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Functional floral traits as mechanistic explanation for community structure

Inaugural-Dissertation

zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Heinrich-Heine-Universität Düsseldorf

vorgelegt von

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Düsseldorf, Mai 2016

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der Heinrich-Heine-Universität Düsseldorf

Gedruckt mit der Genehmigung der
Mathematisch-Naturwissenschaftlichen Fakultät der
Heinrich-Heine-Universität Düsseldorf

Referent: Prof. Dr. Klaus Lunau

Korreferent: Prof. Dr. Arnold Janssen

Tag der mündlichen Prüfung: 26.07.2016

Abstract

Ecological communities are composed of multiple species. These co-occuring organisms are entangled in a complex web of interactions, interdependences and connections, which is the basis of ecological and evolutionary dynamics and processes. Thus, many ecosystem functions such as pollination, seed dispersal and nutrient cycling as well as community structure and stability depend on biotic interactions. Within plant-animal communities, functional plant traits, such as morphology, scent or phenology, mediate interactions and consequently affect community structure. This thesis explores functional floral traits as mechanistic explanation for flower-visitor community structure, with a focus on two topics: Impact of intraspecific floral trait variation in flower-visitor communities and floral traits as mechanism underlying alterations in communities due to changes in the species assemblage and disturbances, *e.g.* due to invasive species.

Within flower-visitor communities, we begin to understand how intraspecific variation in behavioural characteristics within an animal species is affecting the dynamics and structures of interactions. However, to what extent intraspecific variation in floral traits leads to differences in flower-visitor interactions between plant individuals is poorly understood. In a common garden experiment, we studied differences between plant individuals in their interactions with flower visitors and the correlation of these differences to intraspecific variation in phenotype and reproductive success. Therefore, all interactions between arthropods and flowers of 97 *Sinapis arvensis* individuals throughout their lifetime were recorded and linked to plant individuals' phenotypes. We showed that plant individuals significantly differed in their quantitative and qualitative interactions with arthropods on flowers. These intraspecific differences remained stable over the entire season and thus were time-invariant. Variation in interacting arthropod communities was driven by a marked intraspecific variability in the floral phenotype (i.e. phenology, morphology and scent) and resulted in differences in reproductive success. Further, this variation may subsequently affect network statistics that are commonly used to characterize the structure of interaction networks since these statistics classically summarise interactions at species level and neglect intraspecific variation. In a resampling approach using the field data complemented with the recordings from the common garden experiment described above, we evaluated whether and how intraspecific variation in interactions alters commonly used aggregate statistics. Our results show that commonly used network statistics are sensitive towards changes in the interaction patterns of one plant species within a multi-species network, which may affect the ecological interpretation of the stability of communities or other network properties. Our results show that intraspecific variation in functional floral traits and interactions of plant species has pronounced effects in community and network context, potentially with implications for the persistence of communities and populations, and their ability to withstand environmental fluctuations. Further, by challenging the robustness of commonly applied network indices our findings have important methodological implications for the investigation of community and network structure and especially emphasize the urge for a sufficient and representative sampling of interactions.

The structures and dynamics of a given community can be severely altered by the establishment and spread of introduced species (*i.e.* invasive species). Driven by the strong competitive abilities of invasive, native and endemic species often suffer from resource depletion, which may even lead to the displacement of these species. We quantified the niche sizes and overlaps of native and introduced flower visitor taxa in Hawaii Volcanoes National Park in order to reveal the ecological mechanisms underlying competition. We developed and used a novel trait-based approach (*dynamic range boxes*) adopting the concept of *n*-dimensional hypervolumes. This approach improves the concept of multivariate range boxes by accounting for the distribution of the data within their range, while still no assumptions on the underlying distributions are needed. Each dimension of the hypervolume represents one functional floral trait that affects foraging choices of flower visitor species. We could show that on average introduced flower visitor taxa were more generalized in resource use (larger niches) than native taxa. Small niche sizes of native taxa partly resulted from their specialization on native flowering plant species whereas introduced flower visitors interacted with both native and introduced plant species proportional to their abundance. Additionally, natives shared a larger proportion of their niches with introduced taxa than *vice versa*, suggesting a higher competitive ability of introduced taxa. Our results showed that the functional composition of plant communities as well as the ecological and evolutionary background of consumers are important factors in explaining the structure of interaction networks, and help to reveal competitive patterns within communities. Predicted range expansion of invasive plant and flower visitor species may further reduce the availability of resource for native flower visitors; at the same time competition for the remaining resources may increase. Thus, introduced species with a strong competition potential can cause severe current and future threats for native species.

In summary, this thesis analyses the linkage between intraspecific floral trait variation and interaction patterns as well as floral trait variation as mechanistic explanation for alterations in community structure due to invasive species. This work highlights the importance of intraspecific trait variation for interaction patterns within communities and shows how functional traits can explain and may predict the impact of alterations within communities. All chapters demonstrate that functional traits as an interface of plants and plant-visiting animal species provide a central mechanism explaining community structures. Thus, considering functional plant traits at different hierarchical levels can improve our knowledge of community structure and dynamics and thereby help to generate a general understanding of the fate of communities under global change.

Zusammenfassung

Ökologische Gemeinschaften bestehen aus zahlreichen Arten. Die Organismen innerhalb einer Gemeinschaft bilden ein komplexes Netzwerk aus Interaktionen, Abhängigkeiten und Wechselwirkungen, welches die Grundlage für ökologische und evolutionäre Dynamiken ist. Folglich sind viele essentielle Ökosystemfunktionen wie Bestäubung, Samenausbreitung und Nährstoffkreisläufe, aber auch die Stabilität von ökologischen Gemeinschaften von biotischen Interaktionen abhängig. Innerhalb von Pflanze-Tier-Gemeinschaften beeinflussen funktionelle Pflanzenmerkmale, wie Morphologie, Duft oder Phänologie, die Interaktionen und somit auch die Gemeinschaftsstrukturen. In meiner Dissertation wurde der Einfluss von funktionellen Blütenmerkmalen auf die Struktur von Blütenbesuchergemeinschaften untersucht. Der Fokus lag dabei auf zwei Themen: Den Auswirkungen von innerartlicher Variation in Blütenmerkmalen auf Blütenbesuchergemeinschaften sowie Blütenmerkmale als erklärendem Mechanismus für Veränderungen in Gemeinschaften aufgrund von Veränderungen in der Artenzusammensetzung und Störungen.

Während es bekannt ist, dass die innerartliche Variabilität einer Tierart in Verhalten und Besuchermustern die Strukturen von Blütenbesuchergemeinschaften stark beeinflussen kann, ist es unklar, ob innerartliche Variation einer Pflanzenart ähnliche Effekte auslösen kann. In einem „Common Garden“-Experiment wurde untersucht, inwieweit sich Pflanzenindividuen in ihren Besuchsmustern unterscheiden und ob diese Unterschiede durch den individuellen Phänotyp erklärt werden können *oder* den individuellen Reproduktionserfolg beeinflussen. In diesem Experiment wurden während der gesamten Lebensdauer von 97 *Sinapis arvensis*-Individuen alle Interaktionen mit Blüten aufgenommen und anschließend mit dem individuellen Phänotyp korreliert. Es konnte gezeigt werden, dass Pflanzenindividuen sich in ihren quantitativen und qualitativen Interaktionen mit Arthropoden auf Blüten unterscheiden. Diese innerartlichen Unterschiede waren über die gesamte Lebensdauer der einzelnen Individuen konstant und somit unabhängig vom Alter des Pflanzenindividuums. Diese gefundenen Unterschiede sind auf eine ausgeprägte innerartliche Variabilität im Blütenphänotyp (Phänologie, Morphologie und Duft) zurückzuführen und wirkten sich zudem auf den Reproduktionserfolg der einzelnen Individuen aus. Netzwerkstatistiken, die häufig genutzt werden, um die Strukturen von Interaktionsnetzwerken zu beschreiben, fassen Interaktionen klassischerweise auf Artniveau zusammen und berücksichtigen innerartliche Variabilität nicht. Basierend auf einer Feldstudie und den Resultaten des oben beschriebenen „Common Garden“-Experiments wurde mittels eines Resampling-Verfahrens untersucht, inwieweit innerartliche Variabilität in Interaktionen oft genutzte Netzwerkstatistiken beeinflusst. Unsere Ergebnisse zeigen, dass Netzwerkstatistiken sehr empfindlich auf kleine Änderungen in den Besuchsmustern einer Pflanzenart reagierten. Die Schwankungen in den Statistiken waren in einem Rahmen, der die ökologische Interpretation in Bezug auf die Stabilität von Gemeinschaften und andere Merkmale beeinflussen kann. Diese Ergebnisse zeigten, dass

innerartliche Variation in funktionellen Blütenmerkmalen und Interaktionen einen starken Einfluss im Kontext von Gemeinschaft und Netzwerken ausüben kann. Dies hat möglicherweise Auswirkungen auf die Beständigkeit von Gemeinschaften und Populationen sowie deren Fähigkeiten, Umweltschwankungen standhalten. Von einem methodischen Standpunkt aus betrachtet unterstreichen diese Ergebnisse die Wichtigkeit einer repräsentativen und ausführlichen Beprobung.

In einer Gemeinschaft können sich deren Strukturen und Dynamik durch die Ansiedlung und Ausbreitung von gebietsfremden Arten (d.h. invasiven Arten) erheblich verändern. Invasive Arten sind häufig sehr konkurrenzstark und folglich in der Lage, Ressourcen vor einheimischen und endemischen Arten auszubeuten. Dies kann dazu führen, dass heimische Arten unter Ressourcenmangel leiden, *was* wiederum zum lokalen Aussterben dieser Arten führen kann. Um die zugrunde liegenden Mechanismen der Konkurrenz zwischen heimischen und eingeführten Arten zu untersuchen, haben wir in einer Feldstudie im Hawaii Volcanoes National Park, USA, die Nischengröße und -überlappung von einheimischen und eingeführten Blütenbesuchern quantifiziert. Dafür haben wir basierend auf dem Konzept des *n*-dimensionalen Hypervolumes eine neue Methode ‚*dynamic range boxes*' entwickelt und genutzt. In dieser stellt jede Dimension des Hypervolumens ein funktionelles Blütenmerkmal dar, welches die Besuchsentscheidung von Blütenbesuchern beeinflusst. Grundsätzlich kann diese Methode nicht nur für Pflanzenmerkmale, sondern auch in anderen Bereich eingesetzt werden. Zudem verbessert diese bisher existierende Methoden wie z.B. ‚multivariate range boxes', da unsere Methode die Verteilung der Daten berücksichtigt, aber keine bestimmte Verteilung der Daten voraussetzt. Wir konnten zeigen, dass eingeführte Blütenbesuchertaxa im Durchschnitt generalisierter in ihrer Ressourcennutzung (= größere Nischen) sind als einheimische Taxa. Die kleinere Nischengröße einheimischer Taxa beruhte zum Teil darauf, dass diese eher auf einheimische Blüten spezialisiert waren, während eingeführte Blütenbesucher einheimische und invasive Pflanzen gemäß ihrer Häufigkeit besuchten. Darüber hinaus teilten einheimische Taxa einen größeren Anteil ihrer Nische mit eingeführten Taxa als umgekehrt, was auf eine höhere Konkurrenzfähigkeit der eingeführten Taxa schließen lässt. Unsere Ergebnisse zeigen, dass die funktionale Zusammensetzung von Pflanzengemeinschaften sowie der ökologische und evolutionäre Hintergrund der Blütenbesucher wichtige Faktoren sind, die die Gemeinschaftsstrukturen und die Konkurrenz innerhalb von Gemeinschaften erklären können. Es wurde prognostiziert, dass invasive Pflanzen- und Blütenbesucherarten in Zukunft ihren Verbreitungsbereich auf Hawaii ausweiten werden. Dies könnte zu einer Verschlechterung der Ressourcenlage für einheimische Blütenbesucherarten führen, wobei gleichzeitig die Konkurrenz durch invasive Blütenbesucherarten zunimmt. Somit bedeuten eingeführt Arten eine große Bedrohung für die heimischen, hawaiianischen Blütenbesucherarten.

Zusammenfassend wurde in dieser Dissertation der Einfluss von innerartlicher Variation in Blütenmerkmalen auf Interaktionsmuster sowie Blütenmerkmale als mechanistische Erklärung für

Veränderungen in den Strukturen von Gemeinschaften durch invasive Arten untersucht. Diese Arbeiten unterstreichen die Bedeutung innerartlicher Merkmalsvariation für die Interaktionsmuster in Pflanze-Tier-Gemeinschaften und zeigen, dass funktionelle Blütenmerkmale die Auswirkungen von Veränderungen in Gemeinschaften erklären und möglicherweise auch voraussagen können. Die Ergebnisse in allen Kapiteln zeigen, dass funktionelle Merkmale als Schnittstelle von Pflanzen und Blütenbesuchern von zentraler Bedeutung für Gemeinschaftsstrukturen sind. Die Berücksichtigung von funktionellen Pflanzenmerkmalen auf verschiedenen Hierarchieebenen innerhalb von Gemeinschaften (d.h. Individuen, Art und Gemeinschaftsniveau) trägt zu einem besseren Verständnis dieser Strukturen und Dynamiken sowie den Veränderungen durch Klimawandel und anderer Faktoren bei.

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General introduction

An estimated total number of 8.7 million eukaryote species live on earth (Mora *et al.*, 2011). A combination of those organisms can be found in (nearly) every area on earth, forming communities, which can be defined as “a combination of plant (and fungi), animal, and bacterial (microbial) populations, interacting with one and another within an environment, thus forming a distinctive living system with its own composition, structure, environmental relations, development and function” (Whittaker, 1975). Within communities a single plant species for example can interact with over hundreds of other species such as mycorrhizal fungi, endophytes, nitrogen-fixing bacteria, plant-pathogens, herbivores and their natural enemies or pollinators (Stam *et al.*, 2014). Thus, the combination of all organisms and interactions within a community form a highly complex web of interdependencies and connections.

Difficulties in understanding community structures and dynamics arise from their complexity. The structure of a community can be defined as the composition and diversity of species and their interaction patterns. Community dynamics refer to changes over time in the composition and diversity of species and their interactions. To reduce complexity within communities, ecologists mostly focus on manageable subsets and not the whole community itself (Morin, 1999). Often used subsets are consumer-resources networks like host-parasite, plant-herbivore or plant-pollinator networks (Ings *et al.*, 2009). Despite their complexity these networks possess identifiable structures and dynamics (Jordano *et al.*, 2003; Petanidou *et al.*, 2008). One of the most persuasive mechanistic explanations for these structures and dynamics are functional traits (McGill *et al.*, 2006; Violle *et al.*, 2007). Usually a functional trait is defined as measurable property of an organism with a strong influence on the organisms’ performances (McGill *et al.*, 2006). In this thesis, we extended this definition to include traits that influence the behaviour or performance of other organisms interacting with it. These interactions of course also influence the performance of the organism displaying the trait. In both cases, functional traits can include morphological, physiological or life history traits (McGill *et al.*, 2006). For example, floral traits influence the performance of the plant (*i.e.* its reproductive success), but also the behaviour/performance of the pollinator (*e.g.* due to search for specific flowers or higher efficiency in foraging) (Morris *et al.*, 2007; Ne’eman *et al.*, 2010).

The phenotype and trait distribution within a species can change due to multiple disturbances, *e.g.* climate change, habitat alteration or invasive species (Mouillot *et al.*, 2013). The changes in functional traits can influence interaction patterns, performance of plants and animals and consequently community composition and dynamics. Thus, functional traits cannot only be used to investigate the underlying mechanisms of structures and dynamics in species interactions and species niches (Violle *et al.*, 2007; Junker *et al.*, 2013), but also of changes induced by environmental and anthropogenic alterations (Mouillot *et al.*, 2013).

Changes, *e.g.* the introduction of new species, can severely alter the structure and dynamics of these webs and may even have cascading effects beyond the biotic community itself. In the Northern American oak forest the invasive gypsy moth (*Lycaena dispar)* causes increased tree mortality as a result of a severe increase in tree defoliation due to herbivory. The increased mortality leads to alterations in the tree composition with consequences for the whole faunistic community. These changes in community structure can ultimately result in altered ecosystem processes such as carbon allocation and nitrogen fixation, which may have further consequences such as acidification of stream waters (Lovett *et al.*, 2002, 2006). This example also illustrates the different hierarchical levels within a community. At individual level, trees are influenced by increased defoliation. The resulting increased tree mortality alters the population dynamics of different species (*i.e.* species/population level) and ultimately leads to changes in the faunisitic composition of the community (*i.e.* community level). As all hierarchical levels are interconnected, we need to understand the structure and dynamics at all levels, to fully understand the responses and the stability of community in the face of alterations (Hooper *et al.*, 2012; Lefcheck *et al.*, 2015).

Within this thesis, I explored the structuring role of functional plant traits for plant-insect interactions and use functional floral traits to estimate the impact of invasive flower visitors on native communities.

Communities, interactions & functional traits as structuring mechanism

Interactions & network structure

Plant-animal interactions (*e.g.* prey-predator or flower-visitor interactions) influence community dynamics and diversity as they play a central role in plant reproduction and life histories of animals (Bascompte & Jordano, 2007). To reveal structures within these complex webs of interactions (*i.e.* communities), network approaches are commonly used. These approaches allow us to summarize and analyse the complex structure of interaction networks and their role in ecosystems (Kaiser-Bunbury & Blüthgen, 2015). An interaction network consists of nodes and edges, where each node represents a species and each edge an interaction between two species. There is a large number of different network statistics (*e.g.* interaction evenness, connectance, and modularity), which provide a single value derived from the networks' interaction structure. These statistics describe the network structure (Olesen *et al.*, 2007, 2012; Vázquez *et al.*, 2007) and can inform on different important properties of the network, *e.g.* specialization or stability (Blüthgen *et al.*, 2006; Hagen *et al.*, 2012; Olesen *et al.*, 2012).

Within this thesis the focus was on six commonly used indices: connectance (*C*), interaction evenness (*IE*), complementary specialization (network level: H_2'; species level: *d'*), modularity (*M*) and nestedness (*N*) (Dormann *et al.*, 2009). *C* is based on presence/absence data and is the realized proportion of possible edges (*i.e.* interactions) within a network. For example, a network with four plant and four animal species has 16 possible edges (each plant species can potentially interact with each animal species). If only five edges are present the connectance would be low (5 / (4*4) = 0.3125; full range connectance: 0-1, Fig. 1a). *IE* is a measure of the homogeneity of the interaction frequencies between species within a network. A low *IE* describes a high variation in interaction frequencies between different species pairs (Fig. 1b). *d'*, H_2', and *M* describe the interaction patterns of each species relative to the other species. *d'* is calculated for each species within a network and depicts if the interaction frequencies of a species are similar to or different from other species (Fig. 1d). H_2' is closely related to the weighted mean *d'* of all species in a network (weighted by the total number of observations for each species). It describes the "exclusiveness" of interaction frequencies within the whole network, *e.g.* in a network where most species interact with different partners the H_2' would be high (Fig. 1c). Thus, species-level index *d'* can be used to describe the variation within a network and the network-level index H_2' is especially useful for comparison of different networks (Blüthgen, 2010). *M* describes the extent to which species are organized in subcommunities within networks. Species within a subcommunity (*i.e.* module) are linked more tightly together than to species in other modules (Fig. 1e, Olesen *et al.*, 2007). *N* characterizing the generalist-specialist balance in a network (Lewinsohn *et al.*, 2006). A nested network features two properties. First, it has a core of generalist species in which generalists (*e.g.* plants) interact with other generalists (*e.g.* flower visitors). Second, the interactions strength is asymmetric meaning that specialist species only interact with generalists but not with other specialists (Fig. 1f). Empirical and theoretical studies have shown that valuable information can be derived from these network statistics for the maintenance of biodiversity and ecosystem functioning (*e.g.* Dunne *et al.*, 2002; Kaiser-Bunbury *et al.*, 2010; Junker *et al.*, 2015). The ecological interpretations of these network indices are summarized in Figure 1. However, the empirical and theoretical evidence for some of these ecological interpretations is ambiguous or under debate (*e.g.* James *et al.*, 2012; Staniczenko *et al.*, 2013; Kaiser-Bunbury & Blüthgen, 2015) and some network indices (*e.g. IE* or *C*) are susceptible to sampling bias or incompleteness (Blüthgen, 2010; Kaiser-Bunbury & Blüthgen, 2015).

Classically, these indices are used to describe networks at species level, where the mean interaction frequency between species pairs is considered. However, each species consists of different individuals representing the hierarchical level where interactions actually take place. Aggregation on species level thus may mask intraspecific variation and result in a loss of valuable information (Ings *et al.*, 2009; Gómez *et al.*, 2011; Tur *et al.*, 2014). The influence of animal individuals on the structure and dynamics recently received more attention (Dupont *et al.*, 2011; Song & Feldman, 2014; Tur *et al.*, 2014, 2015). Variable behavioural characteristics and preferences of individuals can account for part of the structures found within populations and communities (Tur *et al.*, 2014). In plant-centred networks, variation in the structure of individual networks (Gómez *et al.*, 2011; Gómez & Perfectti, 2012) indicate that intraspecific variability affects community structure and ecological dynamics of plants and their interactions partners (Bolnick *et al.*, 2011; Violle *et al.*, 2012). However, we are lacking knowledge about driving mechanisms of intraspecific variation in interactions and their influence on plant-centred network structure and dynamics.

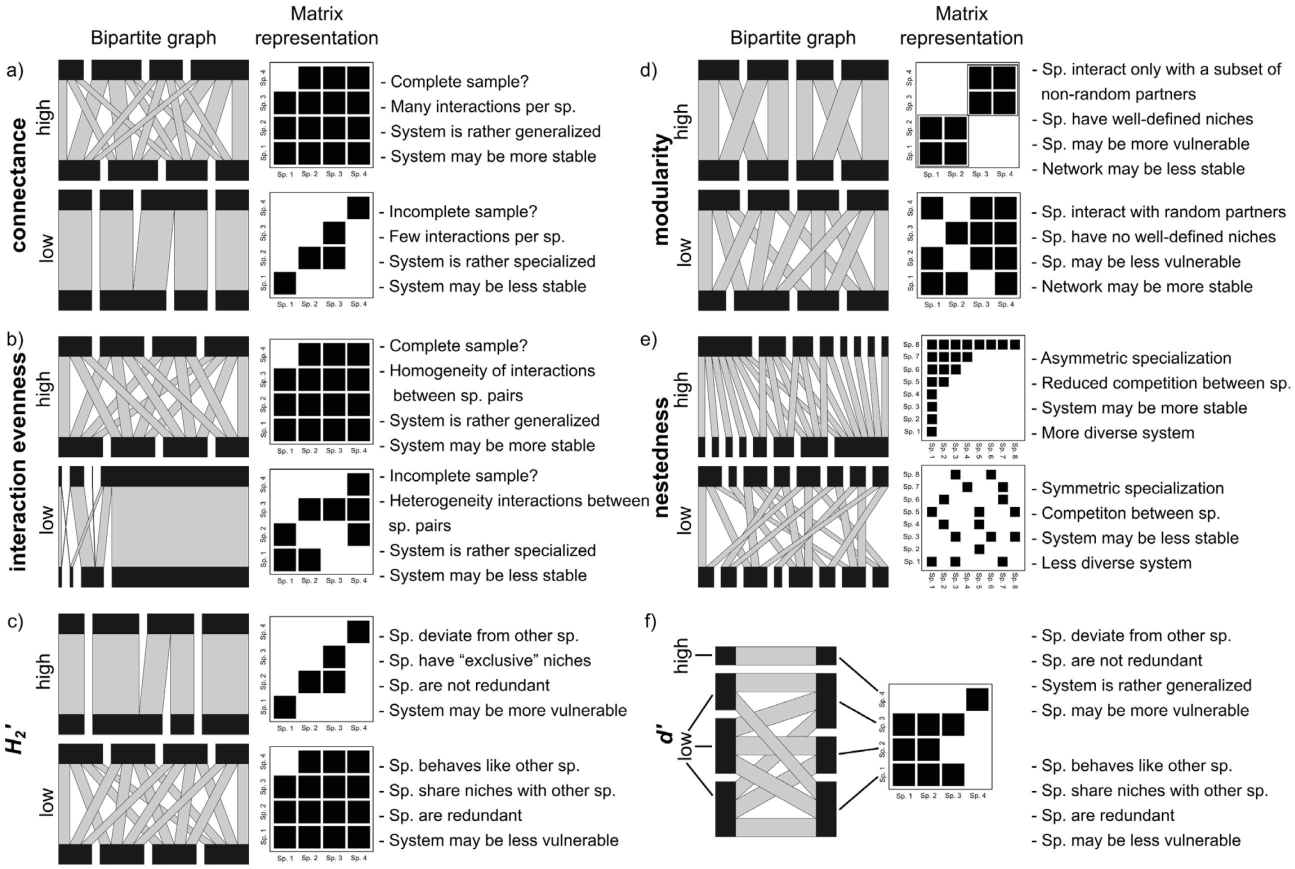

Figure 1. Visualization of several common network statistics and overview of their ecological (and methodological) interpretation. Bipartite graphs and matrix representations for hypothetical 4x4 or 8x8 bipartite interaction networks with high and low value of each network statistics. In bipartite graphs, each node (black) represents a species and each edge (grey) an interaction. The width of the edges corresponds to the interaction frequency between both species. In matrix representation, each black square indicates that both species are interacting and each empty square indicates that both species are not interacting. a) – e) Network statistics at community level: connectance (*C*), interaction evenness (*IE*), complementary specialization (H_2'), modularity (*M*), nestedness (*N*). f) Network statistic at species level: complementary specialization (*d'*). (Junker 2015 Mastermodul „Bestäubungsbiologie von Wild- und Nutzpflanzen", University Salzburg; Bascompte *et al.*, 2003; Olesen *et al.*, 2007; Blüthgen *et al.*, 2008; Bastolla *et al.*, 2009; Kaiser-Bunbury & Blüthgen, 2015).

Functional Traits

Several possibilities, *e.g.* species' abundances, body sizes, phenology, traits such as floral scent or colour and other factors, have been discussed as explanation for the structure of networks in flower-visitor communities (Vázquez *et al.*, 2009). This thesis further explored functional floral traits as mechanistic explanation for interaction, niche and community structures in flower-visitor communities, with a focus on morphology and scent as functional floral traits, while colour and resource quality and quantity can also play an important role (Stang *et al.*, 2006; Lunau *et al.*, 2011; Junker *et al.*, 2013; Junker & Parachnowitsch, 2015; Larue *et al.*, 2015). These traits are displayed by flowers not independently but synchronously and thus they often mediate interactions in combination (Junker & Parachnowitsch, 2015). Globeflowers (*Trollius europaeus*), for example, are pollinated by highly specialized flies. For a successful pollination the combination of floral colour and floral scent is required. The visitation rate of these flies is strongly influenced by small variations in floral colour, and floral scent plays an important role guiding the flies into the flower as well as in long-distance attraction (Ibanez *et al.*, 2010).

Trait variation can be large between species, but also between different populations of the same species (*e.g.* Junker *et al.*, 2013; Gómez *et al.*, 2014; Junker & Parachnowitsch, 2015). Between species variation in floral traits can be driven by selection due to pollinators as well as antagonists (*e.g.* Irwin *et al.*, 2004; Junker & Blüthgen, 2010; Lunau *et al.*, 2011; Van der Niet *et al.*, 2014), while between different populations it may be driven by selection due to differences in local pollinators assemblages (Johnson, 2010; Gómez *et al.*, 2014). Therefore, variation in floral phenotypes may directly translate in variation in visitation patterns between species and populations (Herrera, 2005; Ollerton *et al.*, 2011; Gómez *et al.*, 2014). Even within the population of one plant species flower visitors are able to discriminate plant individuals of the same species based on subtle differences in their floral phenotype (Conner & Rush, 1996; Mothershead & Marquis, 2000), which may lead to intraspecific variation in interaction patterns. However, variation in floral traits may be constraint if a plant species is pollinated by rather specialized flower visitors. In this case a successful pollination often depends on a precise pollen deposition, which is rather ensured by an invariant floral phenotype. This may be more relaxed in plant species with a generalised pollination system (Armbruster *et al.*, 2004) and in populations confronted with a fluctuating environment (*e.g.* changing pollinator assemblages, Pérez-Barrales *et al.*, 2007). Accordingly, in more generalised plant species floral traits like morphology, colour or scent, can feature a considerable intraspecific variation (Parachnowitsch *et al.*, 2012). Overall, variation in floral traits mediates interactions of plants at individual, population and species level.

To understand the impact of functional floral traits in structuring networks and communities a growing number of studies investigate the microstructure (pairwise interactions) of networks (*e.g.* (Junker & Blüthgen, 2010; Kaiser-Bunbury *et al.*, 2014). For example, it has been shown that scent emission promotes the visitation of some flower-visitors, but repels others, which is reflected in the interaction strength between plants and insects (Junker & Blüthgen, 2010). Further, by experimentally manipulating floral scent the visitation patterns as well as the network structures (*i.e.* network statistics) are altered (Larue *et al.*, 2015). In both studies floral scent provides a mechanistic explanation for the flower-visitor interactions. As mentioned above, floral traits are displayed in combination, thus using a set of floral traits can lead to a more detailed understanding of interaction patterns (Junker *et al.*, 2013).

Using a set of floral traits, we can define species-specific niches (Junker *et al.*, 2013). The niche of a species is often conceptualized as *n*-dimensional hypervolume (Hutchinson, 1957). In the hypervolume each axis (*i.e.* dimension) represents a factor (*e.g.* environmental factor) that is required by an organism to live and reproduce. Accordingly, each floral trait can be viewed as a niche dimension (*i.e.* dimension of *n*-dimensional hypervolume) that determines whether a flower visitor is able to exploit the resources offered by flowers (Junker *et al.*, 2013). Thus, the niche concept provides a mechanistic explanation for structures within communities and the co-existence of species

Trait-based niches

First introduced by Grinnell (1917), over the years the niche concept has been wildly debated and changed (*e.g.* Chase & Leibold, 2003). Commonly, there is a distinction between fundamental and realized niches (Hutchinson, 1957; Townsend *et al.*, 2003). Fundamental niches are defined as the entirety of abiotic factors (*e.g.* soil type or temperature), but also biotic factors (*e.g.* interaction partners of other trophic levels) that allow a species to survive and reproduce in a given habitat (Townsend *et al.*, 2003). However, in nature species interact and compete with other species, which reduces the expansion of the niche resulting in the realized niche (Figure 2a, (Townsend *et al.*, 2003; Sargent & Ackerly, 2008).

Within a community each species inhabits a specific niche. According to niche theory the competition potential of two species for *e.g.* a limiting resource increases with the similarity of their ecological niches (Townsend *et al.*, 2003). Thus, if two species share parts of their fundamental niches (*i.e.* overlap) the realized niches of one or both species may largely include the shared part of their fundamental niches (Fig. 2b top). In case the fundamental niche of a species is nested within the niche of another species or several other species the first species may be displaced as the first species cannot shift towards non-shared niche space (Fig. 2b bottom, Funk *et al.*, 2008). This is a situation indicated to be especially relevant if a new competitor of the same family or guild is introduced to a community (Duyck *et al.*, 2004). Further, the overlap in the realized niche of two co-occurring species may even more strongly affect the coexistence of these species than the overlap in the fundamental niche as species may not be able to shift to non-shared niche space. Accordingly, realized niche overlap may potentially lead to competition with disadvantages for those species that share larger proportions of their niches with competitors than species that can avoid competition due to exclusive occupancy of parts of their niches (Fig. 2c). Thus, an asymmetry in niche overlap may define which species suffers more from competition (Reitz & Trumble, 2002).

Within this thesis, niches of species were based on the observed frequency distribution of a species within a niche dimension. This approach inform about current niche sizes and overlaps, but not about past patterns. However, the current niche patterns may be a product of past alterations due to interspecific competition – "the ghost of competition past" (Connell, 1980). Thus, species that do not overlap in their observed niches can potentially compete. Further, whether niche overlap between two species indicates competition is dependent on whether the overlapping niche dimension is limiting for one of the two species. Nevertheless, overlap in observed niches shows that species can directly interfere with each other and that they exploit the same resources (overlap in resources dimensions); both are strong indicator for apparent competition.

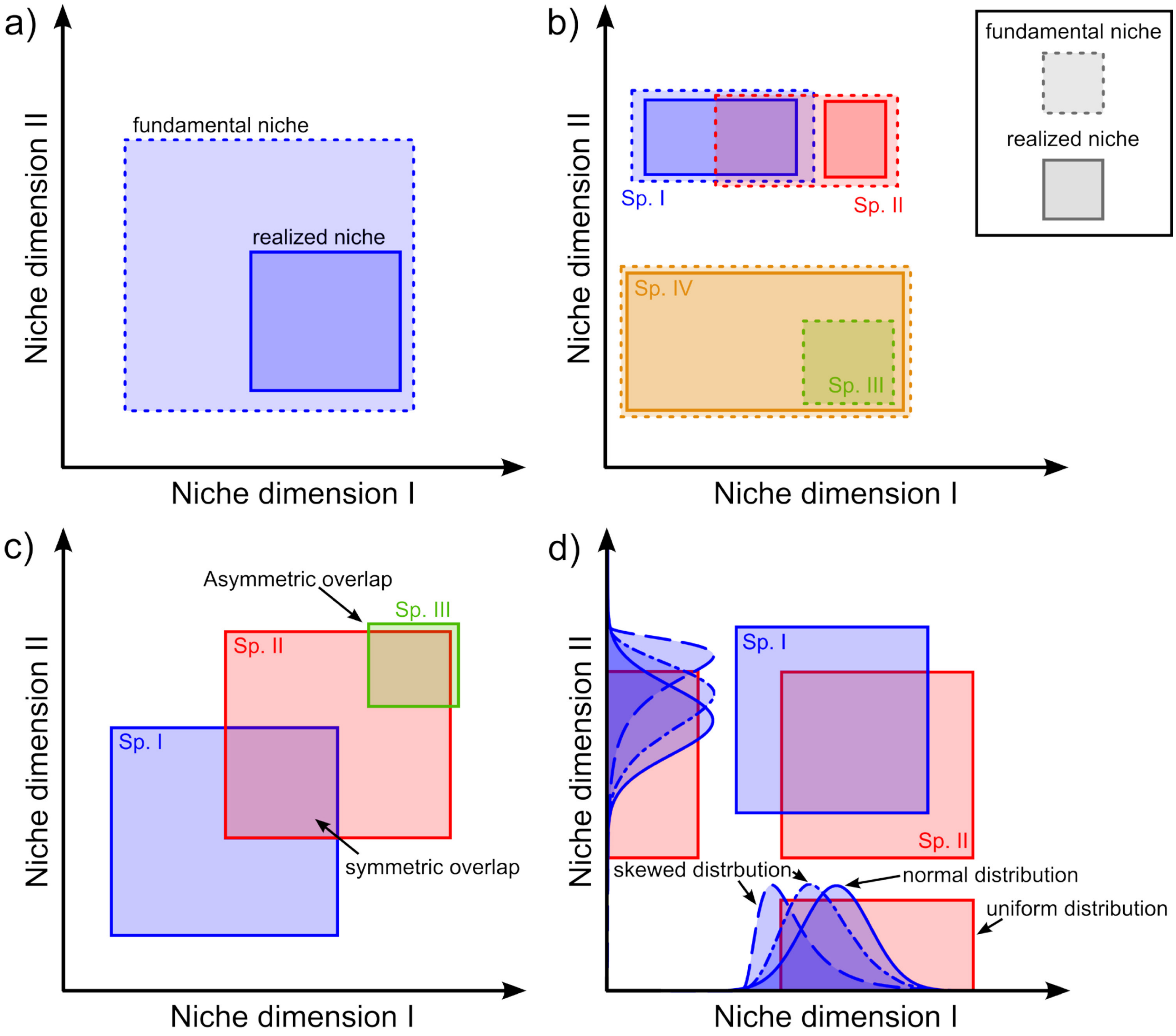

Figure 2. Conceptualization of niche size and overlap a) Visualization of fundamental (dashed box) and realized (solid box) niches as two-dimensional range boxes. b) Two examples for the potential outcome of overlap in fundamental niches. Assuming that Sp. I and Sp. IV are strong competitors compared to Sp. II and Sp. III, the realized niche of Sp. II shifts to non-shared niche space while Sp. III is displaced as it cannot shift to non-shared fundamental niche space c) Potential overlap in realized niches. If two species symmetrically overlap both species share the same proportions of their niches (Sp. I and Sp. II). If two species asymmetrically overlap one species share larger proportions of their niches with another species than *vice versa* (Sp. II and Sp. III). d) Two-dimensional range boxes based on uniform distribution. Uniform distribution implicates the same observed frequency at each point within the species range in a niche dimension. However, observed frequencies may follow other distributions (*e.g.* normal or skewed). Blue curves (curve height = observed frequency at a niche dimension) depict different distributions (normal and skewed) that indicate shifts in the overlap between species compared to uniform distribution (red) and each other. All curves cover the same range in both niche dimensions.

So far, several methods have been proposed to estimate niche spaces (*i.e.* n-dimensional hypervolumes) and their overlaps. Multivariate range boxes (Hutchinson, 1957) and convex hull

(Cornwell *et al.*, 2006; Villéger, 2008) both use the full range of the data in each niche dimension, *e.g.* temperature or moisture. Thus, the distribution (*i.e.* the observed frequency of a species in each dimension) of the data is not considered or a uniform distribution for all data is assumed. The distribution, however, may vary between data and also provides important ecological information. For example, two normal distributions with the same range may overlap strongly, but two skewed (one left, one right) with the same range may have a much smaller overlap (Fig. 2d). Recently, to overcome this shortcoming two new approaches have been introduced: multivariate kernel density estimation (Blonder *et al.*, 2014) and niche regions (Swanson *et al.*, 2015). Multivariate kernel density estimation accounts for each gap in the data (Blonder, 2016), which potentially strongly overstates the biological meaning of gaps as they often may be sampling artefacts in multivariate data. While niche regions do not overstate gaps in the data, it requires multivariate normal distribution of the data. This may be applicable to some biological data, but not to other distributions like skewed or bimodal. Thus, despite the long prevalence of the niche concept and its explanatory power for structures and dynamics in communities, we still lack a robust and widely applicable method for its estimation of niche size and overlap (*i.e.* the *n*-dimensional hypervolume).

Communities, interactions & the impact of invasive species

In the last 150 years many plant and animal species were introduced into non-native areas due to anthropogenic activities (Lockwood *et al.*, 2013). Once established these introduced species begin to interact with resident species (Hobbs *et al.*, 2006) and thereby alter the interaction patterns within communities (Pyšek *et al.*, 2012; Ricciardi *et al.*, 2013; Simberloff *et al.*, 2013). Mostly these alterations are detrimental for native species, *e.g.* result in population decline, and may even lead to their displacement by invasives and thus result in (local) extinctions (Pyšek *et al.*, 2012; Ricciardi *et al.*, 2013; Simberloff *et al.*, 2013; Traveset & Richardson, 2014). For instance the Nile Perch (*Lates niloticus*) introduced into Lake Victoria, East Africa, wiped out nearly 150 native fish species and altered the whole ecosystem (Pringle, 2011). Another example of extreme impact is the Burmese python (*Python molurus bivittatus*) that is massively spreading through the Everglades National Park and Southern Florida, USA, and is regarded as primary cause for the decline of several regional native mammal species (Dorcas *et al.*, 2012). In Australia, numerous introduced animals like rabbits, foxes, cane toads or cats severely impacted native species and ecosystems (*e.g.* Burbidge & Manly, 2002; Shine, 2012). Further, alien flower-visitors like honey bees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) are now introduced in nearly all parts of the world (Goulson, 2003). For example, the African honey bee (*Apis mellifera scutellata*) was first introduced to Brazil in 1956 and from there it colonized South and Central America and parts of the southwestern USA together with its hybrids (*i.e.* Africanized honey bees; hybrids of African and European honey bees) in less than 50 years (Schneider *et al.*, 2004; Hall *et al.*, 2014). Africanized honeybees receive a lot of attention due to their potential threats for humans, their economic impact and their replacement of the European honey bee (Schneider *et al.*, 2004; Hall *et al.*, 2014).

Further, they also strongly alter the structure and topology of native flower-visitor communities (Santos *et al.*, 2012).

In general, introduced flower visitors (especially bees) often interact with co-introduced plant species (Simberloff & Von Holle, 1999) but can also reach high interaction frequencies with native plant species (Junker *et al.*, 2010). This may cause competition with native species that are adapted to and potentially specialized on native plants (Bezemer *et al.*, 2014). Competition can arise when introduced species deter natives from floral resources (interference competition, *e.g.* Lach, 2008; Hanna *et al.*, 2014) or when they deplete resources (exploitation competition, Goulson, 2003; Stout & Morales, 2009). Hence, the floral visitation rate of many native insect species decreases when invasive flower visitors are present (Montero-Castaño & Vilà, 2012). However, the magnitude of these effects strongly depends on the identity of the native and introduced flower visitors as well as other factors such as species densities or resource availability (reviewed in Goulson, 2003; Stout & Morales, 2009; Dohzono & Yokoyama, 2010). Furthermore, introduced species do not only affect single native species, but their impact can scale up to community level and lead to a rearrangement of the interaction patterns within networks. Often aliens account for most interactions within a community (Santos *et al.*, 2012; Traveset *et al.*, 2013; Albrecht *et al.*, 2014). This monopolization increases the cohesiveness of the network (*i.e.* most plant species share the same generalistic alien visitors) and induces changes in the network structure/topology. However, this may not necessarily result in altered network indices (*e.g.* connectance) (Padrón *et al.*, 2009; Kaiser-Bunbury *et al.*, 2011). The alterations induced in interaction patterns are largely driven by the competitive ability, a broad resources use (*i.e.* generalist) of introduced species and their ability to rapidly and efficiently exploit resources, factors that are also attributed to a successful invasion (Pianka, 1981; Levine *et al.*, 2003; Lach, 2008b; Junker *et al.*, 2010; Lockwood *et al.*, 2013). However, our understanding of the underlying ecological mechanisms of the strong competition ability, the integration of introduced species into native networks and their impact on community structure and dynamics is still limited (Traveset *et al.*, 2013).

Commonly, the niche overlap (*i.e.* competition potential) between native and invasive flower visitors is calculated based on the number of shared plant species used as resources (*e.g.* Goulson *et al.*, 2002; Paini & Roberts, 2005; Lye *et al.*, 2010). However, there is accumulated evidence that competitive interactions and potentially replacement or establishment of species are, at least partly, driven by the species' functional traits (Mouillot *et al.*, 2013). Multiple floral traits can be used to define the niche of a floral visitor (see paragraphs *functional traits* & *trait-based niches*, Junker *et al.*, 2013). This approach may provide a more accurate and mechanistic understanding of the species-specific niches within communities than using species identities only (Junker *et al.*, 2013). It especially allows to assess similarity of trait use and functional overlap of two species, which are both important predictors for functional similarity of native and invasive species (Baiser & Lockwood, 2011). Thus, incorporating functional traits into niche models may allow drawing concise conclusions about the mechanisms that structure communities and determine the effects of invasive species on native communities (McGill *et al.*, 2006).

Hawaii as a natural laboratory for invasion biology

Communities on oceanic islands feature several conditions that suggest a high susceptibility to invasions like a low species and functional group diversity and a disharmonic flora and fauna compared to other terrestrial habitats (Denslow, 2003; Krushelnycky & Gillespie, 2010). Indeed, invasive species are frequently found in most habitats of the Hawaiian Islands, one of the world's most geographically isolated archipelagos (Vitousek, 1990). Today, it is estimated that 33 non-indigenous passerine bird species have been established on at least one of the six Hawaiian Islands (Moulton *et al.*, 2001) while presumably only 26 of the historical 77 native species (including species only known from fossils) are still present in the wild (Lockwood, 2006). Similar patterns can be found for plant species where nearly 50 % of the natural occurring species are non-native (Wagner *et al.*, 1990). Within flower visiting insects, fourteen bee species including honey bees have been introduced, but not all are wide-spreaded (Magnacca, 2007). Besides bees, ants (approximately 45 ant species established in Hawaii) and social wasps can also heavily interfere with native flowers visitors (Krushelnycky *et al.*, 2005; Traveset & Richardson, 2014). The effects may be especially severe in Hawaiian communities as historically such social hymenopterans were not present at the Hawaiian Islands (Krushelnycky *et al.*, 2005). Therefore, Hawaiian endemic plants often lack adaptations to avoid exploitation of their flowers by ants (Junker *et al.*, 2011). In consequence of the strong competition between native and introduced flower visitors, which sometimes is accompanied by predatory activities of introduced species (in the case of social wasps), the populations of native animals are often in decline (Paini, 2004; Traveset & Richardson, 2006; Wilson & Holway, 2010; Hanna *et al.*, 2013). Thus, the increased abundances of invasive flower visitors are one reason for the strong decline of pollinators endemic to the Hawaiian Islands, especially birds (honeycreepers) and *Hylaeus* bees (Scott *et al.*, 1988; Banko *et al.*, 2002; Magnacca, 2007). In summary, due to its history Hawaii provides excellent conditions to investigate the changes induced by introduced flower visitors within the niche and interaction structures of native communities and to understand the spread and success of introduced species and the associated threat for native species.

Outlook on thesis

Within this thesis, I first explored the influence of functional plant traits on interaction structure at individual level. Classically, in trait-based as well as community ecology most studies summarize traits and interactions at species level (McGill *et al.*, 2006; Violle *et al.*, 2012; Shipley *et al.*, 2016). However, interactions as well as traits are not a species but an individual property. Thus, we investigated if plant individuals differed in their qualitative and quantitative interaction patterns and if these differences are time-invariant, meaning if they are ecologically relevant and not just stochastic effects and mediated by functional traits (Chapter 1). Further, we evaluated if the intraspecific variation in visitation patterns of one plant species scales up and influences the volatility of commonly used indices (aggregated network statistics) of interaction networks (Chapter 2).

Second, I explored the influence of multiple floral traits on interaction structure at species level. As described above, multiple functional traits can determine the niche of an interaction partner, *e.g.* flower-visitor can only exploit the resources of a flower with certain trait expression. Thus, floral traits can define the resource niche of the flower visitor species. By defining traits as niche dimensions, we developed a non-parametric approach to estimate the volume and overlap of *n*-dimensional hypervolumes (*i.e.* niche space, Chapter 3) and tested several hypotheses regarding niche differences of native and invasive flower-visitor species in the Hawaii Volcanoes National Park (Chapter 4). In summary, by exploring the interplay of traits, interactions and community structure at different hierarchical levels and in the context of multiple traits, this thesis aids to fill recent knowledge gaps in functional traits and community ecology.

Chapter 1 – Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent

This chapter *is published* as:

Kuppler J, Höfers MK, Wiesmann L & Junker RR. Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent. ***New Phytologist*** (2016) DOI: 10.1111/nph.13858

ABSTRACT

- The basic units of ecological and evolutionary processes are individuals. Network studies aiming to infer mechanisms from complex systems, however, usually focus on interactions between species, not individuals. Accordingly, the structure and underlying mechanisms of individual-based interaction networks remain largely unknown.
- In a common garden, we recorded all interactions on flowers and leaves of 97 Sinapis arvensis individuals from seedling stage to fruit set and related interindividual differences in interactions to the plant individuals' phenotypes.
- The plant individuals significantly differed in their quantitative and qualitative interactions with arthropods on flowers and leaves. These differences remained stable over the entire season and thus were time-invariant. Variation in interacting arthropod communities could be explained by a pronounced intraspecific variability in flowering phenology, morphology and flower scent, and translated into variation in reproductive success. Interestingly, plant individuals with a similar composition of flower visitors were also visited by a similar assemblage of interaction partners at leaves.
- Our results show that the nonuniformity of plant species has pronounced effects in community ecology, potentially with implications for the persistence of communities and populations, and their ability to withstand environmental fluctuations.

INTRODUCTION

In community ecology, food webs and networks summarizing trophic interactions are classically recorded at species level, for example counting interactions between producers and consumers. In this species-centric approach where the mean interaction frequency between a species pair or the mean phenotype of a species is considered, the intraspecific variability in interaction patterns as well as in traits is often regarded as noise rather than as an important feature of ecological interactions. However, intraspecific variability in functional traits has long been recognised in evolutionary (e.g. Newton et al., 1999) but also in ecological studies. Recently, the importance of differences between individuals has been re-emphasised and it has been attempted to incorporate them into community ecology (Violle et al., 2012). Thus, not accounting for intraspecific variability may lead to an underestimation of the functional diversity and complexity of communities.

Between plant populations the qualitative and quantitative visitor composition can vary to a large extent (Herrera, 2005; Gómez et al., 2014a) and variation in floral traits between populations may be driven by the selection by different local pollinator assemblages (Johnson, 2010; Gómez et al., 2014a). However, even within populations, flower visitors have the ability to discriminate between conspecific plant individuals based on subtle differences in their floral phenotype (Conner & Rush, 1996; Mothershead & Marquis, 2000), which may be the basis for interindividual differences in flower visitor patterns. From an animal-centred (top-down) point of view, we began to understand how individuality affects the dynamics and structure of flower–visitor interactions within communities and populations (Dupont et al., 2011, 2014; Song & Feldman, 2014; Tur et al., 2014, 2015). These top-down effects imposed by the variable preferences and behavioural characteristics of animal species and individuals can account for part of the structured interactions within communities and populations (Junker et al., 2013; Tur et al., 2014). Bottom-up effects – that is, effects mediated by the plant individuals' genotype or phenotype – have also been described to influence the foraging behaviour of herbivores (e.g. Johnson & Agrawal, 2005; Hersch-Green et al., 2011; Barbour et al., 2015). Similar effects in flower–visitor interactions have been shown for plant genotype (Burkle et al., 2013), but to what extent the intraspecific variation in a set of multiple floral traits affects the variability of flower–visitor interaction patterns between plant individuals is still poorly understood.

Intraspecific variation can constitute up to 30% of the total variation in leaf and life-history traits within a plant community (Albert et al., 2010). By contrast, for flower traits it has been discussed that successful pollination of many plant species depends on precision in pollen deposition, which is facilitated by a rather invariant floral morphology – a precondition that may, however, be relaxed in plant species with a generalised pollination system (Armbruster et al., 2004) and in populations confronted with a fluctuating environment (Pérez-Barrales et al., 2007). Accordingly, in more generalised plant species floral morphology and other flower traits such as scent, colour and phenology are known to feature considerable intraspecific variation (Parachnowitsch et al., 2012). Because plant–animal interactions are mediated by functional plant traits (Stang et al., 2006; Junker et al., 2013; Larue et al., 2015), intraspecific differences in these traits may affect the interaction structure among plant individuals, with potential consequences for the plant's reproductive success (Gómez & Perfectti, 2012). The functional position (sensu the 'Eltonian niche') of species within communities is defined by functional traits and trophic interactions, a concept that can also be applied to plant individuals of the same species either originating from different (Gómez et al., 2008, 2014a; Gómez & Perfectti, 2012) or even the same populations (Gómez et al., 2011). Nonuniform functional positions of plant individuals within communities potentially affect community structure and the ecological dynamics of plants and their interaction partners (Bolnick et al., 2011; Violle et al., 2012), which is indicated by a variable network structure across natural plant populations (Gómez et al., 2011; Gómez & Perfectti, 2012).

In a common garden setting, we quantitatively recorded all interactions between arthropods and flowers and leaves of 97 plant individuals of a highly generalistic plant species (Sinapis arvenis, Brassicaceae) throughout their lifetime (i.e. from germination to the end of the flowering period and seed set). This setting minimized environmental heterogeneity, allowing a direct assessment of the importance of plant intrinsic factors (i.e. traits such as morphology or floral scent emission) in controlling the composition and abundance of different interaction partners and reproductive success, and thus the functional position of plant individuals within a population. Accordingly we tested the following hypotheses. First, plant individuals differ in the quantitative and qualitative composition of their interaction partners. Second, these differences are time-invariant, that is, plant individuals systematically differ in interaction patterns independent of time and age. To test for the time-invariance of interactions, we adopted an approach used in animal behaviour research to investigate behavioural differences among animal individuals. Third, the differences in interactions are the result of bottom-up effects mediated by intraspecific variation in flower and leaf traits. Fourth, intraspecific variability in the plant's phenotype and visitation pattern result in differences in the reproductive success.

MATERIAL AND METHODS

Study organism and experimental design

Sinapis arvensis L. (Brassicaceae) is an annual, self-incompatible plant native to southern and middle Europe, which attracts a broad taxonomic range of flower visitors, mostly bees and hoverflies (Kunin, 1993). We used seeds in equal numbers from two wild populations (one from South-Germany, one from South-England, purchased from Templiner Kräutergarten, Germany and Herbiseed, England, respectively). Seeds were treated with aqueous gibberlic acid solution (1000ppm, Roth, Germany) and remained on wet filter paper in complete darkness at room temperature until germination. Seedlings were transferred into 3.5 l pots containing standard soil (Einheitserde Classic N:P:K 250:300:400 mg/l, Topferde, Einheitserde Werkverband e.V., Germany). Half of the plants from each population were additionally supplemented once with a slow release fertilizer (ten pellets Osmocote Exact Standard 3-4M (N:P:K:Mg 16:9:12:2, Osmocote, South Africa) to investigate how controlled environmental variation potentially influences the phenotype of plant individuals. After one week in a green house, the pots were moved to common garden in the Botanical Garden of the University of Salzburg, Austria (47°47'12.4"N, 13°03'32.3"E, 422 m a.s.l.) in May 2013. In the common garden (11 x 5 m), a total of 97 pots containing one plant each (from one of the two populations and either supplemented with fertilizer or not) were arranged in a full-factorial pseudo-randomised block design. Plants were covered in groups of nine or twelve individuals with a removable net (Monofil-Gaze, bioform, Germany) to prevent animals from interacting with the plants. Pots were recessed into the ground, but were removable for trait measurements. Approximately 250 *S. arvensis* plants surrounded the experimental plants to have an arthropod community specific for *S. arvensis* locally available once the experimental plants were made accessible. For further information see Methods S1.

