Nectar resource diversity organises flower-visitor community structure

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Abstract

Communities of nectar-producing plants show high spatio-temporal variation in the patterns of volume and concentration presentation. We illustrate a novel approach for quantifying nectar reward structures in complex communities, demonstrating that nectar resource diversity (defined as the variety of nectar volume–concentration combinations available) may be a fundamental factor organising nectarivore communities. In a series of diverse bee and entomophilous flower communities in Israel, our measure of nectar resource diversity alone explains the majority of variation in bee species richness, while other nectar variables (volume, concentration, energy value, and water content) have little predictive value per se. The new measure of nectar resource diversity is highly correlated with floral species richness and particularly with the species richness of annuals, yet it is additive in its effect on bee diversity. We conclude that relying solely upon measurements of mean nectar volume and mean nectar concentration overlooks a key characteristic of community-level reward structure, nectar resource diversity, so that previous studies may have failed to identify an important determinant of flower-visitor community structure.

Introduction

Most studies to date have used single quantitative nectar characteristics of floral communities in an attempt to explain how nectar-feeding communities are organised. The two principle measures employed have been the spatial and temporal patterning of nectar volume, and nectar concentration. Changes in these nectar parameters have been shown to influence the visitation rate of bees (Frankie & Haber, 1983; Klinkhamer et al., 2001), butterflies (May, 1985; Hainsworth & Hamill, 1993), and birds (Willmer & Corbet, 1981; Gass & Garrison, 1999) in a variety of systems.

Some pollinator guilds, such as bumblebees (Heinrich, 1976) and bats (Nassar et al., 1997), are dependent upon flowers providing relatively high volumes of nectar to support their foraging activities; whereas other guilds, such as hoverflies and small solitary bees, specialize on flowers

with very small nectar volumes (Proctor et al., 1996) from which large (high-volume demanding) consumers are effectively excluded. In addition there are guilds which require very dilute nectar to maintain water balance during foraging activity, such as bats (Proctor et al., 1996) and large bees (Willmer, 1988), and this constraint is particularly marked in hot arid environments (Willmer & Stone, 1997). At the other extreme, highly concentrated nectar is often viscous and only accessible to flower visitors with specialised morphological and behavioural adaptations that allow them to extract and ingest the nectar (Gilbert, 1981). The two parameters, nectar volume and concentration, are the basis upon which nectar energy is calculated, and the abundances of the dominant species of flower visitors within some ecosystems are linked to the amount of energy provided by nectar (Roubik, 1989). Daily changes in available nectar clearly affects the identity and abundance of flower feeders (Potts et al., 2001), as do seasonal changes (Petanidou & Ellis, 1996; Bosch et al., 1997).

Undoubtedly these aspects of nectar reward structure play a prominent role in defining the suite of flower-visiting

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fauna present; however, on their own they fail to take into account how nectar feeders respond to the diversity of volume–concentration associations available in a given habitat. The manner in which a floral community is partitioned, in terms of the type and frequency of volume–concentration combinations, will define the variety and relative abundance of foraging niches that can be exploited, and must ultimately limit both the number of feeding guilds and the relative abundance of their members.

We demonstrate that simply viewing nectar availability in terms of mean volumes and concentrations available in a flower species or habitat is, at best, only a crude reflection of the actual nectar characters important to visitors and, at worst, potentially misleading as to their role in determining the associated fauna. We have taken the first steps towards moving beyond viewing floral communities only in terms of average nectar characteristics by constructing a simple index of nectar resource diversity that takes into account the variety of nectar resources available, in terms of both nectar volume and concentration, in a series of habitats. Furthermore, we show that this index, and no other nectar characteristic alone, is an important predictor of the species richness of nectar-feeders in our study system. We have chosen an ecosystem particularly rich in both nectar-providing flowers and nectar-feeding bees to demonstrate this linkage; Israel is a globally recognised hotspot for entomophilous floral diversity and bee species richness. The huge variation in both nectar providers and consumers presented the ideal system in which to explore the importance of nectar resource diversity as a key component structuring flower-visiting communities.

Methods

Study sites and general description of floral communities

Mount Carmel National Reserve, Israel, comprises a ca. 150 km^2 mosaic of different aged areas of regenerating post-fire vegetation. Several major fires have resulted in a series of contrasting patches with distinct age-specific community composition. Areas of mature vegetation (>50 years post-fire) are characterised by *Pinus halepensis* Mill woodland, with many multistem dwarf trees and shrubs. Freshly burnt areas (1–5 years post-fire) are dominated by a flush of annuals; and following the first few years post-fire, perennial shrubs become an increasingly important component of the flora. Zohary (1982) gives full descriptions of these community types. We selected seven vegetation types having distinct fire histories (to encompass the full spectrum of burn ages available and to give a full representation of all the major post-fire vegetation types on Mt Carmel), and selected three replicate sites within each to give a total of 21 sites.

