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Generalist social bees maximize diversity intake in plant species-rich and resource-abundant environments

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Abstract. Numerous studies revealed a positive relationship between biodiversity and ecosystem functioning, suggesting that biodiverse environments may not only enhance ecosystem processes, but also benefit individual ecosystem members by, for example, providing a higher diversity of resources. Whether and how the number of available resources affects resource collection and subsequently consumers (e.g., through impacting functions associated with resources) have, however, been little investigated, although a better understanding of this relationship may help explain why the abundance and richness of many animal species typically decline with decreasing plant (resource) diversity. Using a social bee species as model (*Tetragonula carbonaria*), we investigated how plant species richness—recorded for study sites located in different habitats—and associated resource abundance affected the diversity and functionality (here defined as nutritional content and antimicrobial activity) of resources (i.e., pollen, nectar, and resin) collected by a generalist herbivorous consumer. The diversity of both pollen and resin collected strongly increased with increasing plant/tree species richness, while resource abundance was only positively correlated with resin diversity. These findings suggest that bees maximize resource diversity intake in (resource) diverse habitats. Collecting more diverse resources did, however, not increase their functionality, which appeared to be primarily driven by the surrounding (plant) source community in our study. In generalist herbivores, maximizing resource diversity intake may therefore primarily secure collection of sufficient amounts of resources across the entire foraging season, but it also ensures that the allocated resources meet all functional needs. Decreasing available resource diversity may thus impact consumers primarily by reduced resource abundance, but also by reduced resource functionality, particularly when resources of high functionality (e.g., from specific plant species) become scarce.

Key words: functional complementarity; functional redundancy; Meliponini; nutritional ecology; plant–insect interactions; pollinator decline.

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INTRODUCTION

Biodiversity is a critical driver of ecosystem functioning, as it maintains the stability of ecosystem processes and provides insurance against changing environmental conditions (Loreau et al. 2001). Diverse ecosystems typically contain more producers and consumers than less diverse ecosystems

(Gamfeldt et al. 2005, Hines and Hendrix 2005), resulting in more interactions within or across trophic levels which can further stabilize ecosystem services (Ives et al. 2005, Balvanera et al. 2006). The same ecosystem process can be supported by multiple species or functional groups in diverse ecosystems which are functionally redundant, thus increasing resilience of the whole system (Blüthgen and Klein 2011). This increased resilience in ecosystem functioning due to higher biodiversity has frequently been demonstrated (Brittain et al. 2013, Garibaldi et al. 2013). However, whether single organisms in ecosystems also benefit from increasing biodiversity has received little attention.

Biodiverse systems provide a variety of resources to be exploited by consumers (Duffy et al. 2007). Higher resource diversity can in theory either benefit consumers by providing a constant supply of various resources to choose from and to compose ideal (e.g., nutritionally well balanced) resource mixtures, or negatively affect consumers by diluting preferred resources (as shown for several specialist insect herbivores; Yamamura 2002, Otway et al. 2005). Yet we still do not fully understand whether and, if so, how increased resource diversity affect resource collection in generalist consumers. They could, in theory, respond to increased available resource diversity in two ways: (1) by maximizing collected resource diversity (henceforth referred to as "diversity maximization") or (2) by targeting a specific number of collected resources sufficient to cover all functional needs, leading to a saturation in collected resource diversity (henceforth referred to as "diversity restriction"). While "diversity restriction" will always require the time-consuming active selection of preferred resources in a resource diverse environment, "diversity maximization" may be either passive (through foraging on any resource encountered next in diverse habitats) or active (through seeking for a maximum of different resources). Active maximization should consequently result in a constantly more even distribution of different resources, while passive maximization should lead to a more uneven resource distribution (as some plant sources are typically more abundant in environments than others).

Increasing resource diversity positively correlates with higher health and performance of (herbivorous) consumers (Alaux et al. 2010, Di Pasquale et al. 2013, Drescher et al. 2014), for example, through improving nutritional balance or toxin dilution (in mammals; Freeland and Janzen 1974, Glander 1982, and insect herbivores: Bernays et al. 1994, Singer et al. 2002, Simpson and Raubenheimer 2012, Irwin et al. 2014). These positive effects of resource diversity may render diversity maximization a reasonable strategy, although it may increase resource handling and search time and thus impair maximization of short-term energy gain as predicted by optimal foraging theory (Pyke et al. 1977).

To explore how resource diversity affects resource foraging in a generalist herbivore, we monitored resource diversity intake and its effect on resource functionality in relation to plant species richness (and thus resource diversity) using a generalist social stingless bee species (i.e., the tropical stingless bee *Tetragonula carbonaria* Smith) as a model consumer. Here, resource functionality refers to any function that specific resources fulfill for a consumer. For example, food resources typically have to provide the right balance of all essential macro- and micronutrients in order to allow consumers to grow and reproduce (Simpson and Raubenheimer 2012), while resources used as nest material have to protect the inhabitants against various biotic and abiotic adversities (Roubik 1989).

The diversity of plant resources is usually closely linked to habitat quality and composition and thus foraging landscapes (Williams and Kremen 2007). Natural or semi-natural habitats are typically richest in plant species and thus resources collected by bees, while habitats altered by humans for agriculture or intense urbanization often have reduced plant diversity and thus provide only limited resources (McIntyre and Hostetler 2001, McKinney 2008, Decourtye et al. 2010, Williams et al. 2012). Thus, the type of habitat investigated strongly determines the availability and composition of plant resources, which in turn directly influence the foraging patterns of consumers, for example, bees (Roulston and Goodell 2011).

Herbivore foraging patterns are regulated by both plant resource diversity and (seasonal) plant resource abundance (here defined as the overall amount of resources currently available to a forager; in bees: Williams et al. 2012, Jha and Kremen 2013, Jha et al. 2013), but resource diversity and abundance have hitherto rarely been considered separately, as they are mostly strongly correlated.

In our study, we investigated how the resource intake of a generalist consumer responds to changes in plant resource diversity and abundance, and whether and how resource diversity and abundance affect the functionality of the allocated resources (the latter here defined as nutritional content of pollen and nectar and antimicrobial activity of resin). To address this question, we placed colonies of *T. carbonaria* in different habitats with varying plant species richness and thus varying resource diversity and abundance (Kaluza et al. 2016). We chose different habitats, which differ in land-use intensity and anthropogenic influence (henceforth referred to as landscapes), ranging from undisturbed natural forest habitats to anthropogenically altered habitats (agricultural plantation and urban gardens), and monitored foraging patterns and the diversity, abundance, and functionality of resources collected by colonies over two consecutive years.

Social bees typically collect a variety of plant resources, that is, pollen, nectar, and resin. Pollen is primarily fed to larvae as protein source, while nectar is consumed as an energy source by both larvae and adults (Nicolson 2011). Resin is collected mainly from tree wounds and used as nest material and to protect colonies against predators and microbes by many social insect species (Roubik 1989, Leonhardt and Blüthgen 2009, Simone-Finstrom and Spivak 2010, Drescher et al. 2014). Bees are known to benefit from both a more diverse pollen diet and a higher diversity of resin. For example, a polyfloral diet increases larvae weight of bumble bees, improves immunocompetence in honey bees, and prolongs honey bees lives when parasitized (Tasei and Aupinel 2008, Alaux et al. 2010, Höcherl et al. 2012, Di Pasquale et al. 2013), while increased resin diversity provides better protection against multiple stressors (Drescher et al. 2014).