Plant-arthropod interactions

Interactions between arthropods and plant individuals were recorded on non-rainy days (in total 33 days including 26 days during flowering period) between 8:00 and 16:00 h beginning at seedling stage until the end of the flowering period (13th May to 02nd August 2013, start of flowering period: 28th May 2013). An interaction was defined as a visit by an arthropod on one or more flowers or leaves of one plant individual, i.e. an individual flower visitor that visited several flowers of one plant individual consecutively was regarded as one interaction. The sampling was conducted by up to three persons within one day and on most days all 97 individuals were observed. We aimed to maximize the daily observation time for each plant individual and thus the observation time was adjusted depending on weather conditions and interaction frequency of plant visitors. Therefore, the observation time of plants differed among days between 10 and up to 295 minutes and each person simultaneously observed between 4 (high floral abundance and high interaction frequency) and 49 (seedling stage and low interaction frequency) plant individuals at a given time. On most observation days all observed plant individuals were observed for the same amount of time and both in the morning and in the afternoon. The total observation time was approximately 45 h per individual. To make sure that all interactions that occurred in the lifetime of the plants were recorded, nets were removed only during observation times. All interactions on leaves and flowers were recorded and visitor taxa were separated into groups (afterwards referred as insect taxa) that were easily recognisable in the field (see Fig. 1, Table S1). Further, a few individuals of each group were collected for identification. Flower visitor behaviour has been reported to be size-dependent (e.g. Stout, 2000), thus we divided solitary bees and Syrphid flies into two size groups (small and large, Table S1).

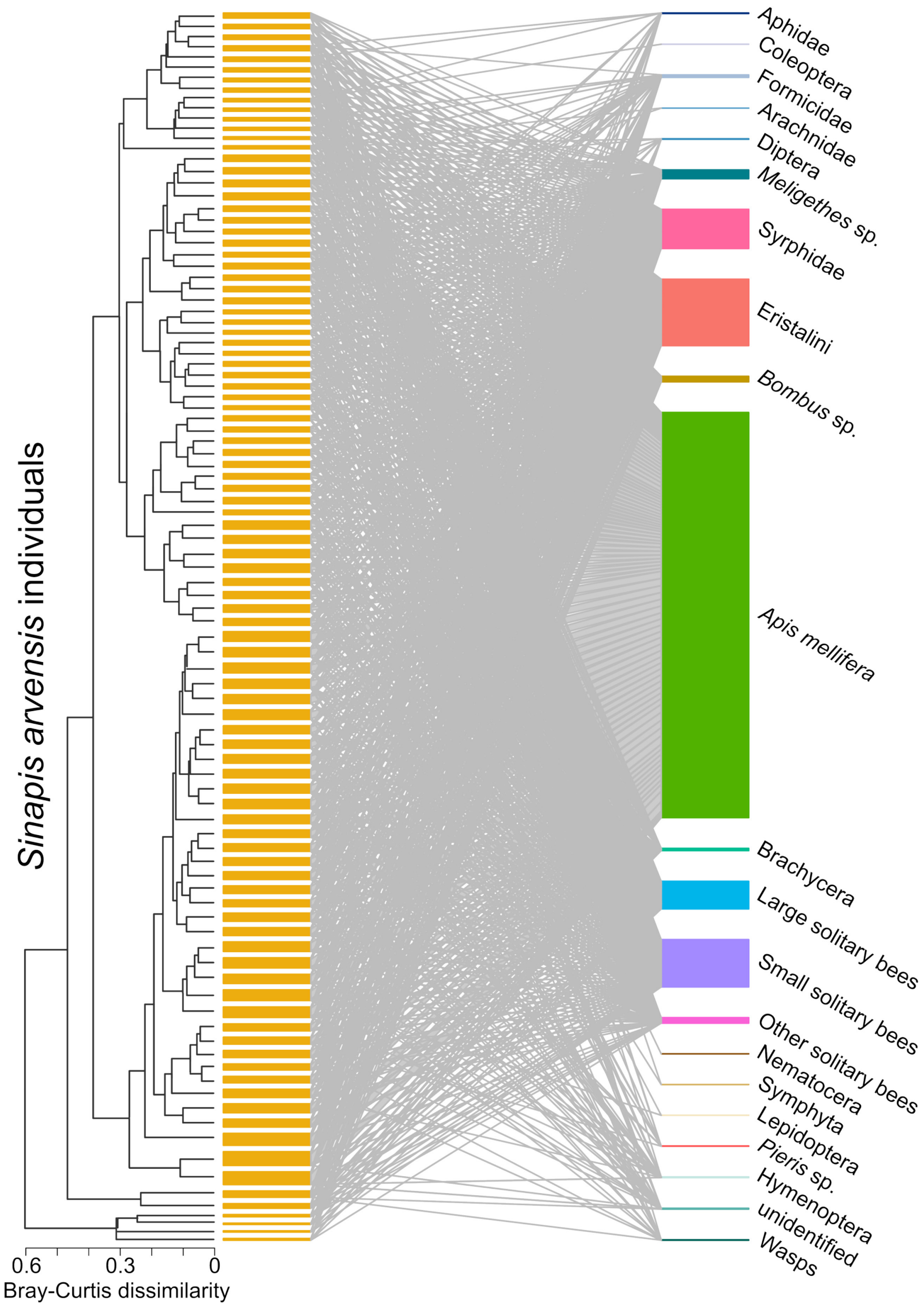

Figure 1. Bipartite individual-based flower-visitor network observed at 97 *Sinapis arvensis* individuals. The network is based on interactions per plant individual per h. Nodes represent plant individuals (left) or flower visitor taxa (right). The width of the nodes denotes the proportional interaction frequency of partners. Dendrogram illustrates Bray-Curtis dissimilarities between plant individuals. Flower visitor taxa: Coleoptera = all Coleoptera excl. *Meligethes* sp., Diptera = all Diptera that could not be identified further; Syrphidae = all Syrphidae excl. Eristalini; Brachycera = all Brachycera excl. Syrphidae & Eristalini; Other solitary bees = all solitary bees that could not be identified further; Lepidoptera = all Lepidoptera excl. *Pieris* sp; Hymenoptera = all Hymenoptera that could not be identified further.

Traits and reproductive success

For each plant individual, we measured several vegetative and floral traits including morphological and chemical traits (Table S2). Twenty-three traits were quantified once per plant (between 10th June and 15th July) and three (number of leaves, number of inflorescences and number of flowers per inflorescence) on a weekly basis (between 13th May and 02nd August). For the standardised measurements of the 23 traits, three or six haphazardly chosen plant individuals per day were carefully transferred to the lab. Each morphological trait was measured on three leaves and flowers from a low, middle and high position to avoid position and age effects; the mean was used for statistical analyses. Leaf traits (number, length, width, area, number of trichomes) were quantified directly on the plant; for the quantification of the floral traits (petal length and width, anther length, stamen length, display size, shape) three flowers per plant were removed (details see Methods S1, Table S2).

Dynamic headspace scent samples were collected from one inflorescence per plant. The inflorescence was enclosed within a polyester oven bag (Toppits®, Germany) for 10 min and the emitted volatiles were then trapped on 1.5 mg Tenax (mesh 60– 80; Supelco, Bellefonte, PA, USA) and 1.5 mg Carbotrap B (mesh 20– 40, Supelco) in a quartz vial (Varian Inc.; length 15 mm, inner diameter 2 mm) for 2 min using a membrane pump (G12/01 EB, ASF Rietschle-Thomas, Puchheim, Germany) with a flow rate of 200 ml min^{-1}. All samples were collected between 8:00 and 12:00 h. Scent samples were analysed using an automatic thermal desorption system (TD-20, Shimadzu, Japan) coupled with a GC–MS (model QP2010 Ultra EI, Shimadzu, Japan) (further details see Methods S1).

Stalks with mature siliques were cut and all siliques from one plant individual were placed in separate boxes for after-ripening. Ripe seeds were collected, counted and partly used to quantify the germination rate of seeds treated with water or an aqueous gibberlic acid solution (methods see above). We used 64 seeds (eight seeds from eight siliques each) per individual for each of the two germination assessments, i.e. a total of n = 128 seeds per plant individual. For the first week new seedlings were counted and removed on a daily bases. In the following four weeks they were checked all three days; afterwards every two weeks for additional ten weeks. We calculated seed viability and dormancy following Luzuriaga *et al.* (2006).

Degree of intraspecific variation

To evaluate the degree of intraspecific variation in plant traits (expressed as coefficient of variation CV) and interaction patterns (expressed as Bray-Curtis dissimilarity and Whittaker's beta diversity) compared to the interspecific variation, we a) measured several plant traits (height of the inflorescences, display size inflorescence, anther and stamen length) as well as the interaction patterns of a set of sympatric plant species (co-occurring at the meadow were the common garden was located) and b) extracted these data from a study performed on a grassland in Germany (Junker *et al.*, 2013, Notes S1).

Statistical analyses

Structure of plant individual-based networks

We investigated the structure of networks based on plant individuals (flower and leaf) by calculating common aggregate statistics characterising the structure of networks: one at individual level (complementary specialization d') and three at network level (connectance, interaction evenness, complementary specialization H_2') (Dormann *et al.*, 2009). The networks were constructed using the visitation frequency per hour for each visitor group. To evaluate the differences of individual- and species-based networks, we compared the values of these indices to values obtained from a number of networks consisting of multiple plant and animal species, which were obtained from the *bipartite* package (Dormann *et al.*, 2008) in R (R Core Team, 2013) and the Interaction Web Database (Guimaraes *et al.*, 2012).

Inter-individual differences in interaction patterns

In order to test whether differences between plant individuals in their interaction patterns do not represent random differences and are invariant over time, we compared independent observation events recorded over time. Such an approach is commonly used in behavioural ecology to define animal personalities that behaviourally differ from other individuals regardless of time, environment or situation (Wolf & Weissing, 2012). This concept is the key feature to investigate individual differences as well as the ecological and evolutionary consequences of intraspecific variability in behavioural traits (e.g. Gracceva *et al.*, 2011) and is directly transferable to study differences in interaction patterns of plant individuals. Thus, we tested whether the ranking of plant individuals based on the daily interactions frequency with different insect taxa was consistent over the whole growing season. This approach allows detecting time-invariant differences between individuals independent of (variable) environments or conditions. For instance, the activity of animal taxa interacting with the plants in our study was highly variable over time due to variable weather conditions or the animals' phenology, which affected evenly all plant individuals but does not inform about the inter-individual differences between plants.

For each observation day, the residual number of interactions N_i for each plant individual i was calculated (i.e. the deviation of the observed interaction strength from a null model expectation E_i assuming an equal number of interactions per individual i per observation time t_i; compare to Junker *et al.*, 2011). If the interactions are driven by random effects all plant individuals should receive the same number of interactions as expected by the null model. However, if other structuring mechanisms (i.e. traits and animals' preferences) are involved the observed number of interactions should deviate from the null model expectation. Residual number of interactions N_i per plant individual i was calculated as $N_i = O_i t_i^{-1} – E_i$ with O_i as the number of observed interactions at plant individual i and t_i as the observation time of individual i. Expected number of interactions E_i is defined as $E_i = Tt^{-1} / I$ with T as the total number of observed interactions with all plant individuals, t as the total time of observation and I as the number of plant individuals observed at a day. Based on N_i, plant individuals i received a rank r_i between 1 and I; subsequently, r_i was standardised between 0 and 1 as standardised rank $R_i = (r_i - 1) / (I - 1)$. Thus, plant individual i with $R_i = 1$ received the most interactions at the day under consideration; i with $R_i = 0$ the least. R_i was calculated for each individual for each observation day (n = 10.8 ± 0.27 days for each plant individual, mean ± SE) for seven visitor groups: the total interactions at flowers (all visitor taxa), as well as the interactions of flowers with honeybees (*Apis mellifera*), small solitary bees (<10mm), large solitary bees (>10mm), Syrphid flies of the tribe Eristalini, Syrphidae (excluding the tribe Eristalini), and the total number interactions at leafs (all visitor taxa). The five most abundant visitor species or taxa (*Apis mellifera*, small and large solitary bees, Eristalini, Syrphidae) are known to pollinate *Sinapis arvensis* (Kunin, 1993).

The effects of plant individual, population and fertilizer treatment on interaction patterns (i.e. mean ranks $\overline{R}_i$) were analysed using linear mixed-effects models (LMMs) with population and treatment as fixed factor and plant individual as random factor and ranks of each observation day as response variable using restricted maximum likelihood. To assess the significance of plant individuals we followed a model building strategy that uses likelihood ratios tests to compare models with and without a given random effect (Pinheiro & Bates, 2000). Further, we estimated the relative contribution of the model factors to the variation in interaction patterns by calculating two types of R^2-values (R^2_{marginal} and $R^2_{\text{conditional}}$) for all LMMs (Nakagawa & Schielzeth, 2013). R^2_{marginal} is the relative contribution of all fixed factors (in our case population and fertilizer treatment) to variation and $R^2_{\text{conditional}}$ is the relative contribution of all fixed and random factors (in our case population, treatment *and* plant individual). Model assumptions were checked visually and if necessary data were log-transformed to achieve normal distribution.

To test whether individual differences can be solely explained by the number of flowers per plant individual, which is a proxy for total resource availability, we repeated the rank calculations using a second null model expectation based on the number of flower per individual. Here the expected number of interactions is defined as $E_i = (Tt^{-1} / F) * F_i$ with T as the total number of observed interactions with all plant individuals, t as the total time of observation, F as the total number of flowers open at the observation day and F_i as the number of flowers of individual i. For number of flowers values from weekly flower counts were used (Table S2, each observation day was in a two day range to the weekly counts). Then, E_i was used to calculate the residual number of interactions N_i per plant individual i as described above.

Additionally, to test for consistency in flower visitor diversity per individual over time we calculated the visitor taxa richness, Inverse Simpson index and Hurlbert's PIE for each plant individual for all observation days and compared the mean richness and diversity using LMMs. The inverse Simpson index as well as Hurlbert's PIE can be used as a surrogate for relative generalization in interaction partners per plant individual, but note that Hurlbert's PIE is corrected for species abundance (Lázaro *et al.*, 2010; Gómez *et al.*, 2014b).

To test whether plant individuals with similar flower visitor communities also have similar interactions at leaves, we correlated distances matrices for flower and leaf interactions consisting of Bray-Curtis dissimilarities between plant individuals based on number of interactions O_{ij} between plant individual *i* and visitor taxon *j* (Mantel Test, Pearson's correlation, 9,999 permutations).

Influence of plant traits on interaction patterns and reproductive success

To investigate the effect of plant traits on the visitation patterns (i.e. mean ranks $\overline{R}_i$) and reproductive success (i.e. total number of seeds (seed set), number of seeds per flower, seed viability, seed dormancy, and seed size) we correlated (Pearson's product moment correlation) trait characteristics of plant individuals *i* with mean ranks $\overline{R}_i$ based on visits of all animals and individual taxa. To correct for potential effects of sampling date (plant age) on the trait values that have been measured only once per plant individual, we used residuals of linear regressions as trait values in cases where Pearson's product moment correlation indicated an age-dependency (Table S2). In order to investigate the effect of trait sets (further referred to as phenotype) on the quantitative composition of the visitor community (on flowers and leaves, separately) and the reproductive success (i.e. number of seeds per flower), we correlated distance matrices based on Bray-Curtis (community data) or Euclidean (trait data) distances between plant individuals *i* based on a set of traits, visitors or number of seeds per flower using a Mantel test (Pearson 's correlation, 9,999 permutations). For this analysis, we used the following trait sets: plants' morphology (separately for floral and vegetative morphology Table S2), floral scent bouquet (Table S3) and phenology (i.e. for each observation day the number of flowers F_i for each plant individual *i* was counted and standardised ($F_i / max(F_i)$)). To assess the effects of the fertilizer treatment and the populations on plant phenotype (floral & vegetative morphology, scent, phenology; Table S2) we used permutational multivariate analysis of variance (PERMANOVA, 9,999 permutations). Further, to test for the effects of population and treatment on single plant traits and reproductive success we used analysis of variance (ANOVA). Statistical analyses were performed with the statistical computing software R (R Core Team, 2013) and the packages *vegan* (Oksanen *et al.*, 2013), *bipartite* (Dormann *et al.*, 2008), *piecewiseSEM* (Lefcheck, 2015) and *nlme* (Pinheiro *et al.*, 2015).

RESULTS

Structure of plant individual-based networks

In total we observed 27,988 interactions (25,730 on flowers and 2,258 on leaves) with an average of 265.4 ± 109 (mean ± SD) interactions on flowers and 23.3 ± 11.1 on leaves per plant individual. Both the flower- and leaf- visitor networks revealed a high degree of generalisation (Fig. 1, Fig. S1, Table 1). The individual-based leaf-visitor network had a higher connectance and a lower complementary specialization (H_2') than the individual-based flower-visitor network. Although differences in interactions between individuals are mostly due to quantitative shifts in the relative composition of visitor taxa and not due to qualitative shifts in visitor taxa composition, mean intraspecific dissimilarities between individuals was pronounced (Bray-Curtis dissimilarities: mean ± SD 0.33 ± 0.15) but, as expected, smaller than inter-specific mean dissimilarities (Salzburg 2015: 0.87 ± 0.17, Junker *et al.*, 2013: 0.95 ± 0.09; Notes S1). Thus, the network based on plant-individuals was also less specialised than species-based flower-visitor networks (Table 1). Note, that individuals with a similar proportional composition of visitor taxa were not similar in numbers of interactions per hour (Mantel Test, Pearson's product-moment correlation, 9,999 permutations: r = 0.01, p = 0.36, Fig. S2).

Inter-individual differences in interaction patterns

Visitation frequency (i.e. mean ranks $\overline{R}_i$) by arthropod taxa differed between plant individuals, i.e. plant individuals significantly differed in their mean ranks $\overline{R}_i$ based on the visits of all and individual visitor taxa except for Eristalini and large solitary bees (Table 2; Fig. 2). While treatment did not affect the visitation patterns, population had a significant effect on the visitation patterns of *Apis mellifera*, large and small solitary bees (Table 2). However, plant individuals explained more variation in interaction patterns than population (Table 2) and the effects of plant individuals on visitation patterns were also present within populations (Table S4, Fig. S3). Similar patterns were found for the mean ranks $\overline{R}_i$ using the second null model expectation (number of interactions is proportional to the number of flowers) while the visitation frequency of Eristalini and large solitary bees also differed significantly (Table S5, Fig. S4). Additionally, mean ranks $\overline{R}_i$ based on the two null model expectations for each taxa and the total number of flowers correlated with each other (Pearson's product-moment correlation: $t > 2.1$, $r > 0.21$, $p < 0.039$) except in the case of *Apis mellifera* ($t = 1.79$, $r = 0.18$, $p = 0.077$, Pearson's product-moment correlation). This indicates that the use of the different null model expectations (equal number of visits and visits proportional to number of flowers) did not strongly influence the results and that the individual visitation patterns (i.e. mean ranks $\overline{R}_i$) are not explainable by varying resource availability across individuals, only. Thus, all following results are based on the mean ranks $\overline{R}_i$ from the first null model expectation (equal distribution of visitors) allowing to gauge the relative effects of number of flowers or phenology on interaction patterns compared to other traits such as flower morphology and scent.

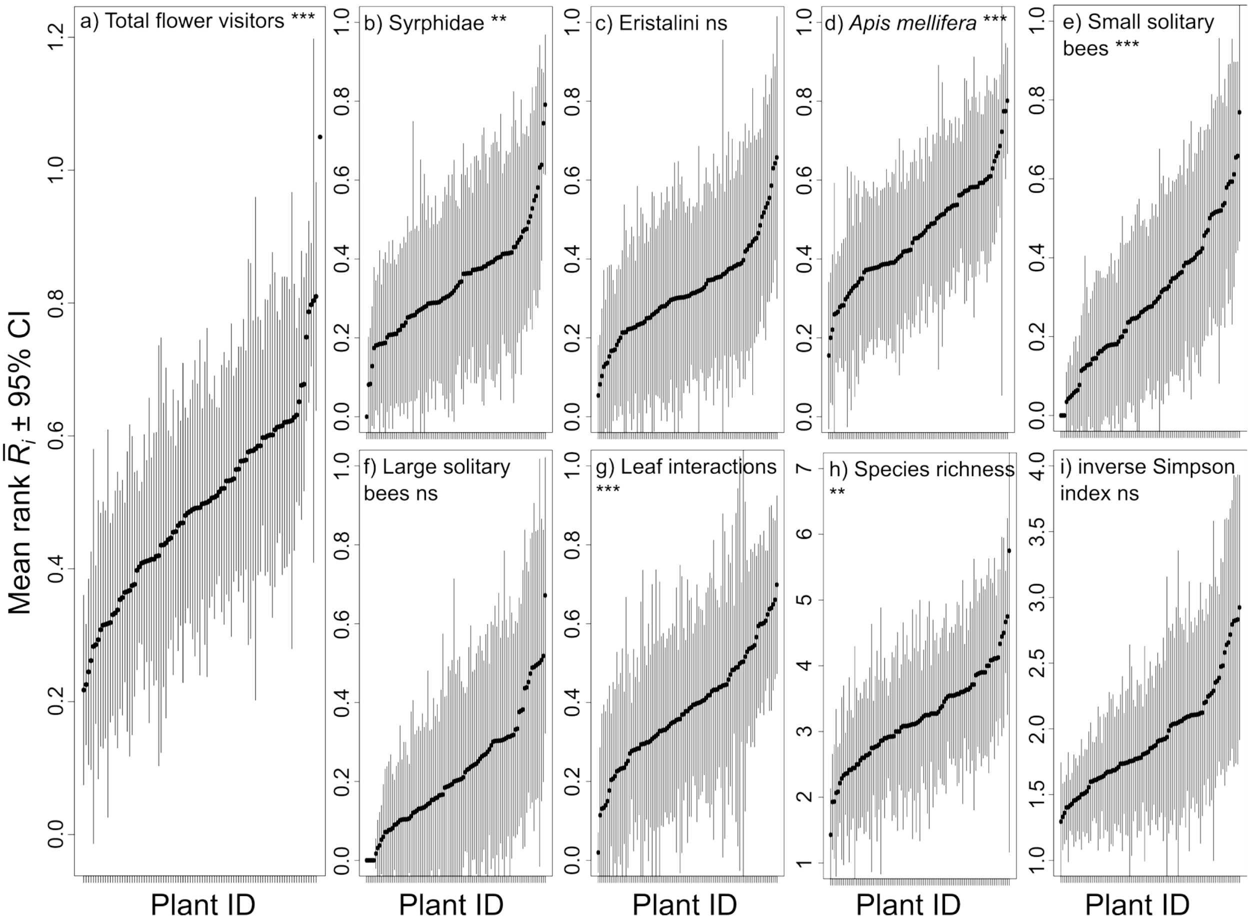

Figure 2. Time-invariant differences in visitation frequencies between plant individuals of *Sinapis arvensis*. a) – g): Each plot shows the mean ranks $\overline{R}_i$ with 95% confidence intervals (CI) of all 97 plant individuals for total number of flower/leaf visitors or different visitor taxa. On each observation day, the plant individuals *i* were ranked based on increasing interaction frequencies with arthropod taxa. h): Mean species richness and i) mean inverse Simpson index of visitor community was calculated on each observation day, shown is the mean ± 95% CI. Mean ranks $\overline{R}_i$ and means of each plant individual were compared using linear mixed-effect models and -likelihood ratio test, significance levels are given as asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

Table 1. Aggregate network statistics for individual-based networks based on qualitative flower or leaf interactions of *Sinapis arvensis* and flower-visitor networks considering multiple plant species. Shown are connectance, interaction evenness, mean complementary specialisation of the individual plant (*d'*) and specialisation of the whole network (H_2'). The values for the flower-visitor networks considering multiple plant species were calculated based on 25 (binary indices) or 20 (quantitative indices) flower-visitor networks (see Material and Methods). For all indices mean ± SE are given.

Network	**Connectance**	**Interaction evenness**	***d'* (mean ± SE)**	***H_2'***
Plant individuals				
Flower visitors	0.414	0.735	0.004 ± 0.001	0.092
Leaf visitors	0.269	0.795	0.002 ± 0.0001	0.21
Plant species				
Flower visitors	0.18 ± 0.11	0.60 ± 0.10	0.41 ± 0.17	0.51 ± 0.16

Table 2. Results of linear mixed-effect models (LMM) testing for differences in interaction patterns between plant individuals (*Sinapis arvensis*). Each model included population (Pop.) and fertilizer treatment (Treat.) as fixed factors and plant individual (PlantID) as random factors. The relative contribution to the variation in interaction patterns of the three factors was assessed using two types of R^2-values: $R^2_{\text{conditional}}$ and R^2_{marginal} (Nakagawa & Schielzeth, 2013). $R^2_{\text{conditional}}$ is the relative contribution of both fixed and random factors, R^2_{marginal} is the relative contribution of the fixed factors only. Significant results are highlighted in bold.

LMMs	**PlantID** (χ^2_1)	**Pop.** ($F_{1,94}$)	**Treat.** ($F_{1,94}$)	$R^2_{\text{conditional}}$	R^2_{marginal}
Visitor taxa					
Total flower interactions	**25.03*** **	3.91	1.36	0.09	0.009
Apis mellifera	**14.71*** **	**11.97*** **	1.09	0.08	0.02
Eristalini	0.21	0.0290	0.74	0.008	0.0008
Small solitary bees	**25.96*** **	**19.54*** **	0.08	0.13	0.04
Large solitary bees	2.02	**21.36*** **	1.39	0.06	0.03
Syrphidae (without Eristalini)	**6.93** **	0.09	0.003	0.04	0.0001
Total leaf interactions	**12.75*** **	0.87	0.04	0.06	0.002
Diversity indices					
Inverse Simpson index	1.58	**39.15*** **	0.001	0.06	0.04
Species richness	**8.39** **	**35.28*** **	0.67	0.09	0.05
Hurlbert's PIE	0.13	**22.1*** **	0.08	0.03	0.02

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; significance of fixed effects assessed with LMMs, significance of random effect with likelihood ratio test

Plant individuals also showed time-invariant differences in the mean species richness of interaction partners (Table 2; Fig. 2h), but did not differ in the diversity measured as inverse Simpson index (Fig. 2i) or Hurlbert's PIE (Table 2). Further, treatment did not affect the diversity of visitor either, but population had a significant effect on all diversity measures. Therefore, models including plant individual explained the same or a little more of the variation in visitation pattern than models including population, only. Overall, these results indicate that plant individuals interact with specific flower visitor communities that quantitatively and qualitatively vary in their compositions (Fig. S2, Fig. S5) and these plant-individual specific communities are time-invariant over the whole flowering period.

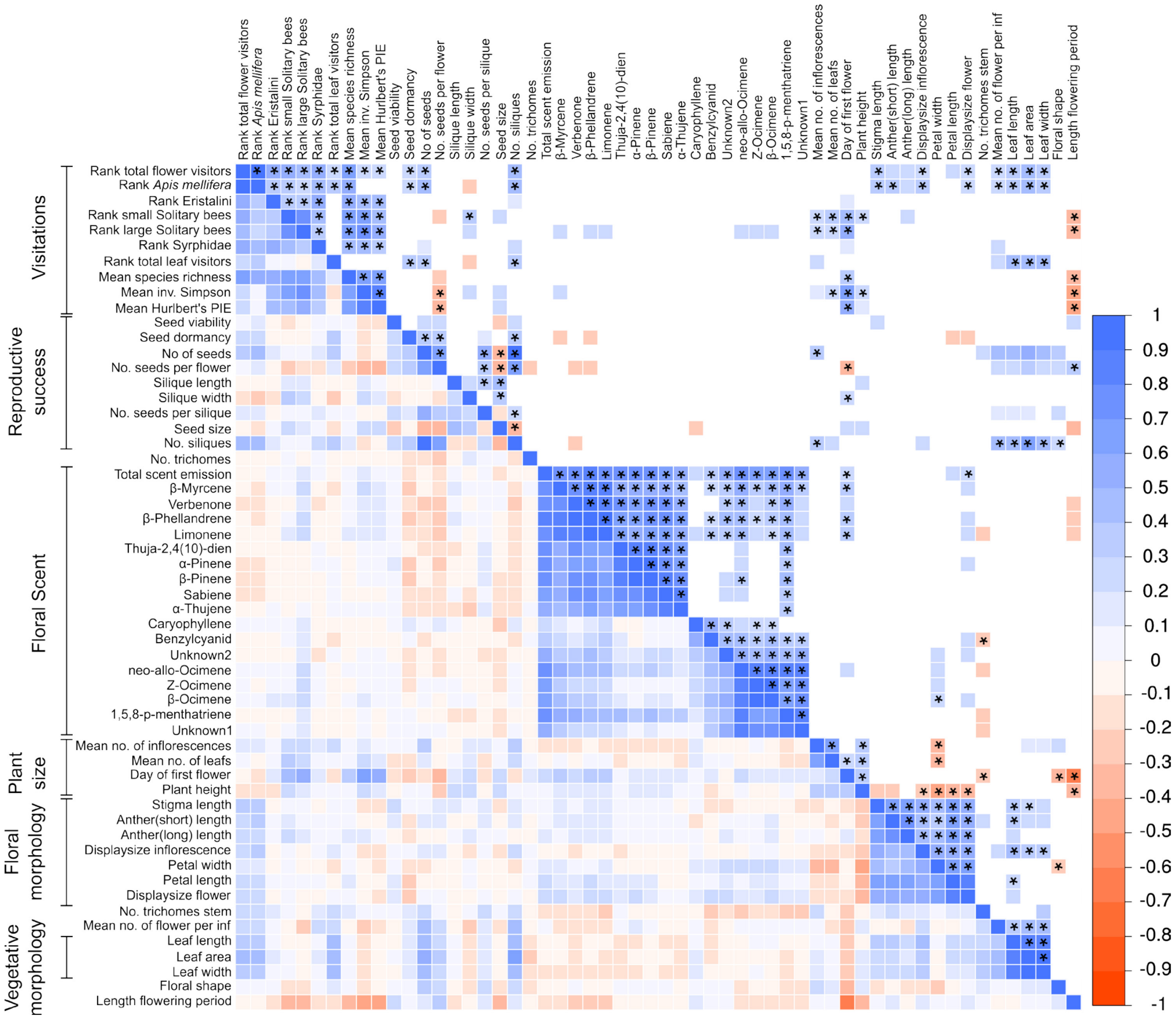

Figure 3. Heatmap on Pearson's product moment correlation coefficients *r* between plant traits, visitation frequencies (i.e. mean ranks $\overline{R}_i$) and reproductive success of plant individuals (*Sinapis arvensis*). Blue squares positive correlations, red squares indicate negative correlations. In the upper right half of the matrix only significant correlations ($p < 0.05$) are shown; asterisks denote correlations remaining significant after False discovery rate-correction for multiple comparisons. In the lower half all *r*-values are shown regardless their significance.

Influence of plant traits on individual interaction patterns and reproductive success

We found a considerable degree of intraspecific variation of plant traits (coefficient of variation CV ranging from 0.127 to 0.22, Notes S1, Table S2, S3), which is up to 70.6 % of the CV measured across several plant species (0.323 – 1.04, Notes S1). The intraspecific variation in individual traits explained variation in the visitations patterns of plant individuals (i.e. mean ranks $\overline{R}_i$). The significant correlations between visits and phenotype often were associated with traits representing the plant size (inflorescence height, mean number of inflorescences, display size of inflorescences, mean number of leafs, leaf length/width/area), phenology as well as anther and stamen length. We found no significant correlations between individual scent compounds or total scent emission and visitation rates after correcting for multiple tests (false discovery rate, Fig.

3). However, large solitary bees showed a trend towards higher visitation frequency on plants that had high emission rates of several scents compounds (e.g. ocimene or limonene) compared to plants with little emissions of these compounds (Fig. 3). Variation in visitation patterns ($\overline{R}_i$) and plant traits also correlated with reproductive success of plant individuals (Fig. 3). For a multivariate visualisation (Co-Inertia analysis) of the association between traits and visitation rate of the different animal taxa see Notes S2.

Individuals from different populations varied in their phenology, seed set, phenotype as well as several traits that can be used as surrogate for plant size (Table S6, S7). In contrast, fertilizer treatment had little effect on the plants' phenotype (Table S6, S7) and consequently did not affect interactions with arthropods (Table 2).

Additional to individual traits that explained part of the intraspecific variability in interaction patterns, the plant phenotype described by more than one individual trait (i.e. one scent compound) was also predictive for interaction structure. Plant individuals that were similar in floral scent bouquets, phenology, vegetative and floral morphology (each described by a number of individual traits) were also similar in their flower visitor communities (Mantel test, Table 3). Furthermore, plant individuals with a similar visitor community had a similar reproductive success (i.e. number on seeds per flower, Table 3).

DISCUSSION

Plant species occupy specific functional niches in communities that determine the species-specific composition of their interaction partners (McGill et al., 2006; Junker et al., 2013), which results in nonrandom associations of plant and animal species in communities (Ings et al., 2009). Our study clearly reveals similar patterns within plant species whereby plant individuals differ in their quantitative and qualitative interactions with flower- and leaf-visiting arthropods resulting in nonrandom interaction patterns, too. These differences were invariant over time (throughout the entire season) and were largely independent of the number of flowers, emphasizing the importance of other traits in controlling differences in interactions, such as morphology and floral scent emission. The plant individual-specific arthropod assemblages also varied in species richness largely independent of the visitor abundance. The constancy in plant individual-specific interaction patterns adds complexity to community structure and suggests that plant individuals occupy specific functional positions in ecosystems. Thus, plant species may not necessarily be uniform entities regarding their ecological function.

The identity, composition and relative abundance of pollinators can be regarded as important components of the niches of plant species (Sargent & Ackerly, 2008; Johnson, 2010). These components vary between plant species, but also between different populations of single plant species (Herrera, 2005; Gómez et al., 2014a). Recently, Gómez et al. (2014a,c) showed that in generalised species the relative visitation frequency of animal species to flowers contributes more to differences between populations than the animal species identity and composition. Even minor shifts in relative frequencies of diverse pollinator assemblages across plant populations can have major consequences for plant performance (Gómez et al., 2011). In these studies the differences between populations may (at least partly) result from top-down effects of local flower visitor communities on plant reproduction and population dynamics. Our data clearly indicate a bottom-up effect of plant species shaping interactions between plant individuals and specific flower visitor assemblages recruited from a shared local species pool. In our common garden study the variation in environmental factors and the local arthropod species pool between plant individuals was kept to a minimum. Thus, plant intrinsic factors – that is, the phenotype as well as the phenology of plant individuals – are the cause for the well-structured intraspecific visitation patterns.

Table 3. Results of mantel statistic testing for correlations between the following distance matrices: plant individuals' visitor communities (flowers, leafs) (Bray-Curtis distance), scent, phenology, vegetative and floral morphology, number of seeds per flower as surrogate for the plant individuals' reproductive success (Euclidean distance) of *Sinapis arvensis*. Significant positive correlations indicate correlating distance matrices, e.g. plant individuals with similar interaction patterns on flowers were also similar in interactions on leaves. Mantel statistic r-values are given. Significant correlations are highlighted in bold.

	Flower visitor community	**Leaf visitor community**	**Nr. of seeds per flower**
Leaf visitor community	**0.086***		0.013
Flower scent	**0.155***	-0.01	-0.011
Phenology	**0.345*****	0.029	**0.12****
Vegetative morphology	0.04	**0.18*****	0.025
Floral morphology	**0.106****	**0.136****	-0.017
Nr. of seeds per flower	**0.176****	-0.013	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Plant individuals with similar flower visitor communities also had similar leaf visitor communities, indicating that interactions at both plant organs may not be independent of each other, possibly due to attraction or aversion to the same plant traits. It has been shown that, for example, pollinators and herbivores prefer the same trait characteristics (Strauss & Whittall, 2006) or that herbivory may alter flower and leaf traits (Strauss et al., 1996; Lucas-Barbosa et al., 2015). Thus, several constraints and ecological trade-offs may underlie multitrophic interactions mediated by functional traits. We found plant traits to be predictive for the visitation pattern of plant individuals, both when tested uni- or multivariately. However, our results suggest that a plant's phenotype rather than the characteristics of individual traits is important for the structuring of individual interactions. Note that groups of traits were highly integrated, that is, the characteristics of several traits (e.g. scent compounds or floral morphology) were strongly correlated, preventing a clear identification of individual traits as a cause for visitation frequency of individual animal taxa.

Such clusters may have evolved as adaptations to interaction partners (Pigliucci, 2003) or may be caused by ontogenetic constraints or pleiotropic effects (Jernigan et al., 1994); our data do not allow a differentiation between these effects. However, regardless of their evolutionary/physiological causes, these clusters clearly affected ecological processes, for example the partitioning of flower visitors within our experimental common garden. Divergences and convergences of phenotypes explain interspecific as well as intraspecific differences amongst spatially distinct communities in flower–visitor assemblages (Gómez et al., 2014c; Junker et al., 2015). Here, we show that these quantitative and qualitative shifts in flower–visitor interactions also occur within populations mediated by rather small differences in the phenotypes of plant individuals.

Variation in the phenotype and the phenology of plant individuals not only correlated with the flower–visitor composition, but also translated into variation in the reproductive success of the plants. The phenotype may affect the reproductive success directly (Gómez, 2000; Strauss & Whittall, 2006; Lay et al., 2011), for example due to differences in pollen germination or pollen loss (Song et al., 2013), or indirectly, for example due to effects on flower visitor communities. However, our data do not allow separating direct effects of the plant's phenotype from indirect pollinator-mediated effects on individual female fitness (i.e. seed set). Differences between plant individuals in the number of flower visits (total and per flower) as well as in the visitor composition may lead to differences in the reproductive success due to differences in pollinator efficiency across species (Sahli & Conner, 2007; Ne'eman et al., 2010). This variation in pollen deposition may lead to differences in seed production whereas other vital functions (i.e. germination rate) remain stable (Ashman et al., 2004; Knight et al., 2005). The plant individuals originated from two populations that experienced unknown but most likely different flower visitor communities to which the plants may have been adapted (Gómez, 2000). Differences in the plants’ phenotypes and reproductive success may indicate that one of the populations was better adapted to the local flower visitor pool, possibly due to a similar local flower visitor pool at their origin.

Community stability is facilitated by a high species and functional diversity (Loreau & de Mazancourt, 2013; Turnbull et al., 2013). Scaling down to species level, we may assume that a high variability in traits across plant individuals and in flower visitor composition also positively affect the stability of plant populations (Waser et al., 1996). Furthermore, intraspecific trait variation is an important factor in ecological functioning (see Bolnick et al., 2011; Violle et al., 2012 for full review) and may help plant populations to cope with environmental change. Variability increases the probability that at least some phenotypes are able to reproduce under changing conditions and thus stabilises the population (Hooper et al., 2005). In annual self-incompatible plant species such as Sinapis arvensis pollinators are crucial for reproduction and thus for the persistence of plant populations. Therefore, a high inter-individual variation in traits mediating visitation patterns could facilitate the population's ability to buffer changes in the local pollinator pool; which changes both naturally (Herrera, 1988; Basilio et al., 2006) and due to anthropogenic disturbances (e.g. Potts et al., 2010).

Our results demonstrate that intraspecific variation in plant traits can have strong effects on interaction patterns, which may also affect community structure and ecosystem processes, and these factors need to be tested in future studies. Intraspecific variation as a prerequisite for selection has been intensively examined in evolutionary studies (Conner & Hartl, 2004). Acknowledging intraspecific variation in floral traits and visitation patterns in an ecological context indicates that plant species are not necessarily uniform entities, which leads to the conclusion that plant individuals occupy distinctive functional positions within populations and communities. Thus, our study clearly suggests that studies considering intraspecific variability in community ecology could facilitate a more detailed understanding of the persistence of communities or populations and their ability to withstand environmental fluctuations.

ACKNOWLEDGEMENTS

We would like to thank Elisabeth Egger and the gardeners of the Botanical Garden of the University of Salzburg for help with the establishment and maintenance of the common garden; Anne-Amelié C. Larue-Kontić and Mathias Hoffmeister for fruitful discussions; Carola Helletsgruber for performing the germination experiments; Stefan Dötterl, Klaus Lunau, Irmgard Schäffler and Martin Zimmer for logistic support; and Angela Moles, Sébastian Ibanez, Hélène Deraison, José María Gómez and anonymous reviewers for valuable comments on an earlier draft of the manuscript. The project was supported by the Graduate School ‘Evolutionary Networks: Organisms, Reactions, Molecules’ (E-Norm) of the Heinrich-Heine-University, Düsseldorf, Germany and the Deutsche Forschungsgemeinschaft (DFG JU 2856/2-2).

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Chapter 2 – Volatility of network indices as a result of intraspecific variation in plant-insect interactions

This chapter *is submitted* as:

Kuppler J, Grasegger T, Peters B, Popp S, Schlager M & Junker RR. Volatility of network indices as a result of intraspecific variation in plant-insect interactions.

ABSTRACT

Classically the structure of interaction networks is derived from summarizing trophic interactions at species level, e.g. counting interactions between plants and flower-visitor species. This approach, however, neglects intraspecific variation in the composition and diversity of interaction partners, which can be pronounced. Intraspecific variation in interactions may thus affect both quantitative and qualitative network indices. In a resampling approach using field data, we evaluated whether and how intraspecific variation in interactions alters commonly used aggregate statistics. Our results showed that aggregate statistics as well as module structure are sensitive towards changes in the interaction patterns of one plant species within a multi-species network, which may affect the ecological interpretation of the stability of communities or other network properties. These findings challenge the robustness of commonly applied network indices, urge for a sufficient and representative sampling of interactions, and emphasize the significance of intraspecific variation in the community and network context.

INTRODUCTION

Network theory strongly contributed to the understanding about the structure of biotic interactions and their importance for community dynamics, function and stability (Heleno *et al.*, 2014). Classically network statistics summarize trophic interactions at the species level and thus consider the mean interaction frequency between species. Although recent studies emphasized the pronounced intraspecific variability in interactions in flower-visitor networks (Gómez *et al.*, 2014a; Tur *et al.*, 2014b; Hoffmeister *et al.*, 2015; Kuppler *et al.*, 2016), it remains unclear whether variation among individuals of a single species is relevant at the community level comprising all species of a habitat.

Network structure is commonly described by aggregate statistics such as connectance, complementary specialization or modularity (Olesen *et al.*, 2007; Blüthgen *et al.*, 2008). These properties may be explained by the abundance distributions of plants and animals, phenology, morphological matching and other factors (Vázquez *et al.*, 2009; Junker *et al.*, 2013). Further, several of these aggregate statistics appear to be relatively invariant between different species-based networks (Jordano *et al.*, 2003; Petanidou *et al.*, 2008). It has been suggested that this invariance reflects a general pattern of flower-visitor networks or that it is the result of methodology such as sampling at species level (Jordano *et al.*, 2003; Tur *et al.*, 2014b). In this context, it is valuable to understand how interactions at the individual level may drive the structure and dynamics at the species level (Olesen *et al.*, 2007) and how they affect the robustness of network indices and the ecological evaluation of communities.

We evaluated the sensitivity of aggregate network statistics to differences in visitation patterns of plant individuals. Therefore, we resampled the interactions of one plant species from a pool of interactions recorded at plant individuals and tested how the (natural) variation in the interactions of one plant species affect the properties of a multi-species network. Our simulation study aims to improve our understanding about the robustness of network analysis, which has implications for the interpretation of the structure and dynamics of species-based interaction networks.

MATERIAL AND METHODS

Flower-visitor interactions

Flower-visitor interactions were recorded on a 30 x 30 m meadow plot in the Botanical Garden of the University Salzburg, Austria in June 2015. We observed all flowering plant species (n = 13 species) and added 20 potted individuals of *Sinapis arvensis* that were homogenously distributed in the plot. To facilitate homogenous monitoring, the plot was divided into four subplots (15 x 15 m, each). Flower-visitor interactions were recorded in random walks on four days between 9:00 and 16:00 h (1 or 2 h in the morning and 1 h in the afternoon) resulting in a total observation time of 10 h per subplot (i.e. total observation time = 40 h). All interactions on flowers were recorded and visitor taxa were assigned to easily recognisable groups (Kuppler *et al.*, 2016). Additional to the sampled flower-visitor interactions we used recordings of flower-arthropod interactions of 64 plant individuals of *S. arvensis* L. (Brassicaceae) that we recorded in a common garden setting in 2013 on the same meadow (Kuppler *et al.*, 2016). In the further analysis, we thus used the data resulting in a total of 84 individuals.

Network resampling and statistics

To test the relative effect of time-invariant intraspecific differences between plant individuals on commonly calculated network indices and thus the ecological interpretation of the properties of multi-species networks, we generated interaction matrices containing the interactions of the 13 plant species naturally occurring in the plot and the interactions of one or several (n = 1, 2, 3, ..., 84) randomly sampled *S. arvensis* individuals. We resampled 84,000 (84 x 1000) networks $N\binom{n}{k}$ with n = total number of *S. arvensis* individuals (84) and k = number of included *S. arvensis* individuals (1, 2, …, 84). For each k we resampled 1000 combinations without replacement. Each network consisted of the interaction frequency (per flower per hour) of the 13 plant species and the mean interaction frequency of $N\binom{84}{k}$ randomly selected *S. arvensis* individuals (Figure S1). Further, as quantitative network statistics are sensitive to differences in interaction frequencies, the resampling was repeated with a constant interaction frequency for each *S. arvensis* individual (proportional interaction strength per *S. arvensis* individual times the mean number of interactions of all *S. arvensis* individuals).

For each resampled network $N\binom{84}{k}$ we calculated common aggregate statistics characterising its structure: one at species level (complementary specialization *d'*) and five at network level (complementary specialization H_2', connectance, nestedness (WNODF), interaction evenness, and QuanBiMo modularity (Dormann *et al.*, 2008)). The QuanBiMo modularity algorithm (Dormann & Strauss, 2014) assigns species to modules based on their similarity in quantitative interactions. To test whether the intraspecific differences in interactions in *S. arvensis* affect the assignment of species into modules, we repeatedly (n = 1000) ran the QuanBiMo algorithm (steps = 1,000,000) on each of the resampled networks containing one *S. arvensis* individual $N\binom{84}{1}$. For each of these resampled networks (n = 84) the plant species' assignment to modules in the n = 1000 QuanBiMo runs was compiled in a presence / absence matrix with plant species as rows and identified modules as columns (number of columns = sum of modules of all 1000 QuanBiMo runs). Based on this matrix we calculated Sørensen distances between plant species (small distances between species pairs thus indicate a common co-occurrence in one module). For all resampled networks containing two or more *S. arvensis* individuals $N\binom{84}{k}$ (n = 1000) we conducted the same calculations. To visualize the plant species' affiliation to modules relative to the other species, we performed a principal coordinate analysis (PCoA). To visualize and quantify the deviation of the module composition (represented as PCoA) based on the networks containing the interactions of one or several $N\binom{84}{k}$ and all *S. arvensis* individuals $\binom{84}{84}$ we compared the deviation of the PCoAs using Procrustes analysis. Procrustes sum of squares *ss* were used as measurement for the deviation in the module composition. All analyses were performed with the statistical software R 3.2.2. (R Core Team, 2013) and the packages *vegan* (Oksanen *et al.*, 2013) and *bipartite* (Dormann *et al.*, 2008). Additional methodological details are available in the electronic supplementary material.

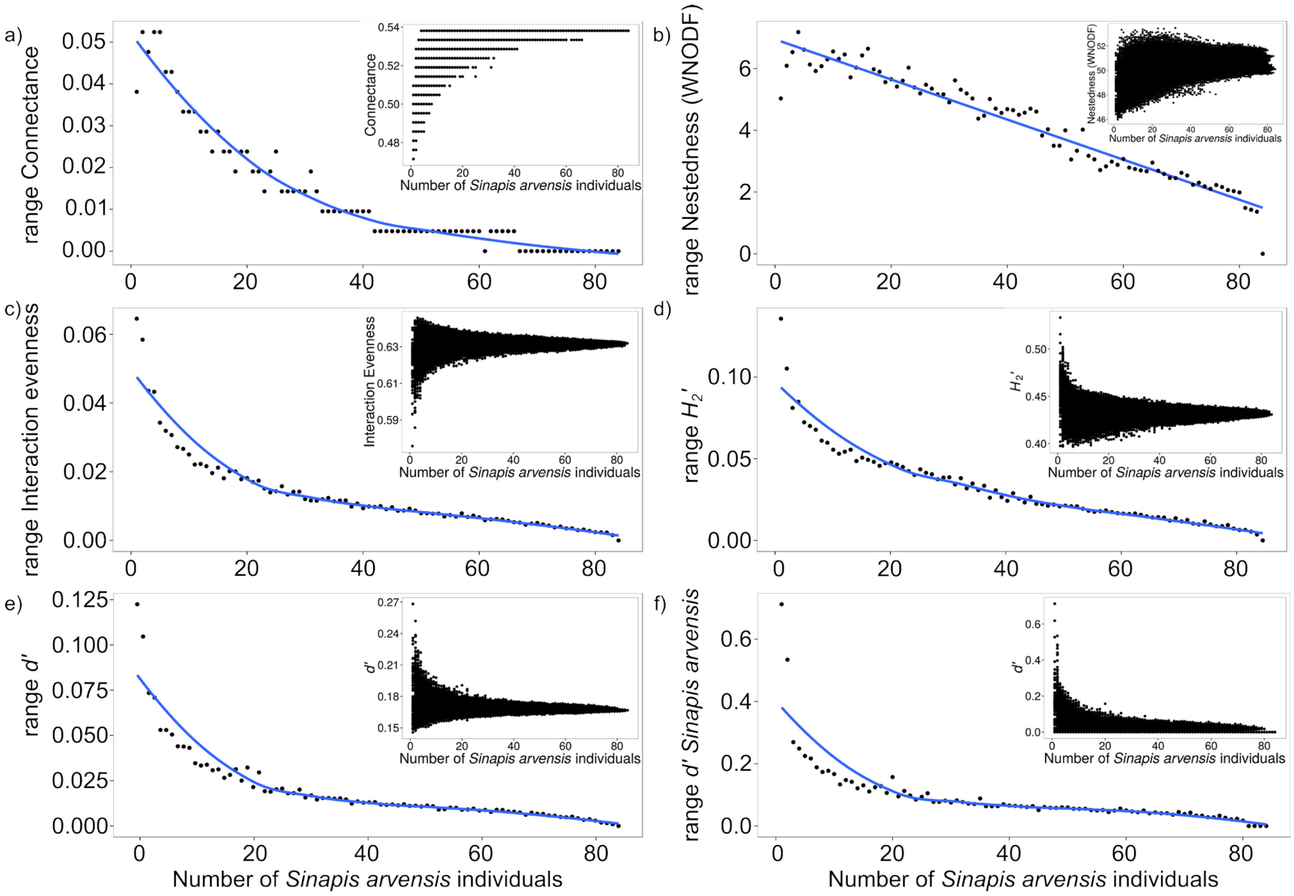

Figure 1. Variation in commonly applied network statistics as a function of the number of *Sinapis arvensis* individuals included in interaction matrix. a – f) Range of values of network indices calculated for all networks *N*$\binom{84}{k}$ with *k* = *S. arvensis* individuals included. Insets visualize the raw values. Nonparametric local polynomial regression curve or linear regression lines (for nestedness) depict the trends in changes in the range of the aggregate network statistics.

RESULTS

In total, we observed 5,411 interactions with a mean interaction frequency per hour per flower of 1.88 ± 0.65 (SE) per plant species including *S. arvensis*. Aggregate statistics were sensitive to the intraspecific variation in interaction patterns in *S. arvensis* (figure 1). Their variation across different networks was largest for the mean complementary specialization *d'*, but relatively small for connectance, nestedness and interaction evenness. Further, different *S. arvens*is or combinations *N*$\binom{84}{k}$induced a considerable variability in the species-specific complementary specialization *d'* of most plant species (networks including one *S. arvensis* individual *N*$\binom{84}{1}$, each: range of *d'* for *S. arvensis*: 0.71; for all other plant species: range between 0 and 0.54;; figure 1f, electronic supplementary material, figure S2).

The modularity analyses clearly showed that plant species that were part of the networks including only one *S. arvensis* individual *N*$\binom{84}{1}$ were assigned in variable combinations to different modules (figure 2). Further, the deviation in module composition in networks with *N*$\binom{84}{1}$ *S. arvensis* individual (measured as Procrustes sum of squares *ss*) was correlated with differences in the interaction patterns, of each *S. arvensis* individual to the species mean (measured as Bray-Curtis distance, Spearman correlation: $S = 68352$, $p = 0.005$, figure 2c). This means that *S. arvensis* individuals that strongly differed in their interactions patterns compared to the species mean also more strongly altered the module composition of the network. Similar results were found for the resampled networks with a constant interaction frequency for *S. arvensis* (see electronic supplementary material).

