in Berlin (Saure 1996), and some studies show positive effects of urbanization on bee richness and abundance (Table 1), especially of certain bee taxa, such as the bumblebees and cavity-nesting bees (Matteson et al. 2008; Hernandez et al. 2009).

Differences in the intensity of land-use change, its spatial scale and the taxonomic group studied are among the main hypothesized reasons for these contrasting findings (McKinney 2008; Cariveau and Winfree 2015).

Table 1. List of studies comparing overall bee richness and/or bee abundance in response to urbanization.

Reference	Study location	Compared land use type	Study design	Outcome variable	Directionality of change
Hostetler and McIntyre (2001)	USA	Desert	Land-use effects	richness	↘
Cane et al. (2006)	USA	Desert	Proportion habitat in landscape	richness	↗
Cane et al. (2006)	USA	Desert	Proportion habitat in landscape	abundance	↗
Winfree et al. (2007)	USA	Farmland	Land-use effects	abundance	↘
Winfree et al. (2007)	USA	Farmland	Land-use effects	richness	●
Verboven et al. (2014)	Belgium	Farmland	Land-use effects	abundance	●
Verboven et al. (2014)	Belgium	Farmland	Land-use effects	richness	●
Baldock et al. (2015)	UK	Farmland	Land-use effects	richness	↗
Baldock et al. (2015)	UK	Farmland	Land-use effects	abundance	●
Dauber et al. (2003)	Germany	Rural	Proportion habitat in landscape	richness	●
Kearns and Oliveras (2009)	USA	Rural	Proportion habitat in landscape	abundance	●
Kearns and Oliveras (2009)	USA	Rural	Proportion habitat in landscape	richness	●
Bates et al. (2011)	UK	Rural	Land-use effects	abundance	↘
Bates et al. (2011)	UK	Rural	Land-use effects	richness	↘
Fortel et al. (2014)	France	Rural	Proportion habitat in landscape	abundance	↘
Fortel et al. (2014)	France	Rural	Proportion habitat in landscape	richness	↗
Senapathi et al. (2015)	UK	Rural	Proportion habitat in landscape	richness	↗
Deguines et al. (2016)	France	Rural	Proportion habitat in landscape	richness	●
Verboven et al. (2014)	Belgium	Seminatural	Land-use effects	abundance	●
Verboven et al. (2014)	Belgium	Seminatural	Land-use effects	richness	↘
Baldock et al. (2015)	UK	Seminatural	Land-use effects	richness	●
Baldock et al. (2015)	UK	Seminatural	Land-use effects	abundance	●
Winfree et al. (2007)	USA	Temperate forest	Land-use effects	abundance	↗
Winfree et al. (2007)	USA	Temperate forest	Land-use effects	richness	●

Positive effect Reference= Reference of the study; Study location=Country or region studied; Compared habitat type=Category of habitat compared to urbanization; Study design = Type of design used. Studies that compare sites along a gradient in surrounding land cover are categorized as "Proportion habitat in landscape". Studies that compare across land-use types, are categorized as "Land-use effects"; Outcome variable= Outcome variable measured; Directionality of change= Response of pollinators (outcome variable) to urbanization; ↗ Positive effect, ● Neutral effect, ↘ Negative effect.

Moderate disturbance in agricultural and urban ecosystems could increase landscape heterogeneity and the availability of suitable pollinator habitats and resources, thus increasing niche diversity and enhancing insect pollinator diversity (Winfree et al. 2009; Kennedy et al. 2013; Clough et al. 2014; Senapathi et al. 2015). Moreover, small-scale habitat features associated with nesting (Murray et al. 2012) and floral resources (Roulston and Goodell 2011) can be limiting factors for pollinator populations, regardless of land-use change (Winfree et al. 2011). Urbanized and agricultural areas, with increased and highly connected semi-natural habitats that provide pollinators with novel foraging and nesting resources, could potentially support pollinator biodiversity (Winfree et al. 2009; Carré et al. 2009; Steckel et al. 2014; Fortel et al. 2014; Senapathi et al. 2015) and thereby enhance the ecosystem service of pollination (chapter I).

Pollinator species diversity and intrapopulation genetic diversity

The majority of studies addressing the impacts of habitat change on pollinator biodiversity have so far been mainly focused on species or functional diversity (Winfree et al. 2011; Rader et al. 2014; Sydenham et al. 2016). However, as originally conceived by the Convention on Biological Diversity (CBD, 2005), biodiversity encapsulates diversity across all scales of biological organisation, from genes, through species to ecosystems. This makes intraspecific genetic diversity one of the fundamental levels of biodiversity. In addition to enhancing population fitness and acting as a surrogate for effective population size, genetic diversity might also have significant effects on ecological processes (reviewed in Hughes et al. 2008, Crutsinger et al. 2006; Kotowska et al. 2010) and could serve as an indirect measure of the evolvability of a population. The greater the genetic diversity of a population, the greater the genetic raw material upon which selection can act; this may be especially important in the context of adaptation to global change, including land-use change (Frankham 1996). Furthermore, species diversity of communities and genetic diversity within a population theoretically co-vary because of parallel local processes (e.g. area, isolation, environmental heterogeneity) acting on both (Fig. 2, case I), or because of direct effects of one level of diversity on the other (reviewed in Vellend & Geber 2005) (Fig. 2, cases II & III).