Pollen nutritional quality is typically measured as protein content (Génissel et al. 2002, Tasei and Aupinel 2008), which can positively correlate with contents of other nutrients (e.g., antioxidants, Di Pasquale et al. 2013, sterols, Vanderplanck et al. 2014). Protein content in pollen largely depends on the plant species' reproductive traits rather than the plant's need to attract pollinators (Roulston et al. 2000), but bees seem to forage preferentially on pollen with high protein content (Rasheed and Harder 1997, Robertson et al. 1999, Leonhardt and Blüthgen 2012) and high amino acid content (Cook et al. 2003, Somme et al. 2015). Moreover, higher protein content in larval food is known to increase body size and weight in bees (Roulston and Cane 2002, Quezada-Euan et al. 2011), and therefore represents one valid (albeit not the only) measure for assessing pollen nutritional functionality.

Regarding nectar nutritional quality, bees are known to target a species-specific optimal nectar concentration, as foraging strategies and handling efficiencies differ (Roubik et al. 1995, Kim and Smith 2000), but can make use of a wide range of nectar concentrations (Biesmeijer et al. 1999, Tatsuno and Osawa 2016). However, Somme et al. (2015) used sugar content to evaluate nectar quality, which we consider one valid nutritional functionality measure, as more highly concentrated nectar represents more energy and would therefore allow bees to maximize energy intake.

Social bees typically collect plant resins from a wide variety of tree species (Roubik 1989, Leonhardt and Blüthgen 2009, Simone et al. 2009), but prefer some tree species over others (Leonhardt and Blüthgen 2009, Wallace and Lee 2010, Wilson et al. 2013, Drescher et al. 2014). Resin from preferred species efficiently repelled predators and microbes (Drescher et al. 2014, Massaro et al. 2014). As its antimicrobial properties are considered the most important function of resin in bee nests (Simone-Finstrom and Spivak 2010), we here use the antimicrobial effect of resin collected by bees as one measure for resin functionality.

In our experimental field study, we consequently related plant species richness as well as the diversity of pollen and nectar collected by colonies (at sites with varying plant species richness and abundance) to resource functionality by determining the overall protein content of pollen loads, overall sugar content of nectar loads, and the antimicrobial activity of resin stored within nests. Note that our functionality measures represent only a limited choice out of the many functions that these resources need to fulfill (e.g., pollen also needs to provide other nutrients, such as lipids, sterols, and micronutrients, and resin also needs to protect bees against predators and parasites). We further compared whether resource foraging patterns were better explained by plant source richness and/or abundance or by landscape per se.

We generally hypothesized (1) plant species richness to be highest at undisturbed sites (i.e., subtropical forests), intermediate at urban sites, and low at intensively managed agricultural sites (i.e., plantations).

Given the benefits of resource diversity previously observed and the expected costs of active "diversity restriction", we expected stingless bees to follow a (passive) resource "diversity maximization" strategy. Thus, we hypothesized that (2) pollen resource diversity collected by bees would increase with the overall surrounding plant species richness in the landscape, while resin diversity collected by bees was expected to increase with the diversity of trees as the main source of resin (Roubik 1989). On landscape level, resource diversity foraged by bees was predicted to be highest in forests, intermediate in gardens, and lowest in plantations. Moreover, as plantations are usually dominated by few plant species, resource evenness was predicted to be lowest in plantations and highest in forests. As bee foraging patterns in these landscapes were found to be significantly affected by seasonal flowering events which differed between landscapes (Kaluza et al. 2016), we always considered resource intake in relation to season.

We further hypothesized that (3) increasing resource diversity in a landscape positively affects the functionality of resources collected (i.e., pollen, nectar, and resin), as higher resource diversity increases the number of different sources to select from. In other words, the chance of finding highly functional resources should be higher in diverse landscapes. In contrast, landscapes with low resource diversity are expected to provide limited choices and the chances of encountering any or larger numbers of highly functional sources are reduced. We therefore predicted the protein content of pollen to increase with increasing plant species richness and collected pollen diversity. We further expected higher sugar intake in landscapes with higher plant species richness, and we predicted the antimicrobial efficiency of resin to increase with increasing tree species richness and thus collected resin diversity.

METHODS

Experimental setup

We investigated how plant resource richness and abundance affect the diversity and functionality of resources collected by bees in different landscapes using the common Australian stingless bee *T. carbonaria* (Apidae, Meliponini; Rasmussen and Cameron 2007). *Tetragonula carbonaria* is native to the study region in South East Queensland, Australia (24°38′–27°29′ S, 152°6′–153°6′ E), but is also commonly kept in hive boxes and used for managed crop pollination (Heard 2016). We established hives of *T. carbonaria* in three landscape types with varying resource diversity: forests, plantations, and urban gardens (Kaluza et al. 2016). Forests were dominated by an overstory of *Eucalyptus* and *Corymbia* species and represented the natural habitats of *T. carbonaria* (Dollin et al. 1997). Plantations were commercial macadamia monocultures (*Macadamia integrifolia* Maiden and Betche × *M. tetraphylla* Johnson) and thus represented anthropogenically disturbed, agricultural landscapes. Australian urban gardens (i.e., in low-density residential areas), another anthropogenically disturbed landscape, typically provide a mix of native and exotic ornamental garden plants (Head et al. 2004).

Four replicates were selected per landscape type (plantation, forest, and garden), and each was divided into two sites with a minimum distance of 55 m in between, creating a nested design of 24 paired sites. In gardens, distances between paired sites were greater (706 ± 129 m) due to limited suitable sites. At each study site, we placed two bee hives with *T. carbonaria*, resulting in a total of 48 original bee hives in 2011 (Kaluza et al. 2016).

Plant species richness and resource abundance in landscapes

We conducted botanical surveys at each study site to assess plant species richness in each landscape and to categorize each site according to the available resource diversity and abundance (Data S1). Plants were recorded along four 500-m transects, starting at the bee hives and extending south, east, north, and west. All plant species within a 5 m wide corridor along these transects were identified and their abundance was estimated according to the following categories:

(1) rare, 1–5 individuals per plant species; (2) uncommon, 6–16 individuals; and (3) common, >16 individuals. For each plant species, typical life form and size were determined according to the literature and each species was categorized as herb, shrub, or tree (Data S1). We excluded grasses and ferns from the data analysis as these were unlikely to provide resources for bees. In plantations and forests, paired study sites were in close proximity and had identical plant assemblages. We thus used the same survey data for plant species richness and abundance for both respective paired sites, but performed separate transect walks for all (paired) garden sites.