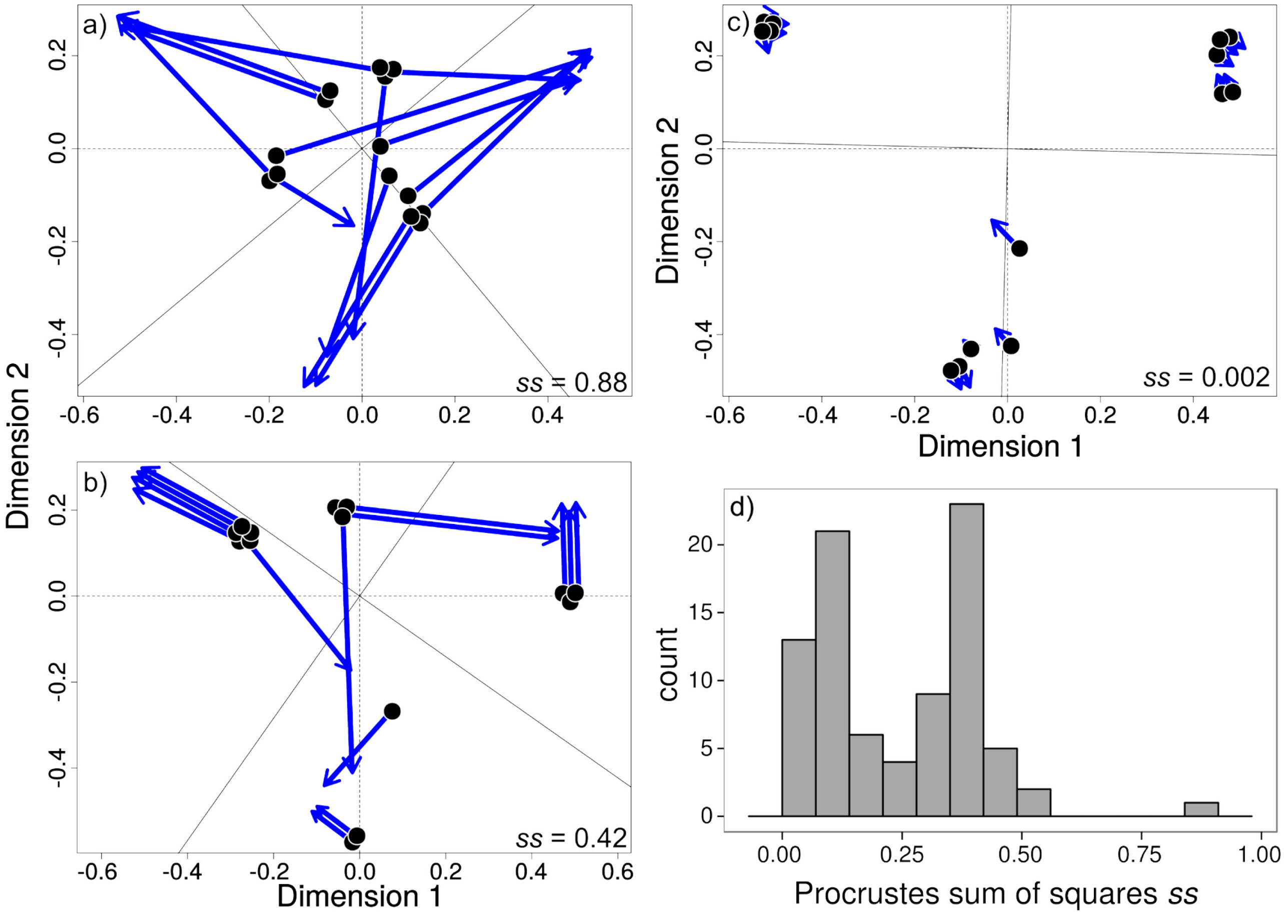

Figure 2. Influence of different *Sinapis arvensis* individuals on module composition. a, b) Procrustes plots comparing principal coordinate analyses (PCoA) based on Sørensen distances of plant species based on module affiliation for networks including only one *S. arvensis* individual $N\binom{84}{1}$ (points) or all individuals $N\binom{84}{84}$ (arrowheads). Procrustes sum of squares *ss* are shown as measurement for the deviation c) Correlation between the deviation in module composition of networks including individuals to network species mean (*ss*-values) and the Bray-Curtis distance (based on interaction patterns) of each individual to the species mean. Inset shows histogram of the *ss*–values from each individual deriving from the species mean $N\binom{84}{84}$.

DISCUSSION

Our simulation study revealed that intraspecific differences in interactions of one plant species in a multi-species network can scale up to community level and influence aggregate statistics that are commonly used to describe network structure. Complementary specialization and module composition were most sensitive towards changes in individual visitation patterns, connectance, nestedness and interaction evenness appeared to be more robust. In a previous study, we showed that the intraspecific differences of *S. arvensis* were time-invariant and driven by differences in functional traits, which suggest that plant individuals occupy specific functional position within communities (Kuppler *et al.*, 2016). This notion is confirmed by the resampling approach where the complementary specialization (*d'*) of *S. arvensis* individuals strongly varied. This shows that different individuals of one species may appear to be generalized or specialized in a community context. Apart from the ecological implication of individual variation, our results show that small quantitative intraspecific differences may alter the ecological interpretation of network descriptors at community level. For example, modularity is used to address the topological role of species within the network and indicate their importance for the integrity of the network structure (Kaiser-Bunbury & Blüthgen, 2015). These roles are defined by the module affiliation and the links to other modules of each species (Olesen *et al.*, 2007). However, different *S. arvensis* individuals altered the module composition of the entire network and consequently the role of a species. Thus, variation in interactions within species may affect modularity to a similar degree as interspecific variation. Likewise other aggregate statistics show a similar pattern, which may be even more pronounced when including intraspecific variation of several plant species. This emphasizes the importance of sufficient and representative sampling (Blüthgen, 2010; Fründ *et al.*, 2015) to get a robust estimate of the species mean and thereby a solid ecological interpretation. Further, the conclusions derived from aggregated networks statistics as indicators for community stability, diversity or impact of environmental change (Hagen et al. 2012, Olesen et al. 2012) should be carefully considered.

In conclusion our study indicated that aggregate networks statistics are sensitive to small quantitative changes in the interactions of one plant species within a multi-species network. This variation may even alter the ecological conclusions derived from network indices emphasize the significance of intraspecific variation in the community and network context. Thus, similar to temporal and spatial variation (Olesen et al. 2012), intraspecific variation is both pitfall and opportunity for a detailed understanding of community structure using network theory.

ACKNOWLEDGEMENTS

We thank the Botanical Garden of the University Salzburg for logistical support and Maren K. Höfers and Lisa Wiesmann for help with fieldwork.The study was supported by the Graduate School “Evolutionary Networks: Organisms, Reactions, Molecules” (E-Norm) of the Heinrich-Heine-University, Düsseldorf, Germany and the Deutsche Forschungsgemeinschaft (DFG JU 2856/2-2).

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Chapter 3 – Dynamic range boxes – A robust non-parametric approach to quantify size and overlap of n-dimensional hypervolumes

This chapter is *under revision* as:

Junker RR, Kuppler J, Bathke A, Schreyer M & Trutschnig W. Dynamic range boxes – A robust non-parametric approach to quantify size and overlap of n-dimensional hypervolumes. ***Methods in Ecology and Evolution***

ABSTRACT

1. *n*-dimensional hypervolumes are commonly applied in ecology and evolutionary studies to describe and compare niches, trait spaces characterizing phenotypes, or the functional composition of communities. Classical ecological surveys, modern analytical tools as well as the establishment of online databases will produce large multivariate datasets, which demands robust statistical tools to analyze and interpret hypervolumes.
2. Existing approaches often have weaknesses, e.g. they rely on multivariate normally or elliptically distributed data, perform poorly in higher dimensions, or their outputs vary arbitrarily with parameter choice. Here we introduce *dynamic range boxes* as a robust non-parametric approach to quantify size and overlap of *n*-dimensional hypervolumes.
3. *Dynamic range boxes* (implemented in the R package *dynRB*) improve the concept of multivariate range boxes by accounting for the distribution of the data within their range, while still no assumptions on the underlying distributions are needed. In addition to calculating the whole *n*-dimensional hypervolume, the package *dynRB* also provides functions for a coordinate-wise analysis and interpretation of the data.
4. The concept of *dynamic range boxes* reliably computes sizes and overlaps of *n*-dimensional hypervolumes, which makes *dynamic range boxes* readily applicable for a broad range of datasets to answer questions related to various disciplines.

INTRODUCTION

Niche theory is one of the most fundamental concepts in ecology. Since the introduction of the term “niche” in an ecological context by Grinnell (1917), the definition of the term and its ecological interpretation has been debated (Whittaker, Levin & Root 1973; Leibold 1995). Commonly, niches are defined as the range of abiotic conditions (e.g., temperature, precipitation, pH) in which a species can survive and reproduce (Leibold 1995; Begon, Harper & Townsend 1998). This definition of the niche as the “habitat” or “requirements” of a species is complemented by the “functional” or “impact” niche definition, which considers the effects of species on their environment, i.e. the functional position of species within a community (Whittaker, Levin & Root 1973; Leibold 1995). The n-dimensional hypervolume proposed by Hutchinson (1957) represents a feasible concept that is broadly applicable for multiple niche definitions, approaches and data sets. It represents a space with n dimensions where each axis represents a factor that is required by an organism. Likewise, traits (i.e., the phenotype) of organisms can be treated as an n-dimensional hypervolume, which is then often referred to as trait space. The possible applications of the n-dimensional hypervolume are well beyond questions on niche sizes and related topics such as competition due to niche overlap (Colwell & Futuyma 1971; Junker et al. 2013), or functional diversity of communities (Villeger, Mason & Mouillot 2008; Villeger, Novack-Gottshall & Mouillot 2011; see Blonder et al. 2014 for examples). For example, in the "omics" era where individuals and species are characterized by a myriad of factors (e.g. by primary and secondary metabolites, (see e.g. Masclaux-Daubresse et al. 2014), approaches that are able to deal with a high number of factors in an n-dimensional space may be particularly useful and a required supplement to ordination approaches where the number of dimensions is reduced.

So far, several approaches quantifying the volume of n-dimensional trait spaces and their overlap have been proposed. However, they often have weaknesses, require multivariate normally distributed data, or are not suited for higher dimensions (Blonder et al. 2014). For broad applicability, an approach to estimate the size and overlap of hypervolumes should a) be independent of the distribution of the data (e.g., no multivariate normally or elliptically distributed data are required), b) consider the abundance and distribution of observed values, c) be robust against outliers, d) yield reproducible results, which do not change arbitrarily when tuning parameters for the procedure are chosen differently, e) be applicable for arbitrary dimensions and return robust results independent of dimensionality, f) return the n-dimensional size and overlap of the hypervolumes, g) provide information on the impact of individual dimensions on overall size and overlap, h) return directional values for the overlap of species pairs (or pairs of other units) accounting for the asymmetry in the portion of shared n-dimensional hypervolumes, and i) account for correlations between values in different dimensions and / or provide an option to inspect the data for correlations prior to the calculation of the sizes and overlap of hypervolumes.

The usage of resources, the ability to survive and reproduce as a function of abiotic factors, or the phenotype of a species is usually delimited by the endpoints of the range with a theoretically continuous distribution of values in between. However, the density of values within the range can deviate from a uniform or normal distribution. That is, skewed, or bimodal / multimodal distributions are possible and commonly observed in biological datasets. Furthermore, gaps in univariate or holes in multivariate datasets may often constitute sampling artifacts. Thus, any approach to quantify the size and overlap of hypervolumes should make no assumptions on the distribution of data, while still acknowledging that some values within the full range are more representative for a species' requirements, function or phenotype than others. Multivariate range boxes (Hutchinson 1957), convex hulls (Cornwell, Schwilk & Ackerly 2006; Villeger, Mason & Mouillot 2008) and the multivariate kernel density estimation (Blonder et al. 2014) represent two extremes where the former two fully neglect the distribution of the data within the range, while the latter may overstate the biological meaning of holes and gaps in the data. Another method to quantify the size and overlap of niches, niche regions as recently introduced by Swanson et al. (2015), considers the distribution of the data and does not overrate the meaning of gaps, but it requires a multivariate normal distribution. Alternatively, distance-based methods to quantify the functional diversity of communities from multiple traits are available (Laliberte & Legendre 2010; Junker et al. 2013). These methods have been shown to perform well but do not allow quantifying the overlap of two trait-spaces.

Here we introduce dynamic range boxes (implemented in the R package dynRB, see http://cran.r-project.org/web/packages/dynRB/index.html), a novel non-parametric approach to quantify size and overlap of n-dimensional hypervolumes and individual dimensions that meets all the criteria discussed above and is thus broadly applicable in ecology and beyond.

METHODS

Our approach improves the concept of multivariate range boxes that envelop all data per dimension within the minimum and the maximum value (Hutchinson 1957). This conservative approach is highly susceptible to outliers and does not take into account the distribution of the data, often leading to an overestimation of the actual niche sizes and the overlap of trait spaces. In order to avoid these disadvantages we introduce *dynamic range boxes* (Fig. 1). Note that contrary to methods for dimensionality reduction such as principal components *dynamic range boxes* – by default – do not correct for correlations between traits. Correlations between trait-values, which are often observed e.g. in morphological data sets, may lead to an overestimation of niche sizes and thus overlaps. Therefore, we strongly recommend inspecting the data for co-varying traits prior to the calculation of niche sizes and overlaps (which is an implemented option in the R package introduced here). In cases where strong correlations between traits are observed, we either recommend to remove a selection of highly correlated traits from the data set or to replace all the measured dimensions with principle components (which is an implemented option in the R package introduced here, too).

Sketch of the method

Roughly speaking, a number of m nested, standardized range boxes are calculated for each species (or other units) under consideration, each box containing a decreasing proportion (1-α_i) of values per dimension n, starting with the interval from 0-quantile (=minimum) to 1-quantile (=maximum) in every dimension, and shrinking in m steps to a degenerated interval only containing the medians (Fig. 1c). Letting $\boldsymbol{R}_n^{\boldsymbol{A}}(\alpha_i)$ and $\boldsymbol{R}_n^{\boldsymbol{B}}(\alpha_i)$ denote the i-th range box for the first and the second species (*A* and *B*) we then calculate their volume and the portion of the second species' range box that is covered by that of the first species, and vice versa (for every α_i). In order to compensate for boxes shrinking too rapidly (which would result in significant underestimations), niche size is corrected (i.e. divided by the volume 1-α of a box formed by the corresponding intervals for the uniform distribution see equation (2) below for a concise definition). Notice that the correction is not needed when calculating the niche overlap between two species since in this case both the numerator and the denominator are shrinking. Calculating the mean of the resulting quantities finally yields what we will refer to in the sequel as niche volume *vol(A)* and overlap *port(A, B)* (of the first in the second species and vice versa). Only working with quantiles yields one the main advantages of the proposed approach, namely that no assumptions whatsoever on the underlying distributions are needed. Additionally, the approach is quite robust, that is, it is not heavily affected by outliers (Fig. 1, see Supporting Information 1).

Mathematical description

Step I: Suppose that $\boldsymbol{A} = (\boldsymbol{a_i})_{i=1}^{n}$ and $\boldsymbol{B} = (\boldsymbol{b_i})_{i=1}^{n}$ are matrices with n column vectors containing trait data for species A and B. For each dimension $i \in \{1, \ldots, n\}$ the minimum and maximum, i.e. $\min\{\min(\boldsymbol{a_i}), \min(\boldsymbol{b_i})\}$and $\max\{\max(\boldsymbol{a_i}), \max(\boldsymbol{b_i})\}$, are calculated and, based on these values, the matrices $\boldsymbol{A} = (\boldsymbol{a_i})_{i=1}^{n}$ and $\boldsymbol{B} = (\boldsymbol{b_i})_{i=1}^{n}$ are linearly transformed (standardized) to the n-dimensional unit box $[0,1]^n$, resulting in two matrices $\hat{\boldsymbol{A}} = (\hat{\boldsymbol{a}}_{\boldsymbol{i}})_{i=1}^{n}$ and $\hat{\boldsymbol{B}} = (\hat{\boldsymbol{b}}_{\boldsymbol{i}})_{i=1}^{n}$. If more than two species are involved in the comparison, minimum and maximum are taken over *all* species.

Step II: To simplify notation, set $\boldsymbol{X} = \hat{\boldsymbol{A}}$. By definition, the α-quantile of $\boldsymbol{X} = (\boldsymbol{x_i})_{i=1}^{n}$ is a vector $\boldsymbol{F}_{\boldsymbol{X}}^{-}(\alpha) = \left(F_{\boldsymbol{x_i}}^{-}\right)_{i=1}^{n}$, where $F_{\boldsymbol{x_i}}^{-}(\alpha)$ denotes the α-quantile of the vector $\boldsymbol{x_i}$ for $i = 1, ..., n$ (for details and mathematical background see Klenke 2007; van der Vaart 2007). For each dimension $i = 1, ..., n$ and $\alpha \in [0,1]$ the α-range interval $I_i(\alpha)$ is given by

$$I_i(\alpha) := \left[F_{\boldsymbol{x_i}}^{-}\left(\frac{1-(1-\alpha)^{\frac{1}{n}}}{2}\right), F_{\boldsymbol{x_i}}^{-}\left(1-\frac{1-(1-\alpha)^{\frac{1}{n}}}{2}\right)\right]. \qquad (1)$$

The n-dimensional range box $\boldsymbol{R}_n^{\boldsymbol{A}}(\alpha)$ of level α is then defined as the Cartesian product of the intervals $I_1(\alpha), \ldots, I_n(\alpha)$, i.e.

$$\boldsymbol{R}_n^{\boldsymbol{A}}(\alpha) := \times_{i=1}^{d} I_i(\alpha).$$

Proceeding analogously for $\hat{\boldsymbol{B}}$ yields the box $\boldsymbol{R}_n^{\boldsymbol{B}}(\alpha)$. Notice that the intervals in each dimension have been chosen this way in order to assure that (under the independence assumption) the range boxes $\boldsymbol{R}_n^{\boldsymbol{A}}(\alpha)$ and $\boldsymbol{R}_n^{\boldsymbol{B}}(\alpha)$ cover $100(1-\alpha)$% of the data. Note that it is mathematically well-established (van der Vaart 2007) that the empirical quantile function converges weakly to the true quantile function from which, using dominated convergence (Klenke 2007), one directly gets consistency of niche overlap, i.e. empirical overlap converges to the true overlap with probability 1.

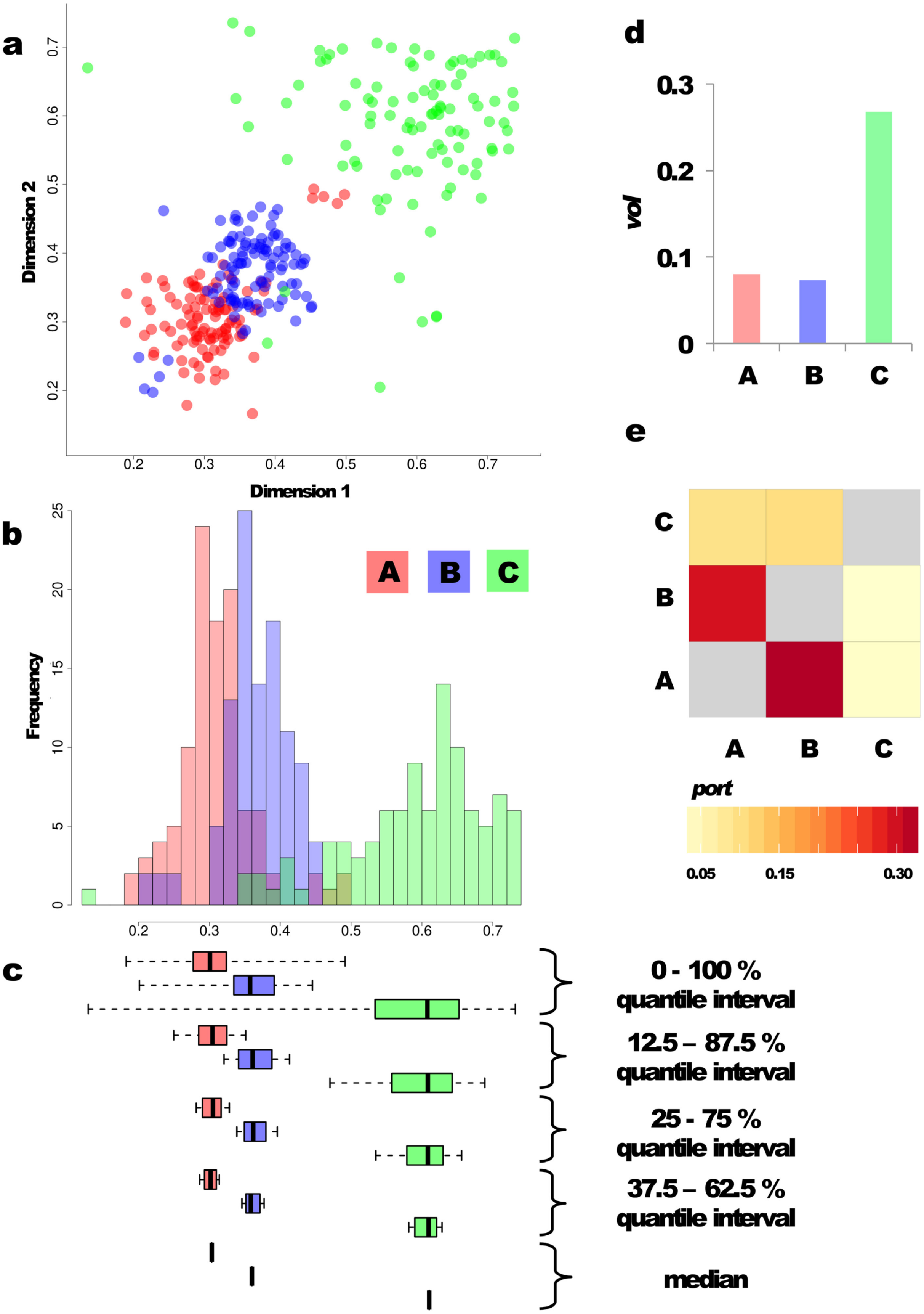

Fig. 1 Graphical overview of the method to calculate the size *vol(A)* and overlap *port(A, B)* of dynamic range boxes (a-c), as well as results of the calculation (d and e) for a data set. a) 2-dimensional trait spaces of A, B and C. b) Marginal histogram of the first dimension of the data for A, B and C. c) Boxplots of dimension 1 of the data for A, B and C for different quantile ranges α. Each boxplot depicts median, 25 – 75 %- quantile interval and range (the latter being the equivalent to the classical range box) for the respective subset.

Boxplots representing the 0 – 100 % quantile interval of original data show size and overlap as represented in classical range boxes. The subsequent quantile intervals of original data show size and overlap for subsets of original data, thereby acknowledging the distribution of the data. Thus, outliers are not overrepresented in the calculation of size *vol(A)* and overlap *port(A, B)* of dynamic range boxes. d) Sizes *vol(A)* of trait spaces of A, B and C as returned by the function `dynRB_VPa(data)`. e) Overlaps *port(A, B)*, *port(B, A)*, *port(A, C)*, *port(C, A)*, *port(B, C)*, *port(C, B)* of trait spaces of A, B and C as returned by the function `dynRB_VPa(data)`. Note that e.g. *port(A, B),* which is A in B or the portion of the trait space of B that is covered by A (first column, second row in the heatmap), is not the same as *port(B, A)* because overlaps are, by construction, asymmetric.

Step III: In the following $\boldsymbol{U} = (\boldsymbol{u_i})_{i=1}^n$ is a matrix with n column vectors containing the trait data for all species. Letting V denote the n-dimensional volume (i.e. the product of the side lengths of the boxes) our quantities of interest are the average portion of the trait space of B that is covered by A, abbreviated A in B, and the average portion of B in A. These quantities are defined as

$$port(A,B) := \int_{[0,1]} \frac{V(\boldsymbol{R_n^A}(\alpha) \cap \boldsymbol{R_n^B}(\alpha))}{V(\boldsymbol{R_n^B}(\alpha))} d\alpha, \quad port(B,A) := \int_{[0,1]} \frac{V(\boldsymbol{R_n^B}(\alpha) \cap \boldsymbol{R_n^A}(\alpha))}{V(\boldsymbol{R_n^A}(\alpha))} d\alpha,$$

The niche volume of A is defined as the average portion of A in the union distribution U on $[0,1]^n$, i.e. it is given by

$$vol(A) := port(A,U) = \int_{[0,1]} \min\left\{ \frac{V(\boldsymbol{R_n^A}(\alpha))}{1-\alpha}, 1 \right\} d\alpha. \tag{2}$$

Thereby the minimum in the integrand makes sure that the quotient can not exceed one. Setting $\alpha_i = \frac{i-1}{m}$ for every $i = 1, ..., m$, these integrals can both be well approximated using the trapezoidal rule.

The package *dynRB* also offers two alternatives to the classical volume V (i.e. the product of the side lengths of the boxes) as aggregation methods, namely mean and geometric mean of the side lengths.

Package dynRB

In order to allow for cross-platform application of *dynamic range boxes*, we have written an R-package called *dynRB,* which is available on CRAN, see http://cran.r-project.org/web/packages/dynRB/index.html. Given datasets of species $A_1, A_2, \ldots, A_k$, the package provides functions to calculate niche volumes *vol(A₁), vol(A₂),…, vol(A_k)*, as well as pairwise overlaps of niche volumes between species $port(A_1, A_2), port(A_1, A_3), \ldots, port(A_1, A_k), \ldots, port(A_k, A_1), \ldots port(A_k, A_{k-1})$.

Additionally, the package contains three aggregation functions allowing for different ways to summarize/aggregate the coordinate-wise (corrected and non-corrected) volumes (interval lengths) and portions: The product $\mathrm{agg_p}\colon \mathbb{R}^n \to \mathbb{R}$, defined by $\mathrm{agg_p}((x_i)_{i=1}^n) = \Pi_{i=1}^n x_i$, the mean $\mathrm{agg_m}\colon \mathbb{R}^n \to \mathbb{R}$, given by $\mathrm{agg_m}((x_i)_{i=1}^n) = \frac{1}{n}\sum_{i=1}^n x_i$, and the geometric mean $\mathrm{agg_g}\colon \mathbb{R}^n \to \mathbb{R}$, defined as $\mathrm{agg_g}((x_i)_{i=1}^n) = (\Pi_{i=1}^n x_i)^{1/n}$. The package uses all three aggregation methods whenever possible, so no additional execution is needed. All functions allow choosing the number m of α-values – for reliable results $m \geq 201$ should be chosen (Supporting Information 1), default is set to $m = 201$. For more details on the functions we refer to Table 1, to the functions themselves, as well as to the help files of the R-package, which also provide examples illustrating how to apply the functions. Fig. 1 gives a graphical overview of the methods to calculate size *vol(A)* and overlap *port(A, B)* of dynamic range boxes, as well as the results using datasets generated for illustration.

Tab. 1 Overview of the functions provided by the R package *dynRB*. Examples for the output of the three functions can be obtained by running the functions with *data(finch2)*, which is included in the package. Data are a data frame, where the first column is a character vector and the other two or more columns are numeric vectors.

Functions and default parameters	**Description**
`r <- dynRB_VPa(data, steps = 201, correlogram = FALSE, row_col = c(2, 2), pca.corr = FALSE, var.thres = 0.9)` `r$result`	Primary function of the package. Returns a data frame containing the niche overlap *port*(A, B) for each pair of objects and dynamic range box sizes *vol(A) for each object* aggregated over all dimensions *n* by all three methods (i.e. product, mean, geometric mean).
`r <- dynRB_Pn(data, steps = 201, correlogram = FALSE, row_col = c(2, 2))`	Function returns pairwise overlaps *port*(A, B) for each pair of objects for each dimension *n* individually.
`r <- dynRB_Vn(data, steps = 201, correlogram = FALSE, row_col = c(2, 2))`	Function returns dynamic range box sizes *vol(A) for each object* for each dimension *n* individually.

Prior to the calculation of size *vol(A)* and overlap *port(A, B)* of dynamic range boxes, data sets should carefully be inspected for correlations between individual dimensions, which is aided by the option to plot a correlogram within the main function of the R package *dynRB*. In cases where two or more dimensions are correlated, we recommend to remove one dimension of the correlated pair of dimensions and to compare the results between the full and the reduced data set. Alternative, we also provide an option in the main function of the R package *dynRB* to replace the original dimensions with principle components, which will be used as dimensions in the subsequent calculation. The number of principle components (PCs) included in the subsequent calculation can be adjusted by defining the minimum of variance explained by the PCs (default = 0.9, a minimum of two PCs is included in any case). Note that dynamic range boxes were designed to be independent of the distribution of the data, which is obviously not true if PCs are used to substitute the original dimensions. If this option is chosen, the same requirements on the data as in any PC analysis (PCA) apply. PCA requires multivariate normally or elliptically distributed data. Zero-inflated datasets, outliers or a highly skewed distribution may cause misleading results (Legendre 2012).

Evaluation of dynRB and comparison to other methods

To evaluate the robustness of the results obtained from the *dynamic range box* approach, we quantified the overlap of two trait spaces as a function of increasing sampling effort ranging from three observations per trait space to the full population of observations. We also evaluated the effect of the number *m* of dynamic range boxes (steps) on the sizes and overlap of trait spaces. Detailed description of the methods and the results of simulations are given in Supporting Information 1. To compare niche-size *vol(A)* with a distance-based method, we compared *vol(A)* with functional dispersion *FDis*, which is the mean distance of each sample in a multidimensional trait space to the centroid of the whole population of samples (Laliberte & Legendre 2010). Both *vol(A)* and *FDis* should increase with increasing standard deviation SD in each dimension. Note that *FDis* does not allow quantifying the overlap of two trait spaces. We generated datasets containing two trait-spaces defined by two dimensions, each. The data defining the trait-spaces had normal distribution (function *rnorm* implemented in R). Each trait-space contained 100 observations. Trait space A had a mean of 100, trait space B a mean of 200 in each dimension. Normal distributions were generated with increasing standard deviations SD ranging from 0.1 to 100 (SD = 0.1, 0.2, …1, 2,…10, 20, …, 100). Per SD, 10 trait spaces A and B were generated, resulting in a total number of 30 SD times 10 replicates = 300 trait spaces A and B. For each trait space, we calculated *vol(A)* and *FDis* of trait space A. To calculate *FDis*, we built a matrix containing the standardized distances [distance = (distance – min(distance)) / (max(distance) – min(distance))] between all samples of trait spaces A and B and subsequently used the distances between the samples of trait space A. Finally, to evaluate whether dynamic range boxes perform well independent of the number of dimensions *n* and to compare these results with other approaches, we quantified overlap *port(A, B)* of trait spaces characterized by two to ten dimensions *n* (for each *n* we generated 100 datasets). For each dimension *n* of trait-spaces A and B we randomly sampled *m* = 2000 observations from different distributions (uniform or normal, with a defined overlap (= 1, 0.66, 0.33, or 0) allowing to calculate the expected overlap of the *n*-dimensional trait-spaces A and B (overlap = o^n, with *o* being the overlap per dimension and *n* the number of dimensions). Expected values of overlap were compared to the overlap quantified with the R packages *dynRB* (`pca.corr=FALSE` and `pca.corr=TRUE`), *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al.* 2015). In all packages, we used default parameters to calculate overlap. To visualize deviations of calculated overlaps using the three R packages from the expected values, we divided the results of the R packages by the expected value (i.e. result / expectation = 1 means that the quantified overlap matches the respective expectation). For datasets with an expected overlap of zero we directly plotted the results.

Testing dynamic range boxes *on ecological data*

To demonstrate the applicability of dynamic range boxes for ecological data, we used existing data sets on trait spaces and quantified their sizes and overlaps. We used a data set on morphological measurements of Darwin finches *Geospiza* sp., which originates from Snodgrass and Heller (1904) and was extracted from the R package *hypervolume* (Blonder *et al.* 2014). The dataset comprises quantitative measurements of nine traits characterizing five (sub-) species of finches, each trait was measured at least in 10 individuals per species.

As a second example, we used our own data on floral scent emissions by *Sinapis arvensis* (Brassicaceae) individuals (Kuppler *et al.* 2016). Ninety-seven individuals from two populations (Southern Germany and England) were cultivated in a common garden, half of the individuals per population ($24 \leq n \geq 22$) were treated with a slow release fertilizer (ten pellets Osmocote Exact Standard 3-4M (N:P:K:Mg 16:9:12:2, Osmocote, South Africa). The plants were arranged in a full-factorial pseudo-randomised block design within an area of 11 x 5 m in the Botanical Garden of the University Salzburg, Austria. For floral scent analysis, one inflorescence per plant individual was enclosed within a polyester oven bag (Toppits®, Germany) for 10 min and the emitted volatiles were then trapped on 1.5 mg Tenax (mesh 60– 80; Supelco, Bellefonte, PA, USA) and 1.5 mg Carbotrap B (mesh 20– 40, Supelco) in a quartz vial (Varian Inc.; length 15 mm, inner diameter 2 mm) for 2 min using a membrane pump (G12/01 EB, ASF Rietschle-Thomas, Puchheim, Germany) with a flow rate of 200 ml min^{-1}. All samples were collected between 8:00 and 12:00 h. Scent samples were analysed using an automatic thermal desorption system (TD-20, Shimadzu, Japan) coupled with a GC–MS (model QP2010 Ultra EI, Shimadzu, Japan). All scent compounds were standardized to emission rate per hour per flower (ng/h/flower). For a detailed description of the methods see Kuppler *et al*. (2016). For both datasets we used *dynamic range boxes* to calculate the overlap *port(A, B)* (and size *vol(A)* in the case of floral scent bouquets) of the *n*-dimensional hypervolumes. Overlaps *port(A, B)* and sizes *vol(A)* were calculate with the default option `dynRB_VPa(data, pca.corr=FALSE)` and the option correcting for correlations between dimensions `dynRB_VPa(data, pca.corr=TRUE)`.

All statistical analyses were performed using R (R Development Core Team 2014) and the package *dynRB*.

RESULTS AND DISCUSSION

Evaluation of dynRB and comparison to other methods

Overlaps *port(A, B)* calculated using subsets of a dataset with an increasing number of randomly drawn observations quickly converged to *port(A, B)* based on all observations (see Supporting information 1 for details). Note that *dynamic range boxes* calculates the realized niche size *vol(A)* and niche overlap *port(A, B)* based on the data measured and does not estimate distributions based on the measured data. The choice of the number *m* of dynamic range boxes *α* (steps) influences the result but only at very low numbers of steps ($m < 50$). Step numbers *m* above 100 mostly resulted in stable results (see Supporting information 1 for details). Therefore, we recommend using $m > 100$ steps and set the default to $m = 201$, which is a good compromise between receiving a robust result while keeping computing time relatively short.

Simulated trait spaces characterized by two dimensions containing normally distributed observations with mean = 100 and increasing standard deviation SD increased in niche size *vol(A)* and functional dispersion *FDis* proportionally to the standard deviation SD (Pearson's product-moment correlation: *vol(A)*: $t_{298} = 58.4$, $p < 0.001$, $r^2 = 0.92$; FDis = $t_{298} = 42.8$, $p < 0.001$, $r^2 = 0.86$, Fig. 2). Niche size *vol(A)* was well predicted by functional dispersion *FDis* (exponential regression model: $p < 0.001$, $r^2 = 0.96$, Fig. 2).

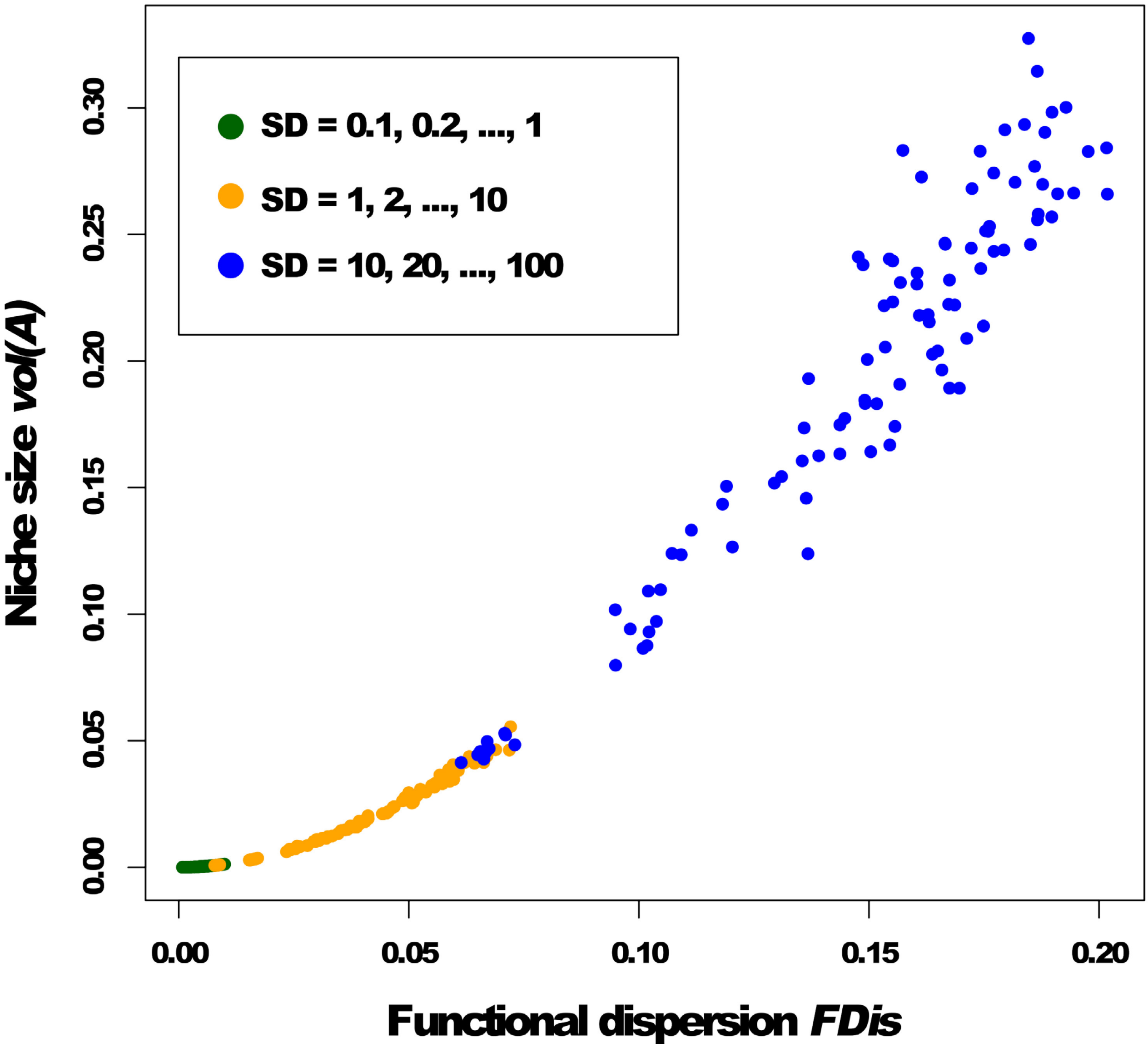

Fig. 2 Comparison of niche size *vol(A)* calculated using the R package *dynRB* with functional dispersion *FDis* using the R package *FD* (Laliberte & Legendre 2010) of the same simulated trait space. Simulated trait spaces were characterized by two dimensions containing normally distributed observations with increasing standard deviation SD (color-coded in the figure).

Overlap *port(A, B)* as returned by the R package *dynRB* was close to (often identical with) the expected values and the magnitude of deviation was largely independent on the number of dimensions *n* characterizing the trait-spaces, demonstrating the robustness of *dynamic range boxes* (Fig. 3, Tab. S2-1). However, note the increase in deviation in higher dimensions in normally distributed data. Overlaps calculated with *hypervolume* (Blonder *et al.* 2014) and *nicheROVER*

(Swanson *et al.* 2015) were highly sensitive to the number of dimensions *n* (Fig. 3, Tab. S2-1) and often strongly deviated from the expected values, particularly in higher dimensions (Fig. 3, Tab. S2-1). Also note that *hypervolume* indicates overlaps significantly smaller than 1 in cases where the distributions of two hypervolumes were strongly overlapping (i.e. overlap = 1 per definition, Fig. 3, Tab. S2-1). Likewise, this approach indicated overlaps above 0 although hypervolumes did not overlap (i.e. overlap = 0 per definition, Tab. S2-1). Deviations of dynRB using the correction for correlated dimensions `dynRB_VPa(data, pca.corr=TRUE)` were usually larger than results of the default option `dynRB_VPa(data, pca.corr=FALSE)` urging for a careful evaluation whether correction should be applied . The data generated to test for the performance of the approaches clearly show no correlation between dimensions (Fig. S2-1) suggesting that the option `dynRB_VPa(data, pca.corr=TRUE)` should be used only if the assumption of independence is violated.

Being able to choose parameters (like bandwidth in density estimation required in the R package *hypervolume*, Blonder *et al.* 2014) may prove useful in many situations where additional expert knowledge may reveal further information – nevertheless any applicable approach should offer a reasonable default parameter setting (parameters chosen by the software taking the current dataset into account) that allows standard users (not willing to study all details) to get reliable results without investing too much time. For the usage of dynamic range boxes, no parameters need to be chosen to yield reliable results. The only parameter that can be chosen is the number *m* of dynamic range boxes *α* (steps) to calculate sizes *vol(A)* and overlap *port(A, B)* of trait-spaces, and our simulation (see Supporting information 1) demonstrated that results are robust with *m* > 100 (default is set to *m* = 201). The results of the simulations thus demonstrate that *dynamic range boxes* yield comparable results as distance-based methods (Fig. 2) and as mathematically expected (Fig. 3, supporting information 2), is independent on the distribution of the data (Supporting information 1) and outperforms other approaches designed to calculate the niche size and overlap in *n*-dimensional hypervolumes (Fig. 3, supporting information 2).

Based on the results of the simulations (see also Supporting information 1), we evaluated whether *dynamic range boxes*, *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al.* 2015) meet the criteria of well performing approaches to calculate the size and the overlap of *n*-dimensional hypervolumes defined in the introduction (Tab. 2). Whereas *dynamic range boxes* meet all the criteria we defined (a correction for correlation between dimensions is optional), the other two approaches revealed weaknesses in some of the criteria. Thus, *dynamic range boxes* is readily applicable for a broad range of datasets to answer questions related to various disciplines.

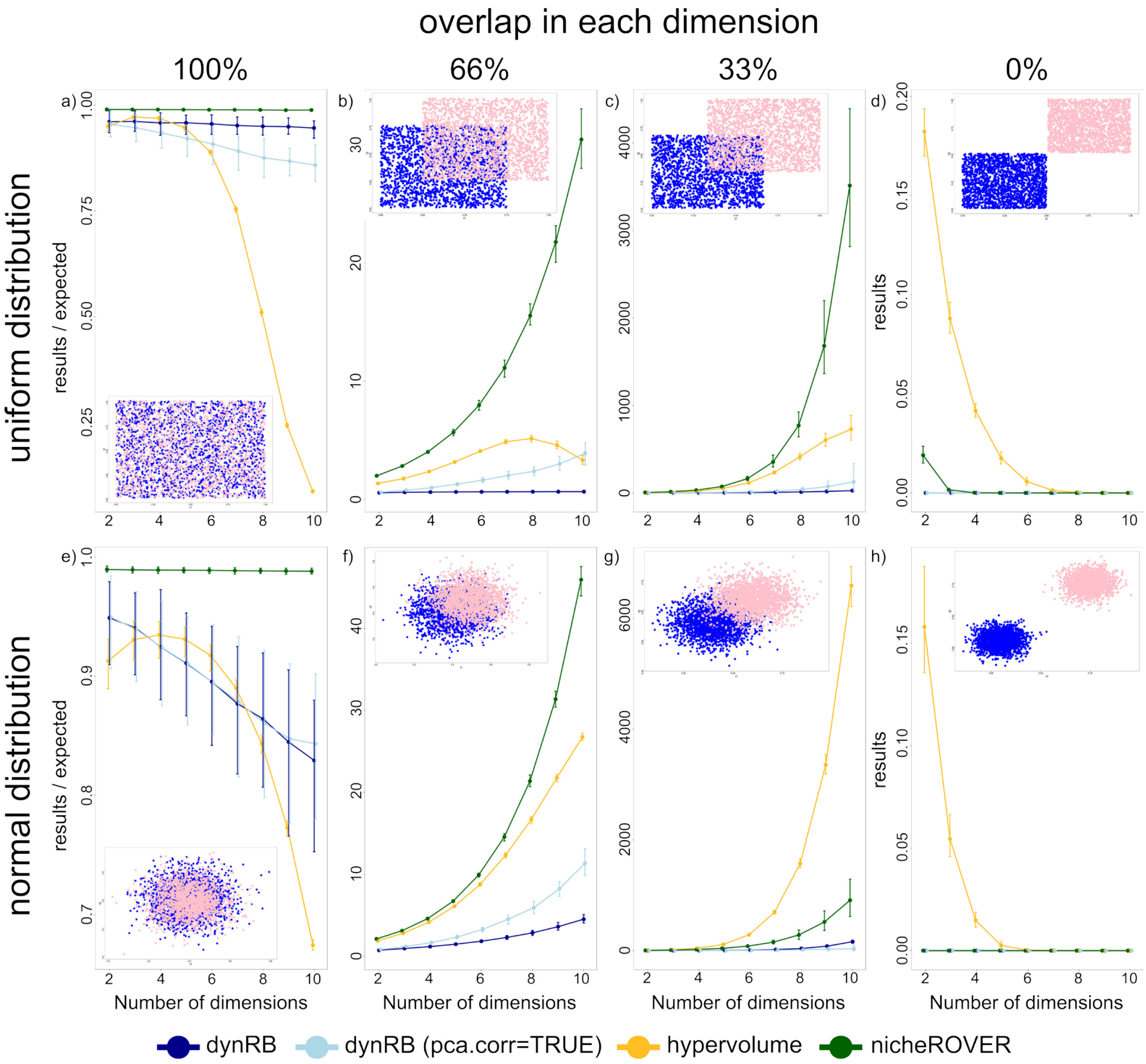

Fig. 3 Overlap of trait-spaces characterized by increasing number of dimensions quantified with the R packages *dynRB* (`pca.corr=FALSE` and `pca.corr=TRUE`), *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al.* 2015). Graphs visualize the deviations of the calculated overlaps (results of the four approaches) from the expected values calculated from the overlap per dimension. Result / expectation = 1 means that overlaps quantified by one of the four approaches match the expectation, i.e. values equal or close to 1 indicate a good performance of the approaches. In cases were the expected values are zero (d and h), original values are displays (expectation = 0). Data in examples a-d have a uniform distribution, e-h have a normal distribution. Insets in panels visualize the distribution of data in two dimensions (dimensions three to ten have the same distributions). Expected values and results are shown in Tab. S2-1.

Testing dynamic range boxes *on ecological data*

We tested *dynRB* on data sets on the morphological trait space of Darwin finches *Geospiza* ssp. and the chemical trait space of *Sinapis arvensis* flowers and demonstrated the applicability of our novel approach. Only two subspecies of *G. fortis* overlapped in a small fraction of their nine-dimensional hypervolumes (aggregation = “product” and “gmean”), whereas the other species’ trait spaces did not overlap (Fig. 4). Dimension-wise overlap revealed that traits characterizing the morphology of the beaks on average overlapped to a smaller portion than traits characterizing the birds' morphology apart from the beak (Fig. 4, Wilcoxon rank sum test comparing all *port(A, B)* in beak traits with those in body traits: $W = 2015$, $p < 0.001$), which is in concordance with the assumption that mainly different beak morphologies allow the finches to exploit different resources and thus avoid interspecific competition (Begon, Harper & Townsend 1998), whereas selection on body morphology may be relaxed.

Tab. 2 Requirements that we believe are necessary to reliably extract the size and overlap of *n*-dimensional hypervolumes met by the approaches *dynamic range boxes*, *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al.* 2015).

	dynamic range boxes	**hypervolume** Blonder *et al.* (2014)	**nicheROVER** Swanson *et al*. (2015)
a) can be used independent on the distribution of the data	✓	✓	✗
b) considers the abundance and distribution of observed values	✓	✓	✓
c) robust against outliers	✓	✓	✗
d) yields robust results, i.e. parameter choice does not affect the ecologcial interpretation of the results	✓	✗[1]	✓
e) applicable for arbitrary dimensions	✓[2]	✓[3]	✓[3]
f) returns the *n*-dimensional size and overlap of the hypervolumes	✓	✓	✓
g) provides information on the impact of individual dimensions on overall size and overlap	✓	✗	✗
h) returns directional values for the overlap of species pairs (or pairs of other units) accounting for the asymmetry in the portion of shared *n*-dimensional hypervolumes	✓	✓	✓

[1]) no clear recommendation is given for the choice of bandwidth, which strongly influences results.

[2]) deviations of the values calculated using *dynRB* from the expected values in Fig. 3 a und e result from slightly different ranges of the values of each group in each dimension despite the underlying theoretical distributions having the same mean and standard deviation (and hence coinciding in case of normality). The small portion of the empirically observed ranges that do not overlap in each dimension multiply with increasing dimensionality, which is visible in the data.

[3]) approaches can deal with an arbitrary number of dimensions but results inconsistently vary with number of dimensions (Fig. 3, Tab. S2-1).

Floral scent bouquets of *Sinapis arvensis* individuals originating from two populations and that were either supplemented with fertilizer or not were highly similar in the qualitative composition, i.e. we found the same compounds in all of the four groups (compare to Kuppler *et al.*

2016). However, the sizes of trait-spaces occupied by the groups showed remarkable differences (Fig. 5), which is a proxy for the variability in the quantitative scent emission across plant individuals within the groups. The data support the notion that species or groups with a larger expansion in the n-dimensional trait-space also have a larger potential to overlap other species (Fig. 5). *Dynamic range boxes* may thus also be a useful tool in studies investigating the metabolome of species, mutants or ecotypes.

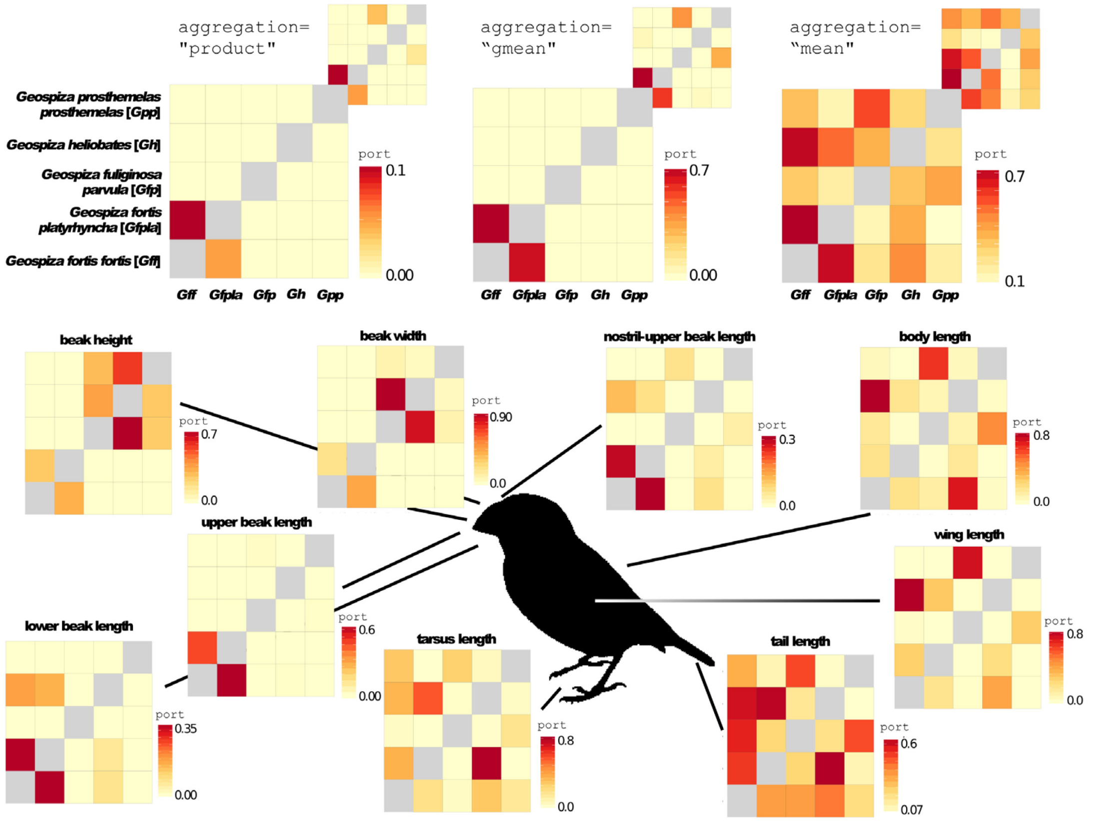

Fig. 4 Heatmaps visualizing the overlap *port(A, B)* of the nine-dimensional hypervolumes as well as of individual dimensions defined by the characteristics of nine morphological traits of Darwin finches *Geospiza ssp.* Data are extracted from the R package *hypervolume* (Blonder *et al.* 2014) and are included in the package *dynRB* as *data(finch)*. Heatmaps in the upper row show overlaps *port(A, B)* of nine-dimensional hypervolumes aggregated as product, geometric mean and mean as returned by function `dynRB_VPa(data)`. Small heatmaps in the upper right corner visualize overlaps *port(A, B)* of nine-dimensional hypervolumes corrected for correlations between dimensions using principle components and aggregated as "product", "geometric mean" and "mean" as returned by function `dynRB_VPa(data, pca.corr=TRUE)`. Scales of heatmaps showing overlaps port(A, B) corrected for correlations between dimensions are the same as for aggregation methods "geometric mean" and "mean", the scale for aggregation method "product" ranges from 0 to 0.4. The nine lower heatmaps show coordinate-wise overlaps *port(A, B)* of individual dimensions as returned by function `dynRB_Pn(data)`. Note that e.g. *port(Gff, Gfpla),* which is *Gff* in *Gfpla* or the portion of the trait space of *Gfpla* that is overlapped by *Gff* (first column, fourth row in the heatmap), is not the same as *port(Gfpla, Gff)* because overlaps are asymmetric. Also note different scales for each heatmap.