Genetic diversity may causally influence species diversity if it affects a population's viability, or if a dominant species determines the biotic environment experienced by the rest of the community (Fig. 2, case II). Conversely, if species diversity of a community influences the local selective regime, genetic diversity may be causally influenced by the diversity and relative abundance of coexisting species (Fig. 2, case III). Yet, there remains a paucity of studies simultaneously analysing species diversity and relative genetic diversity with which to draw firm conclusions on their respective roles in promoting ecological interactions (chapter I).
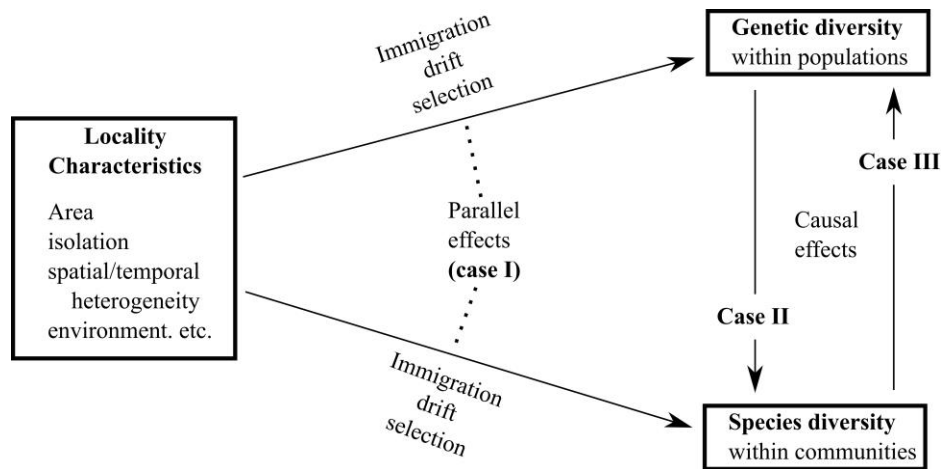
Locality Characteristics

Area
isolation
spatial/temporal heterogeneity
environment. etc.

Immigration
drift
selection

Genetic diversity
within populations

Parallel effects (case I)

Case III

Causal effects

Case II

Immigration
drift
selection

Species diversity
within communities

Figure 2. Potential connections between species diversity and genetic diversity (reprinted from Vellend and Geber (2005) with permission from John Wiley and Sons).

Plant-flower visitor networks

At the scale of an ecological community, the pairwise interactions between individual pollinator species and the plant species that they visit collectively form complex networks (mutualistic networks), which can be visualized and analyzed in a similar manner to food webs (Memmott 1999) (Fig. 3). Most studies have so far focused on the effects of anthropogenic land-use on the diversity of pollinators and their hosts plants as well as on plant-pollinator community composition (e.g. Angold et al. 2006, McKinney 2008, Winfree et al. 2009). However, the effects of land-use change and local habitat on plants and insect pollinators are also likely to influence their mutualistic interactions, thereby impacting the architecture of their networks (Fortuna and Bascompte 2006; Ferreira et al. 2013; Weiner et al. 2014) (chapter II).

In the past decade, several approaches and tools have been developed to describe network topology, quantify the degree of specialization between partners and assess network robustness (Fortuna and Bascompte 2006; Dormann et al. 2009). The topology of those networks is hypothesised to be important in promoting community stability and functioning (Bastolla et al. 2009; Tylianakis et al. 2010; Parrott 2010; Blüthgen and Klein 2011; Kaiser-Bunbury and Blüthgen 2015). For example, increased linkage density characterises more complex biotic interaction networks that could lead to higher network robustness, preventing species extinctions (e.g. Naeem 1998) and potentially leading to more consistent pollination (Blüthgen and Klein 2011). Additionally, defining key elements of networks, such as species specialization and generality, help to guide conservation priorities by identify species roles in local communities and formulate hypotheses regarding the effects of land-use change on plant-pollinator communities, their interactions and consequently pollination (chapter II).
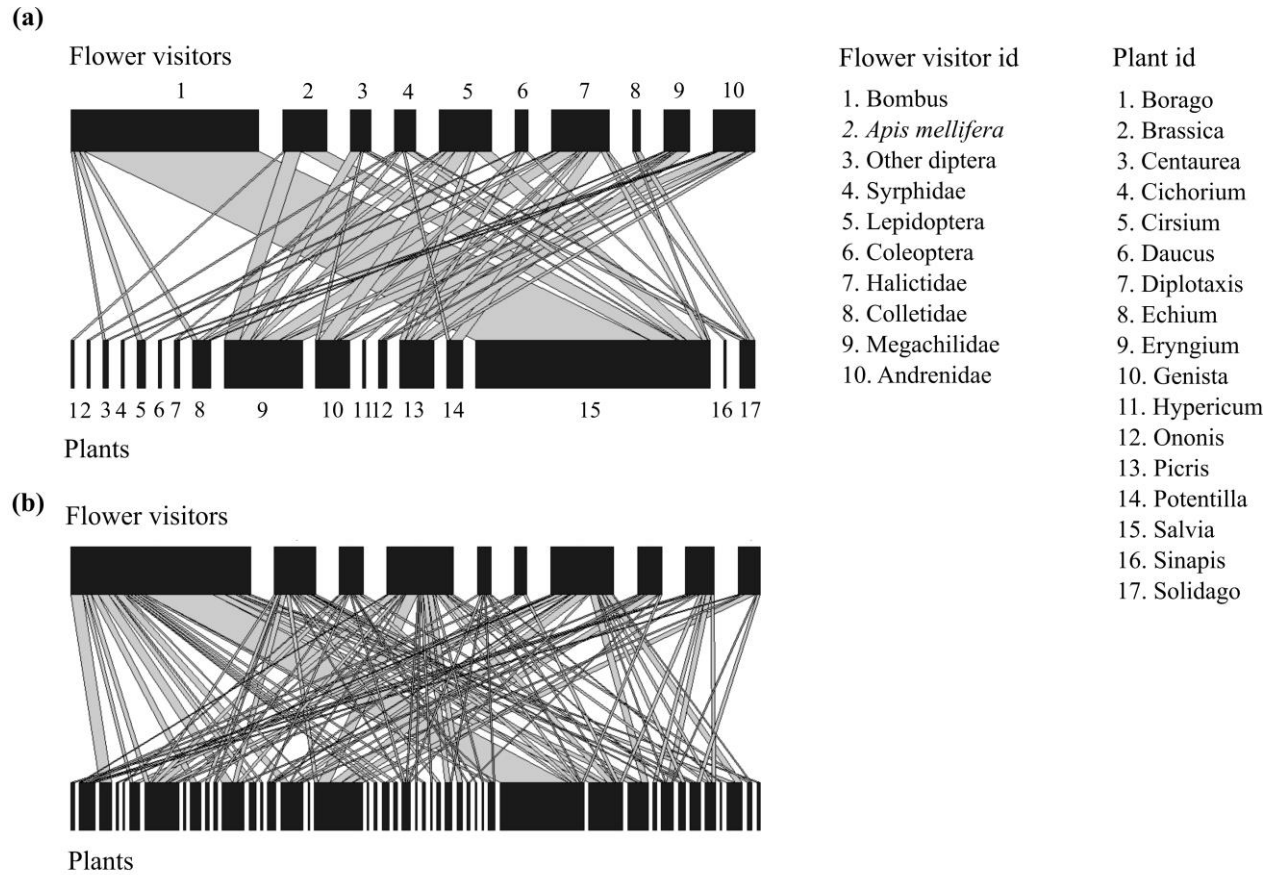
(a)