We estimated plant resource abundance available to bees using a maximum-likelihood search to determine the most appropriate numerical values to replace our abundance categories (rare, uncommon, and common) and life form categories (herb, shrub, and tree). We used mean foraging activity as a response variable to estimate these values, as foraging activity is strongly related to resource abundance in landscapes (see Kaluza et al. 2016). Foraging activity of each hive was assessed by counting the number of returning foragers for 3 min and was recorded for the same days and hives used for conducting observations of resource diversity foraging (see *Resource diversity collected by bees*). Values were optimized for a generalized linear model consisting of the interacting explanatory variables plant abundance and log of plant species richness. In this model, randomly created values were repeatedly tested until a set of values was determined which best explained the model variance for foraging activity (optimized for R^2, see Nakagawa and Schielzeth 2013, R Development Core Team 2013). This optimization process was restricted by fixing herb < shrub < tree, and rare < uncommon < common, which resulted in a factor matrix for rare, uncommon, common × herb, shrub, and tree (Appendix S1). For each newly created category in this factor matrix (e.g., rare herb), a value obtained through the optimization process was assigned as a fixed weighting factor to this specific category. In a corresponding frequency matrix for each study site, the relative frequency of each new category (e.g., rare herb) was calculated by dividing the number of plant species in this category by the total number of plant species at this study site (Appendix S1). Note that this relative frequency is independent of the commonness categories used above. The obtained factor matrix was then multiplied with the frequency matrix for each study site, and the sum of all values in the resulting matrix was used as plant resource abundance value for the respective study site (Appendix S1).

Resin diversity and functionality were expected to be influenced by only tree species richness and abundance. Tree resource abundance was therefore calculated using the same process and the same weighting factors obtained from the likelihood optimization, but restricted to tree abundance in the factor and frequency matrix, thereby emphasizing differences between tree resource abundance categories (rare, uncommon, and common).

Resource diversity collected by bees

Observations of bee foraging and resource intake were conducted from September 2011 to September 2013, for three seasons per year, that is, the dry season (September–December), wet season (January–April), and cold season (May–August). In each season, selected bee hives were visited on three rain-free days within 31 ± 9 d (see Kaluza et al. 2016). For the wet season 2012, hive observations were conducted for all hives at all sites. Observations were then restricted to a subsample of six to eight bee hives located at three to four sites for each landscape type in the remaining seasons to enable a reasonable sampling effort and these hives were re-visited in all following seasons.

Observations were performed when hives had sufficient activity, that is, from 7:30 to 15:30 in the dry season and from 10:00 to 15:00 in the cold season. During each observation, 20 returning foragers were caught at the hive entrance and their load (nectar, pollen, or resin) identified. Individuals were removed for the duration of the experiment to avoid recapturing.

Pollen and resin types were categorized by color (pollen) or color, texture, and smell (resins). Color diversity of pollen or resin loads can be used as a proxy for the diversity of plant species visited by bees (resin: Leonhardt et al. 2011; pollen: Leonhardt and Blüthgen 2012, Leonhardt et al. 2014). Moreover, different eucalypt (i.e., Myrtaceae) species typically have pollen that cannot be distinguished with palynological methods because of their parasyncolpate and tricolpate shape and similar size (Thornhill et al. 2012), rendering assessment by color or costly DNA meta-barcoding a more appropriate approach for comparative analyses. We additionally assessed pollen diversity by (1) palynological analysis via pollen microscopy (see Appendix S2) and (2) pollen DNA meta-barcoding (Appendix S3; Keller et al. 2015, Sickel et al. 2015) for a subset of our samples. These additional analyses revealed that the diversity of pollen colors (exponent of Shannon diversity, $e^{H'}$) was positively correlated with the diversity of pollen morphospecies types (as assessed by palynological analysis: $r = 0.81$, $P < 0.001$; Appendix S2), but that assessment by pollen colors generally underestimated actual taxon diversity (i.e., pollen color diversity was 0.7 times lower than diversity of DNA meta-barcoding; Appendix S3). The assessment by pollen colors therefore provides a valid, but rather conservative diversity estimate. Pollen microscopy was further used to check the purity of pollen loads and confirmed that bees rarely mixed pollen types on single foraging trips (overall 4% polyfloral samples). Categorization of resin loads was validated by comparing the chemical profiles of samples obtained by gas chromatography-mass spectrometry (GC/MS) analysis as described in Leonhardt et al. (2011).

Pollen loads of each pollen forager were removed from hind legs, weighed, and stored in Eppendorf tubes for subsequent analyses. Likewise, resin loads were removed and stored in hexane for control analyses. The numbers of pollen and resin categories were then pooled per site and day to assess pollen and resin diversity per site. Note that we only used pollen and resin samples that were collected by different hives at the same site on one observation day to estimate diversity, to avoid overestimating resource diversity due to mismatching pollen and resin types across days.

We focused on pollen and resin diversity for observations, as nectar diversity cannot easily be assessed in the field, because sugar composition or sucrose concentration can vary greatly within single plant species depending on flower age or time of day (Nicolson and Van Wyk 1998, Torres and Galetto 1998) and do therefore not allow for assessing nectar diversity based on foraged loads.

Resource functionality

Protein content of pollen.—The amino acid content of pollen collected from all pollen foragers at each observation was analyzed by ion-exchange chromatography (IEC: Biotronik, amino acid analyzer LC 3000) as described in Leonhardt and Blüthgen (2012). Pollen was first weighed, then mixed with 200 μL of 6 N HCl, heated for 4 h at 100°C, cooled down to room temperature, and centrifuged (10 min). The supernatant was transferred into a fresh Eppendorf tube and water content reduced at 100°C. The sample was redissolved in 200 μL of purified water and centrifuged again for 10 min. Then, 100 μL of the supernatant was mixed with 20 μL of 12.5% sulfosalicylic acid, extracted in the refrigerator (30 min), mixed, and centrifuged (10 min). Finally, 100 μL of the supernatant was mixed with 100 μL sample rarefaction buffer in a fresh microcentrifuge tube, filtered, and centrifuged (5 min), before the sample was transferred into a fresh microcentrifuge tube for further rarefaction with buffer (1:5) and analysis by IEC.

The resulting amino acid concentration (c in μMol/g) was used to calculate the average protein intake (F_P in μg) per foraging trip for (1) all amino acids and (2) only the essential amino acids for each hive observation:

$$F_P = \frac{2 \times m_P \times \sum_{1}^{n} c \times M}{N_P},$$

where m_P (in g) is the pollen weight (pooled for all pollen foragers caught) × 2 (as we chemically analyzed pollen from only one hind leg), M is the molar mass of the respective amino acid (n), and N_P is the number of foragers whose pollen loads were analyzed. We considered methionine, arginine, tryptophan, lysine, isoleucine, leucine, phenylalanine, histidine, valine, and threonine essential for bees and included proline due to its importance in the flight muscle metabolism in adult bees (de Groot 1953, Micheu et al. 2000).

Sugar content of nectar.—Nectar foragers were carefully squeezed to provoke regurgitation of the crop content. Nectar quantity was measured in 5-μL microcapillary tubes (Camag, Muttenz, Switzerland), and nectar concentration was determined with hand-held refractometers (Eclipse Refractometer, Bellingham + Stanley, Lawrenceville, Georgia, USA). To obtain overall sugar intake, we calculated sucrose loads of individual nectar foragers by converting sucrose concentration (c in %) into x (in μg/μL) following Kearns and Inouye (1993) according to the equation (see Leonhardt et al. 2014, Kaluza et al. 2016):

$$x = -0.0928 + 10.0131 \times c + 0.0363 \times c^2 + 0.0002 \times c^3.$$

*Antimicrobial activity of resin.—*Resin samples were collected in 2012 from resin stores of two to three hives for six sites in each landscape. Resin stores typically contain soft, reusable resin collected by foragers across all seasons and provide resin in sufficient quantities for microbial assays. Resin samples of all hives on both paired sites were mixed (resulting in three samples per landscape type), and microbial assays were repeated five times per resin mix to determine the antimicrobial activity of the overall resin diversity available at landscape level (N = 45 per microorganism).