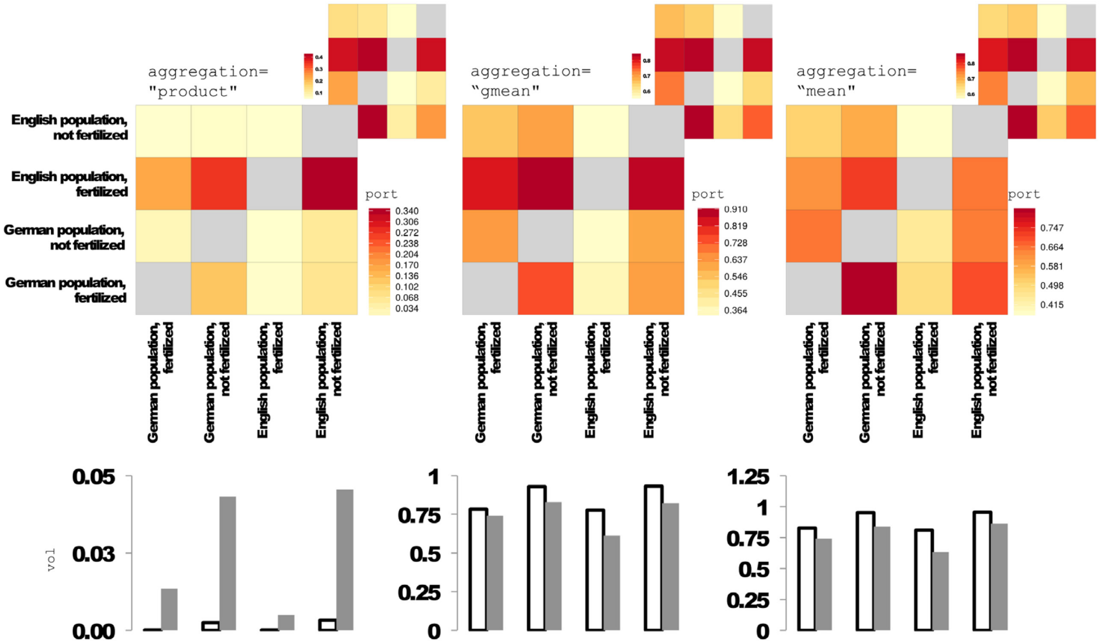

Fig. 5 Heatmaps visualizing the overlap port(A, B) of the n-dimensional hypervolumes defined by the characteristics of floral volatiles emitted by Sinapis arvensis. Heatmaps show overlaps port(A, B) aggregated as product, geometric mean and mean as returned by function dynRB_VPa(data). Note different scales for each heatmap. Small heatmaps in the upper right corner visualize overlaps port(A, B) of n-dimensional hypervolumes corrected for correlations between dimensions using principle components and aggregated as “product”, “geometric mean” and “mean” as returned by function dynRB_VPa(data, pca.corr=TRUE). White barplots show sizes vol(A) of n-dimensional hypervolumes aggregated as product, geometric mean and mean as returned by function dynRB_VPa(data), black barplots show sizes vol(A) as returned by function dynRB_VPa(data, pca.corr=TRUE).

Different aggregation methods facilitated a more detailed interpretation of the patterns. The aggregation method “product” measures the overlap *port(A, B),* which is A in B or the portion of the trait space of B that is covered by A, in the *n*-dimensional hypervolume (sensu Hutchinson 1957) and becomes zero, if two trait spaces do not overlap in a single dimension. Often, a complete differentiation (i.e. no overlap) in a single trait may be sufficient to avoid competition or to represent a completely different phenotype (Fig. 4). However, additional information from the aggregation method “mean” may allow evaluating how similar two niches or trait spaces are based on the mean overlap of the *n* dimensions. For instance, *Geospiza fortis fortis* and *Geospiza heliobates* occupy distinct *n*-dimensional hypervolumes (Fig. 4, aggregation = “product”), but share characteristics in many traits investigated (Fig. 4, aggregation = ”mean” and individual traits). Overlap and niche size resulting from the aggregation methods = “*product*” are highly dependent on the number of dimensions investigated, which prevents direct comparisons across studies. Aggregation methods “*gmean*” (geometric mean) and “*mean*” (arithmetic mean) provide values that facilitate the comparison across studies with different numbers of dimensions. Absolute values for overlaps *port(A, B)* (Fig. 4 and 5) and trait space sizes *vol(A)* (Fig. 5) differ between the default setting `dynRB_VPa(data, pca.corr=FALSE)` and the option correcting for correlated dimensions `dynRB_VPa(data, pca.corr=TRUE)`. However, general patterns remained similar in both approaches (Fig. 4 and 5) suggesting applicability and robustness of both approaches for ecological and chemical data. Nevertheless, we recommend to carefully check datasets for correlations between dimensions as well as to play it safe and analyze the data with both approaches. Additionally, in both data sets the asymmetric nature of overlaps becomes apparent, i.e. *port(A, B)* usually is not the same as *port(B, A)*, which bears important information for the ecological and evolutionary interpretation of the datasets.

CAVEATS

Although *dynamic range boxes* reliably compute sizes and overlaps of *n*-dimensional hypervolumes, some precautions are required in the interpretation of the results. The significance of the outputs of *dynamic range boxes* is, as in any ecological method, dependent on sampling effort. Furthermore, our method does not model the niches of species, but instead calculates the space occupied by the available data, which means that *dynamic range boxes* inform about realized but not fundamental niches. Albeit *dynamic range boxes* consider the abundance and distribution of values in the *n*-dimensional hypervolume, our method represents a simplification, as compared to multivariate density estimation. However, it thus also avoids the well-known problems associated with multivariate density estimation (choice of bandwidth, convergence rate, curse of dimensionality). Often, especially if morphological data are considered, individual traits exhibit a strong positive correlation violating the independence assumption underlying *dynRB*. It is therefore recommendable to carefully inspect the data for strong co-variation prior to the analysis and interpretation of the results, which is facilitated by the option to display a correlogram (*correlogram = TRUE*) in all of the functions provided in the R package *dynRB* (Tab. 1). At first glance it might seem more natural to avoid independence assumptions and to model the data by multivariate normal or elliptical distributions (implying ellipses as contour sets of the densities). Considering, however, that calculating volumes of intersections of n-dimensional ellipses is a non-trivial endeavor, that principal components analysis is highly sensitive to outliers, and that (to the best of the authors' knowledge) there is no (computationally fast) notion of multivariate quantiles (or trimming) that allows for (i) an exclusion of 100α % of the (non-central) data for each α, (ii) a calculation of the convex hulls (or the smallest enveloping ellipse) containing the remaining $100(1-\alpha)$ % and, most importantly, (iii) the subsequent calculation of the intersection of two such convex hulls (or ellipses) and its volume suggests that the dynRB approach offers a good and computationally feasible compromise that yields good results in the majority of cases. We remark that standard notions of multivariate quantiles and depths functions like described in Chaudhuri

(1996) and Serfling and Zuo (2010) and the references therein might manage points (i) and (ii) for a sufficiently small number of dimensions (and directions in which the quantiles are calculated), but it is unclear, how (iii) should be established in the general setting. Although working with principal components has to be done carefully (calculation of principal components jointly for data from different populations might yield directions that do not fit to any of the two datasets and exhibit other odd behaviour, see Rosenbaum (2010)), we provide the option to replace the original dimensions with principle components to avoid dependence in the data.

CONCLUDING REMARKS

The term niche is used for various ecological concepts, either to reveal causes for species' distributions or interactions (response component), or to identify consequences of the presence of a given species for its biotic and abiotic environment (effect component) (McInerny & Etienne 2012c; McInerny & Etienne 2012b; McInerny & Etienne 2012a). These concepts are expressed by the "requirements" or by the "functional" niche definition, respectively (Whittaker, Levin & Root 1973; Leibold 1995). While there is no precise or unifying definition of "the niche", which requires each author to clearly define the meaning of niche in a given study) (McInerny & Etienne 2012c; McInerny & Etienne 2012b; McInerny & Etienne 2012a), a common feature of all interpretations and applications of niches is that a set of *n* factors is used to define it. Thus, the unifying feature of niches is that they are multivariate constructs. In addition to rather classical approaches, advances in analytical methods and the establishment of online databases as well as further developments in biological sciences will yield multivariate datasets on the distribution or characteristics of genotypes, ecotypes, populations, species, communities, ecosystems and biomes, thus requiring robust statistical tools to analyze and interpret the size and the overlap of these multivariate constructs.

Dynamic range boxes provide, as the simulations and examples show, a number of analytical tools that are highly suited to evaluate in detail niches, trait spaces, inter- and intraspecific variability, and other ecological and evolutionary processes that are based on multivariate data. Beyond the calculation of the sizes and overlap of niches and trait spaces, *dynamic range boxes* also allow the deconstruction of niches / trait spaces into individual dimensions to evaluate the impact of each trait on overall size and overlap, which is also facilitated by different aggregation methods. For instance, in selection studies or in studies testing the effects of mutations on the phenotype of organisms, it may be highly relevant to identify those traits that differ most between groups. In ecological studies it may be interesting to pinpoint those biotic or abiotic factors for which the competition potential is highest, or the traits that differ most in the functional composition of communities.

The concept of *dynamic range boxes* lines up with various other approaches to quantify the size and overlap of *n*-dimensional hypervolumes (e.g. Blonder *et al.* 2014; Swanson *et al.* 2015) and it may be advisable to compare results of different approaches and to evaluate the strengths and weaknesses of the approaches for a given dataset. However, the approach presented here satisfies all requirements that we believe are necessary to reliably extract the expansion of hypervolumes composed of multiple factors, which makes *dynamic range boxes* readily applicable for a broad range of datasets to answer questions related to various disciplines.

ACKNOWLEDGEMENTS

We thank David Orme and anonymous reviewers for valuable comments on a previous version of the manuscript and the package *dynRB*. The study was supported by the Graduate School "Evolutionary Networks: Organisms, Reactions, Molecules" (E-Norm) of the Heinrich-Heine-University, Düsseldorf, Germany and the Deutsche Forschungsgemeinschaft (DFG JU 2856/2-2).

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Chapter 4 – Trait-based quantification of floral niche size and overlap reveals mechanisms underlying resource partitioning and competition between native and introduced flower visitors

This chapter is *in preparation*:

Kuppler J, Höfers MK, Trutschnig W, Bathke AC, Eiben JA, Daehler CC & Junker RR. Trait-based quantification of floral niche size and overlap reveals mechanisms underlying resource partitioning and competition between native and introduced flower visitors.

ABSTRACT

Invasive species often cause alterations in the dynamics and structures of native species interactions. Driven by the strong competitive abilities of invasives, native and endemic species often suffer from resource depletion, which may even lead to the displacement of these species. Invasions have had particularly severe consequences on isolated islands such as the Hawaiian Archipelago where thousands of plant and animal species have been introduced. In this study, we quantified the niche sizes and overlaps of native and introduced flower visitor taxa in Hawaii Volcanoes National Park in order to reveal the ecological mechanisms underlying competition. We used a novel trait-based approach (*dynamic range boxes*) adopting the concept of *n*-dimensional hypervolumes where each dimension of the hypervolume represents one functional flower trait that affects foraging choices of flower visitor species. On average, introduced flower visitor taxa were more generalized in resource use (larger niches) than native taxa. Small niche sizes of native taxa partly resulted from their specialization on native flowering plant species whereas introduced flower visitors interacted with both native and introduced plant species proportional to their abundance. Additionally, natives shared a larger proportion of their niches with introduced taxa than *vice versa*, suggesting competitive dominance of introduced taxa. Thus, the functional composition of plant communities as well as the ecological and evolutionary background of consumers are important factors in explaining the structure of interaction networks, and help to reveal competitive patterns within communities. Predicted range expansion of invasive plant and flower visitor species may further reduce the availability of resource for native flower visitors, at the same time competition for the remaining resources may increase. Thus, the large niche sizes of introduced species as well as their strong competition potential pose severe current and future threats for native flower visitor species and the Hawaiian ecosystem.

INTRODUCTION

Anthropogenic activities have facilitated the introduction of many plants and animals into non-native areas in the last 150 years (Lockwood *et al.*, 2013). Oceanic islands offer particularly favorable conditions for the establishment of introduced species as these isolated habitats often feature low species and functional group diversity and disharmonic floras and faunas (Denslow, 2003; Krushelnycky & Gillespie, 2010). Invasional processes and ecological consequences of introduced species can be well observed on the Hawaiian Islands, which are among the most geographically isolated island groups worldwide, where thousands of introduced plants and animals are established (Wagner *et al.*, 1990; Mooney, 2005). Once species become established in new habitats, they start to interact with resident species (Hobbs *et al.*, 2006). Resulting alterations in the interaction patterns within communities are often detrimental for native species, which may even be displaced by invasives (Pyšek *et al.*, 2012; Ricciardi *et al.*, 2013; Simberloff *et al.*, 2013; Traveset & Richardson, 2014). Major factors driving these alterations are the competitive dominance of invasives, their generalized use of resources, and their ability to efficiently and rapidly exploit resources. These factors are also considered as key for the success of invasive species (Pianka, 1981; Levine *et al.*, 2003; Lach, 2008b; Junker *et al.*, 2010; Lockwood *et al.*, 2013). Because these factors commonly cause declines or (local) extinctions of native species, identifying effective conservation strategies for native species requires understaning the ecological mechanisms underlying the strong competition potential of invasive species and associated community-wide alterations of interaction patterns.

Niche theory predicts that the competition potential between two species (e.g. for resources) increases with the similarity of their ecological niches (Townsend *et al.*, 2003). The fundamental niche of a species is defined as the entirety of abiotic (e.g. soil type or temperature), but also biotic (e.g. interaction partners of other trophic levels) factors that allow this species to survive and reproduce in a given habitat, often conceptualized as *n*-dimensional hypervolumes (Hutchinson, 1957). Realized niches are subsets of fundamental niches shaped by interspecific competition (Townsend *et al.*, 2003; Sargent & Ackerly, 2008). Hence, an overlap of realized niches may impede sympatric coexistence more strongly than an overlap in the fundamental niche because alternative resources may not be available. Accordingly, realized niche overlap may potentially lead to competition with a disadvantage for those species that share larger proportions of their niches with competitors than species that can avoid competition due to exclusive occupancy of parts of their niches (asymmetric overlap between species, Reitz and Trumble 2002).

So far, studies investigating the competition potential of invasive and native flower visitors usually focused on the number of shared plant species used as resource as an estimate for niche overlap (e.g. Goulson *et al.*, 2002; Paini & Roberts, 2005; Lye *et al.*, 2010). However, whether a flower visitor is able to exploit floral resources of a plant species is dependent on functional flower traits (e.g. floral morphology, floral scent, or floral colour) displayed by this plant species (Junker *et* *al.*, 2011b, 2013; Kaiser-Bunbury *et al.*, 2014, Larue *et al.* 2015). Hence, these traits can be viewed as floral niche dimensions that determine whether a flower visitor is able to exploit the resources offered by flowers (Junker *et al.*, 2013). Thus, considering functional traits may provide a more accurate and mechanistic description of the floral niche than approaches using the plant species identities only (Junker et al. 2015a). A species-based approach does not inform about the similarity of trait use and functional overlap between two species, which are both important predictors for functional similarity of native and invasive species (Baiser & Lockwood, 2011). Thus, incorporating functional traits into niche models may allow to draw concise conclusions conclusions about the mechanisms that structure communities and determine the effects of invasive species on native communities (McGill *et al.*, 2006).

Introduced flower visitors often interact with co-introduced plant species (Simberloff & Holle, 1999) but also interact frequently with native plants (Junker *et al.*, 2010). Hence, they compete with native animals, which are adapted to and therefore may be more specialized on native plants (Bezemer *et al.*, 2014). The negative effects imposed by introduced flower visitors on native flower visitors are either the results from interference competition when alien species actively deter natives from floral resources (e.g. Lach, 2008; Hanna *et al.*, 2014) or from exploitation competition when aliens deplete the resources (Goulson, 2003; Stout & Morales, 2009). Accordingly, a meta-analysis concluded that the floral visitation rate of many native insect species decreased when invasive flower visitors were present (Montero-Castaño & Vilà, 2012). However, the magnitude of these effects strongly depends on the identity of native and introduced flower visitors as well as others factors such as species densities or resource availability (reviewed in Goulson, 2003; Stout & Morales, 2009; Dohzono & Yokoyama, 2010). Although bees are prominent examples for invasive and competitive dominant flower visitors, other invasive flower visitors, such as social wasps or ants, can also negatively interfere with native flower visitors (Traveset & Richardson, 2014). These effects are especially severe in Hawaiian communities where social hymenopterans had not naturally been present in the species inventory (Krushelnycky *et al.*, 2005). As a consequence, Hawaiian endemic plants often lack means to effectively protect their flowers against exploitation by ants (Junker *et al.*, 2011a), allowing ants to strongly interfere with native arthropod visitations (Lach, 2008b; Junker *et al.*, 2010; Bleil *et al.*, 2011). As a consequence of the strong competition between native and introduced flower vistors, which sometimes is complemented by predatory activities of introduced species (in the case of social wasps), the populations of native animals often decline (Paini, 2004; Traveset & Richardson, 2006; Wilson & Holway, 2010; Hanna *et al.*, 2013). Thus, the increased densities of invasive flower visitors are one reason for the strong decline of pollinators endemic to the Hawaiian islands, especially birds (Honeycreepers) and *Hylaeus* bees (Scott *et al.*, 1988; Banko *et al.*, 2002; Magnacca, 2007).

In this study, we quantitatively recorded interactions between native and introduced flower visitors and flowering plant species within 33 plant communities in the Hawai'i Volcanoes National Park (Hawaii, USA) or adjacent areas and quantified the trait-based niche size and overlap of introduced and native flower visitors. We used *dynamic range boxes* (Junker et al. 2015b), a novel non-parametric approach to quantify size and overlap of *n*-dimensional hypervolumes. Our study will foster a comprehensive functional understanding of the interactions of invasive flower visitors within communities, which may support conservation efforts in highly threatened Hawaiian ecosystems.

METHODS AND MATERIAL

Study sites

The study was conducted in the Hawai'i Volcanoes National Park (HAVO, Hawai'i, USA) between November 2014 and May 2015. Study sites were selected based on their accessibility, the availability of flowers and coverage of a broad range of different habitats. Location, altitude, size, and age (time since last lava flow) of habitats, as well as the number of native and introduced plant species are given in Appendix A: Table A1. In total, 33 sites were selected, 30 within the HAVO and three in adjacent areas. The size of each study site was adjusted to the distribution and abundance of flowering plants and to represent the given habitat. E.g. young lavaflows generally had a low density of plants compared to other habitats, thus these plots were generally larger than in other habitats to include a sufficient number of plants for sampling.

Flower-visitor interactions

At each study site, flower-visitor interactions were observed on one to four consecutive days (between 07:00 – 13:00 h), resulting in 88 observation days and 265 h observation time. For each flowering plant species several individuals (*n* = 3 - 20) were observed for 5 min. All flower visitors were recorded and, if possible, caught for identification. Otherwise the lowest taxonomic unit of the flower visitor that could be determined in the field was noted. Additionally, on plots where birds were present, we surveyed bird-flower interactions using point counts for 30 min in the morning and around noon from a spot overviewing the whole study site (Bibby *et al.*, 2000). Animal species were first separated into morphospecies and then, if possible, identified to species level and categorized as native or introduced to the Hawaiian Islands (Appendix A: Table A2). Flowering plant species (Appendix A: Table A3) were identified, categorized as introduced or native (endemic or indigenous species) and the total number of flowers of each species per plot was counted. Weather conditions (i.e. temperature [°C], humidity [%], wind speed [m/s], and light intensity [μmol/m^2]) were recorded during observations in one min intervals using a mobile data logger (DKS655 "rugged visual", Driesen-Kern GmbH, Bad Bramstedt, Germany) with an external anemometer (WG3400, Driesen-Kern GmbH, Bad Bramstedt, Germany) and an external PAR Quantum Sensor (SKP215, Driesen-Kern GmbH, Bad Bramstedt, Germany). Thus, we could assign every recorded interaction to a specific weather condition to yield information about the activity range of each observed taxon. The data logger recording the temperature and humidity was placed in full shade, the anemometer was mounted on a stick in 1.5 m height, which was in the range of the flower heights on each plot, and the PAR Quantum Sensor was fully exposed to sunlight.

Floral morphology

For all plant species, we obtained nine morphological floral traits that have been shown to affect foraging decision and thus specialization of flower visitors (Fenster *et al.*, 2009; Junker *et al.*, 2013): 1) plant height [cm], 2) flower inclination [°] (the vertical inclination of flowers and if available inflorescences), 3) ratio style length to stamen length, 4) number of stamens, 5) stamen accessibility [mm] (distance from flower tube entrance to stamen; negative values mean that the stamen (and thus pollen bearing anthers) were below the corolla aperture), 6) display size of flowers [mm], 7) display size of largest floral unit [mm] (inflorescence or flower), 8) nectar tube depth [mm] and 9) nectar tube width [mm]. For further analyses the number of anthers was log-transformed. The plant height was measured to the nearest one cm using a measure tape, flower inclination to the nearest 5° using a triangle ruler. All other plant traits were measured to the nearest one mm using a caliper. For common plant species (n = 29) we measured 15-20 individuals (3-7 flowers per individual) and for rare plant species (n = 11) between 2-10 individuals.

For a subset of species, nectar volume [µl] and concentration [%] were quantified and the flower colour was measured as spectral reflectance of the petals (methodological details see Appendix B).

Volatile collection and analysis

Dynamicheadspace scent samples were collected from flowers of each plant species (n = 1-2). First, the flowers were enclosed within a polyester oven bag (Toppits®, Germany), allowing the scent to accumulate in the oven bag. Afterwards, the emitted volatiles were trapped on 1.5 mg Tenax (mesh 60– 80; Supelco, Bellefonte, PA, USA) and 1.5 mg Carbotrap B (mesh 20– 40, Supelco) in a quartz vial (Varian Inc.; length 15 mm, inner diameter 2 mm) for 2 min using a membrane pump (G12/01 EB, ASF Rietschle-Thomas, Puchheim, Germany). All samples were collected between 8:00 and 12:00 h. For plant species were flowers could not be bagged without including green leaves additional samples of only green leaves were taken. Scent samples were analyzed using an automatic thermal desorption system (TD-20, Shimadzu, Japan) coupled with a GC–MS (model QP2010 Ultra EI, Shimadzu, Japan). The GC-MS was equipped with a ZB-5 fused silica column (5% phenyl polysiloxane; 60 m long, inner diameter 0.25 mm, film thickness, 0.25 µm, Phenomenex) and the column flow (carrier gas: helium) was set to 1.5 ml/min. The GC oven temperature started at 40°C (split ratio 1:1), then increased by 6°C per minute to 250°C and held constant for 1 minute. The MS interface worked at 250°C. Mass spectra were taken at 70 eV (in EI mode) from m/z 30 to 350. The GC/MS data were processed using the GCMSolution package

(Version 2.72, Shimadzu Corporation). Compounds were identified by comparison of mass spectra and retention times with standard compounds, which are commercially available. Alternatively, compounds were identified using the mass spectral libraries Wiley 9, Nist 2011, FFNSC 2, Essential oils and Adams 2007 as well as the database available in MassFinder 3. The compounds found in the flowers were compared to those found in the blanks (empty oven bags, samples of green leaves) to determine the compounds that are specifically emitted by flowers. The total scent emission was estimated by comparing peak areas of compounds to the peak area of external standards (monoterpenoids, aromatics, sesquiterpenes and alipahtics). The amount of each compound emitted was standardized by the dry mass of the sampled flowers and the collection time [ng h^{-1} $100mg^{-1}$]. In case of two samples per plant species the mean amounts of individual substances was used for further analysis. In the sample of *Sesbania tomentosa* no scent compounds were detected (Appendix C: Table C1), thus this sample was excluded. Since most substances were emitted by only one or a few plant species, resulting in a zero-inflated matrix and thus preventing a meaningful analysis, we grouped the compounds according to their biosynthetic origin and their functional groups: aliphatics (A), aromatics (AR), C5-branched pathway (C5), irregular terpenes (IT), monoterpenes (MT), sesquiterpenes (ST).

Flower-visitor interaction network analysis

In order to investigate whether plant and animal species that share a long evolutionary history form interaction networks (based on visits per hour) with properties that differ from networks formed by species that just recently settled in Hawaii, we compared properties of networks consisting of either native flower visitors and native plant species, introduced flower visitors and introduced plant species, introduced flower visitors and native plant species, or native flower visitors and introduced plant species, only. Based on these networks we calculated the following aggregate statistics: complementary specialization *d'* of species and four statistics at the network level (connectance, interaction evenness, complementary specialization H_2' using the R package bipartite (Dormann *et al.*, 2009). To assess the potential influence of the spatial distribution of native and introduced flower visitor taxa as well as plant species, we performed the same analysis for flower-visitor interaction networks and calculations of niche size and overlap (see below) including only plots where native and introduced flower visitor taxa and plant species were present (*n* = 11, Appendix A: Table A1)

Calculation of floral niche size and niche overlap

To quantify the niche size of flower visitors and overlap of their niches we adopted the concept of *n*-dimensional hypervolumes proposed by (Hutchinson, 1957). In this broadly applicable framework, a niche is represented by a space characterized by *n* dimensions where each dimension represents environmental conditions or characteristics of resources. In the context of this study, flower traits that may facilitate or prevent flower visitation by a given visitor (Junker & Parachnowitsch, 2015) are considered as niche dimensions. Thus, the *n*-dimensional hypervolume, or floral niche of a flower visitor can be viewed as a trait-space characterized by various floral traits (e.g. nectar tube depth, display size, and scent emission of a flower). This is based on the assumption that animals with preferences or aversion for the characteristics of some traits visit only a subset of available plant species that display a suitable combination of trait characteristics. Thus, the floral niche is defined as the hypervolume containing the characteristics of floral traits that allow an animal taxon to consume floral resources (Junker *et al.*, 2013).

Sizes and overlaps of niches were quantified using *dynamic range boxes*, a novel non-parametric approach to quantify the sizes as well as the asymmetric overlap of *n*-dimensonal hypervolumes (Junker *et al.* 2015b, implemented in the R package *dynRB*, Schreyer et al. 2015). The earlier concept of multivariate range boxes (used to estimate an *n*-dimensional hypervolume) involved enveloping all observed data per dimension within the minimum and the maximum value (Hutchinson, 1957). This conservative approach is highly susceptible to outliers and does not take into account the distribution of the data between the extremes, often leading to an overestimation of the actual niche sizes and the overlap of trait spaces. *Dynamic range boxes* avoid these disadvantages: a number of m nested, standardized range boxes are calculated for each species under consideration, each box containing a decreasing percentage of values per dimension n, starting with the interval consisting of the 0-quantile (= minimum) and the 1-quantile (= maximum) in every dimension and shrinking in m steps to a degenerated interval only containing the medians. Letting $\boldsymbol{R}_n^{\boldsymbol{A}}(\alpha_i)$ and $\boldsymbol{R}_n^{\boldsymbol{B}}(\alpha_i)$ denote the i-th range box of the first and the second species (*A* and *B*) respectively, then their volume and the portion of the first in the second and *vice versa* (for every α_i) are computed. Calculating the product of the resulting quantities finally yields what we will refer to in the sequel as niche size *vol(A)* and overlap *port(A,B).* Both values can be obtained dimension-wise and for the full volume. For a full description of this approach see Junker *et al.* (2015b).

The niche sizes and pairwise overlaps were calculated for all visitor species with at least 10 observations at flowers and available information on their origin, i.e. whether the taxa are introduced / invasive (*n* = 18) or native (*n* = 7, Appendix A: Table A2). First, the size *vol(A)* and the pairwise overlap *port(A,B)* with other species of the niche including all trait categories of the species were calculated. Floral colour as well as nectar properties were not included in this analysis due to incomplete sampling (Appendix B). Second, we calculated sizes and overlaps for each trait category (weather variables, morphological floral traits, floral scent) and each trait separately. *Dynamic range boxes* require non-degenerated variance in each dimension to quantify niche size and overlap. Therefore, we added a small ecologically irrelevant value (0.0001) to some data to run the analyses.

We defined the floral niche of an animal as the *n*-dimensional trait space occupied by the flowers (floral traits) of those plant species visited by the animal weighted by the interaction strength I_{ij} [interactions h^{-1} flower^{-1}] of animal *i* at plant species *j.* Interaction strength I_{ij} was transformed by $I_{ij}' = \log(I_{ij} \cdot 10^6 + 1) \cdot 10$ and I_{ij}' was rounded to the nearest integer $r(I_{ij}')$. For each $r(I_{ij}')$ representing the transformed interaction strength of animal *i* with plant species *j*, we randomly drew one trait value measured for plant species *j* for each trait *t*. Thus, for each animal *i* and trait *t*, we obtained a vector with the length $V = \sum_{j=1}^{J} r(I_{ij}')$ with *J* being the total number of plant species interacting with animal *i* describing the characteristics of trait *t* used by animal *i*. Thus, the floral niche of each animal *i* was expressed as a matrix with *V* rows and *T* columns with *T* as the total number of traits considered.

Temperature, wind speed and light intensity were used to characterize the weather-requirement of visitor species. We excluded humidity from the analyses due to the high correlation with temperature (Pearson correlation coefficient, $R^2 = -0.83$***). Each flower-visitor interaction was associated with weather conditions at the time when the interaction was observed. To correct for the heterogeneous observation times at different weather conditions, which biases the size and overlap of weather niches, we weighted the observations by 1/relative frequency (obtained by kernel density estimates, R function *density*) of specific weather conditions during flower-visitor observations. 1/relative frequencies were rounded to the next integer.

In order to test whether native and introduced flower visitors occupy floral niches of different sizes (i.e. whether they exhibit a different degree of specialization / generalization), we used a Mann-Whitney U test comparing the niche sizes *vol(A)* of animals of both origins. Additionally, to reveal whether native and introduced flower visitors have an asymmetric competition potential, resulting from an asymmetric niche overlap *port(A, B)* of species pairs, we calculated the effect size (log response ratio) of the overlap $L = \log_{10}(port(A,B) / port(B,A))$, with *port(A,B)* and *port(B,A)* as the portion of the trait space of B (introduced taxon) that is covered by A (native taxon), and *vice versa*. In the rare event that *port(A,B)* and *port(B,A)* were 0, zero was replaced by a number close to zero and smaller than the smallest measured overlap (10^{-28}) in order to calculate *L*. Thus, *L* becomes negative if native taxa overlap introduced taxa stronger than *vice versa* and positive if niches of introduced taxa overlap stronger with the niches of natives. To test for a consistent asymmetry in the overlap between native and introduced flower visitors (i.e. for an asymmetric competition potential), we tested whether *L* differs from zero (Mann-Whitney U test).

RESULTS

Flower-visitor interaction network

In total, we observed 3747 interactions between 40 plant species (22 introduced and 18 native species) and 95 flower visitor taxa (32 introduced, 15 native flower visitor taxa, and 48 of unknown origin). Eighteen of the introduced visitor taxa and 7 of the native ones were recorded more than 10 times. Introduced visitor taxa accounted for most of the interactions (68.1 %), while interactions of native taxa were only recorded 371 times (9.8 %). Visitors with unknown origin accounted for 22.1 % of the total interactions. Overall, network structure was relatively complementarily specialized, whereas individual taxa ranged from highly generalized to highly specialized (Fig. 1a, Tab. 1, Blüthgen et al. 2006). Interestingly, the origin of both the flower visitors and the plants strongly affected the pairwise interactions. Native species almost exclusively visited native plant species (94.8 % of all interactions of natives). In contrast, 24.5 % of all interactions observed from introduced flower visitors occurred on introduced plant species, which is proportional to their flower abundance on all plots (26.5 %). Accordingly, interactions of introduced flower visitors were more generalized (high interaction eveness, Tab. 1, Fig. 1b, c) than those of native flower visitors. The latter appeared to be generalistic in interactions with native plant species (Tab. 1, Fig. 1e) but were highly selective in the few flower choices in introduced plant species (Tab. 1, Fig. 1d). The same pattern was observed in plots where native and introduced animal and plant species co-occurred, indicating that the scarcity of interactions between native flower visitors and introduced plant species is not a result of asampling artifact or spatial mismatch of potential interactions partners (Appendix D).

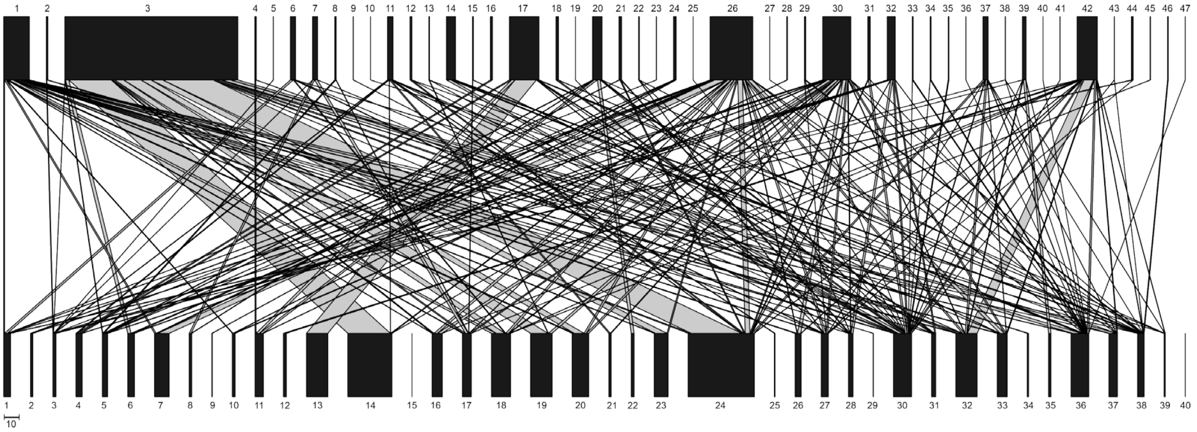
Table 1. Aggregate network statistics for flower-visitor networks. Apart from information regarding the whole community observed in the Hawaii Volcanoes National Park, information on network structure considering plants and animals of specific origins is given. Network structure was calculated for subsets containing either native or introduced flower visitors interacting with either native or introduced plant species. Shown are connectance *C*, interaction evenness *E*, complementary specialization of the individual plant (*d'*) and specialization of the whole network (H_2'). For *d'* mean ± SE across taxa are given.

Animal and plant group	***C***	***E***	***d'***	H_2'
whole community	0.11	0.56	0.38 ± 0.24	0.55
introduced – introduced	0.10	0.51	0.44 ± 0.24	0.65
introduced – native	0.16	0.51	0.35 ± 0.26	0.45
native – introduced	0.03	0.27	0.34 ± 0.37	0.88
native – native	0.14	0.45	0.20 ± 0.26	0.50

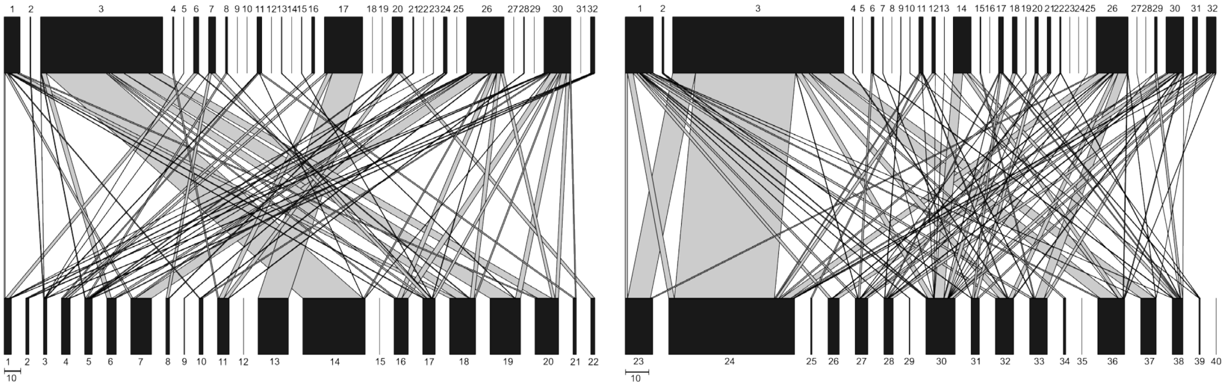
Niche size and niche overlap

Apis mellifera, *Xylocopa sonorina*, and a number of ant species, which were the most common representatives of the introduced flower visitors clearly occupied larger niches *vol(A)* than the endemic bees *Hylaeus difficilis*, *Hylaeus laetus* and the endemic bird *Himatione sanguinea,* prominent representatives of the native flower visitors (Fig. 1). This finding is supported by overall significantly larger niche sizes *vol(A)* of introduced flower visitors compared to natives (Fig. 2a, Mann-Whitney U test: $W = 97$, $p = 0.041$). When the full niche was deconstructed into different parts, i.e. floral morphology and scent as well as weather conditions, the niches of the three most common introduced flower visitor taxa exceeded those of the natives in size *vol(A)* (Fig. 1).

whole community: flower visitor taxa - plant species



b) introduced flower visitor taxa - introduced plant species c) introduced flower visitor taxa - native plant species



c) native flower visitor taxa - introduced plant species d) native flower visitor taxa - native plant species

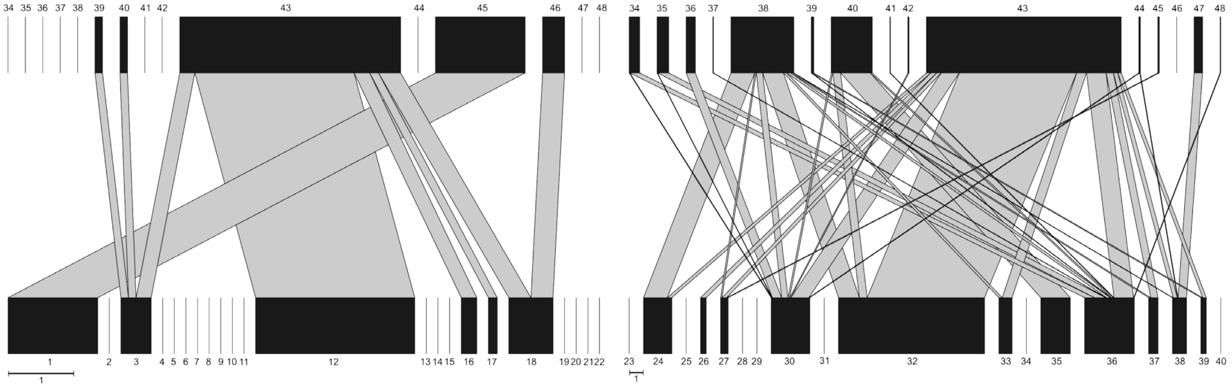


Figure 1. Bipartite flower-visitor networks for the whole community of native or introduced flower visitors interacting with either native or introduced plant species. The networks are based on interactions per plant species per h. Nodes represent plant species (bottom) or flower visitor taxa (top). The width of the nodes denotes the proportional interaction frequency of partners. Numbers denote flower visitor taxa and plant species (names are shown in Appendix A: Table A1 and A2 in Supporting Information): Introduced flower visitors 1 – 33, native flower visitors 34 – 48, introduced plant species 1 – 22, native plant species 23 – 40.

For instance, while *Hylaeus difficilis* was mostly active at warm and dry conditions with high light intensities, *Apis mellifera* was additionally active at colder temperatures and low light intensities (Appendix D). Larger niche sizes *vol(A)* also resulted, for example, from the ability of introduced *Apis mellifera* to exploit flowers that offer nectar in deep flower tubes, resources that are unavailable for *Hylaeus difficilis* (Appendix E). This trend was also apparent when considering all taxa (Fig. 2b, Appendix D), but only significant for floral scent (Mann-Whitney U test: floral scent: $W = 99$, $p = 0.029$, weather: $W = 94$, $p = 0.063$; floral morphology: $W = 89$, $p = 0.12$). Again, the same pattern was observed in plots where native and introduced animal and plant species co-occurred. Niche sizes *vol(A)* regarding floral colour and nectar properties did not differ between native and introduced flower visitors (floral colour: W = 89, p = 0.12, nectar properties: W = 57, p = 0.75, Appendix B: Figure B1). Detailed information on the contribution of single functional traits to the niche size *vol(A)* is given in Appendix F: Table F1, Figure F1.

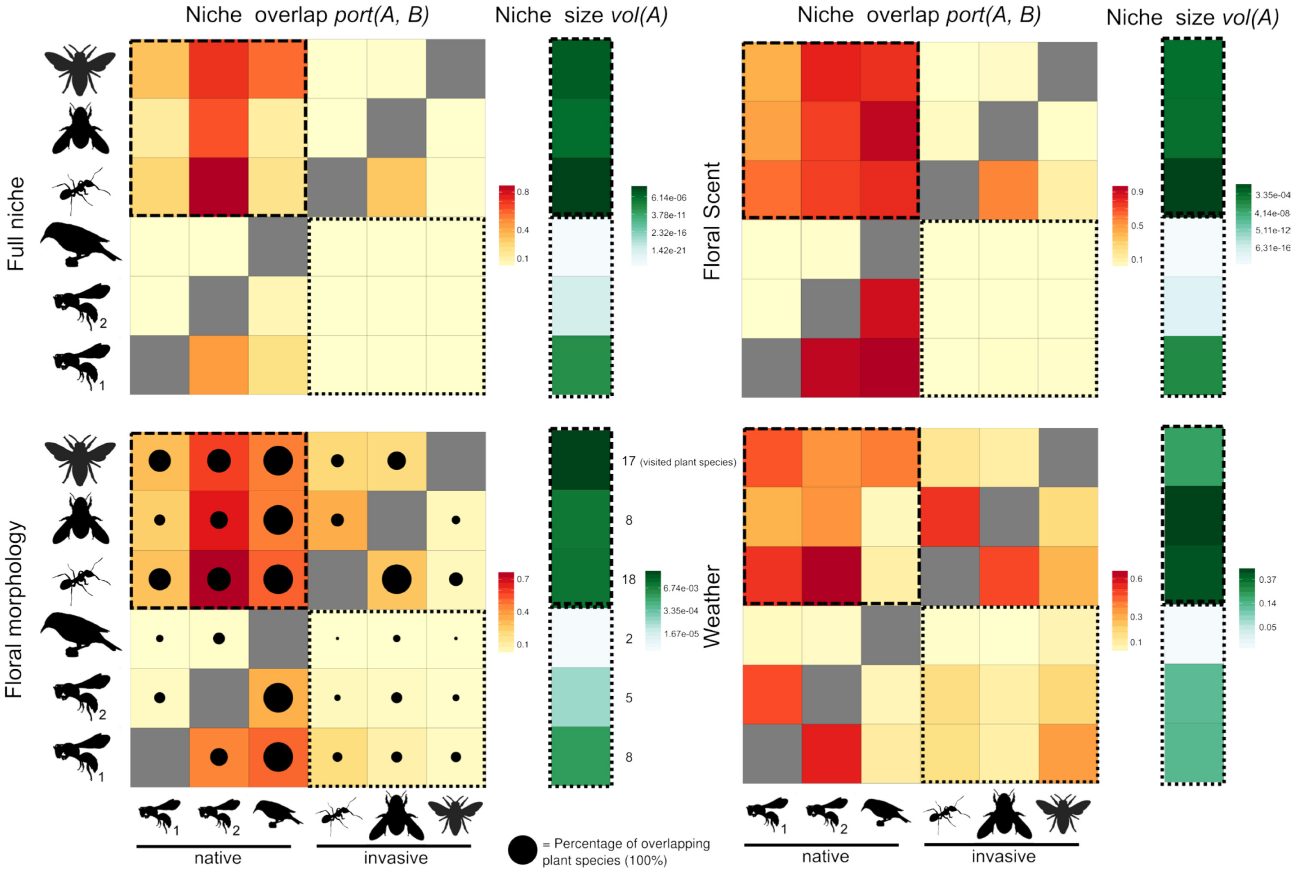


Figure 2. Niche size and overlap of the six most prominent flower visitor taxa (three introduced and three native) in Hawai'i Volcanoes National Park. Flower visitor taxa represented by silhouetes are, starting at the top, *Apis mellifera*, *Xylocopa sonorina*, ants (all species pooled), *Himatione sanguinea*, *Hylaeus laetus* (2), *Hylaeus difficilis* (1). The former three are introduced flower visitors, the latter three are native. Niche size *vol*(A) and overlap *port*(A,B) were calculating for different trait categories (full niche, weather, floral morphology and floral scent) using *dynamic range boxes* – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niches), where each dimension represents one trait (Junker et al. 2015b). Dashed boxes showing the proportion of the niche of native flower visitor taxa covered by introduced species. Pointed boxes showing the proportion of the niche of native flower visitor taxa covered by introduced species. Pointed and dashed boxes indicate the niche sizes of native and introduced flower visitors. Black circles in the lower left heatmap (niche overlap *port*(A,B)) indicate the percentage of overlapping plant species and values next to lower second from left heatmap (niche size *vol*(A)) indicate number of visited plant species).

Even more pronounced than differences in niche sizes *vol(A)* between native and introduced flower visitors were the differences in niche overlap *port(A, B)*. For instance, a large proportion of the niche of native *Hylaeus laetus* bees was covered by introduced taxa, whereas *H. laetus* covered only a minor part of the niches occupied by the introduced taxa (Fig. 1). In general, native and introduced flower visitors showed an asymmetry in their overlap biased towards introduced species that covered a larger proportion of the niches of native species than *vice versa* (Fig. 3, Mann-Whitney U test: Full niche: $V = 3536$, $p < 0.001$; floral scent: $V = 4935$, $p < 0.001$; floral morphology: $V = 5225$, $p < 0.001$; weather: $V = 5985$, $p < 0.001$). The same pattern was found for floral colour (Mann-Whitney U test: $V = 5827$, $p < 0.001$), whereas we found no significant asymmetry for the nectar properties (Mann-Whitney U test: $V = 3650$, $p = 0.58$, Appendix B: Figure B2). The same pattern was observed in plots where native and introduced animal and plant species co-occurred, too (Appendix D). Detailed information on the contribution of single functional traits to the niche overlap *port(A, B)* is given in Appendix B, Appendix F. As expected, trait-based niche overlap *port(A, B)* was correlated to the percentage of plant species shared by a pair of flower visitors (Spearman rank correlation: floral morphology: *rho* = 0.76, $p < 0.001$; floral scent: *rho* = 0.60, $p < 0.001$; Fig. 1 and Fig. 4). However, note that data points of the correlation are widely scattered within the plot (Fig. 4) indicating the non-redundant character of both measures of niche overlap.

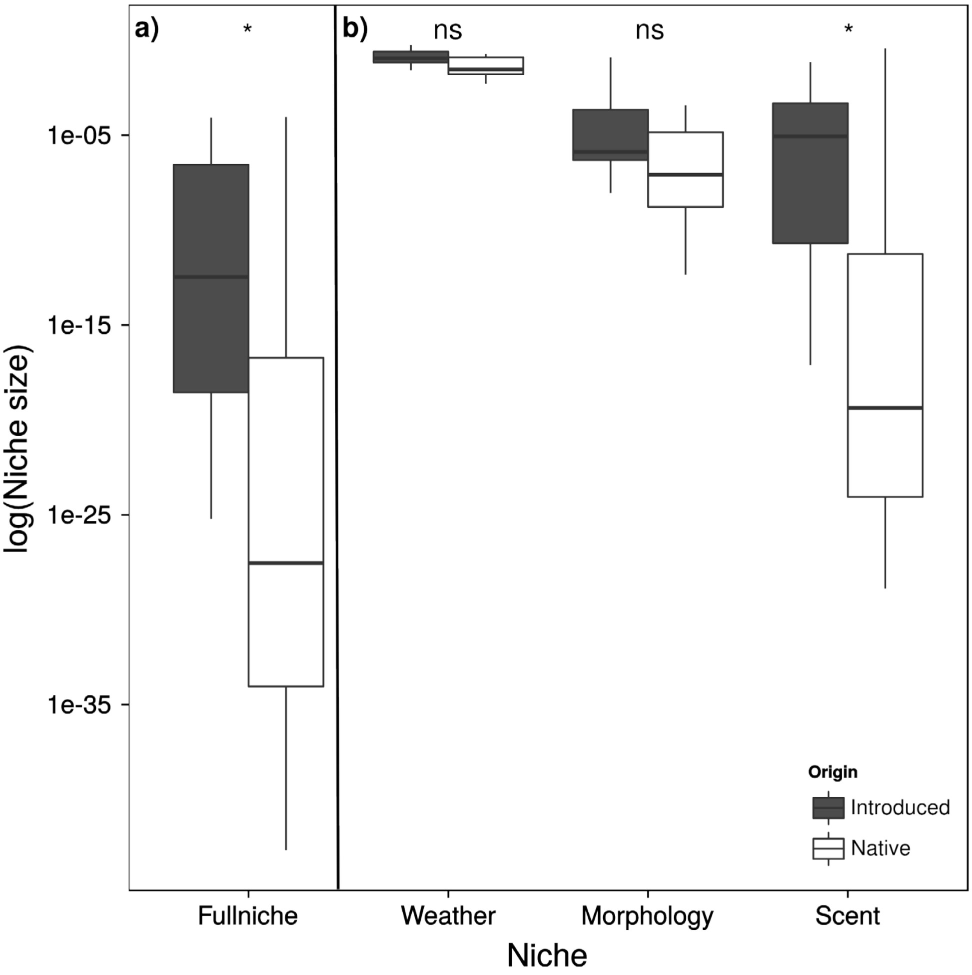


Figure 3. Niche sizes of native and introduced flower visitor species. Niche sizes *vol*(A) were calculated for four different trait categories (full niche, weather, floral morphology and floral scent) using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015b). Note that niche size is dependent on number of dimensions; as each trait category containes a different number of individual traits (morphology: n = 9 traits, scent: n = 6 , weather = 3), niche sizes are not directly comparable between

categories. White boxplots show native taxa ($n = 7$) and grey introduced ones ($n = 18$). ns = non signficiant, *** $p < 0.001$ (Mann-Whitney U test).

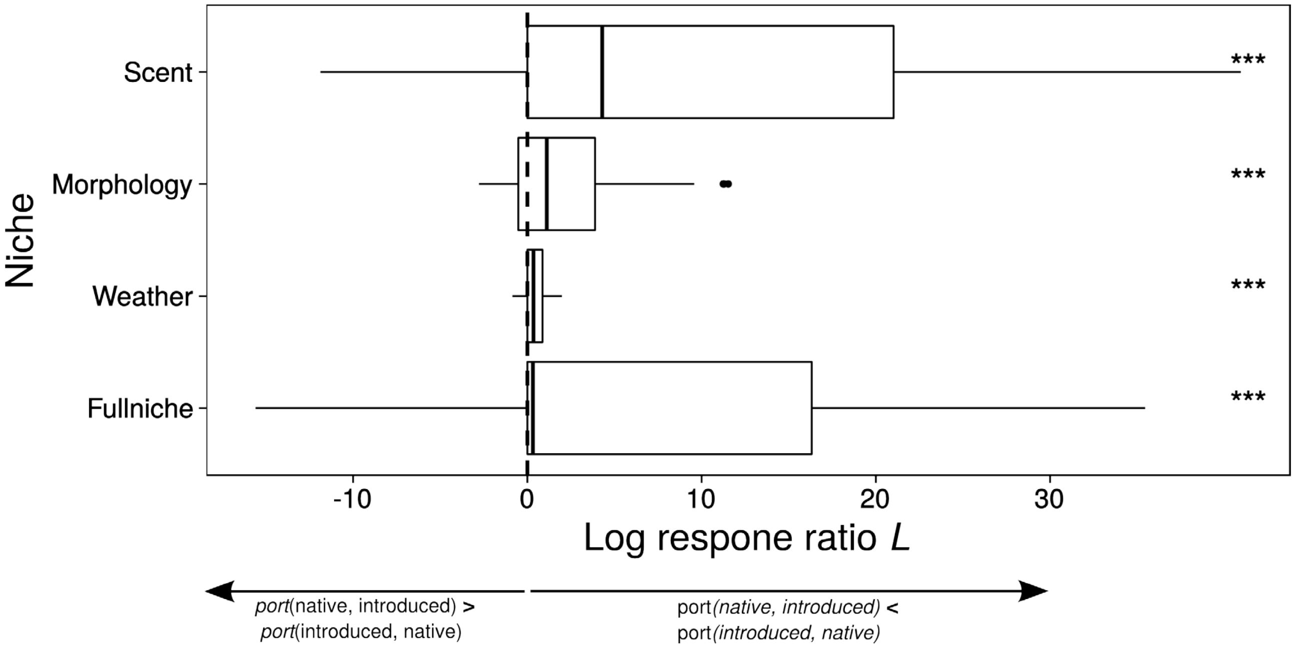


Figure 4. Asymmetric niche overlap between native and introduced flower visitor taxa. Log response ratios L describe the asymmetry of the niche overlap between native and introduced flower visitors. Asymmetry is expressed as the log of the quotient of the portion of the niche of a native taxon covered by the niche of an introduced taxon and the portion of the niche of the introduced taxon covered by the niche of the native taxon L = log(port(A, B) / port(B, A)). $L > 0$ indicates that niches of introduced taxa overlap those of native taxa more than *vice versa*. Boxplots denote range, median and interquantil ranges of log response ratios L for four different trait categories (full niche, weather, floral morphology and floral scent). Niche overlaps *port*(A,B) were calculated using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015b). *** $p < 0.001$ (Mann-Whitney U test).