Bee, flower, and nectar surveys

During the main blooming period (February–May) in 1999 and 2000, we carried out five rounds of surveys. During each round, every site was surveyed for bees, flowers, and nectar, with all sites being visited in a 10 day block and blocks separated by 10–15 days. Given that temperature and humidity are known to have marked effects on insect activity (Willmer, 1983) and nectar properties (Corbet et al., 1979), any day with particularly aberrant weather (e.g., heavy rain or very high winds) was skipped to ensure all data collecting was made under 'typical' microclimatic conditions, and observations were instead made the following day.

Bee surveys. Bees (Hymenoptera: Apoidea) constitute the majority of the flower-visiting fauna of Mt Carmel, and as most communities comprise >90% bees (Potts et al., 2001; O'Toole c. pers. comm.), we selected this group as our nectar-feeding community. Three linear 200 m transects were walked in 20 min at 08:00, 11:00, and 14:00 h, covering the period of maximum bee activity. Each site was surveyed five times during the season and all bees encountered on the transects were recorded to provide both species richness and abundance data. Species unambiguously identifiable while flying were recorded, and the remaining unidentified bees were caught with a hand net and retained for later determination (Bee Systematics and Biology Unit, Oxford University Museum of Natural History). Bee species richness was used as the measure of bee diversity.

Floral surveys. In the floral surveys to obtain a measure of species richness, we included only flowers known to be visited by bees, based on the authors' 25 years of field experience on Mt Carmel. A 50 m transect was laid out and all open bee-visited flowers were recorded in a 0.40 m strip along the transect.

Nectar surveys. A second 50 m transect was laid down independently of the one of floral survey, and along it, 10 1-m^2 quadrats were randomly placed. In each quadrat all the flowers were covered with 1 mm netting cages prior to the start of bee activity (dawn). These quadrats were used to assess nectar standing crop (NSC) without visitation, which gives an approximate index of the 'maximum producible nectar'. Between 10:00 and 12:00 hours, all available nectar was extracted using microcapillaries (Camlab, UK). Nectar volume was determined by measuring the length of the nectar column in microcapillaries of known volumes, and nectar concentration was measured with sugar refractometers modified for small volumes (Bellingham and Stanley, UK). In any quadrat, all the flowers were sampled if there were less than 10 for any given species; if more than

10 were present, then the flowers were counted and 10 representative individuals sampled. When nectar volumes were too small to be extracted with microcapillaries, the flower was scored as having nectar present but in volumes too small to measure. Although fairly crude in its approach, this method represents a time-effective way of estimating the overall NSC in very diverse floral communities. These nectar data were used to calculate the following four mean nectar parameters per m^2 for caged quadrats in each vegetation type: volume, concentration, total sugar energy, and water content. Total nectar energy was calculated from the sum of the total sugar content per flowering species per quadrat, and total water content based on total volume and mean nectar concentration per quadrat (Dafni, 1992).

Calculation of nectar resource diversity

Our index of nectar resource diversity was based on the variety of nectar volume-concentration combinations available in each site during a season. For each site, we pooled data from all quadrats to calculate the mean nectar concentration and volume for each plant species for that site. These values were considered to be independent nectar readings. We constructed a 3×3 matrix of volume categories (<0.1, 0.1–1.0, >1.0 µl) and concentration categories (<25, 25–50, >50%) and each independent nectar reading was assigned to one of the nine cells. Each category can be viewed as a broad ecological niche encompassing all flowering plants providing this particular combination of nectar resources. The number of cells with at least one score was used as our index of nectar resource diversity.

Results

Values for bee and floral diversity and for the different nectar characteristics obtained in the surveys are given in Table 1. Bee and flower species richness and nectar concentration showed a general decline with post-fire age, while nectar volume, energy, and water content was very variable across sites. A two-way ANOVA indicated that there are significant differences in nectar resource diversity between sites ($F_{6,13} = 4.8$, P = 0.039), but no effect of year ($F_{1,13} = 0.0$, P > 0.1). The variety of nectar resources available in two contrasting sites (1–2 years post-burn site and a mature woodland) is represented in Figure 1. The freshly burnt site provides seven resource categories and is characterised by many low and intermediate nectar-volume flowers with relatively high nectar concentrations, both features typical of annual species. In contrast, the mature woodland site provides five categories, with intermediate nectar concentrations and higher volumes being most prevalent.