Microbial assays were performed following Drescher et al. (2014). For each mixed resin sample, 0.6 g resin was extracted in 20 mL of 70% ethanol (3% w/v) and filtered twice. Microbial growth inhibition was determined using the agar well diffusion technique on a 64-well plate (27.9 × 27.9 × 1 cm). Three type-culture strains of microorganisms were tested: *Bacillus cereus* (ATCC 11788, Gram-positive bacterium), *Salmonella* Typhimurium (ATCC 13311, Gram-negative bacterium), and *Candida albicans* (laboratory strain of unicellular fungus). Mueller-Hinton agar (growth media) was liquefied and inoculated with microbial suspension to a final concentration of 3×10^7 CFU/mL. Agar with bacteria was poured onto plates to solidify before punching in holes as test wells. Wells were filled with 150 μL of resin extracts (effective resin amount: 4.5 mg/well) and plates then incubated at 36.5°C for 20 h. Antimicrobial activity was quantified as the mean zone of growth inhibition.

For each microorganism, the growth inhibition of each sample was divided by the mean growth inhibition. The standardized results were then pooled across microorganisms as relative growth inhibition.

Statistical analysis

Generalized linear mixed-effect models (GLMMs) were used to analyze the effect of landscape or plant species richness and resource abundance (fixed explanatory variables) on the response variables: pollen and resin diversity and evenness, as well as pollen, nectar, and resin functionality (i.e., sugar, total protein or essential amino acid loads of foragers, and antimicrobial activity of resin). We always included season as fixed explanatory variable in our models to account for seasonal changes in currently available resources and thus on our response variables.

For each response variable, we generated different models, starting with the most complex model that included all explanatory variables and their interactions. We then simplified models stepwise by excluding interactions and variables and evaluated model quality using Akaike's Information Criterion (AIC). The model with the lowest AIC value was considered the model with the highest explanatory value. To test whether individual explanatory variables explained a significant proportion of the overall variance, we compared the model with a given variable to the same model without this variable using the anova command in the lme4 package which compares two nested models using restricted maximum likelihood (REML) scores (library lme4: Bates et al. 2011). Differences between landscape types were evaluated using Tukey's HSD post hoc test (package multcomp: Hothorn et al. 2008), and effects of plant species richness and abundance were assessed using Spearman's rank correlation tests. Note that plant species richness and resource abundance were independent variables ($r = -0.21$, $P = 0.44$).

To test whether landscape or plant resource richness and/or abundance better explained our findings regarding resource diversity intake and evenness, we always constructed two separate models: one including landscape and season and another including plant species richness and abundance and season. Models were compared using variance explained (R^2) by the best models (library MuMIn; Bartoń 2013, Nakagawa and Schielzeth 2013) following AIC selection.

Pollen and resin diversity were expressed as the exponent of Shannon diversity ($e^{H'}$), which is considered effective diversity (Jost 2006). For the analysis of pollen and resin diversity or evenness and antimicrobial activity, paired site was included as random effect in all models, to account for the nested study design. When analyzing sugar and protein loads, we compared data from several hives located at several study sites for each landscape; thus, hive nested within site was entered as a random effect in all models. Variables were log-transformed (i.e., pollen and resin diversity,

Table 1. Mean (±standard deviation) plant/tree species richness and plant/tree resource abundance for plantation, garden, and forest study sites.

Landscape	Plant species richness	Tree species richness	Plant resource abundance	Tree resource abundance
Plantation	74 ± 42	20 ± 23	0.28 ± 0.06	0.14 ± 0.11
Forest	130 ± 53	48 ± 29	0.35 ± 0.03	0.24 ± 0.07
Garden	328 ± 71	97 ± 31	0.28 ± 0.01	0.17 ± 0.03

protein and essential amino acid loads) or square-root-transformed (sugar loads) where necessary to achieve normality and analyzed by GLMMs with Gaussian distribution. We additionally tested for a correlation between pollen/resin diversity and pollen/resin functionality using Spearman's rank correlation tests. All analyses were performed in R (version: 2.15.0; R Development Core Team 2013).

RESULTS

Plant species richness and resource abundance in landscapes

A total of 1128 plant species were recorded for all study sites, ranging from 40 species at the site of lowest to 411 species at the site of highest plant species richness. Plant species richness strongly varied with landscape type and was on average lowest in plantations, intermediate in forests, and highest in urban gardens (Table 1). Likewise, tree species richness was lowest in plantations and highest in gardens (Table 1). Plant and tree resource abundance estimates were highest in forests, but, while plant resource abundance was similar in gardens and plantations, tree resource abundance was lower in plantations and intermediate in gardens (Table 1).

Resource diversity collected by bees

In total, we assembled a dataset with 8297 recorded foraging trips for 414 hive observations. Bees collected a total of 47 different pollen and 88 different resin types on 4332 pollen and 2894 resin foraging trips. Average (±standard deviation) diversity collected per site and day was 2 ± 2 pollen and 4 ± 3 resin types in plantations, 5 ± 2 pollen and 5 ± 3 resin types in forests, and 6 ± 3 pollen and 4 ± 3 resin types in gardens.

Diversity of pollen types was better explained by the landscape model than by the corresponding plant species richness/abundance model (marginal R^2; Table 2). Pollen diversity was highest in gardens and lowest in plantations, and showed the same seasonal variations in all landscapes (i.e., landscape did not interact with season; Fig. 1A, Table 2). Pollen diversity significantly increased with surrounding plant species richness ($r = 0.43$, $P < 0.001$; Fig. 1B), while plant resource abundance had no influence ($r = 0.01$, $P = 0.95$; Fig. 1C). Pollen diversity intake was further high across seasons and did not drop during resource pulses of single extremely abundant plant species (e.g., mass flowering of macadamia in plantations; Appendix S4).

Resin diversity collected by bees was best explained by the interaction between tree species richness, tree abundance, and season (tree species

Table 2. Comparison of models including landscape (Landscape model) or plant/tree species richness and plant/tree resource abundance (Richness/abundance model) as explanatory variables.

Response variables	Landscape model	ΔAIC	$_{m}R^2$	$_{c}R^2$	Richness/abundance model	ΔAIC	$_{m}R^2$	$_{c}R^2$
Pollen diversity	Lds + Ssn	42.7	0.40	0.50	$_{\mathrm{P}}$Ric* $_{\mathrm{P}}$Abd + Ssn	43.6	0.33	0.48
Resin diversity	Lds * Ssn	25.0	0.17	0.33	$_{\mathrm{T}}$Ric * $_{\mathrm{T}}$Abd * Ssn	40.7	0.29	0.33
Pollen nutritional functionality (protein per foraging trip)	Lds * Ssn	24.5	0.27	0.43	$_{\mathrm{P}}$Ric* $_{\mathrm{P}}$Abd * Ssn	38.8	0.30	0.51
Nectar nutritional functionality (sugar per foraging trip)	Lds * Ssn	226.0	0.09	0.17	$_{\mathrm{P}}$Ric* $_{\mathrm{P}}$Abd * Ssn	232.5	0.10	0.18
Resin antimicrobial activity	NULL	…	…	…	NULL	…	…	…

Notes: Variance of fixed effects (marginal R^2: $_{m}R^2$) and variance of fixed and random effects (i.e., including effects of site; conditional R^2: $_{c}R^2$) of the most parsimonious models following Akaike's Information Criterion (AIC) selection are given, as well as the AIC difference between the presented model and the NULL model (ΔAIC). Fixed effects tested in generalized linear mixed-effect models: Lds: landscapes; Ssn: season; $_{\mathrm{P}}$Ric: plant species richness; $_{\mathrm{T}}$Ric: tree species richness; $_{\mathrm{P}}$Abd: plant resource abundance; $_{\mathrm{T}}$Abd: tree resource abundance. Asterisks (*) indicate interaction between fixed effects, pluses (+) indicate no interaction, and NULL indicates that the NULL model (i.e., random site effects) explained the observed effects best.