DISCUSSION

Our study revealed ecological mechanisms underlying resource partitioning and competition between native and introduced flower visitors. Thus our results can help to understand the causes of the threat for native species and the fragile Hawaiian ecosystems that are increasingly dominated by invasive species. On average, the floral niche sizes of introduced flower visitor taxa were larger than those of native flower visitor taxa. Thus, introduced flower visitors appear to be more generalized and are able to utilize flowering plant species displaying more variable floral traits than native ones. Furthermore, many introduced species were able to forage in a broad range of weather conditions, whereas the foraging activity of many native species was mostly restricted to warm and sunny conditions. The larger niches of introduced flower visitors resulted in an asymmetric niche overlap: native flower visitors shared a larger proportion of their niches with introduced flower visitors than *vice versa*. Apart from the more generalized resource use of invasive flower visitors, they were also more abundant and accounted for over two-thirds of all flower visits. Interestingly, native flower visitors nearly exclusively visited native plant species, whereas introduced species visited both native and introduced plant species proportional to their flower abundance. These findings show that the competition potential between natives and introduced species is asymmetric and that introduced animal species are the dominant flower visitors of both native and introduced plant species. Consequently, the spread of introduced species along with their utilization of nearly the full spectrum of floral resources within the ecosystem may represent a severe threat for native flower visitor species.

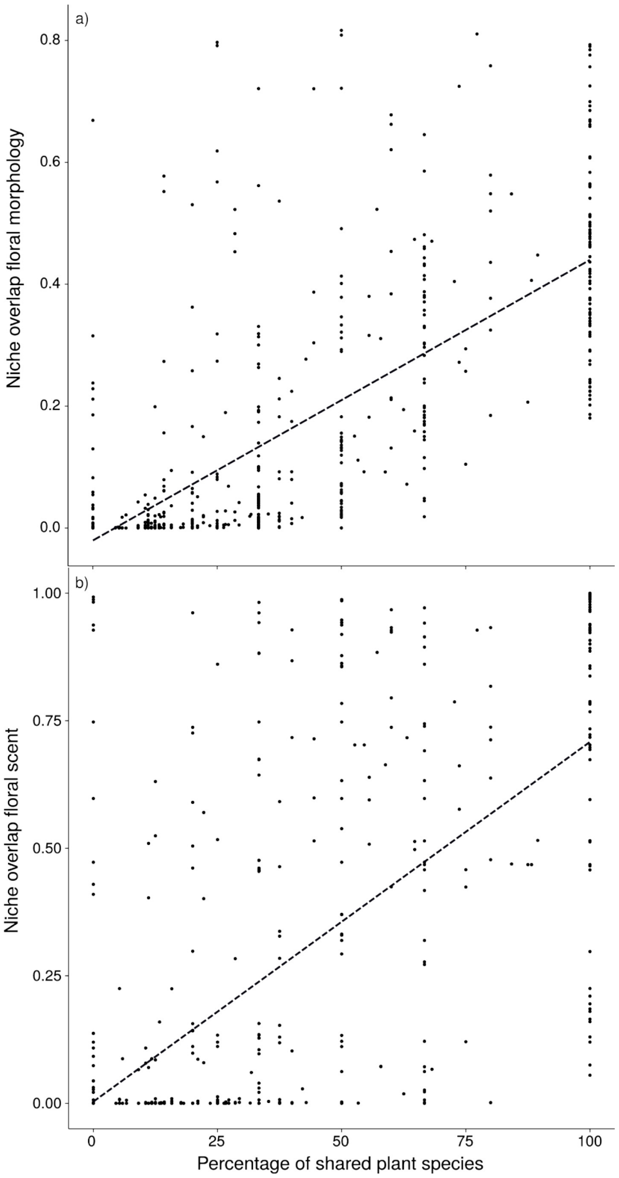


Figure 5. Relationship between number of shared plant species and trait-based niche overlap of native and introduced flower visitor taxa. Niche overlaps *port*(A, B) were calculated using *dynamic range boxes* – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015b). a) Relationship between niche overlap based on floral morphology and number of shared plant species (Spearman rank correlation: $p < 0.001$) b) Relationship between niche overlap based on floral scent and number of shared plant species (Spearman rank correlation: $p < 0.001$).

Native and introduced flower visitors along a specialization / generalization continuum

Native flower visitor taxa were specialized on certain characteristics of flower traits and native plant species and thus are specialized in their resource use. In contrast, invasive flower visitors appeared to be highly generalized allowing them to exploit floral resources from all or most plant species available. Generalized species, i.e. those with larger niches, usually have lower extinction risks in changing environments (Boulangeat *et al.*, 2012), either because these species exhibit a large environmental tolerance (Ackerly, 2003) or because populations have the potential to rapidly adapt to different local environmental conditions (Olsson *et al.*, 2009). In contrast, species with smaller niches potentially are more vulnerable to environmental change such as shifts in abiotic conditions or newly introduced competitors such as invasive species (Slatyer *et al.*, 2013).

Functional floral traits (e.g. morphology or secondary metabolites) determine which plants can be utilized as resources by different animals (Stang *et al.*, 2006; Junker *et al.*, 2011b, 2013; Larue *et al.*, 2015) and thus each functional trait can be viewed as one dimension of the floral niche of a flower visitor species. Consequently, an animal species with a larger floral niche size is able to exploit a broader range of plants displaying various characteristics of functional traits and thus are able to utilize more resources, which may be advantageous if individual plant species offer limited resources, only. If plant species that represent the main resources for animals with smaller floral niches become scarce or are heavily exploited by (introduced) competitors, these animal species may decline (Stout & Morales, 2009). In our study system, native flower visitors occupied small floral scent niches suggesting that these species are restricted in their resource use by this trait. In contrast, introduced flower visitors were more generalized (larger niche sizes) regarding their ability to exploit flowers with different scent bouquets. Floral niches based on morphological traits were smaller in native than in introduced flower visitors. For instance, compared to the native short-tongued *Hylaeus* bees the introduced long-tongued bee species (i.e. *Apis mellifera* and *Xylocopa sonorina*) were able to additionally utilize resources from flowers with deeper nectar-tubes (e.g. *Crotolaria retusa*, Fabacaea). While floral morphology often has been considered to explain resource partitioning among flower visitors (Stang *et al.*, 2006; Junker *et al.*, 2013; Kaiser-Bunbury *et al.*, 2014), floral scent was scarcely included into community-wide assessments to explain the structure of flower-visitor interactions (But see Junker et al. 2011b, Larue et al. 2015). Our results, however, emphasize the importance of scent in structuring the interaction patterns in flower-visitor communities.

Historically, the Hawaiian Islands lacked social hymenopterans as well as other common flower-visitors groups and thus possessed a high proportion of plants that are pollinated by native nectarivorous birds (Honeycreepers, Lammers & Freeman, 1986; Gardener & Daehler, 2006), which may have contributed to a lack of certain floral features (Junker et al. 2011a). Bird-pollinated flowers are often red (e.g. Johnson, 2013) and often are lightly scented (e.g. Knudsen et al. 2004), while insect-pollinated plants often are strongly scented, which is an important signal for these flower visitors (e.g. Raguso, 2008; Dötterl & Vereecken, 2010; Junker & Parachnowitsch, 2015). In other habitats not from isolated Hawaii, a high diversity of mutualistic and antagonistic flower visitors is considered to be an important driver of the evolution of diverse floral scents, that are known to attract pollinators (e.g. honey bees) and repel antagonistic flower visitors (e.g. ants, Raguso 2008, Junker and Blüthgen 2010, Junker et al. 2011a, Schiestl 2015). Thus, the different evolutionary background of the Hawaiian flora maybe explain the differences in the floral scent niches of native and introduced flower vistiors.

While functional floral traits determine the interaction partners of flower visitors, weather conditions strongly influence their foraging activity, especially in ectothermic insects and thus both flower traits and weather conditions are important components of the niches of flower visitor species (Kühsel & Blüthgen, 2015). Native *Hylaeus* bees foraged nearly exclusively at high temperatures and light intensity, while most introduced species, especially *Apis mellifera*, were also active at low temperatures and low light intensity (e.g. earlier in the morning). This could lead to preemption of flower resources, which can result in a shortage of resources for native species contributing to their threatened status (Goulson, 2003; Stout & Morales, 2009).

Asymmetric competition potential between native and introduced flower visitor taxa

Niche overlap can be used as an indicator for the competition potential between two species (Paini, 2004) and its quantification is a feasible approach for community-wide studies. However, niche overlap is a prerequisite for but does not always lead to interspecific competition (Colwell & Futuyma, 1971). Competition may be severe if resources within the shared niche are short, but may be relaxed if resources are available in sufficient amounts (Pianka, 1974; Glasser & Price, 1988). Additionally to shared food sources, similar requirements for habitats and non-food resources such as nesting sites also contribute to the competition between two species (e.g. Stout & Morales, 2009). Thus, inferring from niche overlap to competition is not trivial and requires a detailed knowledge of the ecology of the species under consideration. Nevertheless, strong evidence exists that niche overlap and differentiation play important roles in determining the co-occurrences of species (e.g. Mookerji *et al.*, 2004; Silvertown, 2004; Chu & Adler, 2015). Sizes and overlaps of niches based on functional traits have been shown to be particularly predictive for interspecific competition and resource partitioning (Adler *et al.*, 2013; Junker *et al.*, 2013). Given that ecologically relevant functional traits have been considered, studies that characterize the functional niches of potential competitors can improve our ability to understand species interactions, co-occurrence and responses to environmental change as well as the relative importance of different niche dimensions (Adler *et al.*, 2013; Vannette & Fukami, 2014; Winemiller *et al.*, 2015). Our data on trait-based niches show that native flower visitors shared a larger proportion of their niches with introduced flower visitors than *vice versa*. This asymmetric niche overlap could be observed when floral traits and weather conditions were considered. Thus, our results suggest that native taxa experience a high competitive pressure from introduced taxa.

Most studies that estimate the niche overlap of flower visitors refer to the proportion of shared plant species between flower-visitor species (e.g. Goulson *et al.*, 2002; Paini & Roberts, 2005). As expected, the proportion of shared plant species predicts the trait-based niche overlap as calculated by *dynamic range boxes* (Junker et al. 2015b). Nonetheless, the large residuals in the relationship between the proportion of shared plant species and the trait-based niche overlap *port(A, B)* demonstrate the non-redundant character of both approaches. While both approaches inform about the observed interaction patterns, a trait-based calculation of niche overlaps also allows to identify the traits responsible for the observations and thus to reveal ecological mechanisms behind the interaction structure. Additionally, a trait-based approach allows making assumptions beyond observed interaction partners and thus about the ability of flower visitors to utilize resources in different or altered plant communities, e.g. due to introduced or displaced plant species.

Consequences for species and the Hawaiian ecosystem

Introduced plant species may alter the functional composition, i.e. the abundance, distribution, and diversity of traits of a community. In other regions in the world, native flower visitors are common visitors on flowers of introduced species (e.g. Chittka & Schürkens, 2001; Williams *et al.*, 2010), In contrast, we recorded only very few visits of native Hawaiian flower visitors on introduced plant species (see also Miller *et al.*, 2015). Note that the scarcity of these interactions is not the result of spatial mismatch as native flower visitors that were observed on native plant species also were also observed to ignore introduced plants at the same site. This leads to the assumption that natives are not able to utilize the resources offered by introduced plant species, suggesting that natives are not adapted to the new chemical or morphological flower traits. Introduced flower visitors, however, utilized both native and introduced plants species (approximately 25% of the number of flowers in our study area), and thus may avoid competition by switching to other resources (Denno *et al.*, 1995). Therefore, considering that introduced animal species frequently interact with native plant species, natives experience a strong competition for their resources (Traveset & Richardson, 2006). This asymmetry in competition pressure may even be intensified if introduced flower visitors are competitively superior over native flower visitors and fully deplete the resources of or deter native flower visitors from native plant species (Traveset & Richardson, 2006; Stout & Morales, 2009). Consequently, habitats with a high abundance of introduced plant and animal species may be unsuitable for native flower visitors (especially *Hylaeus* bees). Currently, abundances of native flower visitors in Hawaii are particularly low at low elevations (Banko *et al.*, 2002; Magnacca, 2007, Kuppler, personal observation) where invasive plant species are most abundant (Alexander *et al.*, 2011). Furthermore, facilitated by climate change it is predicted that invasive species will spread to higher elevations (Vorsino *et al.*, 2014) potentially diminishing suitable habitats for native flower visitors and thus, accelerate on-going decline of native flower visitors.

Several of the introduced plants in Hawaii are obligately outcrossing or have a limited degree of self-compatibility (Appendix A: Table A3) and thus depend on introduced flower visitors that nearly exclusively provided pollination service to them. Therefore, our data suggest that introduced pollinators support the establishment and reproduction of introduced plants, which coincides with earlier findings of such positive interactions (Barthell *et al.*, 2001; Stout *et al.*, 2002; Goulson & Derwent, 2004; Traveset & Richardson, 2006). This facilitation may further promote the spread of introduced species into the Hawaiian ecosystems that are already highly susceptible to invasions (Pokorny *et al.*, 2005).

It has been shown that *Apis mellifera* is the most important substitute for the pollination of wide-spread tree *Metrosideros polymorpha* in the abscences of the original native pollinators (i.e. birds) (Junker *et al.*, 2010). Thus, it is likely that *Apis mellifera* provides these services for other common native plant species as well, but it is unknown if this is also true for rare native plants (Hanna et al. 2013). However, while native *Hylaeus* bees show high levels of floral fidelity for native species, *Apis mellifera* often carries mixed pollen of native and introduced species (Miller et al. 2015) indicating differences in pollination efficiency. Overall, we still lacking basic knowledge about the Hawaiian pollinator system to understand the impact of introduced flower visitor on native plant species.

Conclusions

The results of our study show that introduced taxa are able to utilize a broader functional range of flowers than native flower visitors and thus may compete severely with the latter. Introduced plant species were nearly exclusively visited by introduced flower visitors suggesting that introduced plant species benefit from the high densities of introduced pollinators. Our trait-based approach provided a potential functional explanation for this observation showing that native species usually have small floral niches (i.e. are highly specialized), which suggests that native animals are not adapted to the traits of introduced species. Thus, the evolutionary background and the native trait composition of a community are important components determining the impact of introduced species on communities. Integrating functional traits such as flower chemistry and morphology into community ecological studies and the quantification of niche sizes and overlap allows one to identify the mechanisms underlying resource partitioning and interspecific competition, which is particularly important in the context of species invasions. Overall, our results contribute to the understanding of the success and spread of introduced species and the associated threat to native species that experience novel competitors. The presumed range expansion of invasive plant and flower visitor species will further reduce the availability of resources for native flower visitors while simultaneously increasing the competition for the same resources. This suggests further declines of native pollinator species and thus dramatic consequences for the Hawaiian ecosystem.

ACKNOWLEDGEMENTS

We thank Rhonda Loh, Robin Gottlieb, Klaus Lunau, Karl Magnacca, Luc Leblanc, Stefan Dötterl, and Irmgard Schäffler for organizational, technical and logistical support. We thank the United States Department of the Interior (National Park Service) for the permit to conduct our study in the Hawaii Volcanoes National Park (Permit#: HAVO-2013-SCI-0003). The project was supported by the Graduate School "Evolutionary Networks: Organisms, Reactions, Molecules" (E-Norm) and a Wolters-Vollhardt-scholarship of the Heinrich-Heine-University, Düsseldorf, Germany and the Deutsche Forschungsgemeinschaft (DFG, JU 2856/2-2).

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Synopsis

Functional plant traits have been increasingly used for investigating interaction patterns within communities (McGill *et al.*, 2006; Violle *et al.*, 2007; Shipley *et al.*, 2016). As the traits of an organism and not its taxonomy determine its survival, dynamics and interactions (Levine, 2015), functional plant traits provide a mechanistic explanation for interaction structures and species composition within communities (Díaz & Cabido, 2001; Cornwell & Ackerly, 2009). In plant-animal networks, we have currently a general understanding how functional plant traits mediate structures in communities. However, there are still gaps in our knowledge: How is intraspecific variation in functional plant traits related to interaction structures at different hierarchical levels (*i.e.* individual, species and community level)? Do functional plant traits provide a mechanistic explanation for community alterations due to disturbances? Within this thesis, we aimed to fill these gaps and foster our understanding of functional plant traits as a mechanistic explanation for community structure. We focussed on functional floral traits and flower-visitor interactions that are a central part in plant reproduction (*e.g.* Ollerton *et al.*, 2011) and therefore influence community and population dynamics and structure (*e.g.* Parachnowitsch *et al.*, 2012; Junker *et al.*, 2013; Junker & Parachnowitsch, 2015). Specifically, we investigated if intraspecific variation floral traits drive non-random differences in interaction at plant individual level and the influence of these patterns at species level. To quantify the niche size and overlap of *n*-dimensional hypervolumes (Hutchinson, 1957) based on functional traits, we developed a novel non-parametric approach '*dynamic range boxes*'. By applying this approach we tested hypotheses of invasion biology regarding trait-based niche competition of flower visitors. In combination these studies show that functional plant traits provide a mechanism to explore community structure and its response to changes or alterations within communities. Further, they emphasize the importance of considering intra- and interspecific functional trait variation.

Influence of floral trait variation on interaction structures

At individual level – Importance of intraspecific variation

In evolutionary biology, intraspecific variation in functional traits has long been recognized as an important driver for evolution (*e.g.* Newton *et al.*, 1999). In community ecology, classically the focus was laid on interspecific variation and species mean values of plants. However, not accounting for intraspecific variability may lead to an underestimation of functional plant diversity and complexity of communities (Bolnick *et al.*, 2011; Violle *et al.*, 2012). We begin to understand the impact and importance of individual difference of animals for the structure of interaction networks (Dupont *et al.*, 2011; Song & Feldman, 2014; Tur *et al.*, 2014, 2015), while comparable studies for plant species have been scarce. To address the question whether intraspecific variation in functional plant traits mediates non-random interaction patterns of plant individuals, we conducted a common garden experiment. Here, we quantitatively recorded all interactions between arthropods, flowers and leaves through the lifetime of multiple plant individuals of one species and linked these to the individual phenotype. This approach minimized the environmental heterogeneity and thereby allowed us to evaluate plant intrinsic factors (*i.e.* functional traits) as structuring mechanisms. We could show that neighbouring plant individuals differed qualitatively and quantitatively in their interactions with arthropods. These non-random differences were stable over the entire season, *i.e.* time-invariant (Chapter 1). Figure 3 shows the resulting conceptualised niche structure of a flower-visitor community.

Quantitative variation in interaction patterns was the major differentiating factor as most flower visitor species were at least once recorded on nearly all plant individuals of one species. Individuals with a similar phenotype received consistently (over the entire season) more visits of a certain flower visitor taxa than individuals with different phenotypes (Figure 3, Chapter 1). Whether this non-random partitioning is present in a plant species likely depends on the degree of intraspecific variation in functional plant traits/phenotype. Plant species harbouring large intraspecific variation provide more opportunities for partitioning than plant species with small variation. Consequently, large intraspecific variation may allow more flower visitor species to utilize the same plant species without excluding each other. This follows the “competitive exclusion principle” which stats that out of two species one will be excluded if the trait-use patterns of both are too similar (Hardin, 1960; Götzenberger *et al.*, 2012). This is similar to patterns at community level where a functionally more diverse plant community promotes a larger diversity of flower visitors (Junker *et al.*, 2013, 2015).

In addition, functionally diverse communities are more stable towards disturbances and environmental changes than less diverse communities (Turnbull *et al.*, 2013; Loreau & de Mazancourt, 2013). This may also apply for plant species exhibiting a large intraspecific variation. Such species have a greater capacity to respond to disturbances or changes by intraspecific trait shifts or contain already individuals with a certain trait expression that allows them to reproduce under the changing conditions, *e.g.* raising temperatures. In case of floral traits, species with a high intraspecific variability might be more stable against changes in the regional pollinator pool. Community stability can be distinguished into stability towards short-term and long-term environmental change. To explore the relevance of intraspecific variation as response to environmental change, the cause of variation needs to be considered (*i.e.* phenotypic plasticity and genotypic variation) (Ackerly, 2003). If high intraspecific variability arises from phenotypic plasticity it is more likely to correlate with stability towards short-term environmental changes. Genotypic variation (*i.e.* higher potential for evolutionary responses) on the other hand is more important with regard to long-term environmental changes that select for trait values outside the range of plasticity of resident plants (Ackerly, 2003; Ibanez *et al.*, 2016).

At individual level, variation in functional plant traits and visitation patterns indicates that plant individuals occupy distinguishable functional positions in a community. Thus, incorporating intraspecific variation may largely improve our understanding of interactions within community and their vulnerability to alterations, *e.g.* due to global change. .

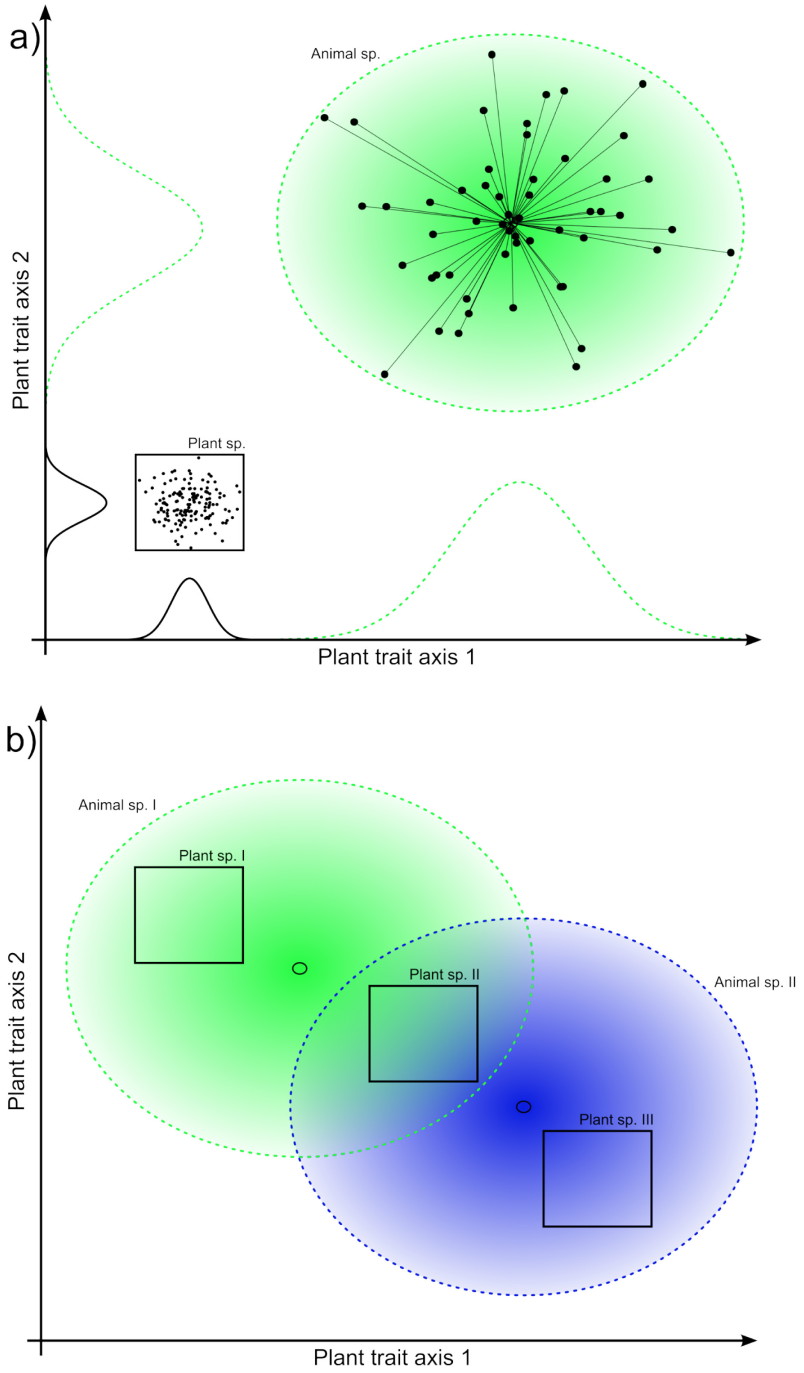

Figure 3. Conceptualised niches within a flower-visitor community. Axes represent functional plant traits (*i.e.* niche dimensions). Each black box represents the trait space of one plant species with the box size corresponding to the degree of intraspecific variation in functional traits. Dotted ellipses depict the full trait space utilized by a flower visitor species (different colour indicate different species). Colour gradient within ellipses correspond to the interaction frequency of the flower visitor within the trait space. Dark colouration indicates high frequencies, light colouration low frequencies. a) Black curves (curve height = observed frequency of a trait value within a plant species in one niche dimension) depict distribution of plant individuals

(black dots) within the trait space (black box). Dotted, green curves (curve height = observed interaction frequency at a trait value in one niche dimension) depict distribution of interactions of flower visitor within the trait space. Each black dot represents a flower visitor individual interacting with a certain phenotype and black lines indicate the distance of the individual to the centroid of the ellipse. b) Different colouration within plant species (*i.e.* black boxes) depicts different interaction frequency of a flower visitor species. Plant individuals with a phenotype closer to centroid of the ellipse may have a higher interaction frequency with the flower visitor species than phenotypes more distant from the centroid. In case a plant species (plant sp. II) interacts with two (or more) flower visitor species, phenotypes that are closer to one of the centroids may receive consistently more visits by this given flower visitor species (compare Chapter 1).

At species & community level – Consequences of intraspecific variation

The prevailing differentiations within a plant species may also influence structures at species/community level. The structures of multi-species interactions/communities species level are commonly described using aggregated networks statistics. These statistics usually use species means and do not incorporate intraspecific variation in interaction patterns (Dormann *et al.*, 2009). In chapter 1, we could show that plant individuals have distinct non-random interaction patterns, which were time-invariant. In this context, it is valuable to understand how interactions at individual level may drive interaction patterns and differentiation at higher hierarchical levels and how they affect the robustness of network statistics and the ecological assessment of communities. Using a resampling approach, we demonstrated that network statistics are sensitive to observed intraspecific variation within one plant species (Chapter 2). This volatility of network statistics stresses the importance of sufficient and representative sampling (Blüthgen, 2010; Fründ *et al.*, 2015) to get a robust estimate of the species mean. The sampling effort for plant species with a low intraspecific variation in functional plant traits may be lower as individuals may not differ largely in their interactions patterns. However, for plant species that show a large variation in functional traits the estimated mean interactions of species may strongly depend on the area of the trait space and the associated interactions sampled (Figure 3b; plant species II). Insufficient sampling of a rather generalized species in terms of interactions patterns may therefore indicate this species as specialized in the network.

Often, networks contain a large number of singletons or doubletons (*i.e.* species that are only observed once or twice) (Olesen *et al.*, 2012). In such cases it is rather unlikely that these observations represent a good estimate of the species mean. This is especially problematic as our results showed that even small quantitative changes in interactions within a single plant species can alter the ecological conclusions derived from network statistics (Chapter 2). Thus, the inclusion of one or several unreliable species means may lead to an inaccurate description of the ecological properties of a community/network. As nowadays network statistics are increasingly used to monitor and explore the ecological impact of global change in communities (*e.g.* Gray *et al.*, 2014; Kaiser-Bunbury & Blüthgen, 2015) such inaccuracies may affect our understanding of these impacts. Consequently, a careful usage of network statistics as indicator for community stability and the impact of environmental change on interactions patterns is necessary to fully utilize the merit of this approach.

Overall, we showed that intraspecific variation in functional plant traits drive non-random differences in individual interaction patterns (Chapter 1) and that those can influence the structure (*i.e.* network statistics) described at species/community level. Thus, hierarchical levels and their interconnections are important to consider in unravelling the structures and dynamics in plant communities. Further, taking intraspecific variation into account may improve our understanding of community responses towards disturbances and global change.

At species/community level - Trait-based niche structure in response to introduced species

Besides network statistics the structures within communities can be investigated by comparing the size and overlap of the trait spaces (*i.e* niches) utilized by different species (Figure 2 & 3). Within this thesis, we developed a novel non-parametric approach '*dynamic range boxes*' to get a robust quantification of the size and overlap of *n*-dimensional hypervolumes. This approach is robust against outliers, considers the distribution of the data, works in high dimensions (*i.e.* multiple traits) and provides the information of the contribution of each single dimension and thus, overcomes the shortcomings and limitations of other methods (Chapter 3).

Trait-based niche size and overlap between species can be used to investigate the alterations within communities induced by disturbances, *e.g.* the establishment of new plant and/or animal species, which can compete and even displace native species (Mouillot *et al.*, 2013; Richardson & Ricciardi, 2013; Simberloff *et al.*, 2013). Here, according to niche theory the competition potential of two species for *e.g.* a limiting resource increases with the similarity of their ecological niches (Townsend *et al.*, 2003). Using our novel approach 'dynamic range boxes' (Chapter 3), we investigated the trait-based niche size and overlap of native and introduced flower visitor species in the Hawai'i Volcanoes National Park, Hawai'i, USA, (Chapter 4) at species/community level.

Niche sizes and overlaps were used to examine two hypotheses explaining the establishment, spread and impact of introduced species: the "superior competitor hypotheses" and the "invasional facilitation hypotheses" (Inderjit *et al.*, 2005). The first states that invaders are more generalized in their interactions and resource use and also more efficient in obtaining limited resources, while the second states that one (or more) invaders positively influence the growth, survival or spread of another invader; the invaders may or may not share a co-evolutionary history (Inderjit *et al.*, 2005). Our results showed that introduced flower-visitors had larger floral niche sizes and overlap the resource niches of native species more strongly than *vice versa*. While niche size and overlap was similar in some floral traits, introduced flower visitors had larger niche size in floral scent and certain morphological traits, *e.g.* nectar tube depth. Further, introduced flower visitors were less constraint by weather conditions while native ones mostly forage in warm and sunny conditions. In contrast to native flower visitors, which rarely visited introduced plant species, introduced flower visitor species similarly utilized introduced as well as native species. This may indicate that native flower visitors were not adapted to utilize the functional traits or their combinations displayed by introduced plant species. In summary, our results revealed functional traits as an ecological mechanism underlying resource partitioning and competition between native and introduced flower visitors. Therefore, using functional traits we could confirm two longstanding hypotheses in invasion biology and provide a mechanistic explanation for both. This adds to the growing body of work that uses functional traits to explain basic principles/hypotheses of invasion biology as well as the impact of introduced species (*e.g.* Funk *et al.*, 2008; Lurgi *et al.*, 2014).

Niche overlap between native and introduced species may not only indicate competition potential, but also a certain degree of functional redundancy, *i.e.* equivalence in trait spaces/niches (Traveset & Richardson, 2014, Figure 3). If an introduced species is functional redundant with a native one it may not only compete with the native one, but also may have the potential to replace it ecologically (Hobbs *et al.*, 2006). In case of flower visitors, introduced species may become novel pollinators of native plant species. However, the effective replacement of native pollinators largely depends on their pollination efficiency compared to native ones (Miller *et al.*, 2015). In cases where introduced species are ecologically equivalent or similar to native ones, they may cause detrimental effects on certain native species, but only small effects on ecosystem functioning (Hobbs *et al.*, 2006; Traveset & Richardson, 2014; Searcy *et al.*, 2016). Identifying the ecological role of introduced species in their new ranges is critical to understand their impact and fate within communities and ecosystems (Simberloff *et al.*, 2013; Searcy *et al.*, 2016). Quantifying niche structures based on functional traits can not only inform us on their ecological role within communities, but also may allow us to predict interactions within new areas. Such information can be valuable in recognizing susceptible habitats for the establishment of invasives and also for the restoration of highly suitable habitats for desired native species (Funk *et al.*, 2008; Pearse & Altermatt, 2013; Ostertag *et al.*, 2015).

Main conclusion

Functional plant traits as an interface of plant and plant-visiting animal species provide a central mechanism explaining community structures. Intraspecific functional trait variation in plants species – similar to animal species – can be an important factor for community structures at individual as well as species level. Along with these findings, our results indicated that functional traits provide a powerful tool to understand and predict the outcomes and responses of communities to global change. Thus, considering functional plant traits at different hierarchical level can improve our knowledge of community structure and dynamics and thereby help generate a general understanding of the fate of communities under global change.

Outlook

Despite our growing knowledge of the structuring role of functional plant traits in communities, we only begin to fully understand the importance of intraspecific trait variation in communities and potentially ecosystem functioning. Further, functional traits provide a promising avenue to understand and predict the impact and fate of introduced species and environmental change. Thus, future research should address the following points to obtain a more comprehensive and complete understanding of functional trait variation within communities and as response to global change:

- In Chapter 1, we demonstrated that plant individuals of one species showed non-random intraspecific interaction patterns. However, we need to experimentally test if these patterns are widespread within plant species and whether these non-random interaction patterns are related to the degree of intraspecific variation in floral traits, *i.e.* if plant species with a small intraspecific variation do not or to a lesser extent show these distinct patterns.

- Intraspecific variation in functional traits may improve our understanding of the response of communities towards environmental change (Chapter 1, Violle *et al.*, 2012; Moran *et al.*, 2015). However, its contribution to community stability is still poorly understood. We need carefully designed experiments that further entangle this contribution. In this context, it is also valuable to investigate the importance of phenotypic plasticity and genotype as driver for intraspecific variation and in response to environmental change.

- Intraspecific variation in functional traits and/or interaction patterns can be large in flower visitor and plant species (*e.g.* Song & Feldman, 2014; Tur *et al.*, 2014, 2015). However, experimentally this has been mostly tested on a single species (Chapter 1, Dupont *et al.*, 2011; Tur *et al.*, 2014, 2015). Despite the logistic difficulties, a multi-species investigation of individual patterns of plants and animals may further improve our understanding of the complex structure and dynamics within communities and the influence of individual level structures on species level structures.

- We used a resampling approach to investigate the influence of intraspecific variation on networks statistics (Chapter 2). Using observational studies in multi-species networks to test for volatility in network statistics to validate our results would greatly improve our understanding of the usefulness of network statistics to describe ecological properties of communities.

- Introduced and native flower visitor can overlap largely in their niches (Chapter 4). Unfortunately, we were not able to include plots in our study where invasive flower visitor species were completely absent. Comparing the niches of native species from such areas with areas were introduced species are present would largely improve our understanding of competition between both.

- The analyses of niche shifts between native and non-native range of a species can provide valuable information about the determinants of species distribution and for potential range expansion. So far, most studies focus only on climatic niche shifts (Gonzalez-Moreno *et al.*, 2015). Using our novel approach, the comparison of niches in the native and introduced range based on functional traits may yield further insights into these complex and important questions.

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Acknowledgements

I am deeply thankful to **Robert R. Junker** for giving me the opportunity to work on fascinating projects, learn tons of new stuff, visit interesting conferences and great places and finish my dissertation. Moreover, thank you for your support and guidance, the discussions, all the things I learned and for being enthusiastic and optimistic, when I was not.

I am grateful to **Klaus Lunau** for always being supportive and uncomplicated in many ways and for being my referent. Further, I would like to thank **Arnold Janssen** for being the second reviewer of this thesis.

During my time in Düsseldorf and Salzburg I had to pleasure to share the office, lab, kitchen and time with a lot different people, thank you all for the discussions, chitchats, coffee breaks, help, cake and cookies & many other things. Especially I want to thank my fellow PhD-colleagues **Anne-Amélie C. Larue-Kontić**, **Sarah Papiorek** and **Mathias Hoffmeister**. **Anni** and **Matti** without you so many things would be far more difficult and definitely less fun, thank you for everything! I am thankful to **Maren K. Höfers** for her company, her effort and her data collection during my thesis and **Irmgard Schäffler** and **Matthias Affenzeller** for your constant help, company and sharing your delicious food.

My thesis would not have been possible without the help and support of many people. I would like to thank **Arne C. Bathke**, **Wolfgang Trutschnig** and **Manuela Schreyer** for the great, easy and fun hours developing 'dynamic range boxes'; **Stefan Dötterl** and **Irmgard Schäffler** for sharing all your knowledge and answering questions regarding scent analyses; **Robin Gottlieb**, **Tobias Grasegger**, **Carola Helletsgruber**, **Johannes Herrmann**, **Birte Peters**, **Susanne Popp**, **Dominique Reiter**, **Martin Schlager** and **Lisa Wiesmann** for help with data collection and great effort in the field or lab; **Annette Eder-Martin** for all your help and support; **Elisabeth Egger** and the **gardeners of the Botanical Garden of the University Salzburg**, Austria, **Martin Zimmer** and **Rocio Perez-Barrales** for logistical, statistical and technical support; **Anja Hörger, Sophie Kuppler** and **Anette van der Aa** for valuable comments and critics on earlier versions of this thesis.

The field season in Hawai'i would not have been possible without **Curtis C. Daehler** and the permission of the United States Department of the Interior (National Park Service) to conduct our study in the Hawaii Volcanoes National Park (Permit#: HAVO-2013-SCI-0003). **Jesse A. Eiben** provided labspace as well as great support. Further, **Jesse A. Eiben**, **Karl Magnacca** and **Luc Leblanc** gave indispensable advice and help in identifying Hawaiian insects.

The work in this thesis was supported by the E-Norm Graduiertenkolleg der Heinrich-Heine-Universität Düsseldorf und der Deutschen Forschungsgemeinschaft.

Appendix

List of Publications

This thesis is based on the following manuscripts:

Kuppler J, Höfers MK, Wiesmann L & Junker RR (2016). Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent. ***New Phytologist*** (2016) DOI: 10.1111/nph.13858

Kuppler J, Grasegger T, Peters B, Popp S, Schlager M & Junker RR (2016). Volatility of network indices as a result of intraspecific variation in plant-insect interactions. *submitted*

Junker RR, Kuppler J, Bathke A, Schreyer M & Trutschnig W (2016). Dynamic range boxes – A robust non-parametric approach to quantify size and overlap of n-dimensional hypervolumes. ***Methods in Ecology and Evolution***, *under revision*

Kuppler J, Höfers MK, Trutschnig W, Bathke AC, Eiben JA, Daehler CC & Junker RR (2016). Trait-based quantification of floral niche size and overlap reveals mechanisms underlying resource partitioning and competition between native and introduced flower visitors. *in preparation*

The authors' contribution

Chapter 1 - Kuppler J, Höfers MK, Wiesmann L & Junker RR (2016). Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent. *New Phytologist* (2016) DOI: 10.1111/nph.13858

JK and RRJ designed the study, JK, LW and MKH collected the data, JK, LW, MKH and RRJ analysed the data, JK drafted the first version of the manuscript and JK and RRJ wrote the final version.

I hereby confirm that the above given information are correct

Prof. Dr. Klaus Lunau

Chapter 2 - Kuppler J, Grasegger T, Peters B, Popp S, Schlager M & Junker RR (2016). Volatility of network indices as a result of intraspecific variation in plant-insect interactions. *submitted*

JK and RRJ designed the study, JK, TG, BP, SP & MS collected data, JK and RRJ analysed the data. JK and RRJ wrote the first draft of the manuscript and all authors contributed to the final version.

I hereby confirm that the above given information are correct

Prof. Dr. Klaus Lunau

Chapter 3 - Junker RR, Kuppler J, Bathke AC, Schreyer M & Trutschnig W (2016). Dynamic range boxes – A robust non-parametric approach to quantify size and overlap of n-dimensional hypervolumes. *Methods in Ecology and Evolution*, *under revision*

RRJ conceived the first idea for the method, RRJ, JK, ACB, MS and TW developed and designed the method, RRJ drafted the first version of the manuscript and all authors contributed to the final version.

I hereby confirm that the above given information are correct

Prof. Dr. Klaus Lunau

Chapter 4 - Kuppler J, Höfers MK, Trutschnig W, Bathke AC, Eiben JA, Daehler CC & Junker RR (2016). Trait-based quantification of floral niche size and overlap reveals mechanisms underlying resource partitioning and competition between native and introduced flower visitors. *in preparation*

JK and RRJ designed the study, JK and MKH collected the data, RRJ, JK, WT and ACB developed the statistical methods used, JK and RRJ analysed the data, JK and RRJ drafted the first version of the manuscript and all authors contributed to the final version.

I hereby confirm that the above given information are correct

Prof. Dr. Klaus Lunau

Declaration of self-contained work

Herewith, I confirm that I composed the dissertation

"FUNCTIONAL FLORAL TRAITS AS MECHANISTIC EXPLANATION FOR COMMUNITY STRUCTURE",

single-handed without utilizing illegitimate resources. I used no other than the cited references and facilities. This work has not been previously handed in to another university and was not subject to miscellaneous examinations.

10.05.2016, Düsseldorf

Jonas Kuppler

Supplementary Material Chapter 1

***New Phytologist* Supporting Information**

Article title: **Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent**
Authors: Jonas Kuppler, Maren K. Höfers, Lisa Wiesmann & Robert R. Junker
Article acceptance date: 9 December 2015
The following Supporting Information is available for this article:

Figure S1: Intraspecific leaf-visitor network
Figure S2: Proportional visitation frequency of the different visitor taxa
Figure S3: Differences of mean ranks within populations
Figure S4: Differences of mean ranks (Null model based on number of flowers)
Figure S5: Individual flower visitor community
Table S1: Species list of observed flower visitors
Table S2: Trait sampling
Table S3: Scent bouquet of *Sinapis arvensis* flowers
Table S4: Differences of mean ranks within populations
Table S5: Differences of mean ranks (Null model based on number of flowers)
Table S6: Influence of population and fertilizer treatments on single plant traits and reproductive success
Table S7: Influence of population and fertilizer treatment on plant phenotype
Methods S1: Additional Materials & Methods
Notes S1: Comparison of intra- and interspecific trait variation and visitation patterns
Notes S2: Multivariate visualisation of the association between traits and visitation rate

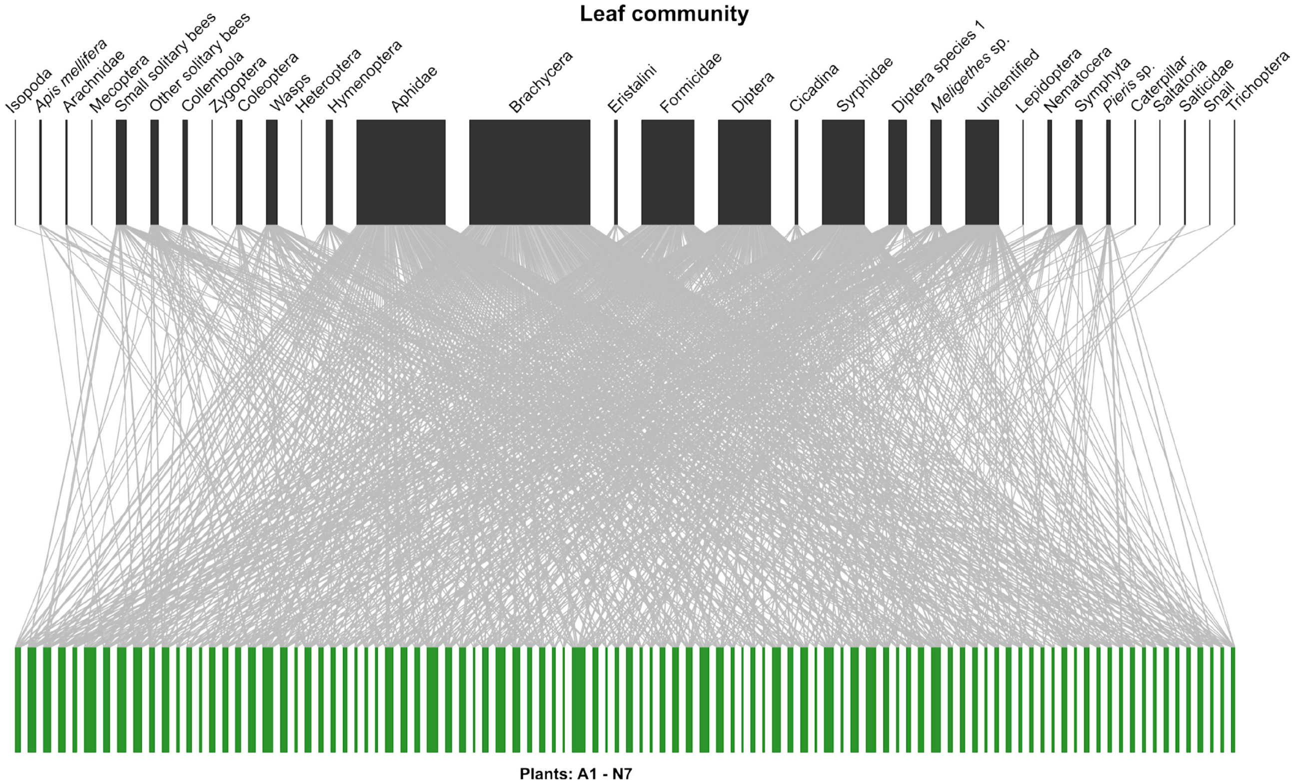


Figure S1. Bipartite networks for leaf community based on individual plants. Plant individual are ordered by their IDs in the experimental field (Starting at the left: A1, A2, A3, …, till N7 at the right).

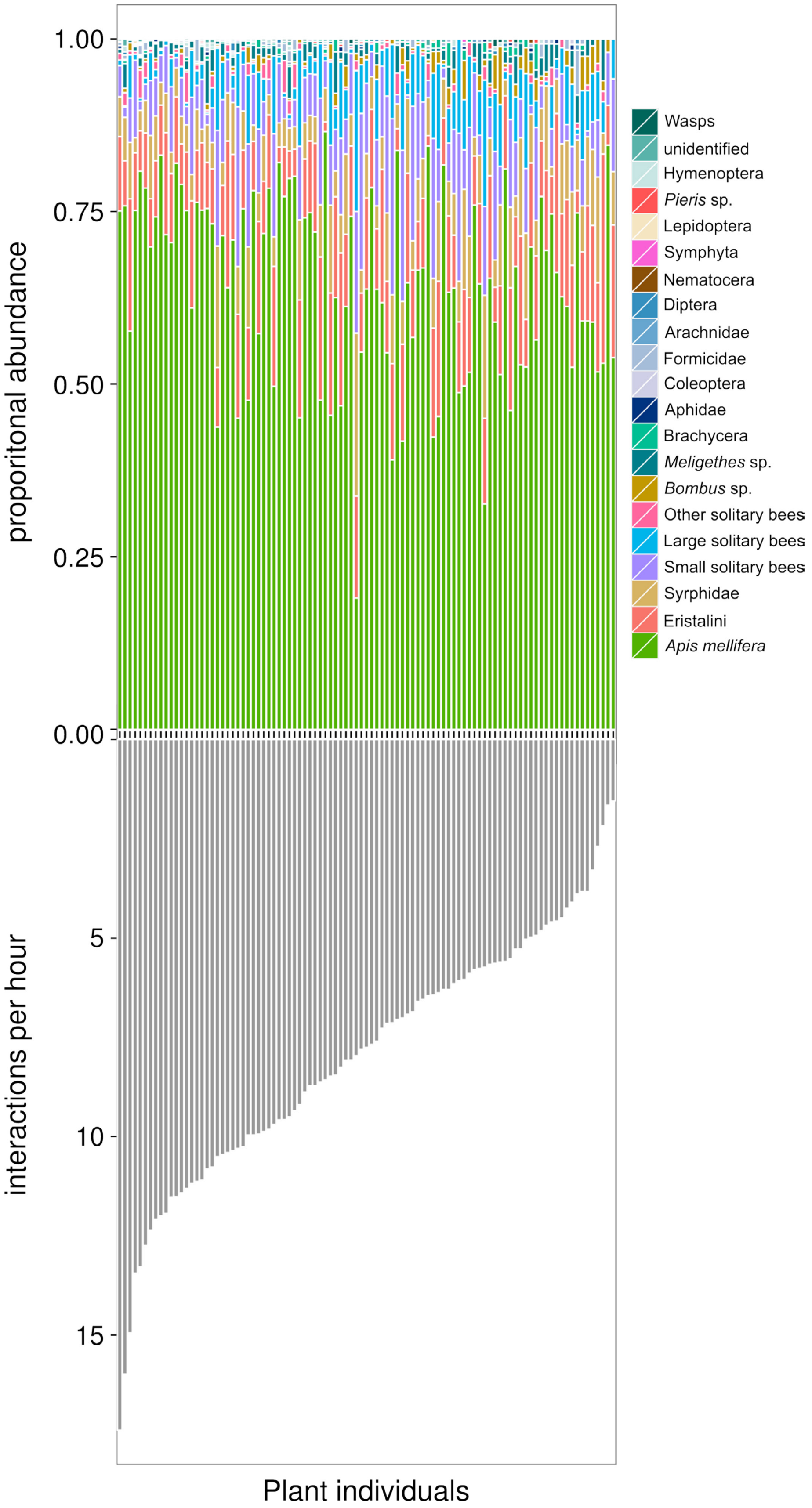


Figure S2. Proportional visitation frequency of the different visitor taxa (upper plot; based on number of interactions per hour) and total number of interactions per hour (lower plot) for each plant individual. The coloured stacked-barplot is ordered by the total number of interactions of all visitor taxa per hour (lower plot).

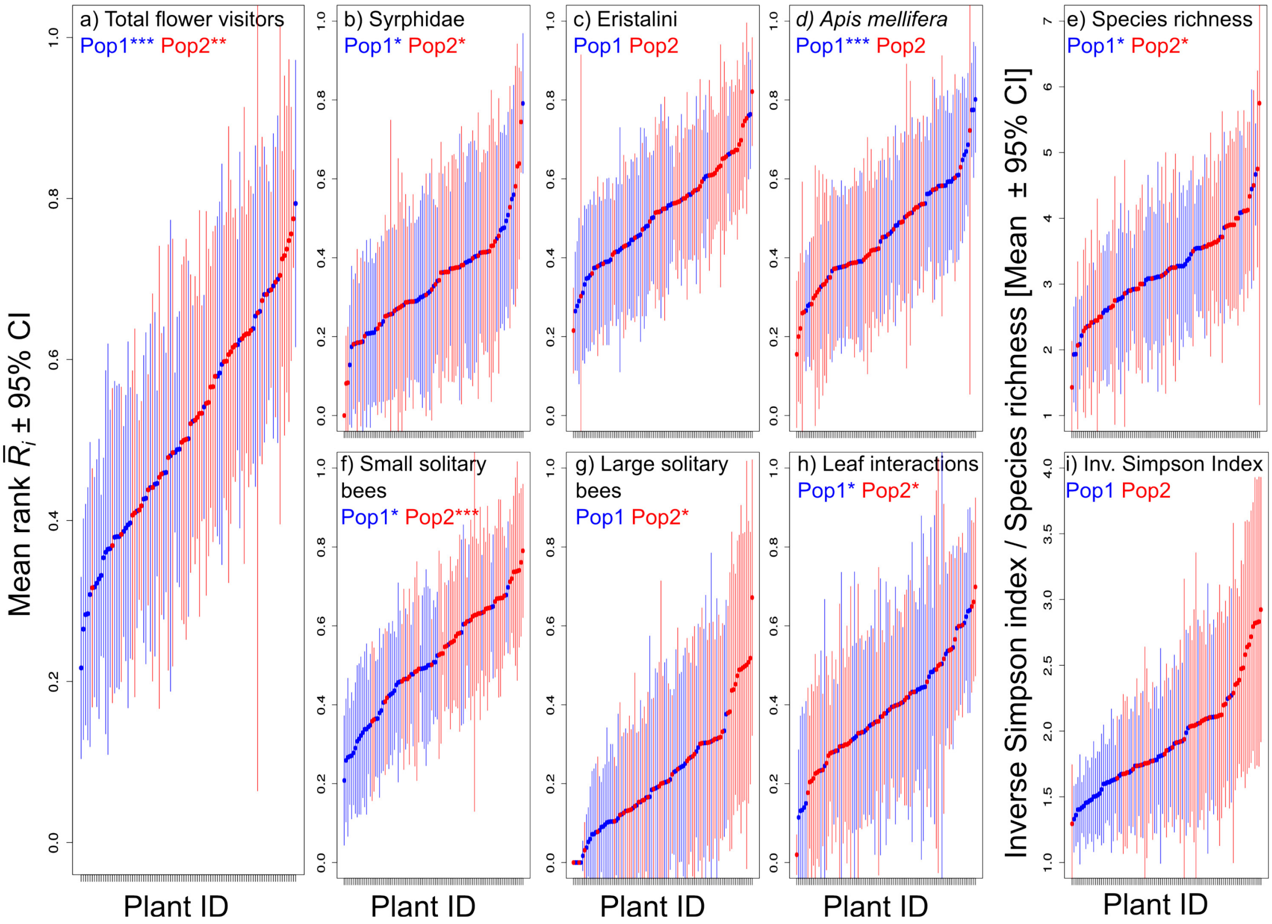


Figure S3. a) – d), f) - h): Mean ranks $\overline{R}_i$ with 95% confidence intervals (CI) for all plant individuals; Plants of the German population (Population 1) are shown in blue, plants of the English population (Population 2) in red. Graphs for different visitor groups are shown. To check if the Ranks R_i for each plant individual *i* were invariant over the observation days ANOVA was used. e): Species richness per day and i) mean inverse Simpson index (upper points) with 95% confidence intervals (CI) for all plant individuals. Mean ranks $\overline{R}_i$ and means of each plant individual was compared using ANOVA. Results are given in Table S4. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

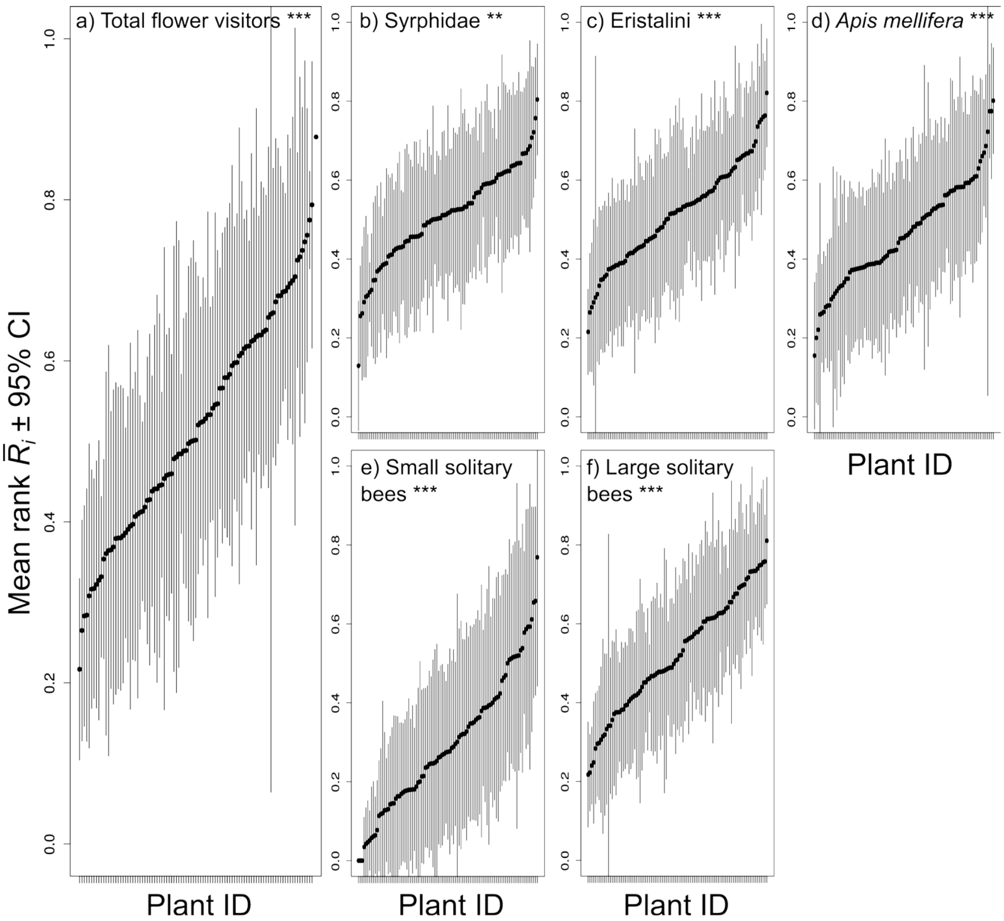


Figure S4. Time invariant differences in visitation frequencies between plant individuals. a) – f): Each plots shows the mean ranks $\overline{R}_i$ with 95% confidence intervals (CI) of all 97 plant individuals for total number of flower visitors or different visitor taxa. Mean ranks were calculated using null model expectation based on number of flowers per individual, number of interaction per individual is proportional to number of flowers per individual. On each observation day, the plant individuals *i* were ranked based on increasing interaction frequencies with arthropod taxa. Mean ranks $\overline{R}_i$ and means of each plant individual were compared using linear mixed-effect models and -likelihood ratio test, significance levels are given as asterisks: *** $p < 0.001$, ** $p < 0.001$. Results are given in Table S5.