Nectar resource diversity is a highly significant positive function of floral species richness across all sites (Figure 2A:

Table 1 Summary of bee and floral species richness and of nectar characteristics in seven vegetation types

Site location (GPS)	Year burnt	Bee species richness	Flower species richness	Nectar volume (ml ha^{-1}day^{-1})	Nectar concentration (%)	Nectar energy (kJ ha^{-1}day^{-1})	Nectar water content (g ha^{-1}day^{-1})	Nectar resource diversity
Wadi Denia 32°45.8′, 35°00.1′	1998	18.4 ± 0.8	34.5 ± 2.3 (40 : 9)	315.0 ± 158.0	53.5 ± 2.4	3.30 ± 1.5	0.37 ± 0.19	6.5 ± 0.5
En Hod 32°41.9′, 34°58.6′	1998	25.6 ± 5.4	54.3 ± 3.3 (61 : 18)	83.3 ± 36.1	53.7 ± 3.9	0.91 ± 0.4	0.10 ± 0.04	7.5 ± 0.5
Hai Bar 32°44.9′, 35°01.2′	1989	13.6 ± 1.1	9.2 ± 1.0 (8 : 11)	136.8 ± 42.0	46.5 ± 2.4	0.86 ± 0.8	0.18 ± 0.06	5.0 ± 0.0
Mitla 32°44.2′, 34°59.6′	1983	8.7 ± 2.1	20.5 ± 5.1 (17 : 17)	32.9 ± 13.5	50.7 ± 3.1	0.30 ± 0.1	0.04 ± 0.02	5.5 ± 0.5
Etzbah 32°42.4′, 34°58.9′	1974	11.2 ± 2.0	16.7 ± 2.6 (23 : 11)	86.1 ± 38.5	39.8 ± 3.5	2.50 ± 1.8	0.12 ± 0.05	4.5 ± 0.5
Etzbah 32°42.4′, 34°58.8′	<1950	10.5 ± 0.9	9.8 ± 0.9 (5 : 5)	202.9 ± 88.6	43.8 ± 2.5	1.00 ± 0.3	0.25 ± 0.10	5.5 ± 0.5
Wadi Denia 32°45.7′, 35°00.4′	<1950	11.2 ± 1.8	11.3 ± 2.3 (12 : 12)	204.0 ± 108.0	29.5 ± 4.0	1.72 ± 1.0	0.31 ± 0.17	4.5 ± 0.5

Values are means ± SEM. Each mean is the average of the three replicate sites for that age of burn over 2 years (n = 6). Values in parentheses under flower species richness indicate the total species richness of annuals: perennials at each site. Nectar resource diversity differs in that it was based on a matrix combining data from the three replicate sites and therefore is a mean across years (n = 2). See text for details on the calculation of nectar parameters.
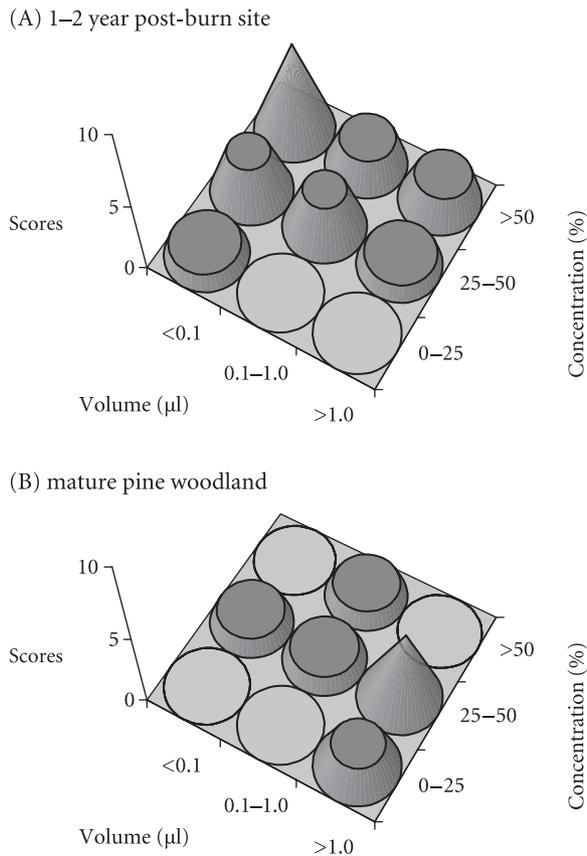
(A) 1–2 year post-burn site

(B) mature pine woodland

Figure 1 The structure of the nectar resources, in terms of volume and concentration, available in characteristic floral communities sampled in 1999 on Mount Carmel, Israel: (A) a freshly burnt site, En Hod (1–2 years post-fire), and (B) a mature pine woodland, Wadi Denia. Scores are the number of flowering plants providing a particular volume–concentration combination.