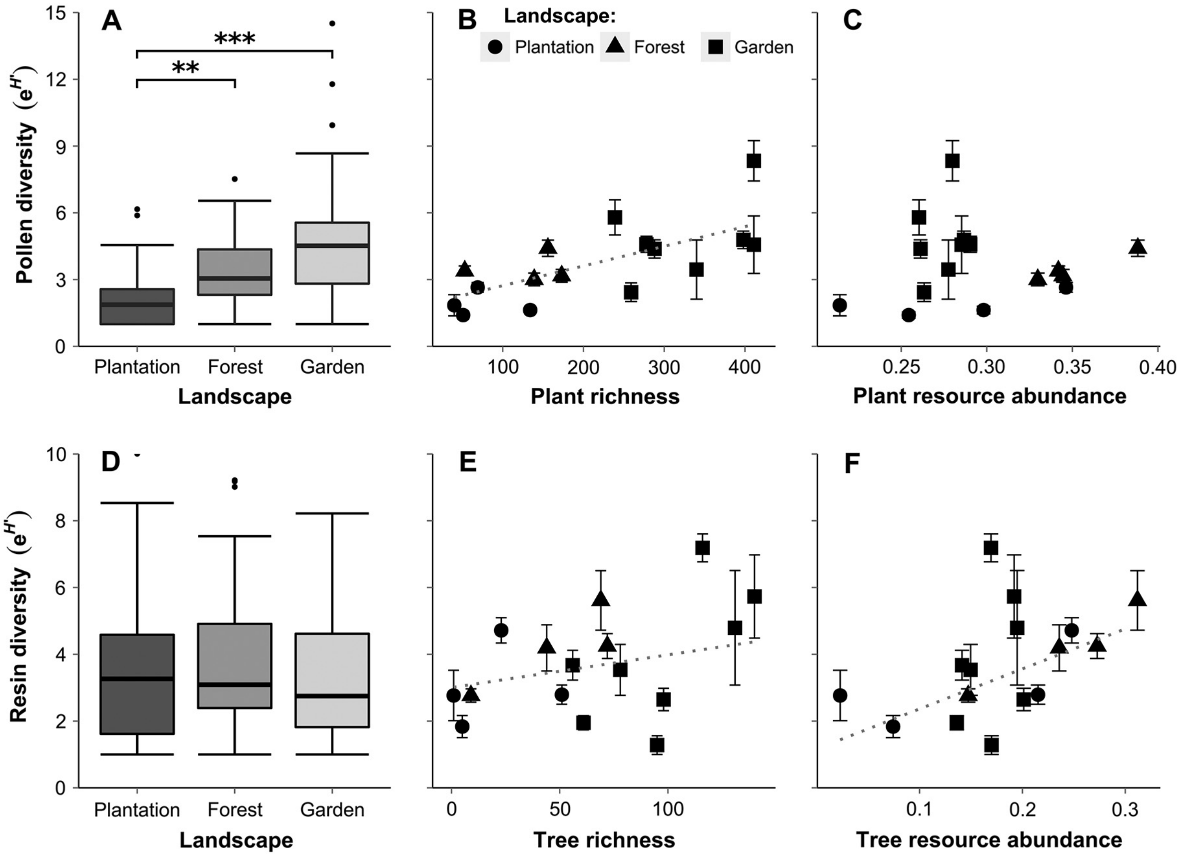

Fig. 1. Diversity of pollen and resin types collected by bees in three different landscapes (A, D) and in relation to plant or tree species richness (Plant richness: B; Tree richness: E) or resource abundance (Plant resource abundance: C; Tree resource abundance: F). Bee hives were placed in plantations (dark gray bars/circle), forests (gray/triangle), and gardens (light gray/squares). Pollen and resin diversity are expressed as effective (i.e., the exponent of) Shannon diversity ($e^{H'}$). Asterisks indicate significant differences between landscapes (following Tukey's post hoc test: $^{**}P < 0.01$, $^{***}P < 0.001$ [A]). Boxplots display the median (thick bar), lower (0.25), and upper (0.75) quartile (gray box), minimum and maximum values (whiskers) and outliers of each dataset (i.e., dots). Means and standard errors of the effective Shannon diversity ($e^{H'}$) are presented (B, C, E, F), and dotted lines indicate significant correlations.

richness/abundance model; Table 2). It was similar across landscapes (Fig. 1D), but significantly increased with tree species richness in the surrounding habitat ($r = 0.16$, $P = 0.014$; Fig. 1E) and even stronger with tree abundance ($r = 0.37$, $P < 0.001$; Fig. 1F). Moreover, foraged resin diversity showed different seasonal trends for each landscape: While it tended to be highest in gardens and lowest in plantations in the cold season, this pattern was reversed in the dry season.

Pollen evenness was best described with a model only including season and was thus high in all landscapes (plantations: $J' = 0.79 \pm 0.16$; forests: $J' = 0.78 \pm 0.14$; gardens: $J' = 0.82 \pm 0.13$), but varied with season. Overall evenness was lowest in the dry season (dry season: $J' = 0.74 \pm 0.16$; wet season: $J' = 0.83 \pm 0.11$; cold season: $J' = 0.80 \pm 0.15$; GLMM: $\chi^2 = 13.84$, df = 2, $P < 0.001$). Pollen evenness increased with plant species richness ($r = 0.15$, $P = 0.036$), but decreased with plant resource abundance ($r = -0.14$, $P = 0.047$).

Resin evenness was best explained by the NULL model (which only considers random site effects). Like pollen evenness, resin evenness was similarly high in all landscapes (plantations: $J' = 0.86 \pm 0.13$; forests: $J' = 0.85 \pm 0.12$; gardens: $J' = 0.86 \pm 0.11$), but did not change across seasons or with increasing tree species richness or abundance.

Resource functionality

Protein content of pollen loads per foraging trip was best explained by the interaction between plant species richness, plant resource abundance, and season (Richness/abundance model, Table 2). Protein content increased with surrounding plant species richness ($r = 0.20$, $P = 0.004$; Fig. 2B), but decreased with higher plant resource abundance ($r = -0.28$, $P < 0.001$; Fig. 2C). However, protein loads per foraging trip showed no direct relationship with the diversity of pollen collected ($r = -0.05$, $P = 0.50$). Protein loads were overall significantly lower in forests compared to gardens and plantations (Fig. 2A), but varied across seasons (i.e., protein content in forests tended to be low in the wet and dry season, but high in the cold season).

Likewise, protein loads of essential amino acids per pollen foraging trip were best described in the Richness/abundance model and increased with surrounding plant species richness ($r = 0.18$, $P = 0.007$), decreased with plant resource abundance ($r = -0.27$, $P < 0.001$), and were lowest in forests (plantations, 55.79 ± 22.84 μg; forests, 40.56 ± 20.24 μg; gardens, 55.83 ± 27.54 μg; GLMM, $\chi^2 = 38.08$, df = 6, $P < 0.001$).