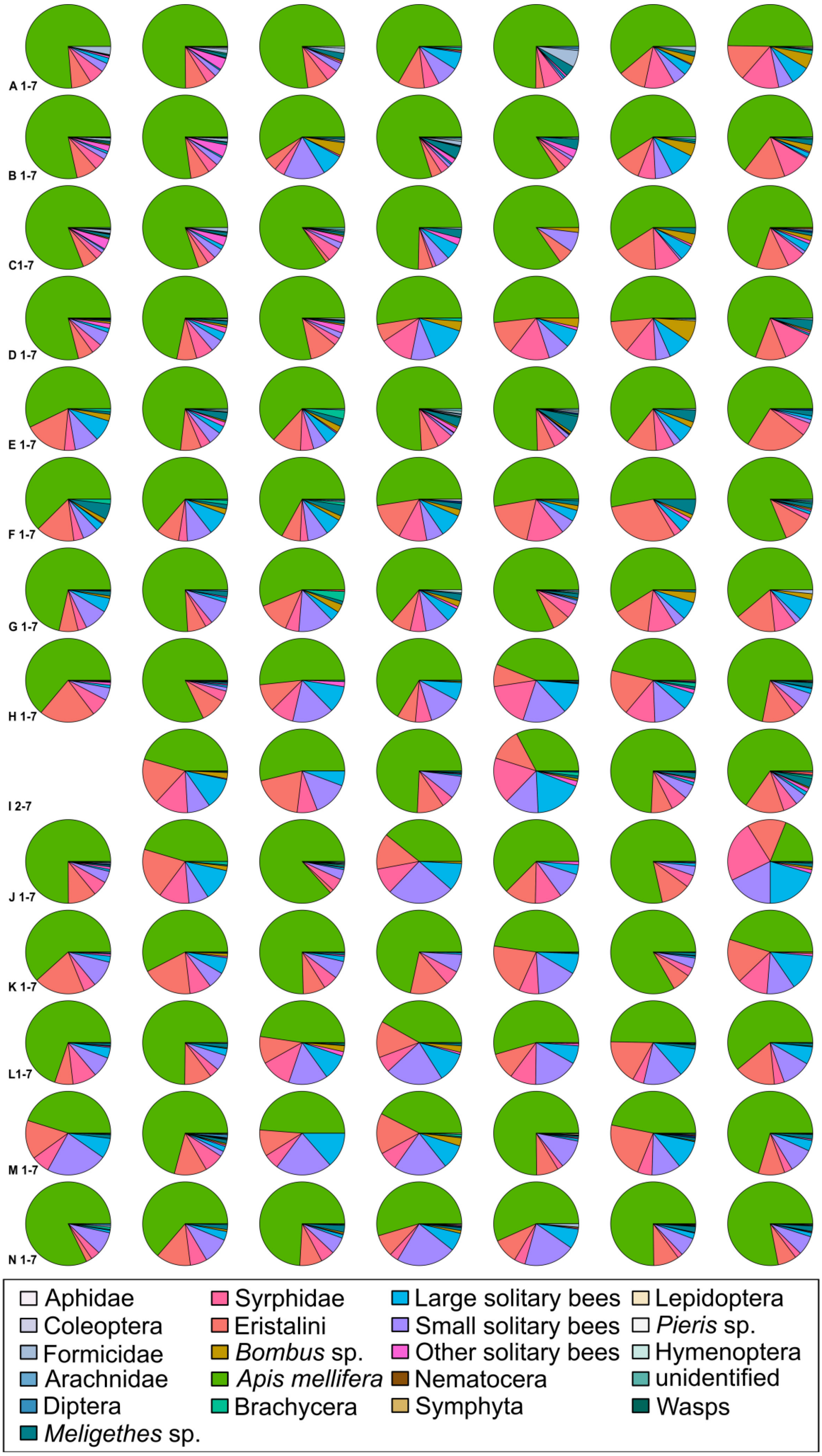


Figure S5. Composition of the flower-visitor communities for each plant individual (A1 – N7).

Table S1. Species list of observed flower visitors.

Family	Subfamily	Species
Large solitary bees		
Andrenidae	Andreninae	*Andrena agilissima* (Scopoli, 1770)
Andrenidae	Andreninae	*Andrena bicolor* (Fabricius, 1775)
Andrenidae	Andreninae	*Andrena chrysosceles* (Kirby, 1802)
Andrenidae	Andreninae	*Andrena cineraria* (Linnaeus, 1758)
Andrenidae	Andreninae	*Andrena haemorrhoa* (Fabricius, 1781)
Halictidae	Halictinae	*Lasioglossum calceatum* (Scopoli 1763)
Small solitary bees		
Andrenidae	Andreninae	*Andrena minutula* (Kirby, 1802)
Andrenidae	Andreninae	*Andrena subopaca* (Nylander, 1848)
Halictidae	Halictinae	*Halictus tumulorum* (Linnaeus, 1758)
Halictidae	Halictinae	*Lasioglossum laticeps* (Schenk, 1870)
Halictidae	Halictinae	*Lasioglossum morio* (Fabricius, 1793)
Halictidae	Halictinae	*Lasioglossum nitidiusculum* (Kirby, 1802)
Halictidae	Halictinae	*Lasioglossum pauxillum* (Fabricius, 1793)
Eristalini		
Syrphidae	Eristalinae	*Eristalinus aeneus* (Scopoli, 1763)
Syrphidae	Eristalinae	*Eristalis arbustorum* (Linnaeus, 1758)
Syrphidae	Eristalinae	*Eristalis tenax* (Linnaeus, 1758)
Syrphidae	Eristalinae	*Merodon equestris* (Fabricius, 1794)
Syrphid flies (without Eristalini)		
Syrphidae	Syrphinae	*Chalcosyrphus nemorum* (Fabricius, 1805)
Syrphidae	Syrphinae	*Dasysyrphus albostriatus* (Fallén, 1817)
Syrphidae	Syrphinae	*Episyrphus balteatus* (De Geer, 1776)
Syrphidae	Syrphinae	*Eupeodes corolla* (Fabricius, 1794)
Syrphidae	Syrphinae	*Helophilus pendulus* (Linnaeus, 1758)
Syrphidae	Syrphinae	*Lapposyrphus lapponicus* (Zetterstedt, 1838)
Syrphidae	Syrphinae	*Melanostoma mellinum* (Linnaeus, 1758)
Syrphidae	Syrphinae	*Melanogaster hirtella* (Loew, 1843)
Syrphidae	Syrphinae	*Neoascia oblique* (Coe, 1940)
Syrphidae	Syrphinae	*Neoascia podagrica* (Fabricius, 1775)
Syrphidae	Syrphinae	*Platycheirus albimanus* (Fabricius, 1781)
Syrphidae	Syrphinae	*Scaeva selenitica* (Meigen, 1822)
Syrphidae	Syrphinae	*Sphaerophoria interrupta* (Fabricius, 1805)
Syrphidae	Syrphinae	*Sphaerophoria scripta* (Linnaeus, 1758)
Syrphidae	Syrphinae	*Syritta pipiens* (Linnaeus, 1758)
Syrphidae	Syrphinae	*Syrphus vitripennis* (Meigen, 1822)

Table S2. Traits quantitatively measured for each plant individual. Abbreviations, sampling methods and mean ± standard error (SE) are given. Mean ± SE for scent compound see Table S3

Trait	Sampling method	Mean ± SE
Floral morphology		
Stamen length[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	6.90 ± 1.21 mm
Short anther length[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	4.53 ± 0.95 mm
Long anther length[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	7.53 ± 0.87 mm
Petal width[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	5.72 ± 0.89 mm
Petal length[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	7.46 ± 0.81 mm
Flower shape[1,2]	Photo taken, see Appendix S1	---
Display size flower[1,2]	Caliper rule	1.61 ± 0.205 cm
Inflorescence height[2]	Tape measure	86.41 ± 17.50 cm
Display size inflorescence[1,2]	Caliper rule	3.57 ± 0.79 cm
Mean number of flowers per inflorescence[3,4]	Mean value of flowers per inflorescence (counted, five blooming inflorescences)	5.38 ± 1.06
Mean number of inflorescence[3,4]	Mean of number of inflorescence per week (counted once per week)	6.62 ± 2.81
Scent[1,2]	See Material & Methods and Methods S1	----
Vegetative morphology		
Leaf hairiness[1,2]	Counted number of trichomes on 1cm² in the middle of the leaf	10.30 ± 12.298
Leaf length[1,2]	Caliper rule	7.33 ± 2.211 cm
Leaf width[1,2]	Caliper rule	4.11 ± 1.20 cm
Leaf area[1,2]	Photo taken incl. scale, measured with Fiji, ImageJ	25.98 ± 13.62 cm²
Mean number of leafs[3]	Mean of number of leafs per week (counted once per week)	10.88 ± 3.02
Stem Hairiness[2]	Counted number of trichome on 1 cm of the stem in the middle between the two lowest leafs	70.31 ± 26.51
Silique morphology		
Number of siliques[2]	Total number of siliques (counted)	128.09 ± 59.62
Number of seeds per siliques[2]	Mean number of seeds per silique (10 siliques per plant)	8.92 ± 1.24
Silique width[2]	Caliper rule	2.84 ± 0.389 mm
Silique length[2]	Caliper rule	2.97 ± 0.33 cm
Phenology		
Day of first flower	Number of days between germination and first flower	33.81 ± 6.01
Flowerperiod	Number of days each plant had open flowers	13.14 ± 3.11

Reproductive success		
Seed set[2]	Number of silique multiple with mean number of seeds per silique	1162.40 ± 622.53
Seed size[2]	Mean of the area of 25 seeds per plant. Photo taken including scale, measured with Fiji, ImageJ	2.03 ± 0.31 mm^2
Number of seeds per flower[2]	Number of seeds divided by mean numbers of flowers	43.78 ± 18.16
Seed dormancy[2]	(Luzuriaga *et al.* 2006), 64 seeds per plant	92.89 ± 11.76 %
Seed viability[2]	(Luzuriaga *et al.* 2006), 64 seeds per plant	98.25 ± 3.12 %

[1] Residuals from regression over time were used for analyses, [2] Traits measured once, [3] Traits measured weekly, [4] If a plant individual started flowering after the weekly counting it was counted again.

References

Luzuriaga A, Escudero A, Perez-Garcia F. **2006**. Environmental maternal effects on seed morphology and germination in *Sinapis arvensis* (Cruciferae). *Weed Research* **46**: 163–174.

Table S3. Scent bouquet of S*inapis arvensis* flowers. For all compounds emission rate (mean ± SE) in ng/h/flower and retention index (RI) are given. For mean and SE calculation, values were not corrected for sampling date. Asterisks * denote compounds, which were identified using standard substances.

Compound	**RI**	**Mean ± SE**
Monoterpenes		
α-Thujene	931	0.48 ± 0.06
α-Pinene*	940	31.54 ± 5.01
Thuja-2,4(10)-dien	961	0.33 ± 0.06
Sabiene*	979	3.51 ± 0.42
β-Pinene*	985	4.53 ± 0.43
β-Myrcene*	992	9.03 ± 0.74
1,5,8-p-menthatriene	1010	2.41 ± 0.30
Limonene*	1035	9.69 ± 0.72
β-Phellandrene*	1037	7.70 ± 0.69
Z-Ocimene*	1038	2.31 ± 0.32
β-Ocimene	1050	40.72 ± 5.12
neo-allo-Ocimene*	1131	1.03 ± 0.16
Verbenone*	1221	6.98 ± 0.77
Sesquiterpenes		
Caryophyllene*	1444	1.64 ± 0.56
Aromatics		
Benzylcyanid*	1144	0.44 ± 0.10
Unknown compounds		
Unknown compound 2	1077	3.28 ± 0.64
Unknown compound 1	1134	0.43 ± 0.07
Total scent emission		126.05 ± 11.53

Table S4. Results for ANOVA for comparison of mean ranks $\overline{R}_i$ for different visitor groups within populations (Population 1 = German population, Population 2 = English population). See also Figure S5. Significant results are highlighted in bold.

Visitor group	**Population 1**	**Population 2**
Total flower visitors	$\boldsymbol{F_{47,528} = 2.39{*}{*}{*}}$	$\boldsymbol{F_{48,406} = 1.68{*}{*}}$
Syrphidae	$\boldsymbol{F_{47,514} = 1.47{*}}$	$\boldsymbol{F_{48,400} = 1.39{*}}$
Eristalini	$F_{47,487} = 1.23$	$F_{48,393} = 0.97$
Apis mellifera	$\boldsymbol{F_{47,516} = 2.17{*}{*}{*}}$	$F_{48,389} = 1.22$
Small solitary bees	$\boldsymbol{F_{47,510} = 1.57{*}}$	$\boldsymbol{F_{48,395} = 2.56{*}{*}{*}}$
Large solitary bees	$F_{47,351} = 0.97$	$\boldsymbol{F_{48,338} = 1.50{*}}$
Leaf visitors	$\boldsymbol{F_{47,400} = 1.41{*}}$	$\boldsymbol{F_{48,\ 404} = 1.76{*}}$
Inverse Simpson index	$F_{47,527} = 1.09$	$F_{48,404} = 1.19$
Species richness	$\boldsymbol{F_{47,529} = 1.46{*}}$	$\boldsymbol{F_{48,406} = 1.52{*}}$
Hurlbert's PIE	$F_{47,529} = 0.85$	$F_{48,406} = 1.108$

$^{*}\ p < 0.05$, $^{**}\ p < 0.01$, $^{***}\ p < 0.001$

Table S5. Results of linear mixed-effect models (LMMs) testing for differences in interaction patterns between plant individuals. Interaction patterns were on the null model expectation the number of interaction per individual is proportional to number of flowers per individual. Each model included population (Pop.) and fertilizer treatment (Treat.) as fixed factors and plant individual (PlantID) as random factors. The relative contribution to the variation in interaction patterns of the three factors was assessed using two types of R^2-values: $R^2_{\text{conditional}}$ and R^2_{marginal} (Nakagawa & Schielzeth, 2013). $R^2_{\text{conditional}}$ is the relative contribution of both fixed and random factors, R^2_{marginal} is the relative contribution of the fixed factors only. Significant results are highlighted in bold.

LMMs	**PlantID** (χ^2_1)	**Pop.** ($F_{1,94}$)	**Treat.** ($F_{1,94}$)	$R^2_{\text{conditional}}$	R^2_{marginal}
Visitor taxa					
Total flower interactions	**41.24*****	**14.53*****	0.25	0.13	0.03
Apis mellifera	**31.05*****	**10.9****	0.52	0.11	0.02
Eristalini	**21.03*****	**14.60*****	1.17	0.10	0.02
Small solitary bees	**23.88*****	**40.72*****	0.14	0.14	0.07
Large solitary bees	**17.36*****	**68.77*****	0.04	0.16	0.10
Syrphidae (without Eristalini)	**9.58****	**14.36*****	1.00	0.07	0.02

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; significance of fixed effects assessed with LMMs, significance of random effect with likelihood ratio test

References

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**: 133–142.

Table S6. Results of ANOVA comparing plant traits and reproductive success between fertilizer treatment and population. Significant results are highlighted in bold.

Trait	Population	Fertilizer
Floral morphology		
Stamen length	$F_{1,88}$ = 1.80	$F_{1,88}$ = 2.78
Short anther length	$F_{1,88}$ = 3.57	$F_{1,88}$ = 1.34
Long anther length	$F_{1,88}$ = 0.01	$F_{1,88}$ = 2.62
Petal width	$F_{1,88}$ **= 5.13***	$F_{1,88}$ = 0.45
Petal length	$F_{1,88}$ = 1.46	$F_{1,88}$ = 0.43
Flower shape	$F_{1,88}$ = 3.57	$F_{1,88}$ = 0.06
Display size flower	$F_{1,88}$ = 3.74	$F_{1,88}$ = 1.26
Inflorescence height	$F_{1,93}$ = **40.36*****	$F_{1,93}$ = 0.003
Display size inflorescence	$F_{1,88}$ **= 7.22****	$F_{1,88}$ = 0.26
Mean number of flowers per inflorescence	$F_{1,93}$ = 3.90	$F_{1,93}$ = 0.56
Mean number of inflorescence	$F_{1,93}$ **= 7.51****	$F_{1,93}$ = 0.38
Scent		
Monoterpenes		
α-Thujene	$F_{1,89}$ = 0.30	$F_{1,89}$ **= 4.54***
α-Pinene	$F_{1,89}$ = 1.59	$F_{1,89}$ = 3.44
Thuja-2,4(10)-dien	$F_{1,89}$ = 0.22	$F_{1,89}$ **= 4.54***
Sabiene	$F_{1,89}$ = 0.58	$F_{1,89}$ = 3.56
β-Pinene	$F_{1,89}$ = 2.40	$F_{1,89}$ **= 4.93***
β-Myrcene	$F_{1,89}$ **= 6.33***	$F_{1,89}$ = 3.72
1,5,8-p-menthatriene	$F_{1,89}$ = 0.01	$F_{1,89}$ = 0.18
Limonene	$F_{1,89}$ **= 5.62***	$F_{1,89}$ = 1.64
β-Phellandrene	$F_{1,89}$ **= 8.10****	$F_{1,89}$ = 3.53
Z-Ocimene	$F_{1,89}$ = 0.32	$F_{1,89}$ = 0.83
β-Ocimene	$F_{1,89}$ = 0.50	$F_{1,89}$ = 0.33
neo-allo-Ocimene	$F_{1,89}$ = 1.06	$F_{1,89}$ = 0.43
Verbenone	$F_{1,89}$ **= 5.13***	$F_{1,89}$ = 3.34
Aromatics		
Benzylcyanid	$F_{1,89}$ = 0.29	$F_{1,89}$ = 0.65
Sesquiterpenes		
Caryophyllene	$F_{1,89}$ = 0.48	$F_{1,89}$ = 0.49
Unknown compounds		
Unknown compound 2	$F_{1,89}$ = 0.86	$F_{1,89}$ = 0.58
Unknown compound 1	$F_{1,89}$ = 0.006	$F_{1,89}$ = 0.019
Total scent emission	$F_{1,89}$ = 3.02	$F_{1,89}$ = 3.46
Vegetative morphology		

Leaf hairiness	$F_{1,93} = 0.38$	$F_{1,93} = 1.12$
Leaf length	$F_{1,93} = 1.29$	$F_{1,93} = 0.04$
Leaf width	$F_{1,93} = 0.86$	$F_{1,93} = 0.02$
Leaf area	$F_{1,93} = 2.08$	$F_{1,93} = 0.25$
Mean number of leafs	$F_{1,93} = \mathbf{20.10***}$	$F_{1,93} = 0.12$
Stem hairiness	$F_{1,93} = \mathbf{11.86***}$	$F_{1,93} = 0.34$
Silique morphology		
Number of siliques	$F_{1,93} = \mathbf{9.61**}$	$F_{1,93} = 0.16$
Number of seeds per siliques	$F_{1,93} = 2.03$	$F_{1,93} = 0.22$
Silique width	$F_{1,93} = \mathbf{14.74***}$	$F_{1,93} = 1.59$
Silique length	$F_{1,93} = \mathbf{8.98**}$	$F_{1,93} = 1.35$
Phenology		
Day of first flower	$F_{1,93} = \mathbf{57.16***}$	$\boldsymbol{F_{1,93}} = \mathbf{3.61*}$
Flowerperiod	$F_{1,93} = \mathbf{15.94***}$	$F_{1,93} = 1.20$
Reproductive success		
Seed set	$F_{1,93} = \mathbf{10.10**}$	$F_{1,93} = 0.10$
Seed size	$F_{1,93} = \mathbf{14.02***}$	$F_{1,93} = 0.05$
Number of seeds per flower	$F_{1,93} = \mathbf{20.58***}$	$F_{1,93} = 0.30$
Seed dormancy	$F_{1,93} = 3.09$	$F_{1,93} = 0.95$
Seed viability	$F_{1,93} = 3.77$	$F_{1,93} = 0.99$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

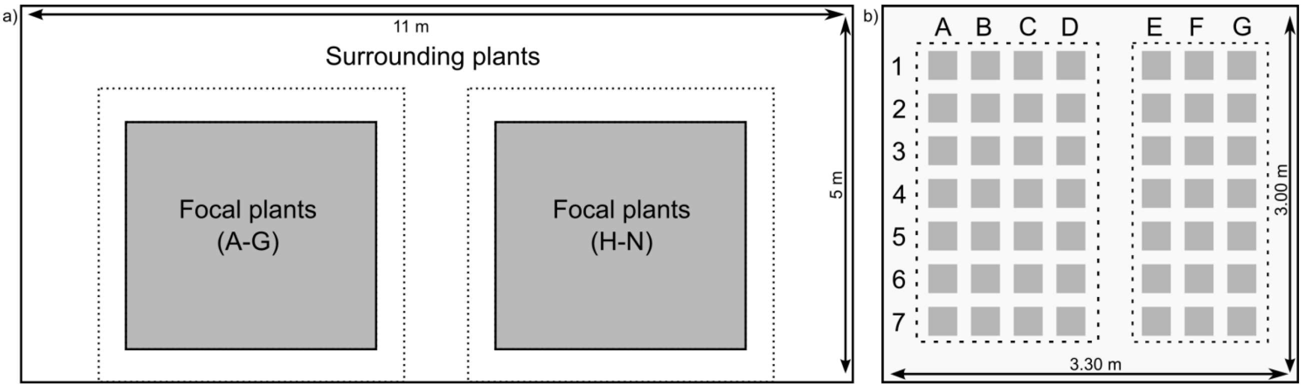
Table S7. Results of permutational multivariate analysis of variance comparing multiple plant traits between fertilizer treatment and population. We compared four trait sets (floral morphology, scent, vegetative morphology and phenology, Table S2) using Euclidean distances. Significant results are highlighted in bold and were assessed using 999 permutations.

Traitset	**Population**	**Treatment**
Floral morphology	**$F_{1,88}$ = 35.28*****	$F_{1,88}$ = 0.01
Scent	$F_{1,88}$ = 1.28	$F_{1,88}$ = 2.03
Vegetative morphology	**$F_{1,88}$ = 5.54*****	$F_{1,88}$ = 0.29
Phenology	**$F_{1,93}$ = 45.95*****	$F_{1,88}$ = 2.96

*** $p < 0.001$

Methods S1

Design of the experimental field



Design of the experimental field. a) Overview. The experimental field (~55m²) was divided into three different areas: two observation units containing the focal plants (grey areas, each ~9.9 m²), access area to the observation units (area within the dotted lines) and the surrounding area (area outside the dotted lines) with approximately 250 additional *Sinapis arvensis* plants. Experimental plants could be accessed from all four sides of the grey areas, depending which plant individuals were observed. b) Detailed view of the observation units, both units had the same setup. The unit was divided into two subunits containing the potted focal plants (grey squares; the left subunit contained 28 plant individuals, the right one 21). The pots were 15 cm in diameter and placed ~15 cm apart from each other, so that the distance between plant individuals was ~30 cm. Each observation unit (n = 4) was covered with a removable insect-net (dashed lines). The nets were ~1.1 m high and the distance from the outer pots to the net was ~20 cm. Each row of plants could be observed separately, while all rows remained covered with the insect-net when they were not observed.

Picture of the experimental field during peak-flowering.

One plant individual (I1) had to be excluded and was removed for the experimental field since it turned out to be a different plant species after the seedling stage. To test for the influence of plant position on traits and visitation pattern, we compared the means of plant traits and interaction patterns (i.e. mean ranks $\overline{R}_i$) between the four observation units via linear mixed-effect models (observation unit as fixed effect and plant individuals as random effect) and post-hoc tests were calculated using the R function *glht*() (package *multcomp*) if necessary. For most traits as well as for most visitor groups (i.e. mean ranks $\overline{R}_i$), we found no invariant differences between the observation units (Table S2-1). Neighbouring plant individuals did not show invariant patterns in their flower visitor composition (Figure S2), implying that there were no neighbouring effects. Further, we found no correlation between position of the plant individuals (distance to the nearest field edge) and their visitor assemblages (Mantel test, Pearson's correlation, 999 permutations: $r = 0.024$, $p = 0.262$) indicating that there is no edge effect that influences the visitor assemblages.

Table A. Results of linear mixed effect models (LMMs) for the comparison of observation units. Differences in the mean of plant traits, interaction patterns and reproductive success are shown. Results of "general linear hypotheses" post-hoc test (glht) are only given for significantly different observation units (OU). All other OU pairs did not differ significantly. Significant results are highlighted in bold.

Trait/interaction pattern/reproduction	**LMM**	**glht**
Stamen length	$F_{3,87} = 0.58$	
Short anther length	$F_{3,87} = 1.36$	
Long anther length	$F_{3,87} = 0.90$	
Petal width	$F_{3,87} = 0.23$	
Petal length	$F_{3,87} = 1.25$	
Flower shape	$F_{3,87} = 0.51$	
Display size flower	$F_{3,87} = 0.63$	
Total scent emission	$F_{3,87} = 0.17$	
Leaf hairiness	$F_{3,92} = 0.31$	
Leaf length	$F_{3,92} = 1.58$	
Leaf width	$F_{3,92} = 1.68$	
Leaf area	$F_{3,92} = 1.24$	
Inflorescence height	$F_{3,92} = 0.72$	
Number of leafs	$F_{3,92} = 1.33$	
Mean number of leafs	$F_{3,92} = 0.32$	
Stem Hairiness	$F_{3,92} = 0.79$	

Display size inflorescence	$F_{3,92}$ = 0.15	
Mean number of inflorescence	$F_{3,92}$ = 2.63	
Mean number of flowers per inflorescence	**$F_{3,92}$ = 6.49*****	OU1>OU2, OU3>OU2
Number of siliques	$F_{3,92}$ = 2.47	
Number of seeds per siliques	$F_{3,92}$ = 1	
Silique width	**$F_{3,92}$ = 6.28*****	OU4>OU1/OU3
Silique length	**$F_{3,92}$ = 3.10***	OU3>OU1
Seedsize	**$F_{3,92}$ = 3.61***	OU3>OU1
Day of first flower	$F_{3,92}$ = 0.45	
Flowerperiod	$F_{3,92}$ = 0.57	
Total number of seeds	$F_{3,92}$ = 1.56	
Number of seeds per flower	$F_{3,92}$ = 0.47	
Seed dormancy	**$F_{3,92}$ = 2.80***	NA
Seed viability	$F_{3,92}$ = 1.21	
Mean Rank Total Flower visitors	**$F_{3,92}$ = 5.38****	OU4/OU3>OU2
Mean Rank Honeybee	$F_{3,92}$ = 2.21	
Mean Rank small solitary bees	**$F_{3,92}$ = 20.7*****	OU3>OU1/OU2, OU4>OU1/OU2
Mean Rank large solitary bees	**$F_{3,92}$ = 9.78*****	OU4/OU3>OU1, OU4>OU2
Mean Rank Eristalini	**$F_{3,92}$ = 6.49*****	OU3>OU1
Mean Rank Syrphidae	**$F_{3,92}$ = 11.0*****	OU3>OU1/OU2/OU4
Mean Rank Total leaf visitors	**$F_{3,92}$ = 5.51****	OU4<OU1/OU3

* $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$, significance levels of LMMs, NA indicates no significant differences found with post-hoc tests.

Scent analyses and compound identification

The GC-MS was equipped with a ZB-5 fused silica column (5% phenyl polysiloxane; 60 m long, inner diameter 0.25 mm, film thickness, 0.25 μm, Phenomenex, Aschaffenburg, Germany) and the column flow (carrier gas: helium) was set to 1.5 ml/min. The GC oven temperature started at 40°C (split ratio 1:1), then increased by 6°C per minute to 250°C and held constant for 1 minute. The MS interface worked at 250°C. Mass spectra were taken at 70 eV (in EI mode) from m/z 30 to 350. The GC/MS data were processed using the

GCMSolution package (Version 2.72, Shimadzu Corporation, Kyoto, Japan). Compounds were identified by comparison of mass spectra and retention times with standard compounds, which are commercially available. Alternatively, compounds were identified using the mass spectral libraries Wiley 9, Nist 2011, FFNSC 2, Essential oils and Adams 2007 as well as the database available in MassFinder 3. The compounds found in the flowers were compared to those found in the blanks (empty oven bags, samples of green leaves) to determine which compounds were specifically emitted by flowers. The amount of each compound emitted was standardized by the number of flowers in the inflorescence sampled.

Shape analyses

Three flowers from each individual were photographed using a digital single-lens reflex camera (Nikon D90 with Nikon AF-S Micro-Nikkor 105mm) with the help of a tripod set at a 180° angle relative to the flowers. A scale bar was included in all photos. These images were converted into tps-files using tpsUtil (Rohlf, 2009). Afterwards eight landmarks and four curves (one for each petal) with 55 semi landmarks were digitalized in the same order for each flower, after setting a scale factor using the software tpsDig (Rohlf, 2006). Semi landmarks, which overlapped with landmarks were deleted and slider-files were created using tpsUtil. To eliminate variation due to size, position, and orientation all landmarks and semi landmarks were superimposed by the least-squares method using tpsRelw (Rohlf, 2007) which returned a mean shape (=consensus). Partial warps, and following relative warps (i.e. the principal components of partial warps scores), analysis were calculated to illustrate shape variation between all individuals. The relative warps axis was used as a surrogate for shape variation.

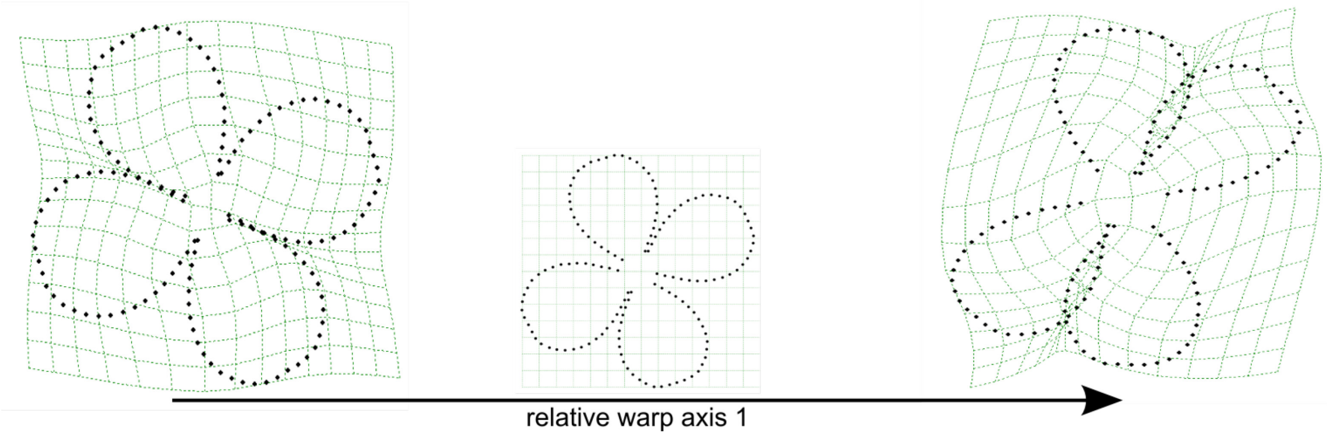


Figure A. Scheme of the relative warps axis used as surrogate for shape variation. The two outer pictures show thin plate spline models representing the shape gradation from the negative (left) to the positive (right) end of relative warp axis 1. The small picture (middle) shows a thin plate spline model of the mean shape (=consensus).

References

Rohlf, F. 2006. tpsDig version 2.10. Department of Ecology and Evolution, State University of New York, Stony Brook.

Rohlf, F. 2007. tpsRelw version 1.45. Department of Ecology and Evolution, State University of New York, Stony Brook

Rohlf, F. 2009. tpsUtil version 1.44. Department of Ecology and Evolution, State University of New York, Stony Brook

Notes S1

Comparison of intra- and interspecific trait variation

To compare the degree of intra- and interspecific trait variation, we used the coefficient of variation (CV, standard deviation divided by mean). The CV was calculated for three datasets. The dataset from this study was used to assess the magnitude of intraspecific variation, while the dataset for Junker *et al.* (2013) as well as a recently obtained dataset from a meadow in the Botanical Garden of the University Salzburg was used for the interspecific variation. In June 2015, the third dataset was obtained on the same meadow were the experimental field of this study was established in 2013. We measured the following five plant traits for all flowering plants species (*n* = 11, *Galium album*, *Scabiosa columbaria*, *Lathyrus pratensis*, *Rhinanthus alectorolophus*, *Vicia sepium*, *Crepis biennis*, *Betonica officinalis*, *Ranunculus* sp., *Lotus corniculatus*, *Trifolium dubium*, *Trifolium pratense*): inflorescence height, anther length, display size of the inflorescence, display size of the flower, and stamen length. Please note that all traits were measured following the methods described in the main text.

Table B. Coefficient of variation (CV) for five plant plant traits comparing intraspecific and interspecific variability. The CVs for intraspecific variation were calculated based on trait measurement for 97 *Sinapis arvensis* individuals. The CVs for interspecific variation were calculated for two meadow communities in Germany (Junker *et al.* 2013, *n* = 31) and Austria (Salzburg, 2015, *n* = 11).

Traits	**CV (intraspecific)**	**CV (interspecific, Junker et al. 2013)**	**CV (interspecific, Salzburg 2015)**
Height inflorescences	0.228	0.736	0.323
Display size inflorescence	0.222	0.704	0.620
Display size flower	0.127	NA	0.767
Anther length	0.208	1.04	0.482
Stamen length	0.175	NA	0.523

‘NA’ indicates that these traits were not measured in the given study.

Comparison of intra- and interspecific variation in interactions

We compared visitation patterns of the same dataset that were used for the trait variation comparison. For the dataset collected in June 2015, we divided the same meadows used in 2013 in four subplots (15 x 15 m) and conducted transect walks on four days resulting in a total observation time of 10 h per subplot. To compare the degree of intra- and interspecific variation in interaction patterns, we used Bray-Curtis dissimilarity (quantitative measure) and Whittaker’s beta-diversity (qualitative measure). For each of the three flower-visitor networks we calculated a distance matrix between all individuals respectively species for both values and then compared their mean dissimilarity and beta-diversity using ANOVAs. Both values show how similar species or individuals are within one network.

Unsurprisingly both indices differed between datasets (ANOVA: Bray-Curtis dissimilarity, $F_{2,6298} = 12000$, $p < 0.001$; Whittaker's beta diversity: $F_{2,6298} = 26579$, $p < 0.001$), but the mean intraspecific dissimilarities between individuals was pronounced (Fig. B). As Whittaker's beta diversity only uses presence/absence data, variation between individuals was less pronounced than for the quantitative Bray-Curtis dissimilarity. Please note, the visitation data obtained from Junker *et al.* (2013) had a higher taxonomic resolution (species level) than our study presented here, which could lead to a higher dissimilarity between species than with lower taxonomic resolution.

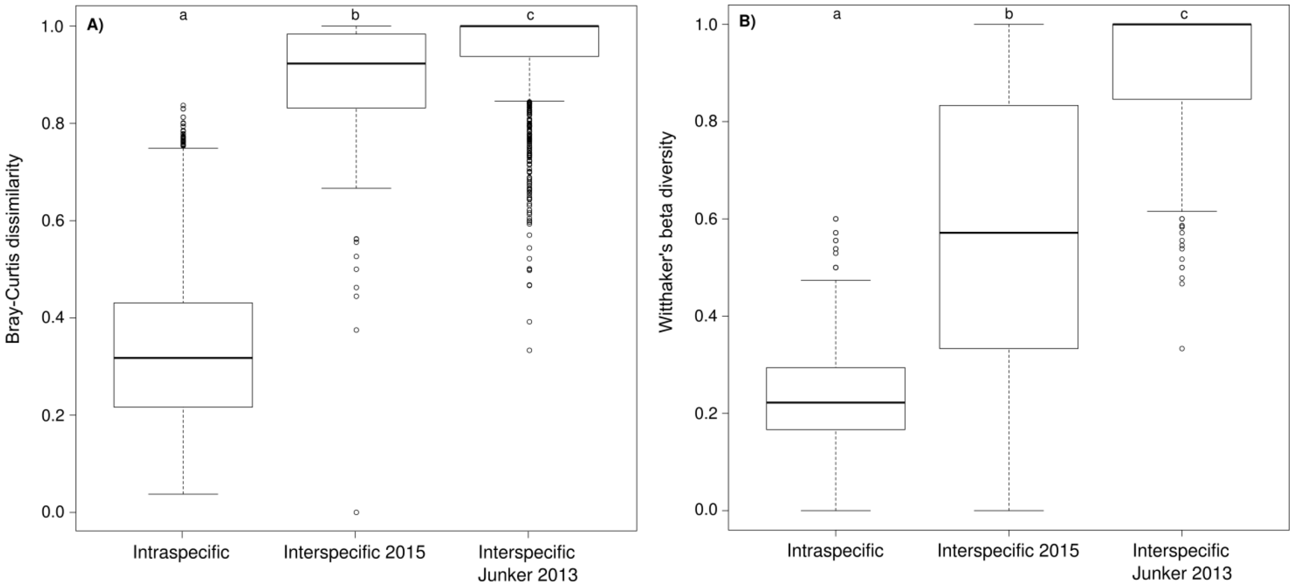


Figure B. Intra- and interspecific differences in flower-visitor interactions. A) shows quantitative differences (Bray-Curtis dissimilarity) in interaction patterns, while B) shows qualitative differences (Whittaker's beta diversity). Both values for interspecific variation were calculated for 97 *Sinapis arvensis* individuals. The values for interspecific variation were calculated for two meadow communities in Germany (Junker *et al*. 2013) and Austria (Salzburg, 2015). Boxplots show the median, the first and third quartiles (top and bottom of the box) and 1.5 times the interquartile range of the data (dashed lines).

References

Junker RR, Blüthgen N, Brehm T, Binkenstein J, Paulus J, Martin Schaefer H, Stang M. 2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. Functional Ecology 27: 329–341.

Notes S2

Multivariate visualisation of the association between traits and visitation rate

To test whether results of the univarite correlation analyses and the Mantel tests are supported by a multivariate analysis, we performed co-inertia analyses (Doledec & Chessel, 1994; Dray *et al.*, 2003). This two-table ordination method is based on a covariance matrix (visitor assemblages and plant traits) which projects two separated PCA-analyses (visitor assemblages and plant traits) onto the same co-inertia space. To assess the strength of the relationship between the two tables the coefficient of variation *RV* was calculated and its significance was tested using a permutation test (999 permutations) implemented in the *RV.rtest*-function in the R package *ade4* (Chessel *et al.*, 2004).

The multivariate visualisation of the association between traits and visitation rates of arthropod taxa (Co-inertia analysis, Figure C) also confirmed that the plant individuals' phenotype significantly explains variation in the interactions patterns (permutation test, $RV = 0.193$, $p = 0.002$) and showed comparable patterns as the univariate correlation analysis (Figure 3) and Mantel tests. Thus, the univariate and multivariate analyses jointly demonstrate that the plant individuals' phenotype significantly affects flower visitor communities and reproductive success.

References

Chessel D, Dufour AB, Thioulouse J. **2004**. The ade4 package - I : One-table methods. *R News* **4**: 5–10.

Doledec S, Chessel D. **1994**. Co-inertia analysis - an alternative method for studying species environment relationships. *Freshwater Biology* **31**: 277–294.

Dray S, Chessel D, Thioulouse J. **2003**. Co-inertia analysis and the linking of ecological data tables. *Ecology* **84**: 3078–3089.

Figure C. Visualization of the co-inertia analysis of based on a covariance matrix (visitor assemblages and plant traits) which projects two separated PCA-analyses (visitor assemblages and plant traits) onto the same co-inertia space. Both variables are projected on the first factor plane of the co-inertia analysis to facilitate interpretation. Each black arrow represents a trait and each blue point a visitor taxa. Correlation coefficient *RV* between the two tables is *RV* = 0.193 and differed significantly from chance (permutation test, 999 permutations: *p* = 0.002).

Supplementary Material Chapter 2

Volatility of network indices as a result of intraspecific variation in plant-insect interactions

Jonas Kuppler, Tobias Grasegger, Birte Peters, Susanne Popp, Martin Schlager & Robert R. Junker

Supplementary Methods

Overview Experimental Design & Flower-visitor interactions (common garden experiment 2013)

Sinapis arvensis L. (Brassicaceae) is an annual, self-incompatible plant native to southern and middle Europe, which attracts a broad taxonomic range of flower visitors, mostly bees and hoverflies (Kunin, 1993). In the common garden (11 × 5 m), a total of 97 pots containing one *S. arvensis* plant each were arranged in a full-factorial pseudorandomised block design. Plants were covered in groups of nine or twelve individuals with a removable net (Monofil-Gaze; Bioform, Nürnberg, Germany) to prevent animals from interacting with the plants. Approximately 250 *S. arvensis* plants surrounded the experimental plants to support an arthropod community specific for *S. arvensis* that was locally available once the experimental plants were made accessible. For observations the nets were removed and all interactions between arthropods and plant individuals were recorded on nonrainy days between 08:00 and 16:00 h. An interaction was defined as a visit by an arthropod on one or more flowers or leaves of one plant individual; that is, an individual flower visitor that visited several flowers of one plant individual consecutively was regarded as one interaction. For a detailed description see Kuppler *et al.* (2016).

Variability in module composition induced by module algorithm QuanBiMo

The QuanBiMo modularity algorithm assigns species to modules based on their similarity in quantitative interactions in an iterative process (Dormann & Strauss 2014). To assess the degree of variability in module composition caused by this algorithm, we repeatedly (n = 1000) ran the QuanBiMo algorithm (steps = 1,000,000) for 84 identical network including the species mean of *Sinapis arvensis* $N\binom{84}{84}$, The deviation (Procrustes sum of squares) in module composition for each network compared to the species mean $N\binom{84}{84}$ (one reference) was calculated as described in the main text.

References

Dormann CF, Strauss, R. 2014 A method for detecting modules in quantitative bipartite networks. *Methods Ecol. Evol.* **5**, 90–98. (doi:10.1111/2041-210X.12139)

Kuppler J, Höfers MK, Wiesmann L, Junker RR. 2016 Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent. *New Phytol.* (doi:10.1111/nph.13858)

Supplementary Results

Results for resampled networks with constant interaction frequency for all Sinapis arvensis individuals

Quantitative network statistics can be sensitive to differences in interaction frequencies. To assess whether variation in the interaction frequencies among the included *Sinapis arvensis* individuals influence our results, we repeated the resampling with a constant interaction frequency for each *S. arvensis* individual. The constant interaction frequency was calculated by multiplying the mean number of interactions of all *S. arvensis* individuals with the proportional interaction strength of each *S. arvensis* individual. Subsequently, the resampling and the analyses were repeated as described in the main text (see material & methods) Aggregate statistics were sensitive to the intraspecific variation in interaction patterns in *S. arvensis* with the range of variation across different networks ($N\binom{84}{k}$ with a constant interaction frequency for each *S. arvensis* individual) being considerable for all calculated network-specific indices (figure S3). Further, the species-specific complementary specialization *d'* of most plant species showed a noticeable variability when including different *S. arvens*is individuals or their combinations $N\binom{84}{k}$ (networks including one *S. arvensis* individual $N\binom{84}{1}$, each: range of *d'* for *S. arvensis*: 0.74; for all other plant species: range between 0 and 0.34; figure S4). The modularity analyses clearly showed that plant species that were part of the networks including the visitation-frequencies of only one *S. arvensis* individual $N\binom{84}{1}$, were assigned in variable combinations to different modules (figure S5), even with the interaction frequency for *S. arvensis* hold constant.

Supplementary Figures

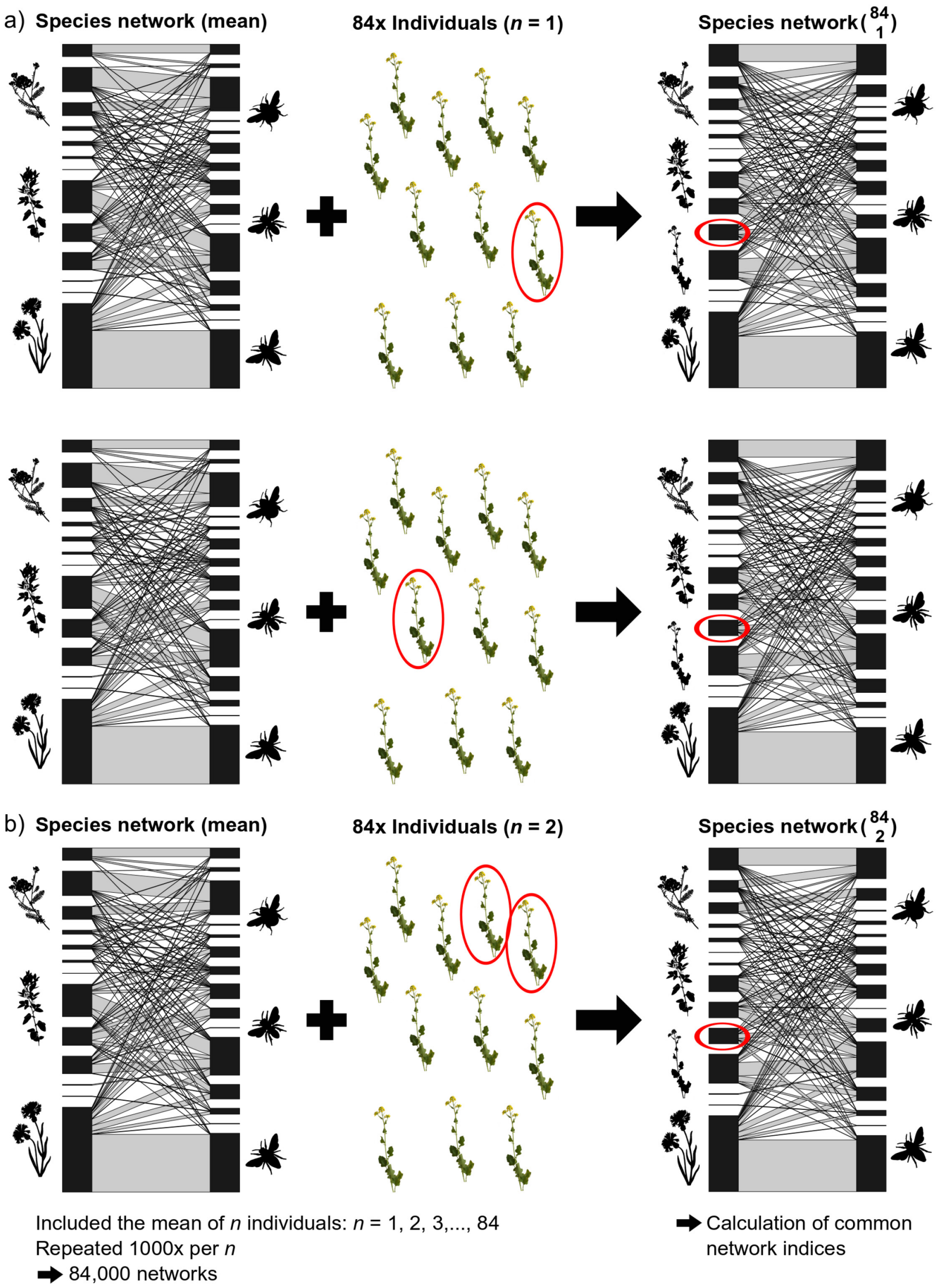


Figure S1. Illustration of resampling approach. a) To the species network based on the thirteen plant species ("species network mean") the species mean interaction frequency of *S. arvensis* was added. In case of *n* = 1 the mean interaction frequency was based on one randomly selected *S. arvensis* individual. For the resulting network ("Species network $\binom{84}{1}$") commonly used network indices were calculated. This step was repeated 1000 times. b) To the species network based on the thirteen plant species ("species network mean") the species mean interaction frequency of *S. arvensis* was added. In case of *n* = 2 the mean interaction frequency was based on two randomly selected *S. arvensis* individual. For the resulting network ("Species network $\binom{84}{2}$") commonly used network indices were calculated. This step was repeated 1000 times. The steps describe in a) and b) were repeated for *n* = 1, 2, 3,…, 84 resulting in 84,000 resampled networks.