r = 0.780, n = 14, P = 0.001) and is correlated with the richness of annuals (r = 0.895, n = 14, P = 0.006) but not perennials (P>0.1). In turn, bee species richness has a highly significant positive relationship with nectar resource diversity (Figure 2B: r = 0.849, n = 14, P<0.001). Even though nectar resource diversity and floral richness are positively correlated, when they are entered together in a multiple regression as predictors of bee diversity (r^2 = 79.2%, n = 14, P<0.001), both factors independently contribute to the model (nectar resource diversity: t = 2.34, P = 0.039, and floral diversity: t = 1.94, P = 0.078).

The multiple regression with bee species richness as the response variable and five nectar variables as predictors was significant (r^2 = 75.4%, n = 14, P = 0.024). Of the individual nectar factors, nectar resource diversity was very significant (P=0.005) while nectar volume, concentration, energy content and water content alone were of no predictive value (P>0.1).
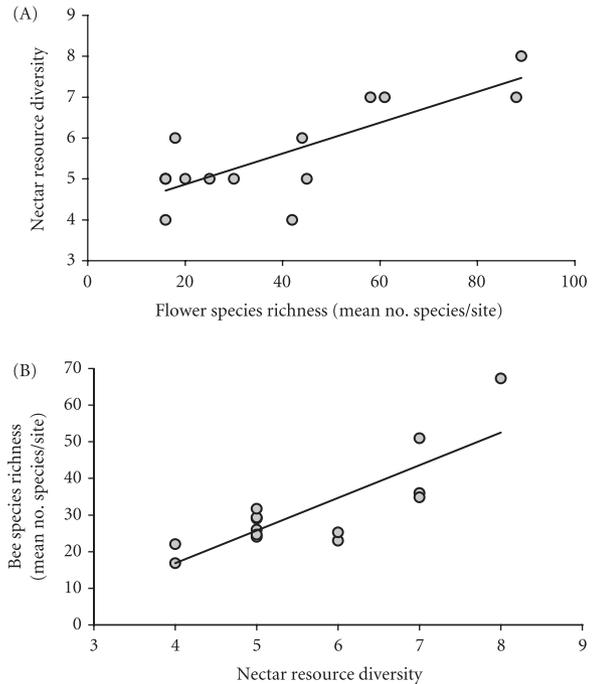

Figure 2 Relationships among bee or flower species richness and nectar resource diversity in a series of post-fire vegetation types on Mount Carmel National reserve, Israel: (A) Nectar resource diversity as a function of floral species richness, and (B) bee species richness as a function of nectar resource diversity.

Discussion

Nectar resource diversity, as measured by our index, and floral diversity, both have strong predictive powers in explaining the diversity within bee communities across a series of habitats on Mount Carmel, Israel. No single nectar characteristic per se other than nectar resource diversity is useful in explaining the observed patterns of bees. The diversity of nectar resources is closely related to floral species richness (especially of annual plants); however, these two properties contribute independently to bee species richness. The annual component of the flora is especially positively linked to bee diversity.

Describing single (or few) species associations between flowers and nectar feeding-visitors is relatively straight-forward (e.g., Potts et al., 2001), but when addressing patterns at the community level our data indicate that an approach only considering single nectar measures may be inadequate, and can fail to identify the key links between flowers and visitors. We demonstrate that nectar resource diversity is the only component of our measured variables that provides useful information on how bee–flower interactions are defined.

We do not, however, suggest that nectar resource diversity is the only factor that is important in structuring communities. Several other components have been shown to have importance, such as pollen availability (Stone et al., 1999), flower morphology (Neal et al., 1998), the combination of sugars present in nectar (Hainsworth & Hamill, 1993), or the presence of other micro-constituents in nectar (Vogel, 1983). Indeed, for Mount Carmel, flower abundance, pollen abundance, site age, nest-site availability, and the ratio of pollen energy to nectar energy availability all play important roles in organising the community structure (Potts et al., 2003). However, the approach described here offers a novel and relatively simple method for relating consumer community diversity to reward structure, and highlights that the use of other single quantifications of nectar variables may miss much of the salient biological information available.

Our findings are a first step to moving beyond single measures of the food resources associated with flower visitors at the community level, and similar approaches should be considered for other types of floral rewards. Pollen resource diversity is amenable to this method, and data on pollen grain abundance and energy content, in terms of lipid and carbohydrate composition, are likely to result in similar patterns. Combining information on nectar and pollen resource diversity, in conjunction with floral morphology, should ultimately explain the structuring of many flower-visiting communities.

Acknowledgements

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