Sugar content (sucrose) of nectar per foraging trip was best explained by the interaction between plant species richness, plant resource abundance, and season (Richness/abundance model). However, sugar content was highly variable, and all composed models explained only little variance (Table 2). As sugar intake patterns varied across seasons in different landscapes (i.e., effects of landscape interacted with strong seasonal effects), model differences between landscapes (Fig. 2D) mainly reflected different seasonal patterns. Sugar loads did not correlate with plant species richness or plant resource abundance alone (plant species richness: $r = 0.002$, $P = 0.92$; plant resource abundance: $r = 0.002$, $P = 0.92$; Fig. 2E, F).

Relative antimicrobial activity of resin was best explained by the NULL model (which only considered random site effects). It was not correlated with foraged resin diversity ($r = 0.02$, $P = 0.95$) and even decreased with increasing tree species richness ($r = -0.35$, $P < 0.001$; Fig. 2H). Antimicrobial activity did also not significantly differ between landscapes when combining all microbes (Fig. 2G). However, for *B. cereus* alone, mean growth inhibition was significantly higher in forests than in gardens (Appendix S5).

DISCUSSION

Generalist consumers living in biodiverse ecosystems may benefit from the surrounding biodiversity through enhanced abundance and diversity of resources. We used a social bee species as model for a generalist herbivorous consumer (which entirely depends on plants for obtaining all resources required for nutrition and nesting) to experimentally investigate how plant species richness and/or plant resource abundance associated with different landscapes/habitats influenced resource intake and corresponding resource functionality. We found that plant species richness and resource abundance better explained the bees' resource intake than landscape categories (except for pollen diversity). We should therefore be more cautious when solely taking into account the effect of different landscape or habitat categories on bee foraging behavior and resource intake.

In agreement with our hypothesis, we found that the diversity of resources collected by bees continuously increased with increasing plant/tree species richness, suggesting that bees maximize resource diversity intake where possible. However, increased resource diversity did not result in increased resource functionality of the specific single functions measured, as both nutritional content and antimicrobial activity were only slightly, if at all, affected by plant/tree species richness or resource abundance.

Plant species richness and resource abundance in landscapes

Plant species richness was closely linked to landscape and varied strongly with habitat type, thereby providing an adequate plant species richness gradient for assessing diversity effects. However, contrary to our hypothesis, our garden sites had an on average two to three times higher richness of plant species than natural forest or plantation sites, which has so far not been shown for a (sub-) tropical region. Urban gardens typically comprise a diverse mix of native and exotic plants, which create a diverse and continuous supply of floral resources (Australia: Head et al.

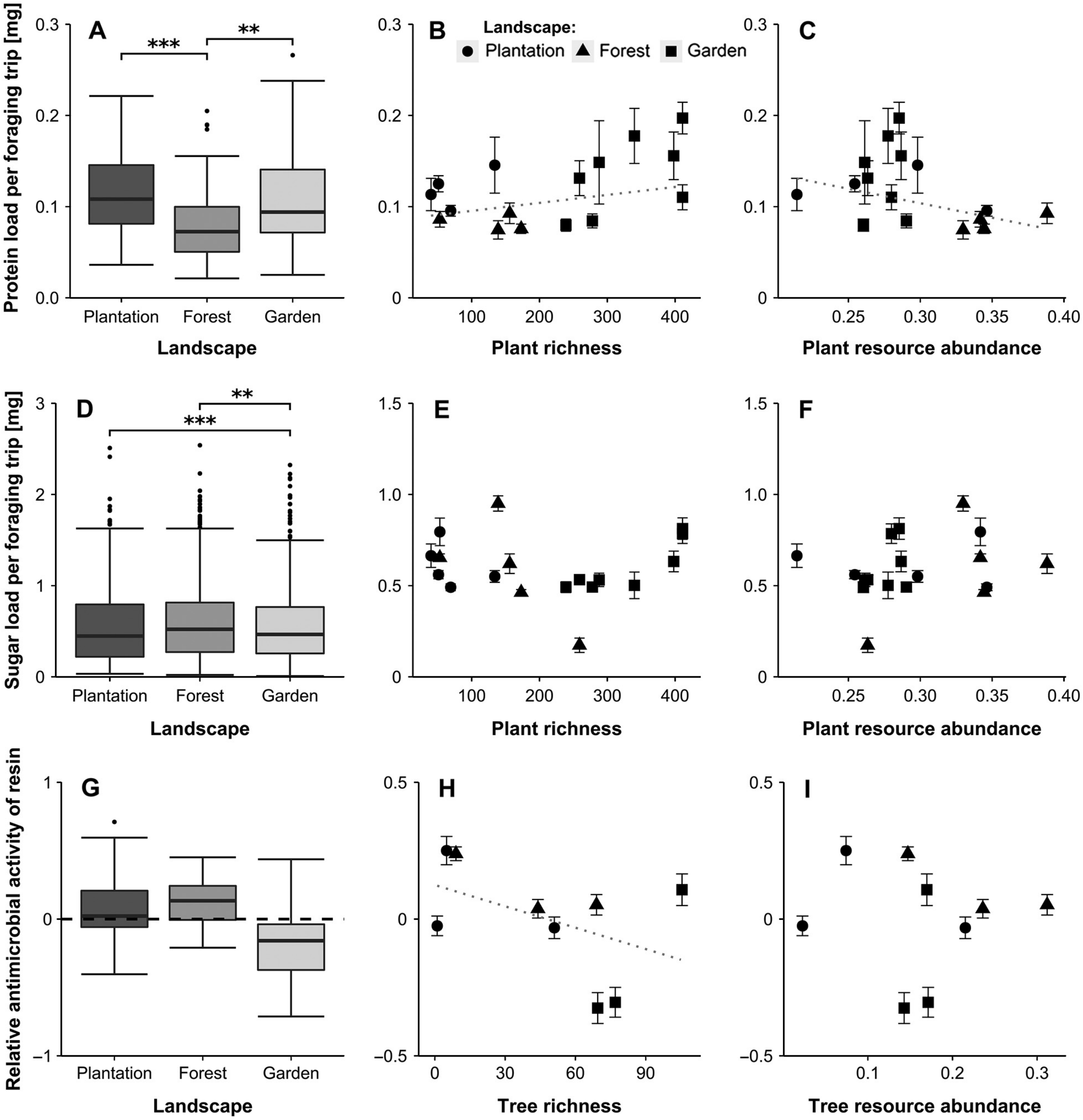

Fig. 2. Functionality of resources collected by bees in three different landscapes (A, D, G) in relation to plant or tree species richness (Plant richness: B, E; Tree richness: H) or resource abundance (Plant resource abundance: C, F; Tree resource abundance: I). Pollen nutritional functionality was measured as protein load per foraging trip (A–C), nectar nutritional functionality as sucrose load per foraging trip (D–F), and resin functionality as relative antimicrobial activity of nest resin (G–I). Bee hives were placed in plantations (dark gray bars/circle), forests (gray/triangle), and gardens (light gray/squares). Pollen and resin diversity are expressed as effective (i.e., the exponent of) Shannon diversity ($e^{H'}$). Asterisks indicate significant differences between landscapes (following Tukey's post hoc test: $^{**}P < 0.01$, $^{***}P < 0.001$ [A, D]) and include (significant) opposing seasonal patterns between landscapes (A, D). Boxplots display the median (thick bar), lower (0.25), and upper (0.75) quartile (gray box), minimum and maximum values (whiskers) and outliers of each dataset (i.e., dots). Means and standard errors of the effective Shannon diversity ($e^{H'}$) are presented (B, C, E, F, H, I), and dotted lines indicate significant correlations. The dashed line (G) indicates average antimicrobial activity of resin.