Flower visitors

Flower visitor id	Plant id
1. Bombus	1. Borago
2. *Apis mellifera*	2. Brassica
3. Other diptera	3. Centaurea
4. Syrphidae	4. Cichorium
5. Lepidoptera	5. Cirsium
6. Coleoptera	6. Daucus
7. Halictidae	7. Diplotaxis
8. Colletidae	8. Echium
9. Megachilidae	9. Eryngium
10. Andrenidae	10. Genista
	11. Hypericum
	12. Ononis
	13. Picris
	14. Potentilla
	15. Salvia
	16. Sinapis
	17. Solidago

(b)

Flower visitors

Plants

Figure 3. Quantitative networks of flying insects and plants (data from chapter II). Flower visitors are shown as rectangles at the top and plants are shown as rectangles at the bottom of each bipartite graph, constructed using the R package 'bipartite'v.2.05 (Dormann et al. 2009). The width of the rectangles reflects the relative frequency of interactions of each species. The number attached to each rectangle (only for (a)) corresponds to the flower visitor and plant identities. Compared to network (a), (b) shows higher linkage density (mean number of links per flower visitor /plant weighted by the number of interactions) and higher flower visitor generality (mean effective number of plants visited per flower visitor, weighted by their relative abundance) (chapter II).

Bumblebees as a model system

Bumblebees have become a model system for studies on behaviour, ecology and evolution and are of great ecological and economic importance (Goulson 2010; Woodard et al. 2015). The majority of bumblebee species are generalist pollinators and can therefore facilitate the reproduction of a large number of wild plants and commercial crops in diverse terrestrial habitats of temperate regions (Goulson et al. 2008; Goulson 2010; Kleijn et al. 2015).

With accumulating evidence of wild (non-managed) bee declines in the Northern Hemisphere (Biesmeijer et al. 2006; Burkle et al. 2013), there is an increasing interest in native pollinator conservation in human altered environments (Potts et al. 2016b). Bumblebees are among the most important pollinators in this biogeographic region that offer an excellent model system to study the effects of land-use on genetic diversity and gene flow (Jha and Kremen 2013; Jha 2015; Woodard et al. 2015) (chapter I). Furthermore, they represent an ideal system to study the potential top-down effects of parasitism on pollination services (chapter III).

Bumblebees are attacked by a number of parasites, including the trypanosomatid *Crithidia bombi* and the microsporidium *Nosema bombi*. *Crithidia bombi* is a common gut parasite that affects colony reproduction and foraging performance (Schmid-Hempel 1998; Brown et al. 2003; Gegear 2005; Gegear et al. 2006). The less common *N. bombi* infects the entire animal and has been shown to reduce worker survival and colony fitness (Otti and Schmid-Hempel 2007; Otti and Schmid-Hempel 2008; Rutrecht and Brown 2009). Thus, these two parasites, which seemingly attack a wide range of bumblebee species, could potentially influence both the quantity and quality of plant-pollinator interactions and alter provision of pollination service to plants (chapter III).

Structural equation modelling (SEM)

The term structural equation modelling (SEM) does not designate a single statistical technique but a family of related procedures, such as explanatory factor analysis and multible regression or path analysis (Kline 2011). Structural equation modelling is also known as "causal modeling" or "analysis of covariance structures" and is often visualised by a graphical path diagram. In the absence of an experimental design, no statistical methodology, including SEM, can by itself demonstrate causation. However, SEM can be used for examining alternative hypotheses and identifying direct and indirect correlations between variables within a defined mechanistic path that incorporates logically plausible causal links; this is potentially a statistically more powerful approach to the analysis of my datasets than other multivariate methods, such as multiple regression, which test all links among all pairs of variables, whether logically plausible or not.

Across all the chapters of the thesis, I use structural equation modelling (SEM) to investigate hypotheses involving the relationships between: (a) environmental variables, urbanization, visitation rates, pollinator biodiversity and pollination (chapter I), (b) environmental variables, urbanization, local plant and pollinator community structure and network topology (chapter II) and (c) environmental variables,

urbanization, abundance of flower visitors and *Bombus* spp. parasite prevalence and pollination (chapter III).

In this thesis, I constructed all *a priori* piecewise SEMs based on previous studies that have tested individual links and hypotheses included in my overall path models (Cussans et al. 2010; Gillespie 2010; Winfree et al. 2011; Goulson et al. 2012; Murray et al. 2012; Gillespie and Adler 2013; Leong et al. 2014).