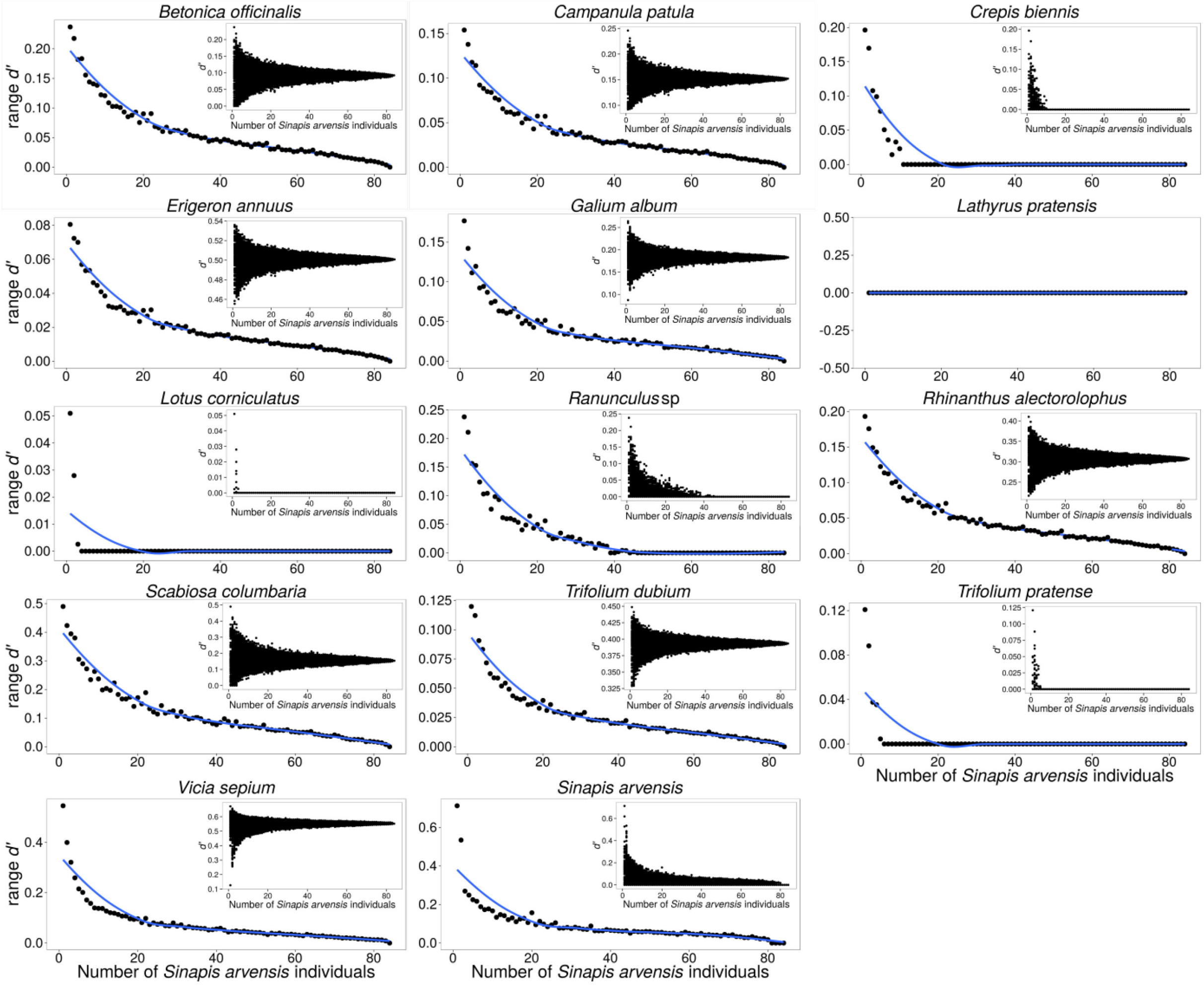


Figure S2. Results of the complementary specialization *d’* of individual plant species for resampled networks. Large plots show the range of values calculated for all networks $N\binom{84}{k}$ for *k* = 1,2,…,84 included *Sinapis arvensis* individuals, while insets show the calculated values. Solid lines visualize the trends of the range of the calculated values. Lines were derived from linear regression or smoothing functions (loess regression).

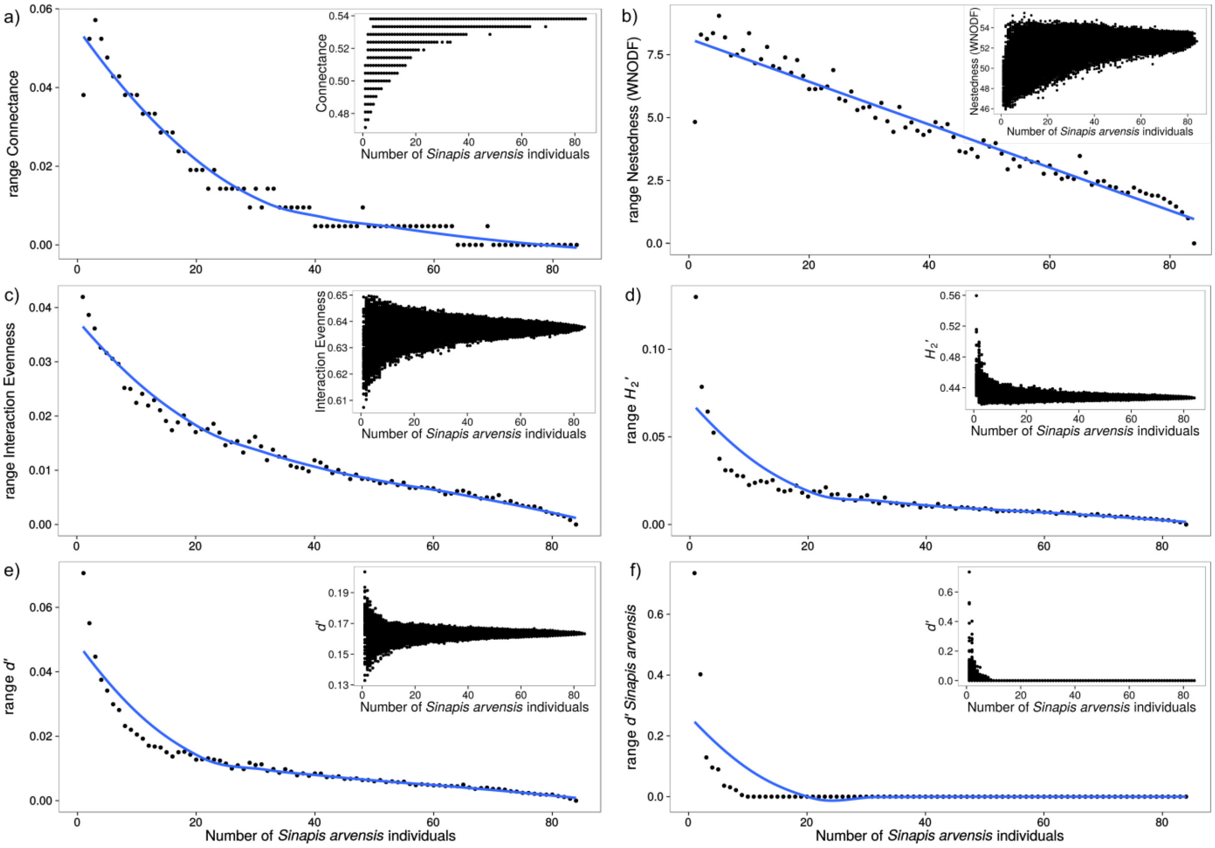


Figure S3. Results for resampling with interaction frequency of all *Sinapis arvensis* individuals held constant: Variation in commonly applied network statistics as a function of the number of *Sinapis arvensis* individuals included in interaction matrix. a – f) Range of values calculated for all networks $N\binom{84}{k}$ with k = *S. arvensis* individuals included. Insets visualize the raw values. Nonparametric local polynomial regression (LOESS) curve or linear regression lines (for WNODF) depict the trends in changes in the range of the aggregate network statistics.

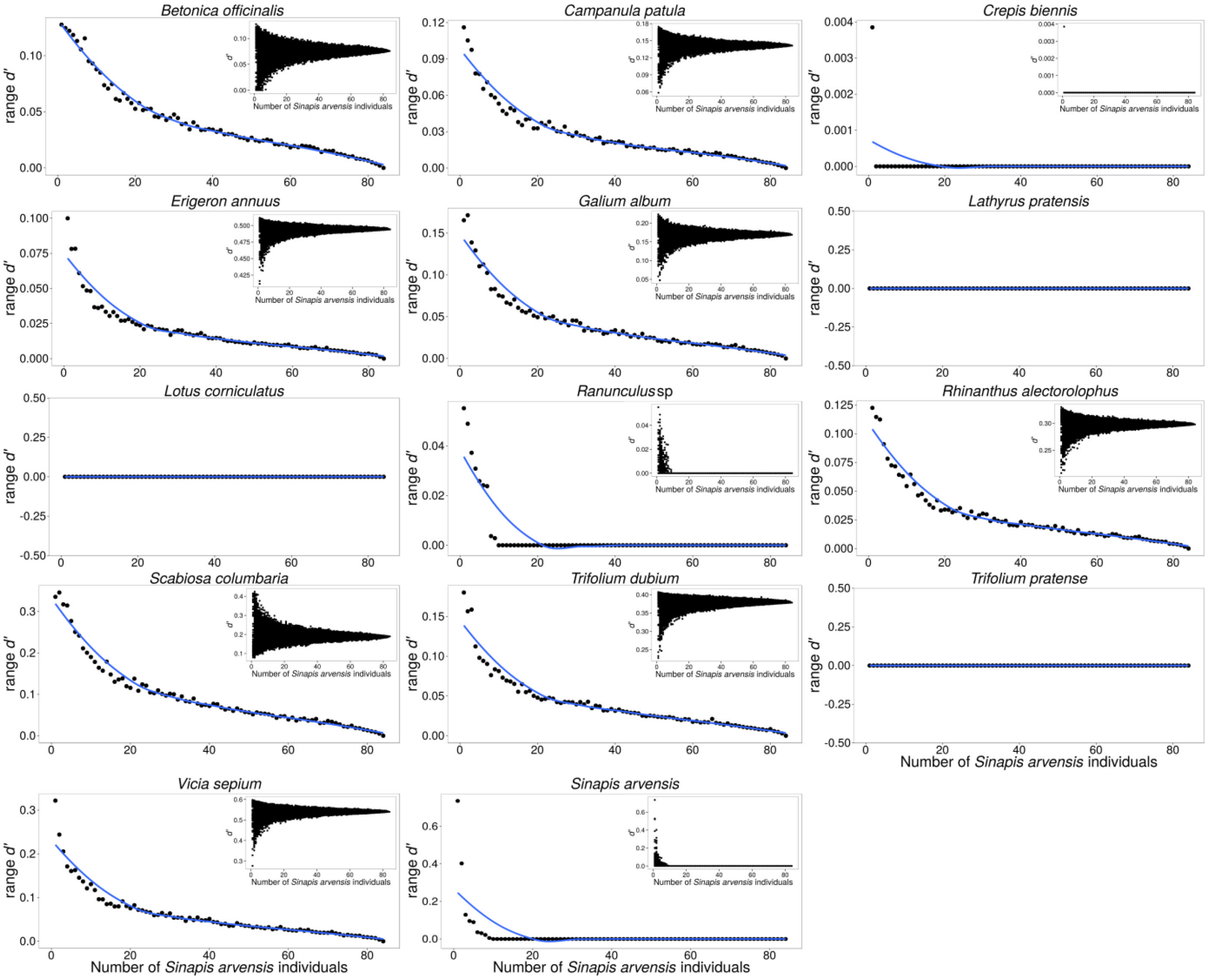


Figure S4. Results for repeated resampling with interaction frequency of all Sinapis arvensis individuals held constant: complementary individual specialization *d'* of each plant species. Large plots show the range of values calculated for all networks $N\binom{84}{k}$ for *k* = 1,2,…,84 included *Sinapis arvensis* individuals, while insets show the calculated values. Solid lines visualize the trends of the range of the calculated values. Lines were derived from linear regression or smoothing functions (loess regression).

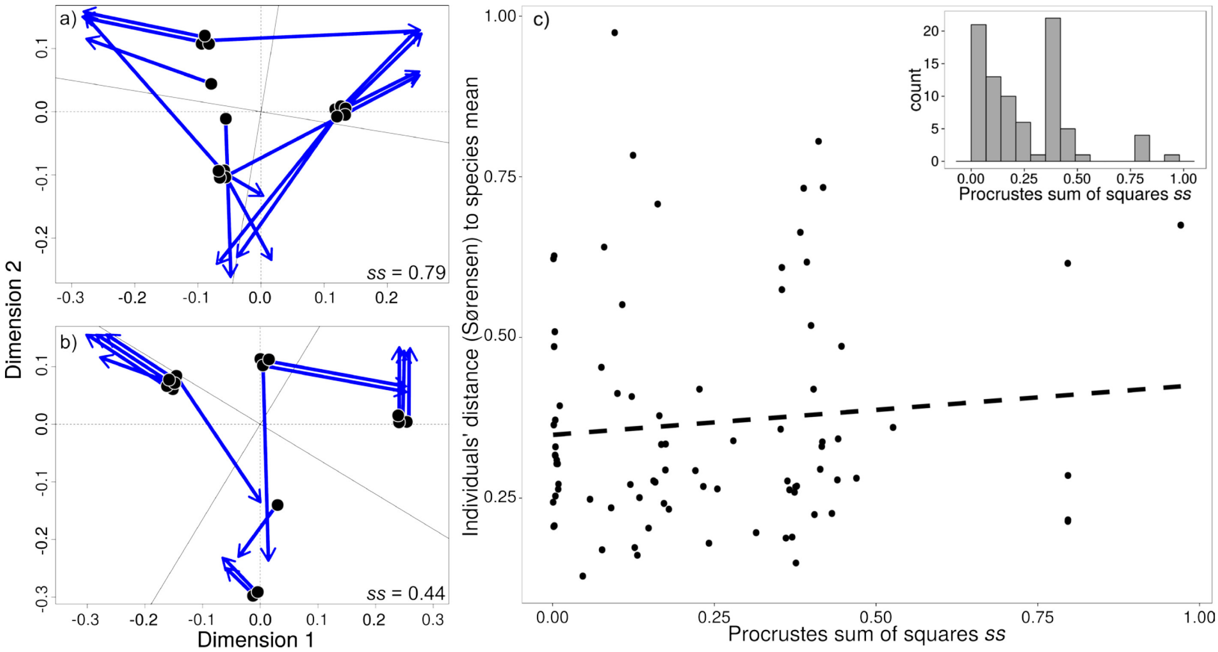


FIGURE S5. Results for resampling with interaction frequency of all Sinapis arvensis individuals held constant: influence of different *Sinapis arvensis* individuals on module composition. a, b, c) Procrustes plots comparing principal coordinate analyses (PCoA) based on Sørensen-distances of plant species based on module affiliation for networks including only one *S. arvensis* individual $N\binom{84}{1}$ (points) or all individuals $N\binom{84}{84}$ (arrowheads). Procrustes sum of squares *ss* are shown as measurement for the deviation d) Histogram of the deviation in module composition of networks including one *S. arvensis* individual (n = 84) to species mean (*ss*-values) $N\binom{84}{84}$.

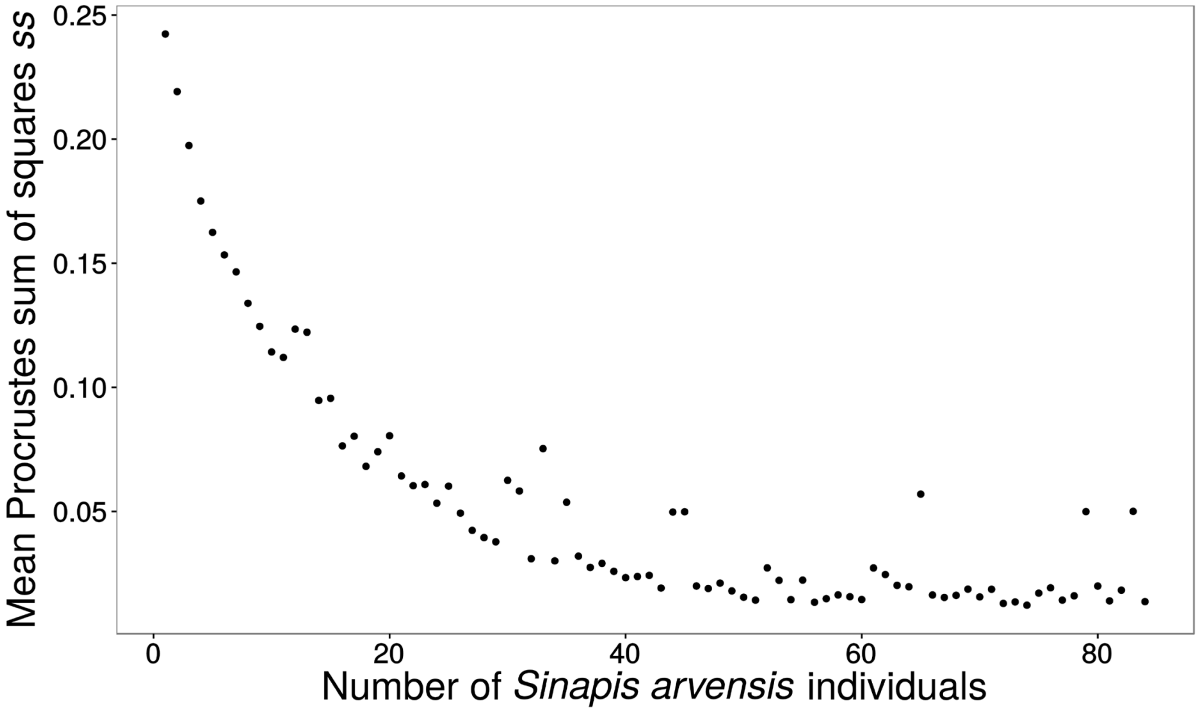


Figure S6. Influence of the number of *Sinapis arvensis* individuals on module composition. Mean procrustes sum of squares *ss* for resampled networks (*n* = 1000) including different numbers of *Sinapis arvensis* individuals ($N\binom{84}{k}$ for *k* = 1,2,…,84) are shown. Procrustes sum of squares *ss* were obtained from comparing principal coordinate analyses (PCoA) based on Sørensen distances of plant species based on module affiliation for networks including different numbers of *S. arvensis* individuals $N\binom{84}{k}$ (for *k* = 1,2,…,84) and all individuals $N\binom{84}{84}$. Procrustes sum of squares *ss* are shown as measurement for the deviation (see also figure 2 and figure S5).

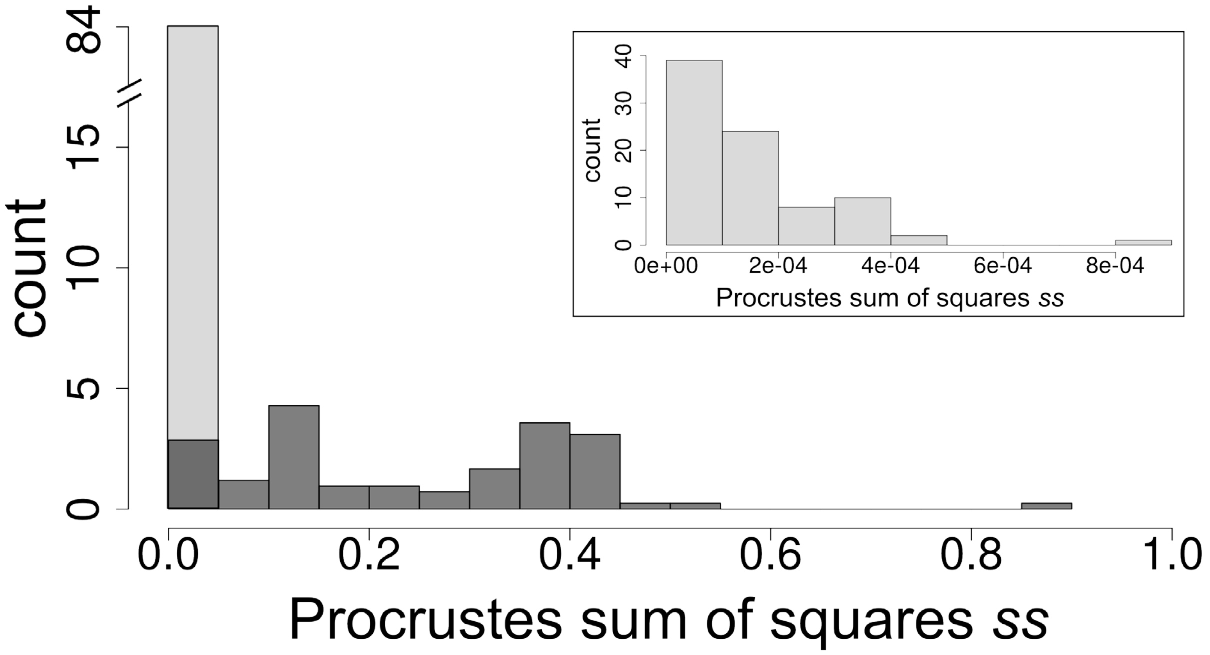


Figure S7. Influence of different *Sinapis arvensis* individuals on module composition. Histogram shows the deviation in module composition (Procrustes sum of squares). Dark grey bars show deviation of networks including one *S. arvensis* individual (*n* = 84) to species mean (*ss*-values) $N\binom{84}{84}$ (figure 2). To assess deviation induced only by the module algorithm used, light grey bars show deviation of networks including the species mean $N\binom{84}{84}$ to species mean $N\binom{84}{84}$. Inset shows the deviation of networks including the species mean $N\binom{84}{84}$ to species mean $N\binom{84}{84}$ only. Procrustes sum of squares *ss* were obtained from comparing principal coordinate analyses (PCoA) based on Sørensen distances of plant species based on module affiliation for networks including different *S. arvensis* individuals $N\binom{84}{1}$ and all individuals $N\binom{84}{84}$.

Supplementary Material Chapter 3

Dynamic range boxes – A robust non-parametric approach quantifying size and overlap of niches and trait-spaces in *n*-dimensional hypervolumes

Robert R. Junker, Jonas Kuppler, Arne Bathke, Manuela L. Schreyer, Wolfgang Trutschnig

Supporting Information 1 – **Simulations**

Methods

To evaluate the robustness of the results obtained from the dynamic range box approach, we quantified the overlap *port(A, B)* of two trait-spaces as a function of increasing sampling effort ranging from three observations per trait-space to the full population of observations. We generated six datasets each containing two trait-spaces defined by two dimensions. The data defining the trait-spaces had either a normal, uniform, binomial distribution; one dataset contained normally distributed data with outliers, two uniformly distributed datasets varied in the degree of their overlap in trait-spaces. Each trait-space contained 100 to 200 observations. For these datasets we randomly drew n_o observations ($n_o$ranging from 3 to the maximum number of observations) and calculated the overlap *port(A, B)* between the trait-spaces based on this subset of observations. This approach was repeated 100 times for each number of randomly drawn observations to obtain mean and 95% confidence interval.

Additionally, we evaluated the effect of the number *m* of dynamic range boxes *α* (steps) on the sizes *vol(A)* and overlap *port(A, B)* of trait-spaces. We used the same datasets as described above and quantified the sizes *vol(A)* and overlaps *port(A, B)* of the trait-spaces using an increasing number of steps (5 - 500).

Results and discussion

The mean of 100 replicates of calculations on the overlap *port(A, B)* of trait-spaces consisting of n_o randomly drawn observations from the total population of observations quickly approached the overlap that was calculated based on all observations, regardless of the distribution of the generated data (Fig. S1-1). However, low sampling efforts resulted in larger 95% confidence intervals of the overlap than found in calculations based on a higher sampling effort (Fig. S1-1). Thus, as *dynamic range boxes* precisely calculate sizes *vol(A)* and overlap *port(A, B)* of niches and trait-spaces the result obtained from a subset of data may under- or overestimate values, especially if sampling effort is below 40%.

The choice of the number *m* of dynamic range boxes *α* (steps) influences the result but only at very low numbers of steps (*m* < 50). Step numbers *m* above 100 mostly resulted in stable results (Fig. S1-1). Therefore, we set the default to *m* = 201, which is a good compromise between receiving a robust result while keeping computing time relatively short.

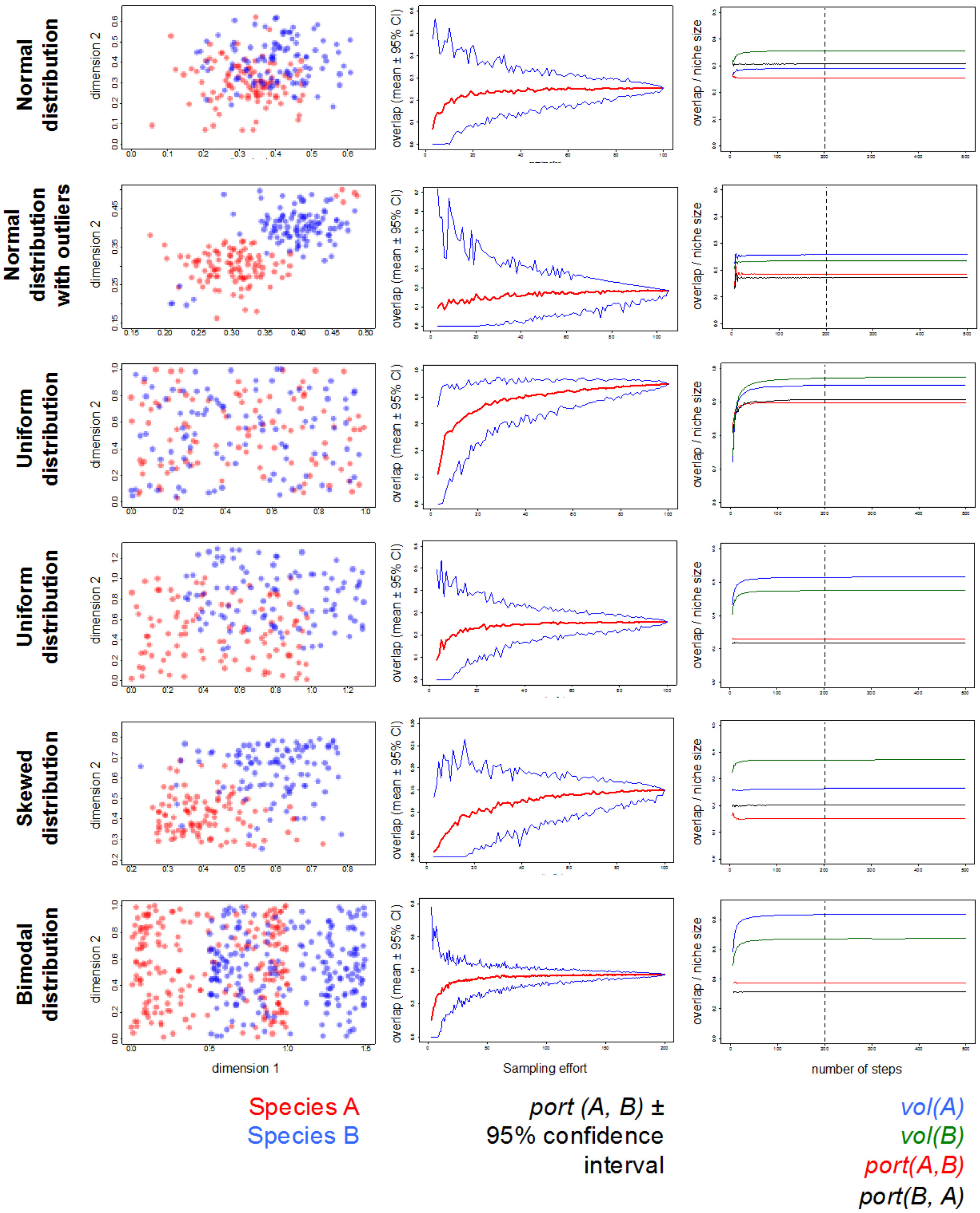


Fig. S1-1 Results of simulation. For six datasets with different distributions (left column), the overlap *port(A, B)* ± 95% confidence interval as a function of increasing sample size is shown (middle column). Additionally, vol(A), vol(B), *port(A, B)* and *port(B, A)* as a function of increasing numbers *m* of *α*-values are shown (right column).

Supporting Information 2 – **Overlap of *n*-dimensional hypervolumes with increasing number of dimensions *n*, comparing dynamic range boxes with other methods**

Additional results

Tab. S2-1 Overlap of trait-spaces characterized by increasing number of dimensions quantified with the R packages *dynRB* (pca.corr=FALSE and pca.corr=TRUE), *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al*. 2015). Data either had a uniform or a normal distribution. Given are expected values calculated from the overlap per dimension and results of the four approaches (mean ± SD) as a function of a increasing number of dimensions.

		uniform distribution				normal distribution			
100% overlap in each dimension									
dimensions	expected	dynRB	dynRB (pca.corr=TRUE)	hypervolume	nicheROVER	dynRB	dynRB (pca.corr=TRUE)	hypervolume	nicheROVER
2	1	0.960682 ± 0.0012972	0.9544 ± 0.0014	0.9501 ± 0.0005	0.9897 ± 0.0089	0.9489 ± 0.0020	0.9494 ± 0.0019	0.9127 ± 0.0011	0.9895 ± 0.0142
3	1	0.961352 ± 0.0012484	0.9482 ± 0.0014	0.9718 ± 0.0002	0.9895 ± 0.0089	0.9408 ± 0.0021	0.9392 ± 0.0021	0.9308 ± 0.0010	0.9892 ± 0.0140
4	1	0.957897 ± 0.0012241	0.9338 ± 0.0018	0.9688 ± 0.0002	0.9894 ± 0.0088	0.9245 ± 0.0024	0.9239 ± 0.0024	0.9348 ± 0.0008	0.9890 ± 0.0144
5	1	0.958052 ± 0.0011302	0.9211 ± 0.0017	0.9468 ± 0.0003	0.9891 ± 0.0083	0.9109 ± 0.0024	0.9105 ± 0.0025	0.9309 ± 0.0007	0.9889 ± 0.0128
6	1	0.955484 ± 0.0011085	0.9079 ± 0.0019	0.8890 ± 0.0002	0.9889 ± 0.0075	0.8953 ± 0.0028	0.8945 ± 0.0025	0.9174 ± 0.0008	0.9888 ± 0.0128
7	1	0.951898 ± 0.0009987	0.8909 ± 0.0019	0.7542 ± 0.0003	0.9888 ± 0.0077	0.8769 ± 0.0031	0.8783 ± 0.0031	0.8900 ± 0.0005	0.9885 ± 0.0148
8	1	0.949838 ± 0.0010773	0.8751 ± 0.0022	0.5103 ± 0.0004	0.9885 ± 0.0079	0.8641 ± 0.0029	0.8604 ± 0.0032	0.8434 ± 0.0004	0.9883 ± 0.0125
9	1	0.948963 ± 0.0039328	0.8875 ± 0.0068	0.2431 ± 0.0012	0.9880 ± 0.0257	0.8448 ± 0.0038	0.8474 ± 0.0035	0.7728 ± 0.0004	0.9882 ± 0.0137
10	1	0.945813 ± 0.0028828	0.8582 ± 0.0052	0.0872 ± 0.0005	0.9883 ± 0.0199	0.8293 ± 0.0033	0.8432 ± 0.0032	0.6743 ± 0.0002	0.9880 ± 0.0128
66% overlap in each dimension									
2	0.4444	0.243907 ± 0.0006353	0.2810 ± 0.0010	0.5955 ± 0.0008	0.8812 ± 0.1052	0.3250 ± 0.0031	0.3598 ± 0.0037	0.8307 ± 0.0053	0.9393 ± 0.1455
3	0.2930	0.174088 ± 0.0003508	0.2248 ± 0.0009	0.5175 ± 0.0007	0.8331 ± 0.1245	0.2833 ± 0.0020	0.3550 ± 0.0028	0.8351 ± 0.0032	0.9191 ± 0.1765
4	0.1975	0.119334 ± 0.0002358	0.1934 ± 0.0010	0.4830 ± 0.0008	0.7901 ± 0.1258	0.2358 ± 0.0028	0.3348 ± 0.0040	0.8228 ± 0.0041	0.9049 ± 0.1754
5	0.1317	0.081578 ± 0.0001494	0.1684 ± 0.0009	0.4158 ± 0.0005	0.7458 ± 0.1758	0.1924 ± 0.0024	0.3031 ± 0.0031	0.8041 ± 0.0027	0.8875 ± 0.1888
6	0.0878	0.054835 ± 9.78E-05	0.1417 ± 0.0010	0.3572 ± 0.0008	0.6984 ± 0.1891	0.1573 ± 0.0018	0.2827 ± 0.0027	0.7881 ± 0.0025	0.8721 ± 0.2513
7	0.0585	0.0389 ± 8.14E-05	0.1180 ± 0.0010	0.2844 ± 0.0008	0.6507 ± 0.2187	0.1338 ± 0.0018	0.2848 ± 0.0040	0.7208 ± 0.0019	0.8533 ± 0.3851
8	0.0390	0.024794 ± 4.21E-05	0.0923 ± 0.0008	0.2004 ± 0.0008	0.6061 ± 0.1924	0.1107 ± 0.0019	0.2323 ± 0.0029	0.6507 ± 0.0019	0.8374 ± 0.3988
9	0.0260	0.016828 ± 3.28E-05	0.0779 ± 0.0008	0.1190 ± 0.0004	0.5684 ± 0.2054	0.0947 ± 0.0015	0.2185 ± 0.0030	0.5852 ± 0.0018	0.8139 ± 0.3285
10	0.0173	0.011111 ± 1.85E-05	0.0675 ± 0.0008	0.0574 ± 0.0004	0.5279 ± 0.2448	0.0788 ± 0.0014	0.1957 ± 0.0035	0.4838 ± 0.0014	0.7901 ± 0.6883
33% overlap in each dimension									
2	0.1111	0.098117 ± 0.0002745	0.1021 ± 0.0008	0.4581 ± 0.0009	0.6534 ± 0.1839	0.0748 ± 0.0009	0.0680 ± 0.0008	0.6759 ± 0.0059	0.5518 ± 0.4159
3	0.0370	0.052438 ± 0.0001385	0.0678 ± 0.0005	0.3498 ± 0.0008	0.5170 ± 0.2029	0.0490 ± 0.0005	0.0435 ± 0.0007	0.6002 ± 0.0058	0.3814 ± 0.5008
4	0.0123	0.027303 ± 6.80E-05	0.0441 ± 0.0004	0.2782 ± 0.0004	0.4004 ± 0.1914	0.0325 ± 0.0005	0.0268 ± 0.0008	0.5322 ± 0.0030	0.2642 ± 0.4941
5	0.0041	0.014039 ± 3.28E-05	0.0291 ± 0.0004	0.2152 ± 0.0005	0.3024 ± 0.1737	0.0212 ± 0.0004	0.0138 ± 0.0008	0.4668 ± 0.0031	0.1738 ± 0.3855
6	0.0014	0.007102 ± 1.40E-05	0.0154 ± 0.0003	0.1595 ± 0.0004	0.2249 ± 0.1728	0.0137 ± 0.0002	0.0074 ± 0.0005	0.3898 ± 0.0024	0.1100 ± 0.2423
7	0.0005	0.003598 ± 9.03E-06	0.0098 ± 0.0002	0.1078 ± 0.0004	0.1620 ± 0.1523	0.0088 ± 0.0001	0.0045 ± 0.0003	0.3178 ± 0.0015	0.0725 ± 0.1729
8	1.524E-04	0.001814 ± 4.08E-06	0.0061 ± 0.0002	0.0632 ± 0.0003	0.1175 ± 0.1185	0.0058 ± 0.0001	0.0022 ± 0.0002	0.2383 ± 0.0011	0.0411 ± 0.1451
9	5.081E-05	0.000913 ± 2.11E-06	0.0038 ± 0.0002	0.0307 ± 0.0002	0.0854 ± 0.1061	0.0040 ± 0.0001	0.0015 ± 0.0001	0.1703 ± 0.0011	0.0257 ± 0.0848
10	1.694E-05	0.00046 ± 1.05E-06	0.0022 ± 0.0001	0.0123 ± 0.0001	0.0595 ± 0.0723	0.0027 ± 0.0001	0.0008 ± 0.0001	0.1100 ± 0.0009	0.0144 ± 0.0532
0% overlap in each dimension									
2	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.1822 ± 0.0007	0.0190 ± 0.02405	0.0000 ± 0.0000	0.0000 ± 0.0000	0.159379733 ± 0.00332	0.0000 ± 0.0000
3	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0880 ± 0.0004	0.0018 ± 0.00375	0.0000 ± 0.0000	0.0000 ± 0.0000	0.054785703 ± 0.001391	0.0000 ± 0.0000
4	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0415 ± 0.0002	0.0001 ± 0.00039	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0145788 ± 0.000503	0.0000 ± 0.0000
5	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0175 ± 0.0002	0.0000 ± 5.0E-05	0.0000 ± 0.0000	0.0000 ± 0.0000	0.000377839 ± 3.4E-05	0.0000 ± 0.0000
6	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0058 ± 0.0001	0.0000 ± 1.2E-05	0.0000 ± 0.0000	0.0000 ± 0.0000	3.84E-05 ± 8.3E-06	0.0000 ± 0.0000
7	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0013 ± 0.0000	0.0000 ± 0.0E+00	0.0000 ± 0.0000	0.0000 ± 0.0000	2.28E-06 ± 1.2E-06	0.0000 ± 0.0000
8	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0002 ± 0.0000	0.0000 ± 0	0.0000 ± 0.0000	0.0000 ± 0.0000	7.45E-07 ± 7.4E-07	0.0000 ± 0.0000
9	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0000 ± 0	0.0000 ± 0.0000	0.0000 ± 0.0000	0 ± 0.0000	0.0000 ± 0.0000
10	0	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0000 ± 0.0000	0.0000 ± 0	0.0000 ± 0.0000	0.0000 ± 0.0000	0 ± 0.0000	0.0000 ± 0.0000

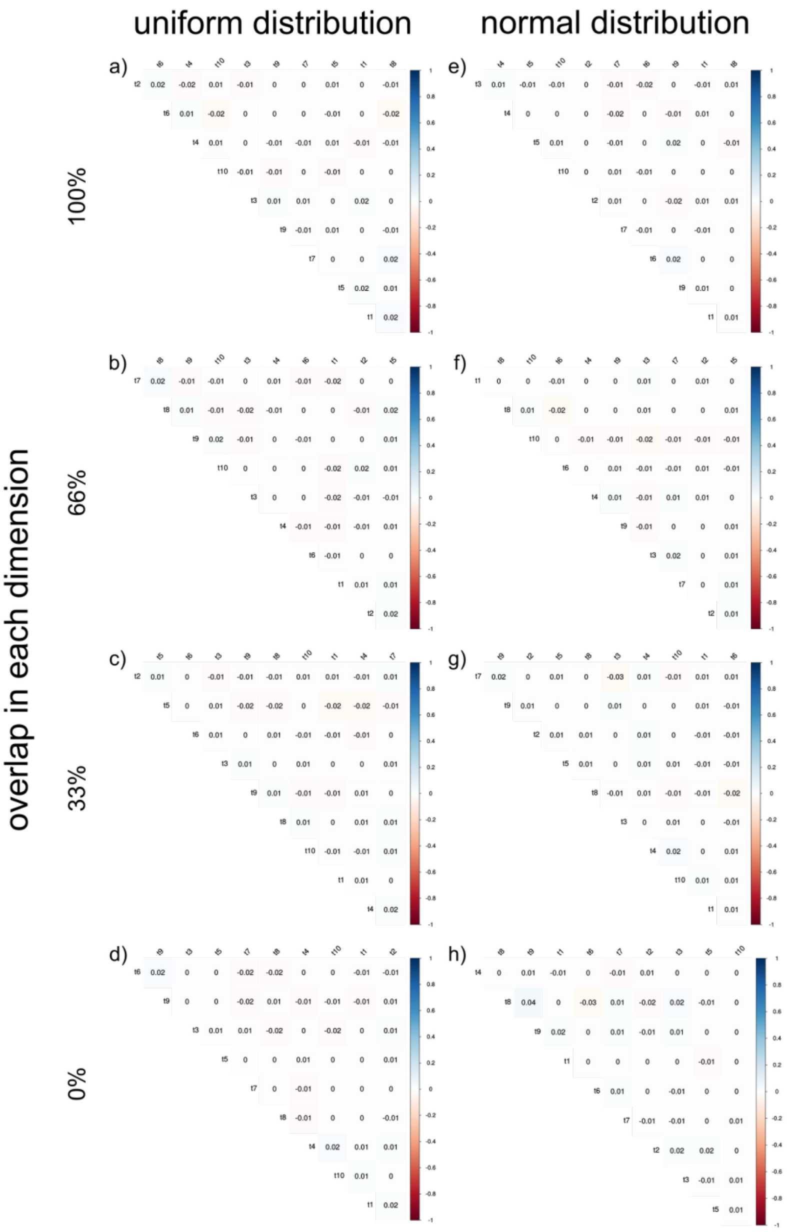


Fig. S2-1 Correlations between generated dimensions used to compare expected overlaps with results of the four approaches *dynRB* (pca.corr=FALSE and pca.corr=TRUE), *hypervolume* (Blonder *et al.* 2014), and *nicheROVER* (Swanson *et al.* 2015) (s. Fig. 3 in the main text and Tab. S2-1). Data in examples a-d have a uniform distribution, e-h have a normal distribution.

References

Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014) The n-dimensional hypervolume. *Global Ecology and Biogeography*, 23, 595-609.

Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D. & Reist, J.D. (2015) A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, 96, 318-324.

Supplementary Material Chapter 4

Article title: **Trait-based quantification of floral niche size and overlap reveals mechanisms underlying resource partitioning and competition between native and introduced flower visitors**

Authors: Jonas Kuppler, Maren Höfers, Wolfgang Trutschnig, Arne C. Bathke, Jesse A. Eiben, Curtis C. Daehler & Robert R. Junker

Article acceptance date: N/A

The following Supporting Information is available for this article:

Appendix A: Plot description, list of plant species and flower visitor taxa
Appendix B: Methods and Results for floral colour and nectar properties
Appendix C: Emission rates of native and introduced plant species
Appendix D: Results for niche size *vol*(A) and overlap *port*(A,B) calculations only including plots where native and introduced plant species and flower visitor taxa were co-occurring.
Appendix E: Distribution of visited trait ranges for three trait categories (floral morphology, floral scent and weather)
Appendix F: Dimension-wise niche size *vol*(A) and overlap *port*(A,B) for three trait categories (floral morphology, floral scent, weather)

Appendix A: Plot description, list of plant species and flower visitor taxa

Table A1. Description of study sites. If not otherwise indicated the study sites were located within the Hawaii Volcanoes National Park.

Name	Geographic coordinates	Altitude [m a.s.l.]	Age [y]	Size [m²]	No. animal species (all/native)	No. plant species (all/native)
N1	19.4939 N, 155.3847 W	2036	1500	750	7 / 5	2 / 2
N2	19.3434 N, 155.2741 W	985	750	780	10 / 1	4 / 4
N3	19.1833 N, 155.0905 W	225	400	495	4 / 0	3 / 1
N5[1]	19.4051 N, 155.2050 W	1595	160	200	5 / 2	4 / 2
N6	19.1755 N, 155.0869 W	109	41	667	10 / 1	8 / 2
N7[2]	19.2641 N, 155.1155 W	991	355	800	5 / 0	6 / 1
N8	19.2050 N, 155.1639 W	986	750	104	8 / 2	3 / 3
N9	19.2177 N, 155.1507 W	1037	400	138	5 / 0	2 / 2
N10	19.2623 N, 155.1808 W	1232	200	230	3 / 0	1 / 1
N11	19.2627 N, 155.1808 W	1215	200	504	8 / 2	6 / 4
N12	19.2637 N, 155.1802 W	1245	200	430	6 / 2	4 / 3
N13	19.2224 N, 155.1242 W	1038	41	7550	9 / 3	4 / 4
N14	19.1966 N, 155.1675 W	923	750	750	8 / 3	5 / 5
N15	19.1874 N, 155.0884 W	508	41	740	3 / 0	3 / 2
N16[3]	19.2129 N, 154.5921 W	42	23	1454	7 / 2	10 / 2
N17	19.2070 N, 155.1644 W	995	1500	617	9 / 3	5 / 5
N18	19.1711 N, 155.0747 W	52	400	1238	5 / 2	3 / 2

N19	19.2902 N, 155.2243 W	1869	1500	336	8 / 3	3 / 2
N20	19.3704 N, 155.2267 W	1020	36	4410	9 / 3	5 / 3
N21	19.2896 N, 155.1075 W	29	400	864	8 / 0	7 / 2
N22	19.3241 N, 155.2775 W	894	750	450	11 / 4	4 / 2
N23	19.3726 N, 155.2349 W	1021	42	2314	8 / 1	4 / 4
N24	19.3076 N, 155.3050 W	810	750	4147	12 / 4	9 / 5
N25	19.3676 N, 155.2129 W	1005	41	2973	13 / 4	5 / 3
N26	19.2978 N, 155.0969 W	49	400	1003	6 / 0	6 / 4
N27	19.3992 N, 155.2571 W	1148	41	924	12 / 4	2 / 2
N28	19.2440 N, 155.2136 W	902	355	553	0 / 0	3 / 3
N29	19.4068 N, 155.2386 W	1118	400	156	9 / 0	2 / 1
N30	19.4017 N, 155.2546 W	1142	355	86	5 / 2	3 / 3
N31	19.3733 N, 155.2408 W	1039	355	578	4 / 0	3 / 3
N32	19.4332 N, 155.2848 W	1248	400	798	7 / 3	3 / 3
N33	19.3146 N, 155.1514 W	556	400	1210	6 / 1	3 / 3
N34	19.3380 N, 155.2055 W	853	41	1644	7 / 4	4 / 4

[1]Saddle Road; [2]Volcano Village; [3]Puna

Table A2. Observed native and introduced flower visiting taxa. Taxa names are given as species names, morphospecies (M1, M2, etc.) or as genera potentially comprising several species. Number in brackets correspond to numbers in figure 1.

Flower visitor taxa	**Number of observations**	**Number of visited plant species**	**Percentage of native plant species visited**
introduced			
Curcolionidae, Coleoptera			
Cylus formicarus (9)	1	1	100
Syrphidae, Diptera			
Allograpta oblique or *exotica* (1)	166	19	63
Syrphid M1 (23)	1	1	0
Syrphid M2 (24)	4	3	0
Syrphid M3 (25)	1	1	100
Syrphid sp. (26)	162	22	45
Toxomerus marginatus (30)	106	19	42
Miridae, Hemiptera			
Lygus elisus (15)	4	2	50
Tingidae, Hemiptera			
Teleonemia scrupulosa (28)	2	1	0
Apidae, Hymenoptera			
Apis mellifera (3)	1182	17	47
Ceratina cf. *dentipes* (7)	23	4	25
Ceratina smaragdula (8)	7	2	0
Xylocopa sonorina (32)	97	8	63
Colletidae, Hymenoptera			
Hylaeus albonitens (12)	16	3	100
Megachilidae, Hymenoptera			
Megachile sp. (16)	2	1	0
Formicidae, Hymenoptera			
Anoplolepis gracilipes (2)	34	3	67
Brachomyrmex obscurior (4)	5	2	50
Cardiocondyla emeryi (5)	1	1	0
Cardiocondyla kagutsuchi (6)	38	5	60
Linepithema humile (14)	318	3	100
Ochetellus glaber (17)	78	8	63
Paratrechina bourbonica (18)	104	2	100
Paratrechina vaga (19)	1	1	100
Pheidole megacephala (20)	31	7	43
Plagiolepis alluaudi (21)	15	3	67
Tapinoma melanocephala (27)	1	1	100
Tetramorium bicarinatum (29)	26	1	100
Vespidae, Hymenoptera			
Dolichovespula maculata (10)	1	1	100
Polistes olivaceus (22)	16	3	100
Vespula pensylvanica (31)	102	3	100
Orthoptera			

Ensifera (11)	23	9	56
Zosteropidae, Passeriformes			
Zosterops japonicus (13)	6	3	67
native			
Drosophilidae, Brachycera			
cf *Scaptomyza* sp. (35)	39	1	100
Miridae, Hemiptera			
Orthotylus sophoricola (47)	1	1	100
Lygaeidae, Hemiptera			
Nysius delectulus (44)	9	2	50
Nysius nemorivagus (45)	2	1	0
Nysius rubescens (46)	12	1	100
Colletidae, Hymenoptera			
Hylaeus conipes (36)	1	1	100
Hylaeus difficilis (37)	62	8	100
Hylaeus flavipes (38)	3	3	66.6
Hylaeus laetus (39)	15	5	80
Hylaeus pele (40)	1	1	100
Hylaeus rugulosus (41)	5	1	100
Hylaeus sp. (42)	181	15	67
Hylaeus volcanicus (43)	5	2	100
Fringillidae, Passeriformes			
Hemignathus virens (33)	17	2	100
Himatione sanguinea (34)	18	2	100
Unknown origin			
Brachycera M1	4	1	100
Brachycera M2	1	1	100
Brachycera M3	1	1	100
Brachycera M4	8	1	0
Brachycera M5	1	1	100
Brachycera M6	1	1	100
Brachycera M7	2	2	100
Brachycera M8	1	1	100
Brachycera M9	2	2	50
Brachycera M10	1	1	100
Brachycera M11	222	1	100
Brachycera M12	2	1	0
Brachycera M13	17	5	60
Brachycera M14	1	1	1
Brachycera M15	3	1	0
Brachycera sp.	28	11	73
Caterpillar M1	1	1	100
Caterpillar M2	70	1	100
Coleoptera M1	1	1	0
Coleoptera M2	1	1	0
Coleoptera M3	1	1	100
Coleoptera M4	7	5	80

Coleoptera M5	162	1	100
Coleoptera sp.	1	1	100
Diptera sp.	73	9	56
Calchid wasps	86	14	57
Heteroptera sp.	6	4	75
Ichneumonoidea M1	1	1	100
Ichneumonoidea M2	1	1	0
Lepidoptera M1	1	1	100
Lepidoptera M2	5	2	50
Lepidoptera M3	4	3	0
Lepidoptera M4	1	1	100
Lepidoptera M5	2	1	100
Lepidoptera M6	1	1	0
Lepidoptera M7	1	1	100
Lepidoptera sp.	15	8	38
Nematocera M2	1	1	100
Nematocera M3	1	1	100
Nematocera M5	1	1	100
Nymph unknown	1	1	100
Thysanoptera	26	6	67
Unknown	7	5	100
Wasp M1	4	2	50
Wasp M2	1	1	100
Wasp M3	1	1	100
Wasp M5	4	1	100
Wasp sp.	18	6	50

Table A3. Native and introduced plant species observed in the study. Given are number of occurrences on plots, number of floral units (inflorescence or flower) on all plots, and reproductive properties of the plant species (V = vegetative reproduction, NV = no vegetative reproduction, SC = self-compatible, SI = self-incompatible, X = no information). Numbers in brackets are corresponding to numbers in Figure 1.

Flower visitor taxa	Occurence	Number of floral units	Reproductive properties
introduced			
Asteraceae			
Ageratina riparia (1)	2	1656	V , X
Emilia sp. (9)	2	1499	V , X
Hieracium sp. (10)	2	39	
Pluchea carolensis (17)	2	6623	NV , X
Fabaceae			
Chamaechrista nictitans (3)	10	12537	NV , SC[1,2]
Crotalaria incana (4)	2	421	NV , SI[2]
Crotalaria retusa (5)	3	929	NV , SI[2]
Desmodium incanum (7)	1	95	V , SC&SI[1,2]
Desmodium triflorum (8)	3	2544	V , X
Lotus subbiflorus (12)	2	1238	
Mimosa pudica (14)	2	370	V , SI[2]
Lamiaceae			
Ajuga reptans (2)	1	160	V , SC[3]
Lythraceae			
Cuphea hyssopifolia (6)	1	1644	NV , X
Onagraceae			
Oenothera stricta (16)	1	6	X , SC[4]
Rosaceae			
Prunus sp. (19)	1	139	NV , X
Rubus argutus (20)	2	729	V , SI[2]
Rubiaceae			
Mitracarpus hirtus (15)	1	80	NV , X
Scrophulariaceae			
Torenia glabra (22)	1	29	V , X
Sterculiaceae			
Melochia umbellata (13)	1	733	X , X
Polygonaceae			
Polygonum capitatum (18)	4	6261	V , X
Verbenaceae			
Lantana camara (11)	4	11912	V , SI[2]
Stachytarpheta jamaicensis (21)	1	454	NV , X
native			
Asteraceae			
Bidens hawaiensis (24)	3	2006	
Dubautia ciliolata (26)	1	46	
Dubautia scabra (27)	5	4677	
Pseudognaphalium sandwicensium (33)	3	11909	

Convolvulaceae		
Ipomoea indica (28)	3	235
Epacridaceae		
Styphelia tamemaeiae (37)	15	10105
Ericaceae		
Vaccinium reticulatum (38)	9	3402
Fabaceae		
Acacia koa (23)	2	5490
Sesbania tomentosa (35)	1	15
Sophora chrysophylla (36)	7	8278
Goodenicaceae		
Scaevola kilauea (34)	4	129
Myrtaceae		
Metrosideros polymorpha (30)	22	3415
Rosaceae		
Osteomeles anthyllidifolia (32)	3	2488
Rubiaceae		
Kadua centranthoides (29)	1	206
Morinda citrifolia (31)	2	81
Sapindaceae		
Dodonea viscosa (25)	3	1859
Sterculiaceae		
Waltheria indica (39)	7	5537
Thymelaeaceae		
Wikstroemia sp. (40)	3	818

[1]hear.org/PIER, [2]cabi.org, [3]BIOFLOR-database, [4] eFlora.org

Appendix B: Methods and Results for floral colour and nectar properties

Flower reflectance measurement

Flower colour was measured as the spectral reflectance of petals between 300 – 700 nm, using a reflectance spectrometer (Jaz spectrometer, Ocean Optics, Ostfildern, Germany) with a standardized light source (Jaz-PX light source, Ocean Optics, Ostfildern, Germany). All measurements were taken in an angle of 45° to the surface. White calibration was done using a standard (Spectralon®) and black calibration was done covering the turned off light source. Flower colour was measured 2 – 10 times for each plant species using flowers from different individuals. Due to logistic constrains (availability of the spectrometer) we were only able to measure the flower colour of 22 plant species (Appendix A: Table A3). From the reflectance spectra we extracted common physical properties of the floral reflectance curve as surrogates for the flower colour: brightness (the sum relative reflectance over the entire spectra), chroma ((maximum reflectance – minimum reflectance)/ mean brightness) and hue (wavelength of the reflectance maximum) (Montgomerie 2006) using the R package *pavo* (Maia et al. 2013).

Nectar properties

Nectar volume [µl] and sugar content [%] were quantified early in the morning. Nectar samples of 2-10 individuals per species were taken with microcapillary tubes and the volume as well as the sugar content (percentage based on mass/mass) were quantified, the later by using a handheld refractometer (Eclipse; Bellingham and Stanley, Kent, UK). The value of either 0.01 µl (species that do produce nectar) or 0 µl (species that do not produce nectar) was assigned to each plant species where we were not able to collect nectar. For nectar concentration these plant species were excluded from the analysis.