2004; Europe: Loram et al. 2008). Generalist bee foragers are known to utilize both native and exotic flowering plants (Tepedino et al. 2008, Stout and Morales 2009, Williams et al. 2011, Threlfall et al. 2015) and in some cases even prefer horticultural plant hybrids over wild types in gardens (Garbuzov and Ratnieks 2014), which renders urban areas with parks and gardens a very suitable foraging habitat for generalist bees. Our garden sites were further often close to patches of remnant vegetation, providing a mixture of habitats with a variety of native plants and trees. This combination of patches with diverse native and exotic plant species most likely explains why we found the greatest plant species richness and high resource abundance around urban sites in subtropical Australia.

Also in contrast to our expectations, plant species richness around our forest sites varied from high richness to unexpectedly low richness. Low plant species richness was found primarily in mature forested landscapes (costal forest dominated by *Banksia* spp.), with dominant tree species well adapted to local climate and fire cycles (Bird et al. 2008). On the other hand, forests with high plant species richness were comprised of species-rich ecotones, like forest edges or transitions from rainforest to wet sclerophyll vegetation. Such moderately disturbed forests are known to have higher plant species richness and to support higher bee diversity than mature forests (Liow et al. 2001, Winfree et al. 2007).

As expected, we found plant species richness to be lowest in macadamia plantations. However, some plantation sites had unexpectedly high plant diversity. Yet many of these plants were ground-covering exotic weeds (51–65%), which were persistently managed with mowing and herbicides and did not actually provide any floral resources for bees.

Resource diversity and evenness

As predicted, the diversity of pollen types collected by bees increased with increasing plant species richness, but not plant resource abundance, and was thus highest in gardens, intermediate in forests, and lowest in plantations. Average pollen diversity per hive at our forest sites was very similar to nest pollen diversity as reported for other bees in tropical forests (Ramirez Arriaga and Martinez Hernandez 1998, Vossler et al. 2010), yet pollen diversity collected in gardens exceeded the reported maximum diversity by 1.2–1.3 (plantations, $H' = 0.77 \pm 0.12$; forests, $H' = 1.04 \pm 0.24$; gardens, $H' = 1.30 \pm 0.31$).

Generalist social bees, such as honey bees and stingless bees, are known to collect pollen from a diverse spectrum of plant species (Ramirez Arriaga and Martinez Hernandez 1998, Odoux et al. 2012, Smith et al. 2012). Our study further showed that pollen diversity collected by *T. carbonaria* continuously increased with increasing plant species richness. Besides pollen, bees also maximized resin diversity intake in tree species-rich environments, indicating that *T. carbonaria* generally follows a resource "diversity maximization" strategy. A similar "diversity maximization" strategy was found in saki monkeys (Palminteri et al. 2016), but has, to our knowledge, not been described in other animal species. However, many animal species, and in particular herbivores, are known to perform better on diets composed of diverse resources rather than only one resource type, as dietary mixing either improves nutritional balance or dilutes toxins (Glander 1982, Hägele and Rowell-Rahier 1999, Unsicker et al. 2008, Groendahl and Fink 2016, Palminteri et al. 2016).

As generalist (social) bees typically combine pollen from a variety of plant species at the colony level, pollen diversity likewise ensures composing a nutritionally balanced diet and the dilution of toxic plant compounds (Eckhardt et al. 2014, Irwin et al. 2014). In fact, bees even incur greater foraging distances and higher energetic costs to maintain a polyfloral pollen diet (Williams and Tepedino 2003). Correspondingly, increasing resin diversity increases protection against multiple antagonists (Drescher et al. 2014). Thus, maximizing resin diversity intake likely benefits stingless bees by increasing the functional diversity of the composed resin storage.

However, in contrast to pollen diversity, the diversity of resin types collected by our hives increased only moderately with tree species richness and strongly with tree abundance. Unlike pollen, which is provided by many flowering plants, resin sources occur randomly, for example, on wounded trees (Howard 1985, Roubik 1989, Langenheim 2003). Thus, only a random subset of trees actually provide resin sources at any given time, which may in part explain the high variability observed between sites. However, increasing tree species richness likely directly increases the number of different potential resin sources. Further, tree abundance, as measured in our study, strongly corresponds to high numbers of common tree species; thus, chances are higher that some trees of these species will in fact secrete resin. Resin availability consequently increases with increasing numbers of tree species and common trees, which explains the observed positive correlation between resin diversity collected and tree species richness and abundance. The distribution of and pattern found for resin sources may be more comparable to non-plant resources, such as animal prey, whose encounter frequency and thus consumption rates also increase with overall abundance (likely driven by few specific prey species) and less (if at all) with species diversity (Hillebrand and Cardinale 2004).

While maximizing resource diversity may benefit bees (and other generalist consumers), it remains unclear how they regulate resource diversity intake. Individual consumers (which forage solitarily) can independently decide whether and when to switch sources in order to forage on diverse resources. In contrast, social (bee) foragers typically specialize on a single plant source for prolonged periods and up to their entire forager lifetime (i.e., flower constancy: Grant 1950, Slaa et al. 2003). Moreover, both stingless bees and honey bees recruit foragers to rewarding food patches (von Frisch 1967, Nieh 2004), which typically favors abundant resources over highly functional resources as colonies forage disproportionally on one to few specific abundant resources (Requier et al. 2015, Aleixo et al. 2016). However, many studies (including ours) investigating resource intake in generalist social bees found a relatively broad spectrum of resources collected in addition to the most abundant ones (Ramirez Arriaga and Martinez Hernandez 1998, Vossler et al. 2010, Requier et al. 2015, Aleixo et al. 2016, Kämper et al. 2016). Such disproportional foraging on few abundant and several less abundant resources may be a consequence of increased overall foraging activity (or the proportion of a specific forager group, e.g., pollen foragers or scouts), which increases the chance that additional scouts or foragers discover and forage on new plant sources, thereby increasing overall resource diversity intake. In fact, *T. carbonaria* responds to increased overall resource abundance in the habitat by increasing foraging activity (Kaluza et al. 2016), which supports the idea that "diversity maximization" is regulated via increasing foraging activity at the colony level. Moreover, collected pollen diversity positively correlated with foraging activity, particularly in the plant species-rich gardens (Appendix S6). Gardens offer a resource landscape with extremely high plant species richness but often comparatively small resource patches (i.e., more herbs; Data S1). Consequently, higher foraging activity likely results in passive resource maximization in diverse habitats, such as gardens, where any outgoing forager is likely to encounter a new patch or plant species. In contrast, higher foraging activity may not necessarily increase collected resource diversity in diverse habitats with larger resource patches (e.g., forests with mass-flowering trees), where most outgoing foragers are recruited to or encounter the same resource patch or plant species.