Aims of this thesis

As a step towards understanding the effects of anthropogenic land-use on insect pollinator diversity, in the first chapter of this thesis (chapter I) I use a replicated landscape scale experiment in nine central eastern German cities and nearby adjacent rural areas to disentangle the relative effects of local habitat resources, landscape composition and configuration on insect pollinator diversity, simultaneously measured as intraspecific genetic diversity, species richness and phylogenetic diversity. I furthermore performed a concurrent landscape-scale pollination experiment using potted, greenhouse-raised, insect-pollinator dependent plants ("pollinometers") to investigate the relationship between insect biodiversity (genetic diversity, species richness and phylogenetic diversity), visitation rates, landscape, local habitat and pollination service provision both within and across urban and rural ecosystems.

In the second chapter of this thesis (chapter II), I use flower-visitor networks to examine how local habitat factors (nesting and floral resources) and the gradual change in dominant land-use type from agricultural to urban in the surrounding landscape affect plant-pollinator communities and their interactions. Despite the growing body of theory and use of visitation networks to provide information about resource use by flying insects, little is known to date about how network structure relates to ecosystem functioning and service provision (Ferreira et al. 2013; Kaiser-Bunbury and Blüthgen 2015). In the second chapter of the thesis (chapter II), by again using potted greenhouse-raised, insect pollinator dependent plants (pollinometers), I investigated whether hypothesised network metrics (e.g. linkage density, flower visitor generality) are related to pollination *per se*.

As terrestrial ecosystems are impacted by multiple pressures, knowledge of the interactive effects between them is necessary to aid biodiversity conservation and maintenance of the ecosystem services provided by pollinators (Didham et al. 2007; González-Varo et al. 2013). For example, in addition to habitat loss, pathogens can also negatively affect pollinator populations and pollination. Pathogens are known to reduce pollinator fitness and abundance and alter their foraging behaviour (Schmid-Hempel 1998), thus

potentially causing cascading, negative multi-trophic effects on pollination. In the third chapter of this thesis (chapter III) I investigate those potential interactive effects (anthropogenic land-use change and pollinator parasitism) on pollination service provision using bumblebees (genus *Bombus*) and their associate parasites as a model system. Gillespie and Adler (2013) recently showed that the prevalence of parasites in *Bombus* spp. could be negatively correlated with seed set of the plant species that they visit (e.g. *Trifolium pratense*). Additionally, urban areas are considered to support high *Bombus* spp. colony densities (McFrederick and LeBuhn 2006; Osborne et al. 2008), which potentially further promote parasite abundance and transmission; across host-parasite systems, parasite prevalence is influenced by host population size, and vice versa (Anderson and May 1981; Goulson et al. 2012). Thus, studying bumblebees and their associated parasites across changing landscapes as well as their effects on pollination (chapter III) can provide further insights into how two of the main global change pressures on pollinator biodiversity, that of parasitism and anthropogenic land-use, may interact and indirectly affect mutualistic ecological interactions.

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I. Flower-rich urban areas can act as bee pollination hotspots

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Abstract

Changes in land use, including urbanization, are a major driver of shifts in biodiversity, with potential consequences for the ecosystem services they provide. At the same time, there is growing interest in the role of cities not only in requiring but also potentially in supplying biodiversity and ecosystem services, including pollination. Here, we investigated whether cities are associated with enhance or diminished pollination by experimentally quantifying the ecosystem service of pollination at nine pairs of flower-rich urban and nine adjacent flower-rich rural sites. To understand the causes of variation in pollination service provision, we compared insect pollinator diversity, spanning intraspecific genomic variability through to community phylogenetic diversity at all 18 sites. Pollination service provision was higher at urban than rural sites despite overall lower pollinator species richness at the former. Diptera and Lepidoptera in particular were less diverse in cities, Coleoptera did not differ, whereas Hymenoptera were more diverse at urban sites, with higher flower visitation rates, suggesting that they drove the pattern in service provision. We also found strong associations between biodiversity and landscape heterogeneity that were common to both urban and rural ecosystems. An increase in insect pollinator species richness was associated with greater landscape connectivity within cities, and with a decrease in agricultural land and increase in flower richness within rural sites. The best predictors of pollination service provision across all sites (urban and rural) were Hymenoptera community diversity and visitation rates. Intraspecific genetic diversity has been hypothesised to enhance ecosystem function. Yet genomic diversity of one of the main flower visitors in our region, the wild bumble bee *Bombus lapidarius*, was not related to pollination.

We conclude that appropriately managed cities could not only enhance the conservation of Hymenoptera, particularly wild bee species, but also act as hotspots for pollination service provision.

II. The structure of flower-visitor networks in relation to pollination across an agricultural to urban gradient

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Abstract

Pollination is a major ecosystem service in which insects, particularly bees, play an important role for the reproduction of most angiosperms. Currently this service is considered under threat due to reported bee declines. Moderately urbanized areas could be important for pollinators and pollination; however, compared to agricultural and natural systems, they are poorly studied. Here, we investigated the relative effects of local habitat quality and anthropogenic land use across an agricultural to urban gradient for local plant and flying insect communities. We quantified local flower-visitor networks and related network architecture to these local and landscape factors using structural equation modelling. Flower-visitor network architecture is often assumed to act as a surrogate for the ecosystem service of pollination. To test this idea, we related network metrics to pollination of four experimental, insect pollinator-dependent plant species. Overall, local land use markedly influenced plant and flying insect communities. Flower richness and bee richness were higher in urban compared to agricultural areas. Flower-visitor network metrics (e.g. linkage density) increased with the proportion of urban area surrounding a site. Also, relative to agricultural areas, urban flower visitors were more generalised and foraged from a higher number of plant species, likely a consequence of higher urban flowering plant richness. However, urban bees also visited a lower proportion of the available flowering plants (higher specialisation). Surprisingly, linkage density, network specialisation and flower visitor generality were not related to pollination of our four experimental plants *per se*. Rather, it was the proportion of urban cover, flying insect abundance and bee richness that were positively related to pollination. Our findings show strong effects of local land use on plant and flying insect communities and flower-visitor interaction networks. We observed increased overall visitation rates and pollination services to our experimental plants in urban compared to agricultural areas, despite increased urban flower visitor generality. Indeed, flower-visitor network metrics were a poor proxy of provision of the ecosystem service of pollination. Nevertheless, our results point to potential facilitating effects of diverse urban floral and bee communities for pollination.