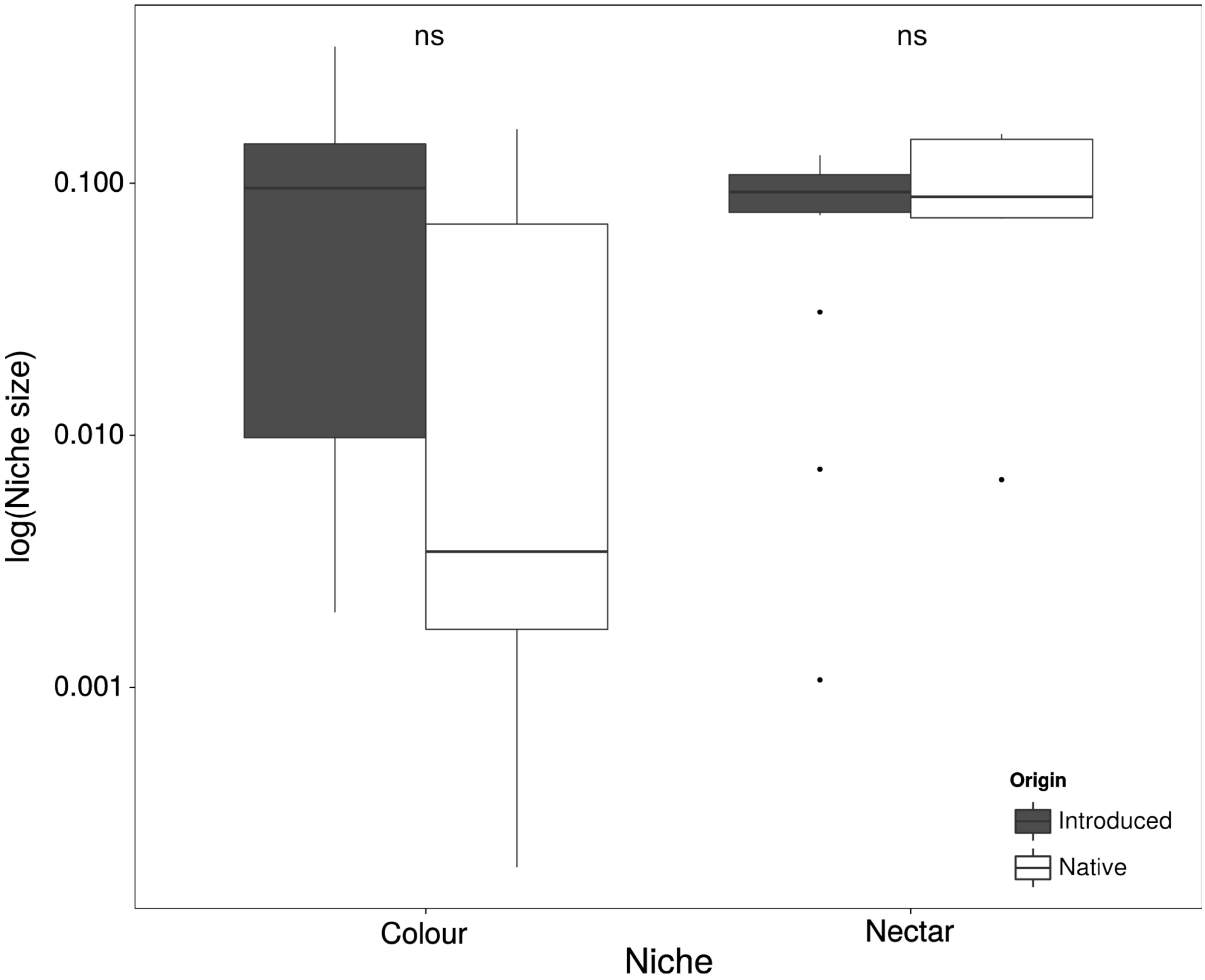


Figure B1. Niche sizes of native and introduced flower visitor. Niche sizes *vol*(A) were calculated for two different trait categories (floral colour and nectar properties) using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). Note that niche size is dependent on number of dimensions; as each trait category containes a different number of individual traits (morphology: n = 9 traits, scent: n = 6), niche sizes are not directly comparable between categories. White boxplots show native taxa (*n* = 7) and grey introduced ones (*n* = 18). ns = non-significant (Whitney-Mann U test).

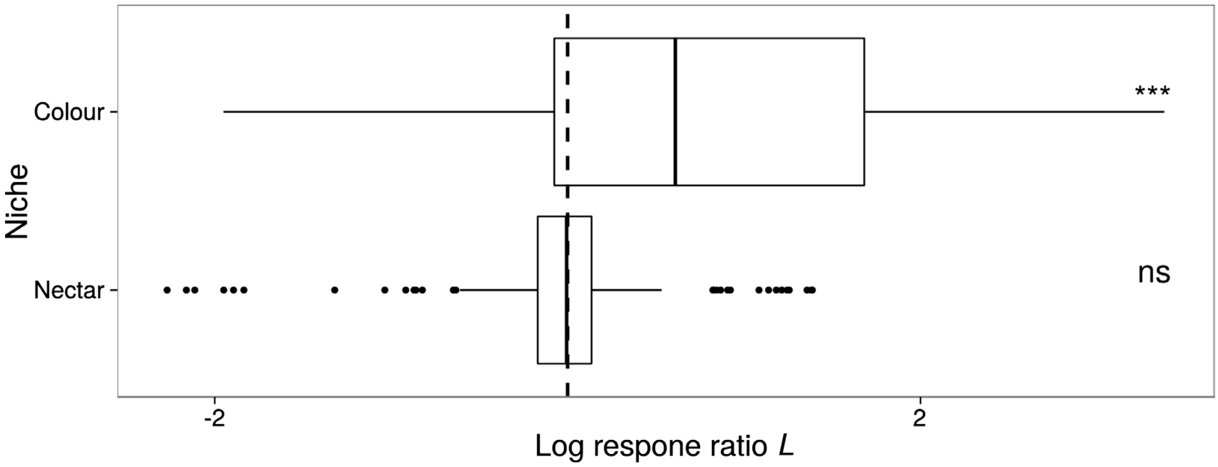


Figure B2. Asymmetric niche overlap between native and introduced flower visitor taxa. Log response ratios *L* describe the asymmetry of the niche overlap between native and introduced flower visitors. Asymmetry is expressed as the log of the quotient of the portion of the niche of a native taxon covered by the niche of an introduced taxon and the portion of the niche of the introduced taxon covered by the niche of the native taxon *L* = log(port(A, B) / port(B, A). *L* > 0 indicates that niches of introduced taxa overlap those of native taxa more than *vice versa*. Boxplots denote range, median and interquantil ranges of log response ratios *L* for two different trait categories (floral colour and nectar properties). Niche overlaps *port*(A,B) were calculated using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). *** p < 0.001, ns = non-signficiant (Whitney-Mann U test).

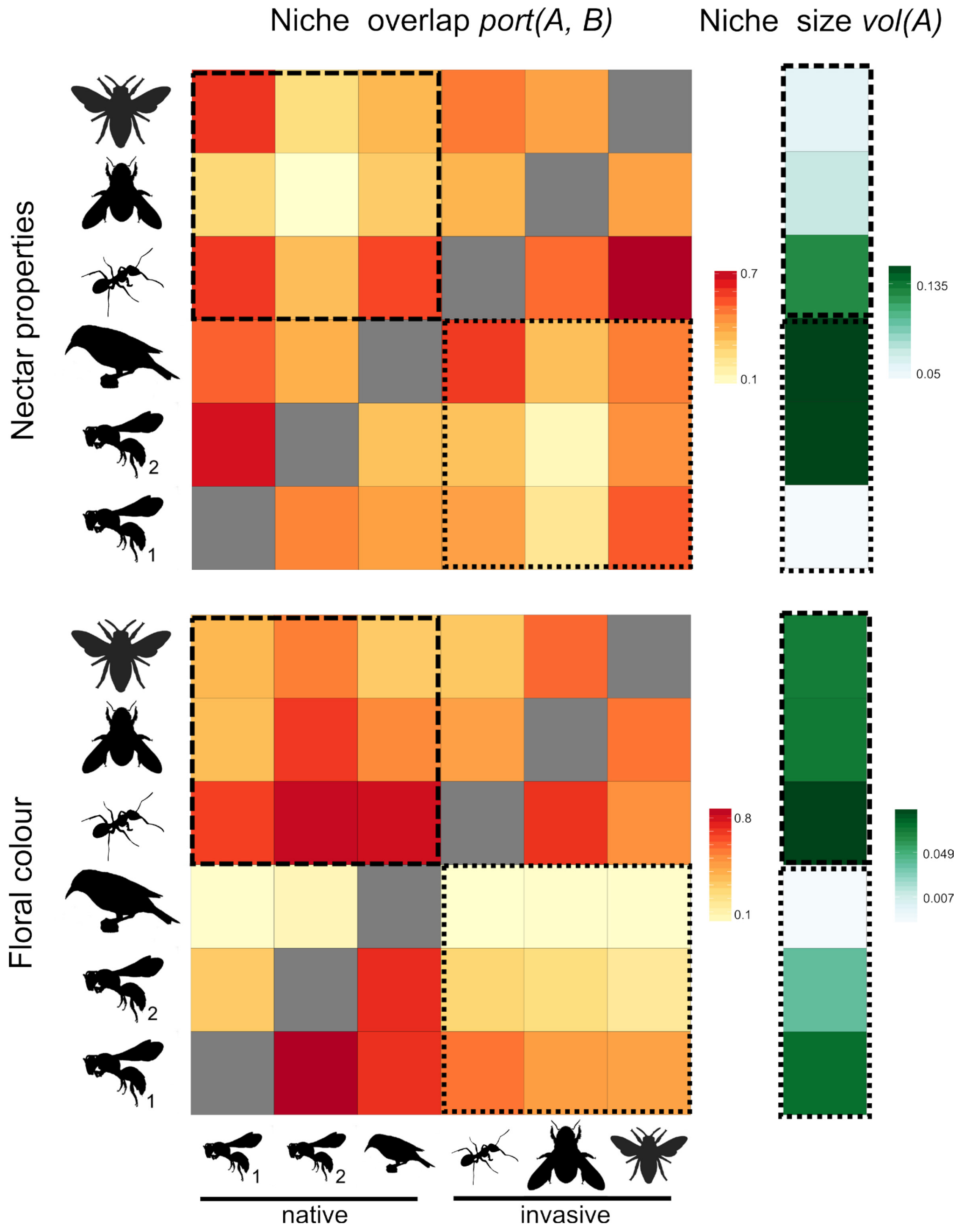


Figure B3. Niche size and overlap of the six most prominent flower visitor taxa (three introduced and three native) in Hawai'i Volcanoes National Park. Flower visitor taxa represented by silhouetes are, starting at the top, *Apis mellifera*, *Xylocopa sonorina*, ants (all species pooled), *Himatione sanguinea*, *Hylaeus laetus* (2), *Hylaeus difficilis* (1). The former three are introduced flower visitors, the latter three are native. Niche size *vol*(A) and overlap *port*(A,B) were calculating for different trait categories (floral colour and nectar properties) using *dynamic range boxes* – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niches), where each dimension represents one trait (Junker et al. 2015). Dashed boxes showing the proportion of the niche of native flower visitor taxa covered by introduced species. Pointed boxesshowing the proportion of the niche of native flower visitor taxa covered by introduced species. Pointed and dashed boxes indicate the niche sizes of native and introduced flower visitors. Black circles in the lower left heatmap (niche overlap *port*(A,B)) indicate the percentage of overlapping plant species and values next to lower second from left heatmap (niche size *vol*(A)) indicate number of visited plant species).

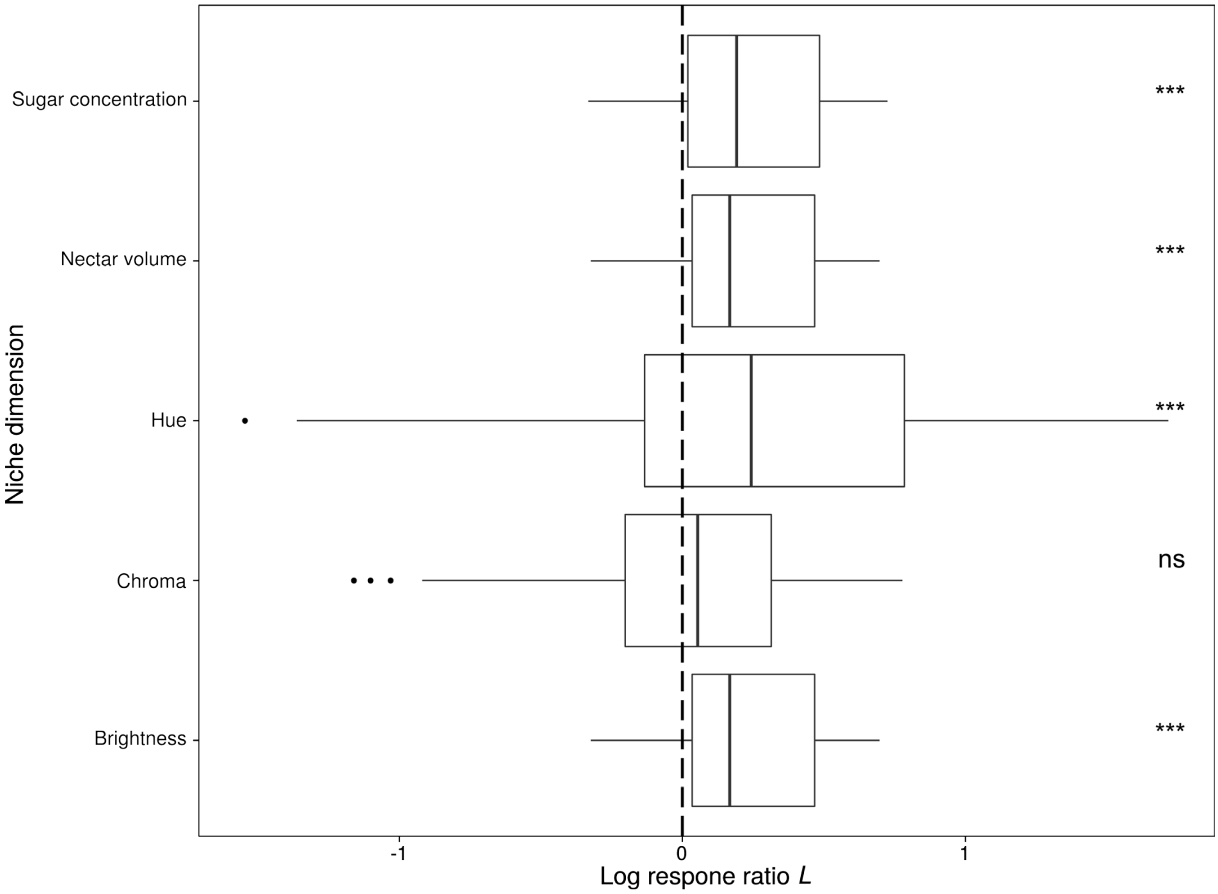


Figure B4. Asymmetric niche overlap between native and introduced flower visitor taxa. Log response ratios *L* describe the asymmetry of the niche overlap between native and introduced flower visitors. Asymmetry is expressed as the log of the quotient of the portion of the niche of a native taxon covered by the niche of an introduced taxon and the portion of the niche of the introduced taxon covered by the niche of the native taxon *L* = log(port(A, B) / port(B, A). *L* > 0 indicates that niches of introduced taxa overlap those of native taxa more than *vice versa*. Boxplots denote range, median and interquantil ranges of log response ratios *L* for all single traits comprising the two different trait categories (floral colour and nectar properties). Niche overlaps *port*(A,B) were calculated using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). *** $p < 0.001$, ns =non-signficiant(Whitney-Mann-U-test).

Appendix C: Emission rates of native and introduced plant species

Table C1. Emission rate of volatiles originating from six biochemical pathways in native and introduced plant species. For all functional groups emission rate in ng/h/100mg dry mass flower are given. Functional groups are aliphatics (A), aromatics (AR), C5-branched pathway (C5), irregular terpenes (IT), monoterpenes (MT), sesquiterpenes (ST).

Plant		A	AR	C5	IT	MT	ST
introduced							
	Ageratina riparia	0	0	0	0.424	0.214	0.035
	Ajuga reptans	0.844	0.055	0	0	0	0.531
	Chamaechrista nicitians	0	0	0	0	4.953	0
	Crotalaria incana	0.1	0.018	0	0.683	0.079	0.093
	Crotalaria retusa	0.151	0	0	0.474	0.003	0.068
	Cuphea hyssopifolia	0.078	0.137	0	0.113	3.834	0
	Desmodium incanum	0	0	0	0	0	0.363
	Desmodium triflorum	0	0	0	0	1.566	0
	Emilia sp.	0.151	0	0	0.247	0	0.51
	Hieracium sp.	0.836	0	0	0	0.228	0.025
	Lantana camara	5.998	0.648	0	2.415	187.67	89.852
	Lotus subbiflorus	0	0	0	0	614.87	32.873
	Melochia umbellata	0	1.508	0	0	1.199	0
	Mimosa pudica	0	0.593	0	0	0	0
	Mitracarpus hitra	0.055	0	0	0.047	0.02	0
	Oenothera stricta	38.947	35.325	0	0	205.82	0
	Pluchea carolensis	0.013	0	0	0.284	5.812	0.728
	Polygonum capitatum	0	0	0	0	0.085	0
	Prunus sp.	0	9.762	0	0	2.049	0
	Rubus argutus	0	0.65	0	0.123	0	0
	Stachytarpheta jamaicensis	4.746	0	0	0	0	0
	Torenia glabra	0	0	0	0	0.862	0
native							
	Acacia koa	0.319	0.132	0	1.697	0.04	0
	Bidens hawaiiensis	3.642	11.174	1.604	3.956	18.301	0.932
	Dodonea viscosa	0.121	0.218	0	0	2.869	0
	Dubautia ciliolata	0	1.513	0	4.04	1.108	18.094
	Dubautia scabra	0	1.021	0	0	30.553	3.739
	Ipomoea indica	0.751	0.11	0	0	0.461	21.637
	Kadua centranthoides	0	0.142	0	0	1.911	0.046
	Metrosideros polymorpha	0.034	0.024	0	0.076	0.137	0.256
	Morinda citrifolia	6.231	71.242	0.645	7.725	4.759	6.457
	Osteomeles anthyllidifolia	0.082	0.128	0	0	0	0
	Pseudognaphalium sandwicensium	2.746	0	0	0.032	3.059	0.797
	Scaevola kilauea	0	0	0	0	194.31	0
	Sophora chrysophylla	0	0	0	0	0.016	0
	Styphelia tamemaeiae	0	0.294	0	0	0.074	0
	Vaccinium reticulatum	0.005	0.081	0.017	0.082	2.675	0.151
	Waltheria indica	10.971	0	0.862	95.65	98.751	120.46
	Wikstroemia sp.	0	0	0	0	2.894	0

Appendix D: Results for niche size *vol*(A) and overlap *port*(A,B) calculations only including plots where native and introduced plant species and flower visitor taxa were co-occurring.

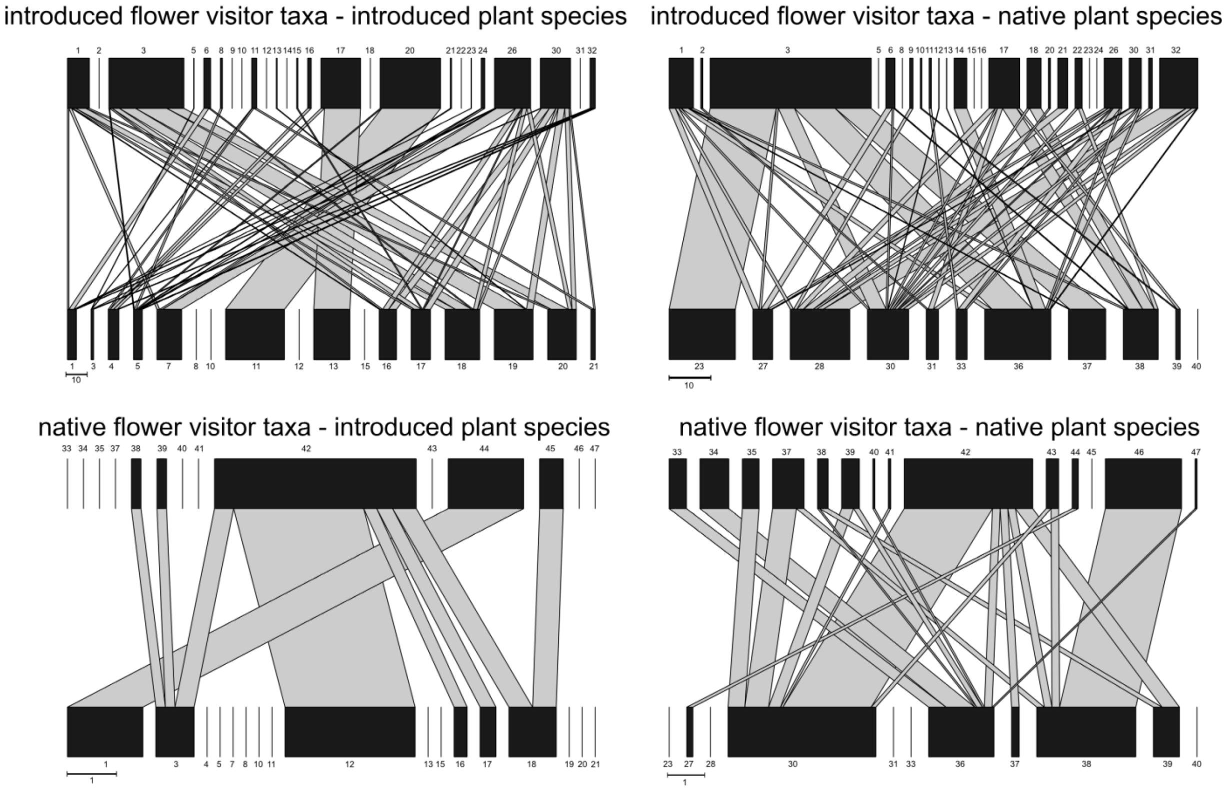


Figure D1. Bipartite flower-visitor networks for native or introduced flower visitors interacting with either native or introduced plant species. The networks are based on interactions per plant species per h observed on all plots where native and introduced flower visitor taxa and plant species were co-occurring (Appendix A: Table A1). Nodes represent plant species (bottom) or flower visitor taxa (top). The width of the nodes denotes the proportional interaction frequency of partners. Numbers denote flower visitor taxa and plant species (names are shown in Appendix A: Table A1 and A2 in Supporting Information): Introduced flower visitors 1 – 33, native flower visitors 34 – 48, introduced plant species 1 – 22, native plant species 23 – 40.

Table D1. Aggregate network statistics for flower visitor-plant networks in the Hawaii Volcanoes National Park. Information on network structure considering plants and animals of specific origins is given. Network structure was calculated for subsets containing either native or introduced flower visitors interacting with either native or introduced plant species. Shown are connectance *C*, weighted nestedness based on overlap and decreasing fills (WNODF), interaction evenness *E*, complementary specialisation of the individual plant (*d'*) and specialisation of the whole network (H_2'). For *d'* mean ± SE across taxa are given.

Animal and plant group	C	E	*d'*	H_2'
introduced – introduced	0.11	0.50	0.53 ± 0.24	0.71
introduced – native	0.17	0.55	0.41 ± 0.20	0.61
native – introduced	0.04	0.32	0.31 ± 0.37	0.89
native – native	0.14	0.49	0.42 ± 0.36	0.66

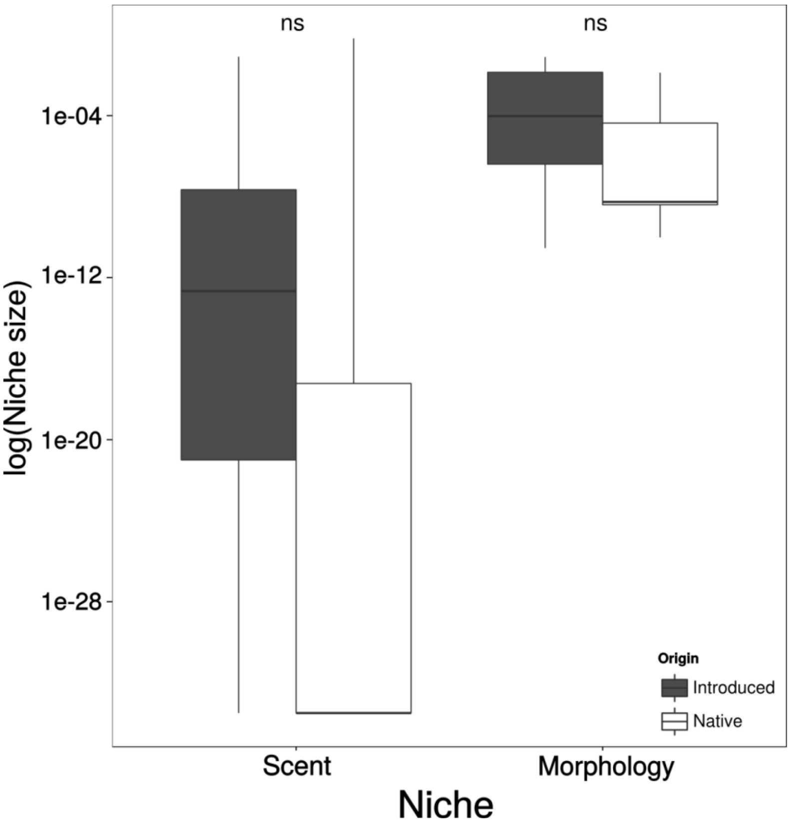


Figure D2. Niche sizes of native and introduced flower visitor. Niche sizes *vol*(A) were calculated for two different trait categories (floral scent and floral morphology) using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). Note that niche size is dependent on number of dimensions; as each trait category containes a different number of individual traits (morphology: n = 9 traits, scent: n = 6), niche sizes are not directly comparable between categories. White boxplots show native taxa (*n* = 7) and grey introduced ones (*n* = 18). ns = non-significant (Whitney-Mann U test: Scent: *W* = 76, *p* = 0.19; Morphology: *W* = 78, *p* = 0.15).

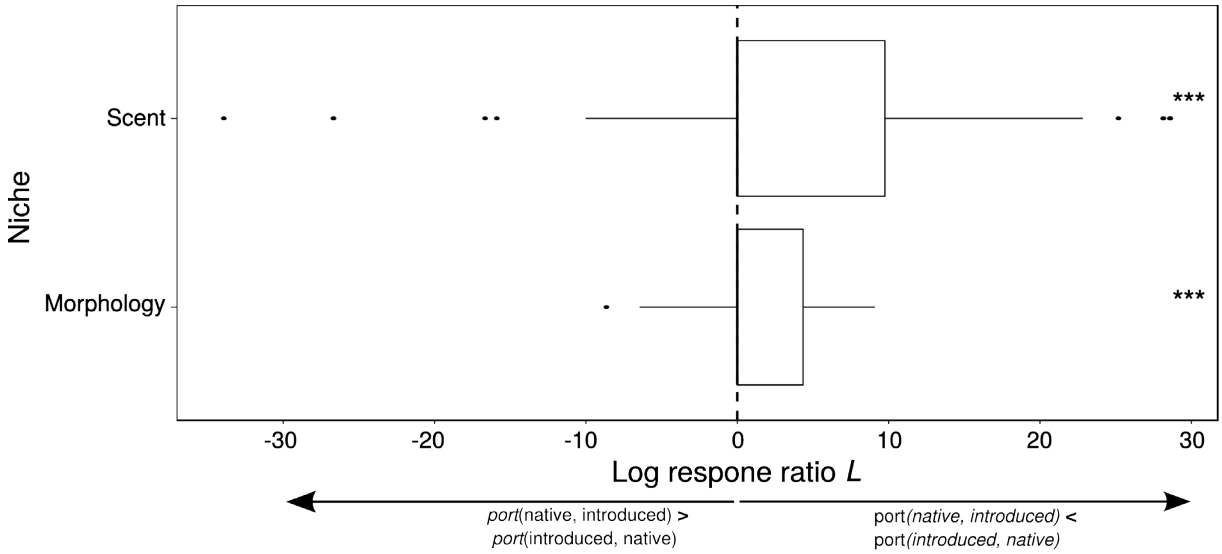


Figure D3. Asymmetric niche overlap between native and introduced flower visitor taxa. Log response ratios *L* describe the asymmetry of the niche overlap between native and introduced flower visitors. Asymmetry is expressed as the log of the quotient of the portion of the niche of a native taxon covered by the niche of an introduced taxon and the portion of the niche of the introduced taxon covered by the niche of the native taxon L = log(port(A, B) / port(B, A). $L > 0$ indicates that niches of introduced taxa overlap those of native taxa more than *vice versa*. Boxplots denote range, median and interquantil ranges of log response ratios *L* for two different trait categories (floral morphology and floral scent). Niche overlaps *port*(A,B) were calculated using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). *** $p < 0.001$ (Whitney-Mann U test: Scent: $V = 1238$, $p < 0.001$; Morphology: $V = 2510$, $p < 0.001$).

Appendix E: Distribution of visited trait ranges for three trait categories (floral morphology, floral scent and weather)

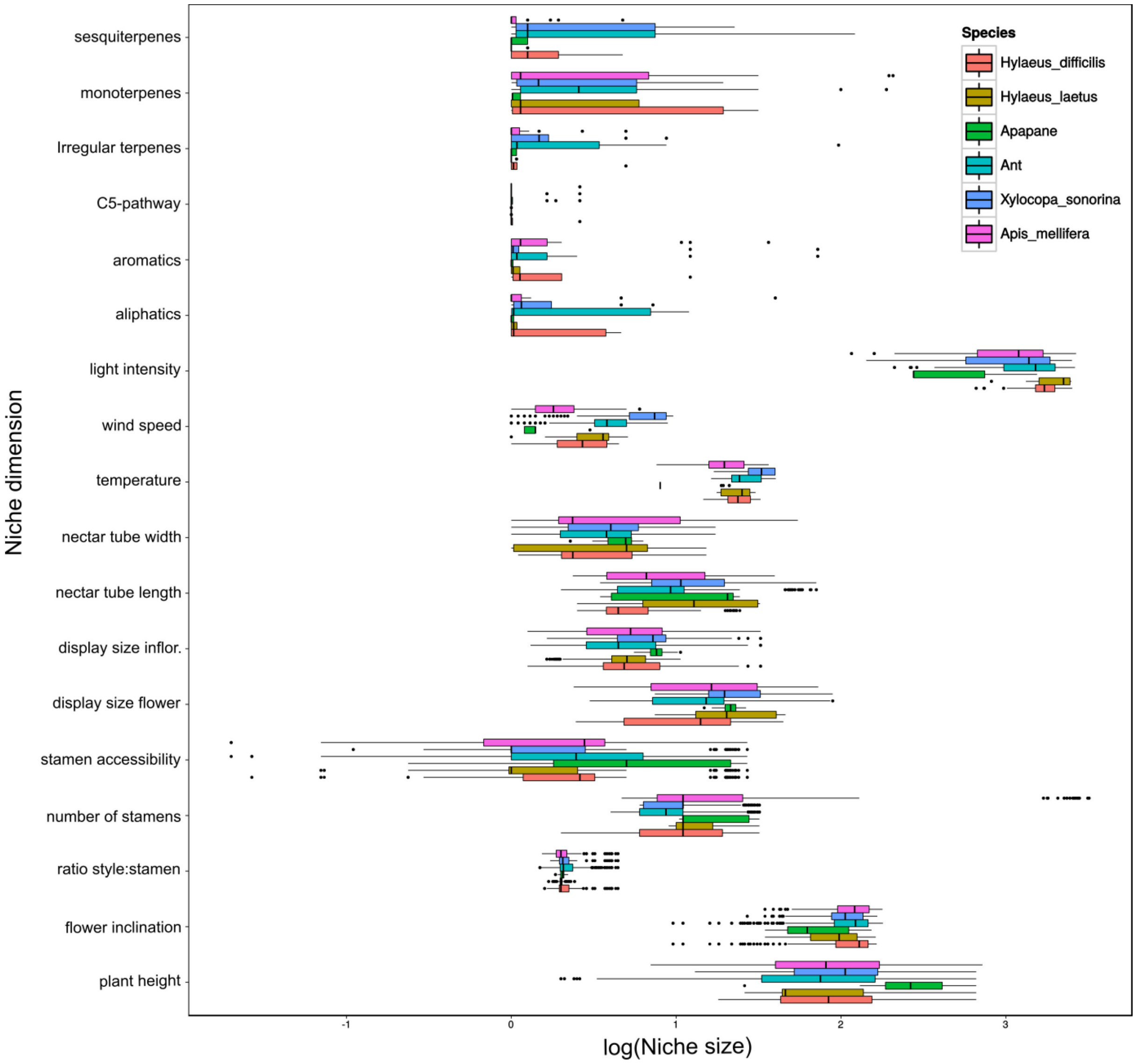


Figure E1. Trait distribution for all traits from the different trait categories (weather, scent and floral morphology) for *Apis mellifera, Xylocopa sonorina, Ants (all ant species pooled), Hylaeus difficilis, Hylaeus laetus and Himatione sanguinea (Apapane)*. Distributions are weighted for the interaction frequency of each visitor taxa with a given trait.

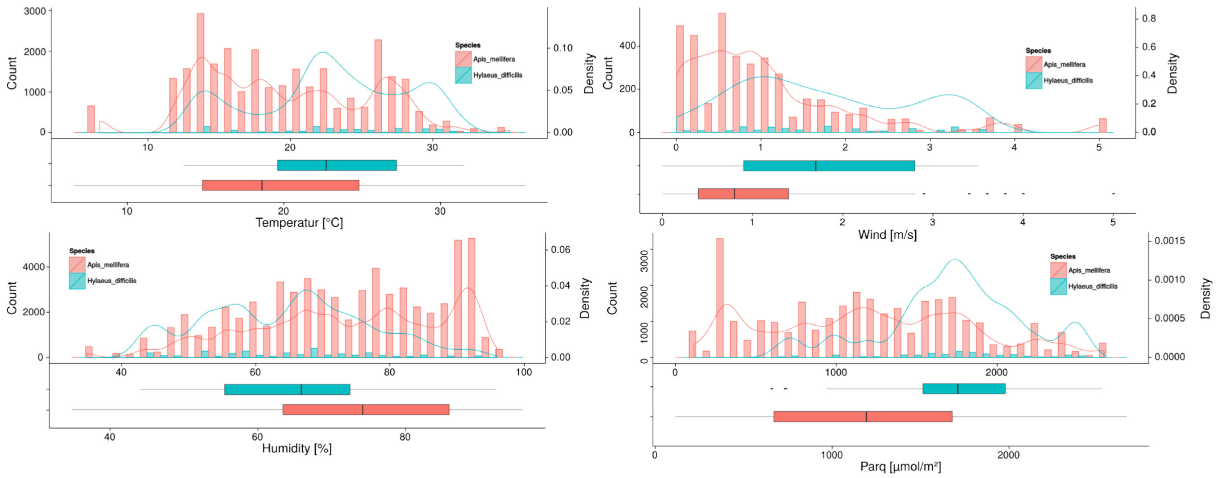


Figure E2. Detailed trait distribution of weather traits for *Apis mellifera* and *Hylaeus difficilis*.

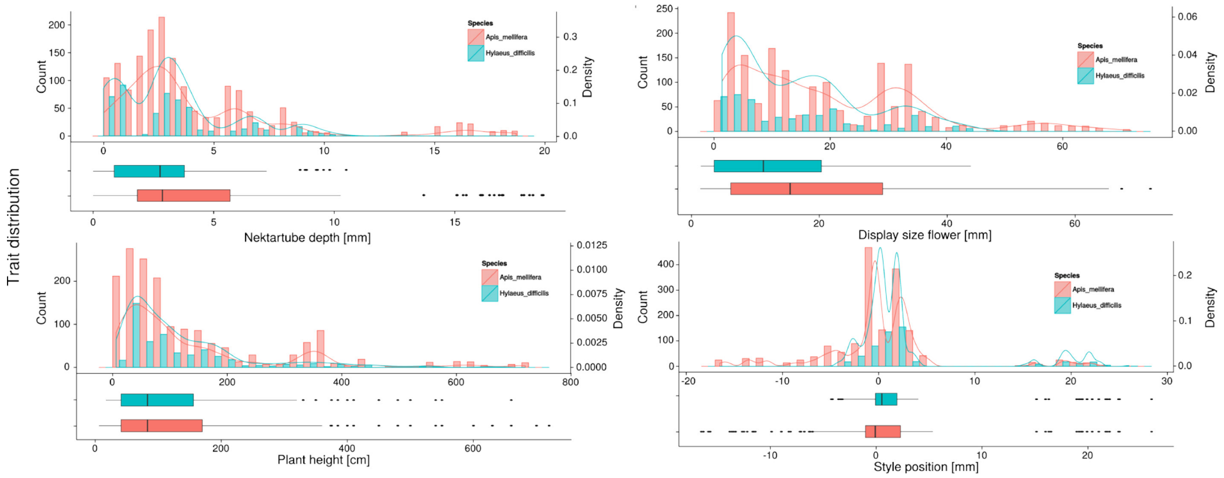


Figure E3. Detailed trait distribution of four floral morphology traits for *Apis mellifera* and *Hylaeus difficilis*.

Appendix F: Dimension-wise niche size *vol*(A) and overlap *port*(A,B) for three trait categories (floral morphology, floral scent, weather)

Table F1. Size for each niche dimension of native and introduced flower visitor species. Dimension-wise niche size were calculated for all measured floral traits, weather conditions and floral scent compounds using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche) (Junker et al. 2015).

Flower visitor taxa	Plant height	Flower inclination	Ratio style:stamen length	Nr of stamens	Stamen accessibility	Display size flower	Display size inflor.	Nectar tube length	Nectar tube width	Aliphatics	Aromatics	C5-pathway	Irregular terpenes	Mono-terpene	Temperature	Wind speed	Light intensity	Sesqui-terpenes
introduced																		
Allograpta oblique or *exotica*	0.3316	0.7277	0.233	0.091	0.2575	0.5609	0.2651	0.3061	0.3682	0.1741	0.1051	0.1135	0.0163	0.0656	0.5115	0.5414	0.7347	0.061
Anoplolepis gracilipes	0.4278	0.3618	0.1839	0.0071	0.3536	0.1225	0.2321	0.1286	0.0815	0.2318	0.7675	0.5361	0.1169	0.0061	0.4144	0.1953	0.7757	0.0772
Apis mellifera	0.4426	0.6548	0.2088	0.1113	0.2326	0.5744	0.4453	0.3485	0.4164	0.1587	0.1434	0.1408	0.0117	0.1187	0.606	0.279	0.7627	0.0049
Brachomyrmex obscurior	0.1544	0.2528	0.2196	0.0134	0.1189	0.2043	0.0314	0.1315	0.4378	0.4332	0.0362	6.05E-05	0.1132	0.6624	0.1908	0.1325	0.0868	0.9596
Cardiocondyla kagutsuchi	0.1842	0.5408	0.51	0.0062	0.215	0.0959	0.1889	0.0839	0.0783	0.0006	0.0131	0.0077	0.0017	0.0479	0.4575	0.3047	0.3846	0.0268
Ceratina cf. *dentipes*	0.264	0.6675	0.1054	0.0022	0.1281	0.153	0.2741	0.1216	0.1214	0.1102	0.4936	0.2731	0.0688	0.0064	0.0596	0.5457	0.3933	0.0642
Ensifera	0.2494	0.6238	0.2057	0.005	0.1277	0.2634	0.4147	0.2058	0.1083	0.1117	0.0413	0.2041	0.0131	0.0167	0.4982	0.8352	0.7628	0.005
Hylaeus albonitens	0.3422	0.4449	0.7025	0.0086	0.2154	0.6603	0.6545	0.0253	0.0352	0.3063	0.434	0.9925	0.1638	0.1259	0.2098	0.2384	0.404	0.0269
Linepithema humile	0.6613	0.7602	0.2396	0.007	0.6882	0.2629	0.2031	0.2802	0.0706	0.0011	0.0012	0.0131	0.0007	0.0052	0.2323	0.3031	0.6644	0.0022
Ochetellus glaber	0.3445	0.7828	0.263	0.0023	0.2212	0.3698	0.2456	0.3212	0.1228	0.2921	0.3013	0.3119	0.2785	0.1522	0.6814	0.8758	0.6299	0.7173
Paratrechina bourbonica	0.7614	0.9458	0.3807	0.016	0.8291	0.4032	0.3122	0.2104	0.0692	0.0022	0.0024	0.0325	0.0002	0.0125	0.3027	0.4772	0.6867	0.0026
Pheidole megacephala	0.3188	0.5798	0.1922	0.0028	0.2137	0.2762	0.2274	0.2585	0.119	0.3299	0.3429	0.3669	0.2978	0.1723	0.3689	0.8919	0.8785	0.5832
Plagiolepis alluaudi	0.2159	0.7071	0.3661	0.0045	0.2109	0.717	0.2917	0.7658	0.282	0.0815	0.136	0.5808	0.0382	0.0259	0.198	0.7629	0.2254	0.2413
Polistes olivaceus	0.3409	0.9823	0.2362	0.0068	0.4715	0.1692	0.1711	0.1049	0.0927	0.0008	0.0164	0.0132	0.001	0.0576	0.3519	0.3865	0.3238	0.0355
Syrphid sp.	0.2641	0.5673	0.1937	0.0777	0.2498	0.5236	0.3209	0.3074	0.3398	0.1746	0.1014	0.1	0.0134	0.0637	0.5301	0.5347	0.5804	0.0473
Tetramorium bicarinatum	0.3042	0.9819	0.3371	0.0059	0.4769	0.142	0.1753	0.1349	0.0863	0.0007	0.013	0.0201	0.0009	0.0457	0.2288	0.2232	0.5396	0.0287
Toxomerus marginatus	0.2609	0.5881	0.2046	0.0083	0.2218	0.6554	0.2581	0.3931	0.5088	0.2338	0.146	0.0982	0.0126	0.0778	0.4814	0.2877	0.7623	0.0607
Vespula pensylvanica	0.531	0.5575	0.5006	0.0092	0.5364	0.4108	0.4689	0.0187	0.0914	0.1205	0.2032	0.7293	0.0531	0.0383	0.4575	0.243	0.7096	0.0088
Xylocopa sonorina	0.4025	0.6149	0.22	0.004	0.1975	0.5629	0.3158	0.4547	0.1776	0.1065	0.3585	0.3785	0.0527	0.0161	0.6907	0.6914	0.8747	0.1109
native																		

cf. *Scaptomyza* sp.	0.7042	0.4465	0.051	0.0026	0.1279	0.0713	0.0769	0.017	0.0207	2.29E-06	1.25E-06	5.56E-05	9.33E-07	1.45E-07	0.2461	0.1171	0.3199	7.40E-07
Hemignathus virens	0.5134	0.6834	0.0794	0.0108	0.7409	0.0758	0.0948	0.527	0.0494	0.0018	0.0007	7.14E-05	0.0016	0.0004	0.0748	0.1563	0.235	0.0044
Himatione sanguinea	0.5255	0.6351	0.0681	0.0084	0.6751	0.0985	0.0923	0.4326	0.0585	0.0014	0.0005	7.29E-05	0.0013	0.0003	0.1815	0.0745	0.3815	0.0034
Hylaeus difficilis	0.3598	0.6089	0.2771	0.0074	0.2299	0.4555	0.3781	0.1187	0.1734	0.078	0.0703	0.3308	0.0179	0.0468	0.4628	0.4187	0.4258	0.0181
Hylaeus laetus	0.3099	0.7771	0.0545	0.0038	0.1754	0.5308	0.1501	0.7337	0.2115	0.0034	0.0025	6.99E-05	0.0004	0.008	0.6142	0.4013	0.7173	0.0011
Hylaeus sp.	0.2537	0.5825	0.1355	0.0043	0.1853	0.3407	0.311	0.1756	0.2431	0.2504	0.1239	0.1993	0.1494	0.3523	0.8053	0.5052	0.5343	0.2653
Nysius rubescens	0.0556	0.1234	0.0892	0.0003	0.0395	0.0674	0.047	0.041	0.0213	2.96E-06	1.62E-06	7.19E-05	1.21E-06	1.88E-07	0.0898	0.0806	0.4191	9.58E-07

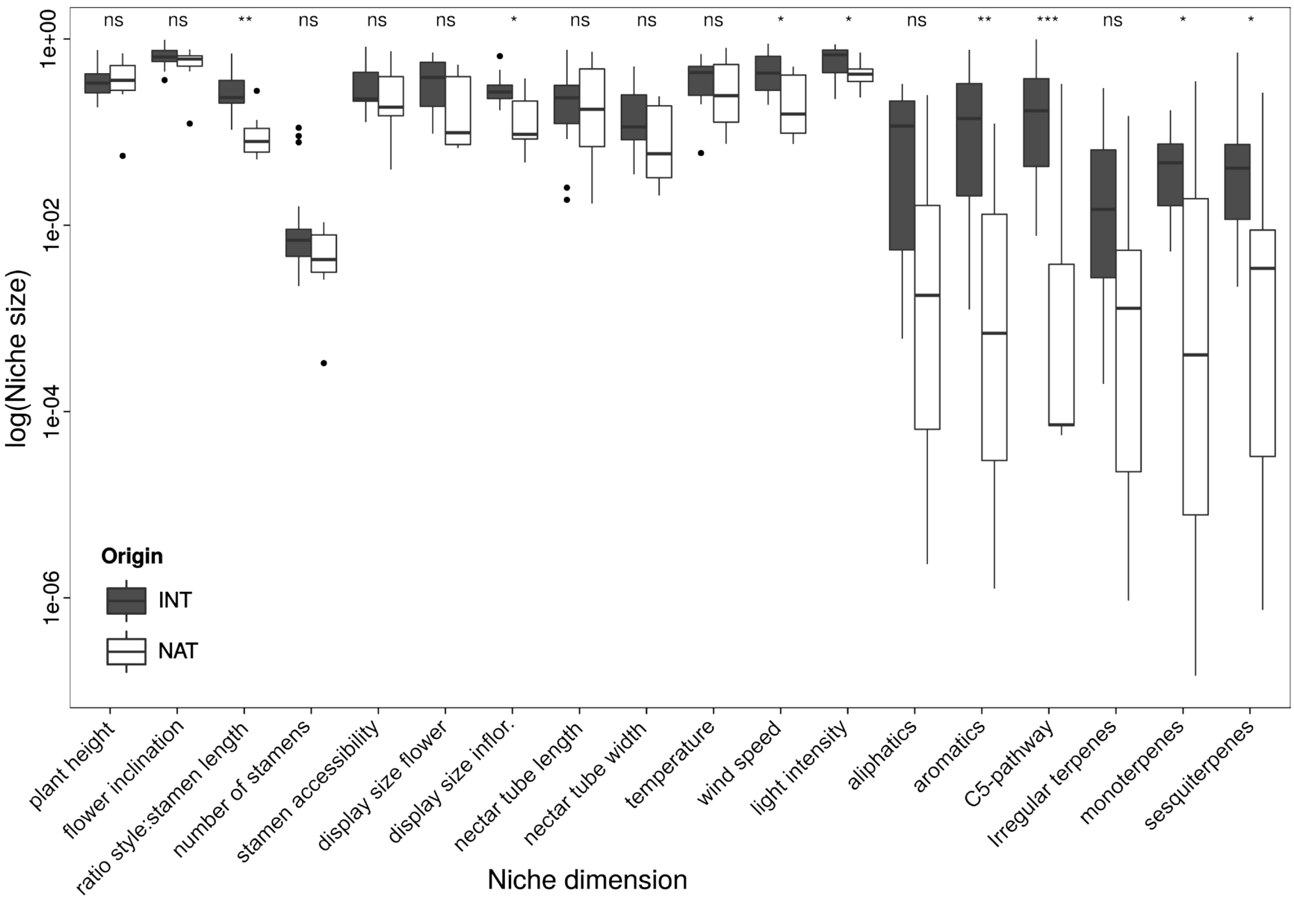


Figure F1. Niche sizes of native and introduced flower visitor species. Niche sizes *vol*(A) were calculated for all measured floral traits, weather conditions and floral scent compounds using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of n-dimensional hypervolumes (i.e. niche) (Junker et al. 2015). Grey boxplots show introduced taxa (*n* = 18) and white native ones (*n* = 7). ns = non-signficiant, *p < 0.05, ** p < 0.01, *** p < 0.001 (Whitney-Mann U test).

Please see Excel-file: Appendix F Table F2.

Table F2. Overlap for each niche dimension of native and introduced flower visitor species. Dimension-wise niche overlap *port*(A, B) were calculated for all measured floral traits, weather conditions and floral scent compounds using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of n-dimensional hypervolumes (i.e. niche) (Junker et al. 2015).

Appendix 15

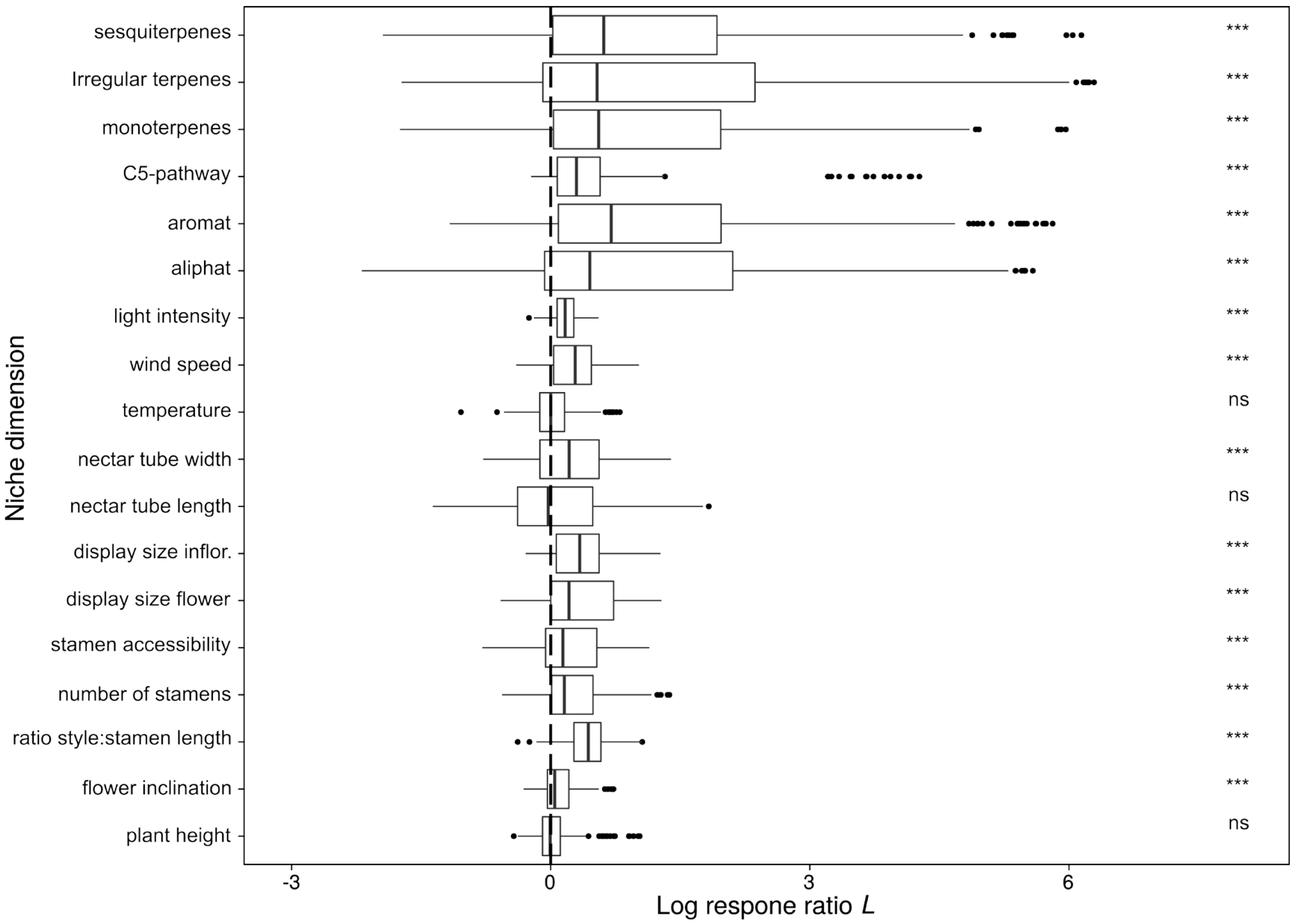


Figure F3. Asymmetric niche overlap between native and introduced flower visitor taxa. Log response ratios *L* describe the asymmetry of the niche overlap between native and introduced flower visitors. Asymmetry is expressed as the log of the quotient of the portion of the niche of a native taxon covered by the niche of an introduced taxon and the portion of the niche of the introduced taxon covered by the niche of the native taxon L = log(port(A, B) / port(B, A). $L > 0$ indicates that niches of introduced taxa overlap those of native taxa more than *vice versa*. Boxplots denote range, median and interquantil ranges of log response ratios *L* for all single traits comprising the four different trait categories (full niche, weather, floral morphology and floral scent). Niche overlaps *port*(A,B) were calculated using dynamic range boxes – a non-parametric approach for quantifying the size and overlap of *n*-dimensional hypervolumes (i.e. niche), where each dimension represents one trait (Junker et al. 2015). *** $p < 0.001$, ns = non-signficiant (Whitney-Mann U test).