Evenness of foraged pollen and resin resources was high across habitats and seasons, indicating that bees always composed a diverse pollen diet or resin bouquet per day and did not show strong preferences for specific sources at particular days. Even in plantations during the short flowering periods of the dominant *Macadamia* trees, collected pollen diversity and evenness remained relatively stable (Appendix S4), suggesting that bees actively maximize daily resource diversity intake in habitats with low plant species richness, as a purely passive mechanism should have reduced pollen diversity due to the disproportional collection of abundant *Macadamia* pollen. This finding indicates that active or passive resource diversity maximization depends on habitat complexity and plant species richness or available resource diversity. However, future studies need to elucidate the precise mechanisms underlying resource diversity maximization in *T. carbonaria* and other generalist consumers.

Resource functionality

Contrary to our predictions, neither resin antimicrobial activity nor pollen nutritional content (i.e., the amount of protein collected per foraging trip) positively correlated with the diversity of collected resin or pollen types, respectively. Thus, increased diversity intake does not necessarily correlate with increased resource functionality of specific functions, but rather results in average functionality for single functional measures. This finding is in accordance with Alaux et al. (2010) and Di Pasquale et al. (2013) who showed that, while specific measures of nutritional content peak in single pollen types, pollen mixtures have average nutritional quality across nutrients.

In fact, in our study, pollen protein (and essential amino acid) was surprisingly low in forests and high in gardens and plantations. The low protein content found in pollen collected in forests cannot be attributed to protein limitations of pollen from plants of the indigenous Australian flora, as Rayner and Langridge (1985) found the protein content of honey bee-collected pollen of Australian plants to often be even higher than in exotic plants. Instead, differences in protein loads may (at least partly) be explained by pollen load size, because pollen loads carried by single foragers in gardens had similar average protein contents (data not shown), but were larger compared to pollen loads in plantations. In plantations, pollen protein content showed high variability across seasons, but bees collected pollen with very high protein concentration during the macadamia flowering in the dry season, which resulted in overall highest protein content in plantations and indicates that macadamia pollen may have comparatively high protein content. Similarly, resin from specific tree species can largely determine overall antimicrobial activity (Drescher et al. 2014), which may explain why resin antimicrobial activity did not correlate with resin diversity in our study. In fact, antimicrobial activity actually decreased with increasing tree species richness, and variation in resin functionality was best explained by site, indicating that it was mostly affected by the specific tree species composition at each site. Moreover, antimicrobial activity against *B. cereus* was highest in forests, further suggesting that antimicrobial properties were primarily driven by the presence of particular tree species, most likely typical and abundant forest trees (e.g., specific eucalypts). These findings suggest that few specific sources of high functionality (e.g., a plant species with protein-rich pollen or highly antimicrobially active resin) may partly compensate low resource diversity, particularly when they are found in large quantities and occur at different times of the foraging season. As they are of high functionality (e.g., provide a protein-rich diet), they likely suffice to periodically cover a specific functional requirement.

In contrast to pollen and resin, nectar nutritional content, that is, sugar loads per foraging trip, was high across landscapes, showing that it was not affected by resource availability and diversity, but that bees had ample nectar foraging opportunities everywhere. *Tetragonula carbonaria* preferentially collects highly concentrated nectar ranging from 60% to 75% sucrose content (Kaluza et al. 2016), which was available from a number of plant species across landscapes. Many Australian plants are bird-pollinated and produce an abundance of nectar (Ford et al. 1979) and thus offer plentiful carbohydrate resources, which in turn favor opportunistic social insects (Morton et al. 2011), as also shown here. Given the uniqueness of the Australian flora, results for interactions between plant diversity and nectar sugar content may be different on other continents.

Overall, our findings suggest that, for specific resource functions, the diversity-resource functionality relationship depends more on plant (resource) community composition than on plant species richness or diversity per se. However, studies investigating the relationship between resource diversity, composition, and functionality are still extremely scarce, rendering broader inferences rather speculative. This relationship may, however, parallel the relationship between biodiversity and the functioning of specific ecosystem processes: Specific ecosystem functions also appear to be determined by the identity and dominance of specific trait groups, and are thus influenced by community composition more strongly than by the number or abundance of species per se, while overall ecosystem functioning (i.e., the sum of all single functions) typically increases with biodiversity (Gagic et al. 2015).

Likewise, while we examined three functional variables in this study, we ignored other measures of resource functionality, for example, overall nutritional composition (of pollen and nectar), the presence of secondary compounds in floral resources, or a repellence effect of resin against predators and parasites. Similar to the positive relationship between biodiversity and overall ecosystem functionality (Hooper et al. 2005, Tilman et al. 2014), the overall spectrum of functional resource effects most likely increases with increasing resource diversity, while specific resource functions may be fully provided by one or a few specific resources (Drescher et al. 2014). Bees and other consumers may consequently need to target a diverse and even resource intake to maintain a variety of functions associated with all resources. A more comprehensive assessment of functions and resource effects would thus be needed to entirely capture the overall functionality of resources in relation to resource diversity. Moreover, further comparative studies on resource intake in relation to biodiversity by different consumer species of ideally various trophic levels (i.e., other bee species and beyond) are needed in order to reveal whether the strategy of maximizing resource diversity is unique to Australian stingless bees or also applies to other generalist herbivores.

In this study, we were further able to separate the effects of plant species richness and plant resource abundance in landscapes on a single consumer, which has not been achieved before. Joined analyses of richness and abundance promise to be a sophisticated tool to identify driving factors in ecosystems, as demonstrated by Winfree et al. (2015) for bee species richness and abundance effects on ecosystem function. However, plant species richness and resource abundance in our study were based on a rapid assessment approach, which limits more thorough conclusions. More detailed plant data, for example, on plant coverage (Hines and Hendrix 2005) or seasonal availability (Williams et al. 2012) could clearly improve deductions.

CONCLUSION

Using bees as a model consumer, we found that this floral generalist attempts, where possible, to maximize the number of sources to collect from (resource "diversity maximization" strategy). This resource-use strategy has also been observed in primates (Palminteri et al. 2016) and agrees with the positive effects of resource mixing observed in herbivores (see *Introduction* and *Discussion*). It suggests that, at least for generalist consumers foraging on plants, resources need to fulfill a multitude of functions which may best be met by a multitude of resources (e.g., nutritional balance, toxin dilution), while specific functions (e.g., high pollen protein content, strong antimicrobial activity of resin) may already be provided by one or a few resources. Depending on the surrounding plant (or prey) community, the functionality of resources may (e.g., pollen protein content, resin antimicrobial activity) or may not (e.g., nectar sugar content) be driven by the occurrence of specific plant sources. Single resources can thus cover specific functional needs even in impoverished landscapes (e.g., agricultural macadamia plantations). However, higher resource diversity likely safeguards overall functionality by bolstering multiple aspects of resource functionality and providing insurance in spatiotemporally dynamic resource landscapes (Williams et al. 2012), which may ultimately determine a consumer's fitness and thus vulnerability.

While time and handling constraints may limit the number of different resources collected by solitary organisms or consumers of higher trophic levels (e.g., predators), resource diversity maximization may be facilitated by the social structure of insect colonies. Here, each forager can be highly specialized on and thus efficiently exploit one or a few resources, while the colony as a whole can increase overall resource diversity intake simply through increasing foraging activity. This unique way of partitioning resource collection renders social insects a very interesting study system for further investigating the relationship between resource intake strategies and resource functionality in relation to available resource diversity.

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