III. Pollination services enhanced with urbanisation despite increasing pollinator parasitism

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Abstract

Animal-mediated pollination is required for the reproduction of the majority of angiosperms and pollinators are therefore essential for ecosystem functioning and the economy. Two major threats to insect pollinators are anthropogenic land-use change and spread of pathogens, whose effects may interact to impact pollination. Here, we investigated the relative effects on the ecosystem service of pollination of: (i) land-use change brought on by agriculture and urbanisation as well as (ii) the prevalence of pollinator parasites, using experimental insect pollinator-dependent plant species in natural pollinator communities. We found that pollinator habitat (i.e. availability of nesting resources for ground-nesting bees and local flower richness) was strongly related to flower visitation rates at the local scale and indirectly influenced plant pollination success. At the landscape scale, pollination was positively related to urbanisation, both directly and indirectly via elevated visitation rates. Bumblebees were the most abundant pollinator group visiting experimental flowers. Prevalence of trypanosomatids, such as the common bumblebee parasite *Crithidia bombi,* was higher in urban compared to agricultural areas, a relationship which was mediated through higher *Bombus* abundance. Yet, we did not find any top-down, negative effects of bumblebee parasitism on pollination. We conclude that urban areas can be places of high transmission of both pollen and pathogens.

General Discussion

Animal pollination is an essential ecosystem service in which insects, particularly bees, play an important role for plant reproduction, including crop production (Klein et al. 2007; Ollerton et al. 2011). However, due to recent reports of bee declines in the Northern Hemisphere, this service is currently considered under threat (Potts et al. 2010; Bartomeus et al. 2013). This has led to the first Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report, which is on pollinators, pollination and food production (Potts et al. 2016a).

Habitat destruction is the primary driver of biodiversity loss in general, and of pollinator diversity loss in particular (Brown and Paxton 2009; González-Varo et al. 2013). (Semi-) natural habitats, rich in diverse floral food resources and pollinator nesting opportunities, are fragmented and degraded during conversion to highly impervious urban and intensively managed agricultural areas.

Urbanization is a major global change phenomenon with threats but also potential benefits for biodiversity (Baldock et al. 2015; Hall et al. 2016). Currently, the study of pollinators in urban areas is the subject of great interest and in several cases more diverse and abundant pollinator populations can be found in cities compared to nearby rural ecosystems (General Introduction, Table 1). Nonetheless, knowledge gaps remain substantial with regards to which features of cities can be improved to enhance functional pollinator biodiversity and whether urbanization interacts with other global change pressures, such as parasitism, to affect pollinator populations and pollination.

Whether and to what extent urbanization influences not only biodiversity but also pollination is still largely unexplored. The work presented in the current thesis provides new insights on the effects of urbanization on insect pollinators and their interactions with plant communities, and at the same time addresses fundamental ecological hypotheses about the relationship between biodiversity and ecosystem services. I used a series of tools spanning from next generation sequencing, landscape ecology approaches, ecological network theory, experimental "pollinometers" and advanced statistical methods to investigate these hypotheses. The implications of my PhD work relate to the understanding of the effects of anthropogenic land-use, with emphasis on urbanization, on insect pollinators. They also point to specific local habitat and landscape ecological interventions to improve the value of cities for pollinators and pollination.

First using replication at the landscape level, I found lower overall pollinator species richness in flower-rich urban compared to flower-rich rural sites. However, richness patterns varied between taxonomic groups, with higher richness of Hymenoptera in cities (chapter I), which is in agreement with a recent large scale study from the UK (Baldock et al. 2015). My study expands their results by investigating biodiversity across all major insect pollinators (Diptera, Lepidoptera, Coleoptera, and Hymenoptera) while also exploring the main environmental drivers, spanning from local habitat quality to landscape heterogeneity, of the richness of each of these insect orders across both urban and rural ecosystems (chapter I). At the same time, my paper is the first large scale study that uses experimental plant communities to evaluate pollination in multiple cities. My results reveal that pollination service provision can be higher in urban compared to rural sites, suggesting that cities could act as pollination hotspots. The relationship was driven by increased Hymenoptera diversity and flower visitation rates in urban areas.

Landscape heterogeneity, and, more specifically, green area edge density was a good predictor of species richness across both rural and urban ecosystems. These results provide important information as they suggest that edges might be valuable pollinator habitats rich in floral and nesting resources. In addition, the positive correlation found between edge density and visitation rates, similarly to previous studies, further suggest that flower visitors might use edges as foraging routes and that edges therefore could facilitate pollinator movement and enhance flower visits (Tewksbury et al. 2002; Hennig and Ghazoul 2011a; Hennig and Ghazoul 2011b). Given the strong associations found between biodiversity and landscape heterogeneity across cities and rural ecosystems, my results highlight the idea that common landscape ecological interventions may be transferred from one ecosystem to another to successfully facilitate biodiversity conservation and ecosystem service provision.

Future research attention should be given to the investigation of both the spatial and temporal stability of pollinator biodiversity and pollination within urban ecosystems. This will provide further insights in how to improve wild pollinator populations in urban areas and contribute to the development of more sustainable urbanization. Additionally, expanding current biased knowledge from temperate cities to include cities in tropical Asia and Africa will be of great importance since those countries will experience most of the predicted global urban expansion in the coming decades (Seto et al. 2012).

An important aspect of my research was also the implementation of next generation sequencing (NGS) for the assessment of insect pollinator richness and genomic diversity of *B. lapidarius* (chapter I). I used NGS-based metabarcoding (Yu et al. 2012; Ji et al. 2013) and, in collaboration with my colleagues, we developed a novel pipeline to determine Operational Taxonomic Units (OTUs) and perform taxonomic

assignment of pan-trapped collected insect pollinators (chapter I). Furthermore, to assess genome-wide genetic diversity of *B. lapidarius*, an important pollinator in our region, I used RAD sequencing, a genome complexity reduction technique that facilitates large-scale SNP marker discovery and genotyping by NGS (Baird et al. 2008). Both of these NGS techniques were important in my investigations of the effects of urbanization on pollinator biodiversity, allowing me to study several of its facets, ranging from intraspecific genomic variability to community phylogenetic diversity. My NGS data suggest that cities can harbour pollinator taxa from a diverse set of lineages, with no detectable effects of urbanization on genetic diversity or gene flow of *B. lapidarius* in central-eastern Germany.

The relationship between genetic diversity and functioning of communities has rarely been explored with regard to ecological interactions, including pollination. My data provide evidence against the hypothesis that intraspecific genetic diversity is correlated with ecological interactions and ecosystem services (Hughes et al. 2008). Rather, my results indicate that the ecosystem service of pollination is promoted by functional complementarity, as expressed by phylogenetic diversity and Hymenoptera OTU richness, particularly for plants whose flowers are visited by numerous wild bee species. Nevertheless, I found a positive correlation between overall insect pollinator richness and *B. lapidarius* intraspecific genetic diversity. The positive species-genetic diversity relationship suggests that conservation actions focusing on community diversity will also enhance population sizes of individual species and help to conserve pollinator intraspecific genetic diversity and *vice versa*. Future research should explore and disentangle the main mechanisms connecting genetic and species diversity. Furthermore, additional studies that survey levels of genetic variance across multiple natural populations and across larger time and landscape scales are also needed to investigate the main mechanisms underpinning the potential ecological consequences of genetic diversity.

In the current thesis, I not only used biodiversity surveys, but also investigate the potential effects of anthropogenic land-use on the interactions between plants and pollinators (chapter II). These interactions form complex structured networks (Bascompte et al. 2003) and network architecture may be important for community stability (Bastolla et al. 2009).

Habitat loss, as described earlier, can affect both species richness and abundance and thus could also affect the network of interactions in a community. In the current work, I used networks as tools to investigate plant-pollinator communities and their interactions along an agricultural to urban land-use gradient (chapter II). By simultaneously assessing local habitat quality and the surrounding land-use, I disentangled their relative contributions in structuring plant-flower visitor interactions; I showed that urbanization not only

can affect plants and their flower visitors, but can also contribute to the reorganization of interspecific interactions in a local community. I found that interaction networks become more specialized in urbanized areas, with increased linkage density and flower visitor generality. Furthermore, I found that increasing nesting resources and flower richness were associated with a higher abundance of flying insects, bee genus richness and increased overall visitation rates to the "pollinometers", further emphasizing the importance of local habitat quality for pollinator communities. I further explored how these multiple environmental factors influence pollination of pollinator-dependent plants. My findings showed that, in moderately urbanized areas providing rich floral resources, both positive effects on bee richness and plant reproduction can be observed. The study emphasizes that knowledge of species interactions is critical for gaining a better understanding of plant-pollinator community structure and also highlights the importance of using networks as tools when investigating plant-pollinator communities.

Multiple studies have attempted to relate habitat loss and urbanization with the architecture of plant–pollinator interaction networks (Geslin et al. 2013; Spiesman and Inouye 2013; Baldock et al. 2015; chapter II). However, we still lack studies linking community network topology to ecosystem function. In my study, I did not find significant associations between network metrics and pollination. This might be due to insufficient sampling and thus lack of statistical power. Alternatively, or in addition, it may indicate the importance not only of the diversity and distribution of interactions to ensure pollination of pollinator dependent plants, but also the potential role of the quality of those interactions in terms of the number of compatible, viable pollen grains deposited on stigmata.

Future studies constructing more informative community networks i.e. distinguishing between mere flower visitors and effective pollinators (e.g. Ballantyne et al. 2015), over longer periods of time and using a wider range of experimental plant species, are needed to further explore the extent to which network metrics are associated with ecosystem function, and specifically how flower-visitor networks relate to pollination.

Finally, pollinator populations are affected not only by habitat loss but also by several other global change pressures such as climate change, non-native species and parasites. These pressures can interact in non-additive ways but are rarely considered together in studies of pollinators or pollination (González-Varo et al. 2013). For that reason, in the last presented study (chapter III), using bumblebees and their associated parasites as a model system, I performed a landscape-scale experiment using self-incompatible plant communities and empirically examined the relative effects of local habitat, anthropogenic land-use and bee parasitism on pollination. My study revealed higher prevalence of a common bumblebee parasite (*C.*

bombi) in urban areas. The relationship was positively mediated through higher *Bombus* abundance. Yet, I did not find evidence for top-down effects of host bee parasitism on pollination. I hypothesize that higher abundance of bumblebees in urban areas results in higher success of pollination, which more than compensates for the putative increase in transmission and prevalence of *C. bombi* due to increasing host bee abundance.

Despite the growing body of research in understanding the effects of individual global change pressures on pollinators and pollination, we still lack studies simultaneously considering multiple pressures. Future studies should benefit from using urban habitats as study systems since they provide spatial concentrations of major global change pressures, such as habitat loss and fragmentation, non-native species, urban warming and environmental contaminants. The combination of these pressures within urban areas provides a great opportunity to test and expand our current theories related to ecology and evolution.

Overall, in the presented work I investigated the effects of urbanization on pollinators and pollination. My findings suggest that relatively simple actions to provide pollinators with local nesting and floral resources at a local scale and the appropriate urban planning to increase the cover and connectivity of semi-natural vegetation at a landscape scale could promote cities as refuges for species affected by agricultural intensification. This would give the expanding urban areas a future role as sources of pollinators and hotspots of the ecosystem service of pollination.

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B. Curriculum vitae

Panagiotis Theodorou
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Born on April 8th, 1983
Nationality: Cypriot

Education	
2013-present	**Ph.D. candidate**, Department of Zoology, Martin-Luther-University (MLU) Halle-Wittenberg, Halle, Germany.
2008-2011	**M.Sc. in Biology,** University of Iceland, Faculty of Life and Environmental Sciences, Department of Biology, Reykjavik, Iceland.
2003-2008	**B.Sc. in Biology,** Aristotle University of Thessaloniki, Faculty of Science, School of Biology, Thessaloniki, Greece.
Research and work experience	
2013-present	**Ph.D. candidate,** department of Zoology, Martin-Luther-University (MLU) Halle-Wittenberg, Halle, Germany. PhD thesis to be submitted: *Biodiversity-from genes to species to communities-and ecosystem services under global change: the case of bees and pollination under urbanization*. Supervisor: Prof. Dr. Robert J. Paxton.
2012	**Internship,** department of Zoology, Martin-Luther-University (MLU) Halle-Wittenberg, Halle, Germany. Training in: Molecular genetics, DNA barcoding, Phylogenetics, Fieldwork with bees. Supervisor: Prof. Dr. Robert J. Paxton.
2009-2010	**M.Sc. research project** at the research centre of the Westfjords, University of Iceland. *Reaching the limit: reduced behavioral flexibility of juvenile Atlantic cod (*Gadus morhua*) at higher temperatures.* Supervisors: Dr. Gudbjorg A. Ólafsdóttir, and Prof. Dr. Sigurdur S. Snorrason.
2008-2009	**M.Sc. research project** at the research centre of the Westfjords, University of Iceland. *Disrupted behavior in hatchery reared juvenile Atlantic cod (*Gadus morhua*).*Supervisors: Dr. Gudbjorg A. Ólafsdóttir, and Prof. Dr. Sigurdur S. Snorrason.
2007	**B.Sc. thesis** at University of Iceland, Faculty of Life and Environmental Sciences, Department of Biology, Reykjavik, Iceland (Exchange student, ERASMUS scholarship). *Interactions related to body size in deciding territorial contest between hatchery and wild juvenile Atlantic cod*. Supervisors: Dr. Gudbjorg A. Ólafsdóttir, and Prof. Dr. Sigurdur S. Snorrason.
Awards and Grants	
2017	Scholarship for conferences. Deutscher Akademischer Austauschdienst (DAAD)
2016	Junior scientist Conference grant. Genetics Society
2015	Conference grants for attendance at non-GS meetings. Genetics Society
2008-2010	M.Sc. stipend. University of Iceland Research fund
2007	6 months Socrates-Erasmus-Scholarship to visit University of Iceland, awarded from the Greek State Scholarship Foundation (IKY)
Conferences	

- British Annual meeting, UK, Liverpool (2016). Insect pollinator diversity and the ecosystem service of pollination in changing landscapes. **Panagiotis Theodorou**, Rita Radzevičiūtė, Guillaume Lentendu, Belinda Kahnt, Martin Husemann, Tesfaye Wubet, Josef Settele, Oliver Schweiger, Christoph Bleidorn, Ivo Grosse, Tomás E. Murray, Robert J. Paxton.
- Ento'15: International Symposium of the Royal Entomological Society (Insect Ecosystem Services) Dublin, Ireland (2015). Interrelationship between pollinator diversity, landscape heterogeneity and pollination service provision in German apple orchards. Rita Radzevičiūtė, Martin Schlegel, **Panagiotis Theodorou**,Robert J. Paxton.

- Ecological Society of Germany, Austria and Switzerland (GfÖ) conference, Göttingen (2015). Plant-pollinator networks, bumblebee pathogens and pollination service provision in anthropogenic habitats.**Panagiotis Theodorou**, Karoline Albig, Rita Radzevičiūtė, Josef Settele, Oliver Schweiger, Tomás E. Murray, Robert J. Paxton
- European Society for Evolutionary Biology (ESEB) ocnference, Lausanne (2015). "Mapping genetic and species diversity of pollinators to the ecosystem service of pollination across changing landscapes". **Panagiotis Theodorou**, Josef Settele, Christoph Bleidorn, Oliver Schweiger, Ivo Grosse, Tomás E. Murray, Robert J. Paxton
- Central European Meeting of the International Union for the Study of Social Insects – IUSSI, Lichtenfels ,Germany. (2015)."Interdependent parasite pressures on social bees".Dino P. McMahon, Myrsini E. Natsopoulou, Matthias A. Fürst, Vincent Doublet, **Panagiotis Theodorou**, John Bryden, Mark J. F. Brown, Robert J. Paxton.
- Hymenopterologen-Tagung, Stuttgart. (2014). "Insights into the systematic relationships of a European fossorial bee species complex in the subgenus Hoplandrena".Matthias Seidel, **Panagiotis Theodorou**, Robert Paxton.
- Bienen AG Tagung, Marburg, GE. (2014). "The impact of lactic acid bacteria on viral (DWV) and Microsporidian (Nosema ceranae) infections in the honey bee (Apis mellifera)" T. Disayathanoowat, D. McMahon, V. Doublet, **P. Theodorou**, T. C. Olofsson, A. Vásquez, R. J. Paxton.
- BES Annual General Meeting, Birmingham, UK. (2012). "Pollination service provision in Co. Armagh apple orchards." Lorraine McKendrick, Tomás E. Murray, **Panagiotis Theodorou**, Sean MacAntSaoir, Robert J. Paxton.

C. Publication list

9. M. Pusceddu, G. Piluzza, **Panagiotis Theodorou**, F. Buffa, L. Ruiu, S. Bullitta, I. Floris, A. Satta. Resin foraging dynamics in *Varroa destructor* infested hives. A case of medication of kin? (accepted in Insect Science)

8. Rita Radzevičiūtė, **Panagiotis Theodorou**, Martin Husemann, George Japoshvili, Giorgi Kirkitadze, Aigul Zhusupbaeva, Robert Paxton (2017). Replication of honey bee RNA viruses across multiple bee species in apple orchards of Georgia, Germany and Kyrgyzstan. Journal of Invertebrate Pathology 146, 12-23. doi http://doi.org/10.1016/j.jip.2017.04.002.

7. Patricia Landaverde-González, J. Javier Quezada-Euán, **Panagiotis Theodorou**, Tomás E. Murray, Ricardo Ayala, José Humberto Moo-Valle, Martin Husemann, Rémy Vandame, and Robert J. Paxton (2017). Sweat bees on hot chillies: provision of pollination services by native bees in traditional slash-and-burn agriculture in the Yucatan Peninsula of tropical Mexico. Journal of Applied Ecology. doi:10.1111/1365-2664.12860.

6. **Panagiotis Theodorou**, Karoine Albig, Rita Radzevičiūtė, Josef Settele, Oliver Schweiger, Tomás E. Murray, Robert J. Paxton (2017). The structure of flower-visitor networks in relation to pollination across an agricultural to urban gradient. Functional Ecology 31(4), 838-847. doi: 10.1111/1365-2435.12803.

5. Antonella Soro, J. Javier G. Quezada-Euan, **Panagiotis Theodorou**, Robin F. A. Moritz, Robert J. Paxton (2016). The population genetics of two orchid bees suggests high Ne, high dispersal, low diploid male production and only an effect of island isolation in lowering genetic diversity. Conservation Genetics. doi: 10.1007/s10592-016-0912-8.

4. **Panagiotis Theodorou**, Rita Radzevičiūtė, Josef Settele, Oliver Schweiger, Tomás E. Murray, Robert J. Paxton (2016): Pollination services enhanced with urbanisation despite increasing pollination parasitism.Proceedings of the Royal Society B: Biological Sciences, 283, 20160561. doi: 10.1098/rspb.2016.0561.

3. McMahon, D. P.; Fuerst, Matthias A.; Caspar, Jessica; **Theodorou, Panagiotis**; Brown, Mark J F; Paxton, Robert J. (2015). A sting in the spit: widespread cross-infection of multiple RNA viruses across wild and managed bees. Journal of Animal Ecology, 84, 615-624. doi: 10.1111/1365-2656.12345.

2. **Theodorou, P.** , Snorrason, S. S. and Ólafsdóttir, G. Á. (2013). Habitat complexity affects how young of the year Atlantic cod *Gadus morhua* perceive predation threat from older conspecifics. Journal of Fish Biology, 82, 2141-2146. doi: 10.1111/jfb.12140.

1. **Theodorou, P.** , Ólafsdóttir, G.Á. and Snorrason, S.S., (2012). Reaching the limit: constrained behavioural flexibility of juvenile Atlantic cod (*Gadus morhua*) at current costal temperatures. Journal of Experimental Marine Biology & Ecology, 413, 192-197. doi: 10.1016/j.jembe.2011.12.009.

D. Declaration of own contribution to the original articles presented in this thesis

I. **Panagiotis Theodorou**, Rita Radzevičiūtė, Guillaume Lentendu, Belinda Kahnt, Martin Husemann, Christoph Bleidorn, Josef Settele, Oliver Schweiger, Ivo Grosse, Tesfaye Wubet, Tomás E. Murray, Robert J. Paxton. Flower-rich urban areas can act as bee pollination hotspots (1st revision under re-review in *Global Change Biology*)

Design of the project: 80%
Collection of field data: 100%
Experimental work: 100%
Data analysis: 90%
Wrote the paper: 80%

II. **Panagiotis Theodorou**, Karoine Albig, Rita Radzevičiūtė, Josef Settele, Oliver Schweiger, Tomás E. Murray, Robert J. Paxton (2017). The structure of flower-visitor networks in relation to pollination across an agricultural to urban gradient. Functional Ecology 31(4), 838-847. doi: 10.1111/1365-2435.12803

Design of the project: 80%
Collection of field data: 50%
Data analysis: 100%
Wrote the paper: 80%

III. **Panagiotis Theodorou**, Rita Radzevičiūtė, Josef Settele, Oliver Schweiger, Tomás E. Murray, Robert J. Paxton (2016): Pollination services enhanced with urbanisation despite increasing pollination parasitism. Proceedings of the Royal Society B: Biological Sciences, 283, 20160561. doi: 10.1098/rspb.2016.0561

Design of the project: 80%
Collection of field data: 90%
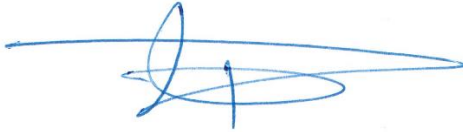Experimental work: 100%
Data analysis: 100%
Wrote the paper: 80%

E. Eidesstattliche Erklärung

Halle, den 10.08.2017

Hiermit erkläre ich, dass diese Arbeit von mir bisher weder bei der Naturwissenschaftlichen Fakultät I der Martin-Luther-Universität Halle-Wittenberg, noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht wurde.

Ich erkläre, dass ich mich bisher noch nicht um den Doktorgrad beworben habe.

Ferner erkläre ich an Eides statt, dass ich dies Arbeit selbstständig und nur unter Zuhilfenahme der angegebenen Hilfsmittel und Literatur angefertigt habe.

Panagiotis Theodorou