Temporal turnover of plant-pollinator interaction networks

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Abstract

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2.1 Study area

The Cerrado spans across most of Central Brazil while extending marginally into Bolivia and Paraguay. It comprises of vegetation ranging from open grasslands to scrublands with a sparse distribution of trees, and smaller regions of gallery and close canopy forests. These patches exist side-by-side, resulting in a highly heterogeneous ecosystem (**?**).

Plant-pollinator interactions were surveyed in the Protected Area of the Jardim Botânico de Brasília (Brasília's Botanical Garden Protected Area; hereafter 'BBG') and in the Reserva Ecológica do IBGE (hereafter 'IBGE') . The two study sites are located on the Brazilian plateau (1,100m a.s.l.), within the federally protected conservation site "APA-Gama-Cabeça-de-Viado", located approximately 30km south of Brasília (15°56'S, 47°53'W). This region is characterized by a well-defined wet summer season that lasts from November until March followed by a dry winter period that extends from May until September (**?**).

The BBG site comprised of a denser type of vegetation with a predominance of large shrubs, lianas, and trees. In contrast, the IBGE site consisted of a 8-hectare plot (200 x 400m) covered with mainly grasses mixed with herbaceous plants and shrubs, with a sparse distribution of lianas and trees. (**?**).

2.2 Sampling methods and species identification

Bees are the predominant pollinators in the Cerrado (∼70%) followed by moths (∼12%), hummingbirds (∼3%), bats, (∼2%) and beetles (∼2%) (**???**). Hence, this study focused only on bee-flower interactions. A plant or pollinator species was included in the surveys only if the flowering plant received visits or if the bee was seen foraging on flowers. For every interaction observed, the plant was tagged with a unique identification number, photographed and vouchered. Plant vouchers were identified by using comparative herbarium material, a checklist of local angiosperms and local botanical expertise (Refer to Acknowledgements). In both sites, bees were collected with an entomological net and killed either in individual vials with paper pellets moistened with ethyl acetate or frozen after each observation. Insect vouchers were thereafter mounted, preserved, and identified to species level by comparison with reference collections, taxonomic literature, local records (**????**) and by local entomological experts (Refer to Acknowledgements).

The BBG area was sampled weekly (0730h to 1700h) by M. C. Boaventura from June 1995 to June 1997 using two predefined transects (5,280m and 4,130m in length) located 4 km apart (**?**). Sampling in this site totaled 125 days over 25 months (mean = 5 days/month). Interactions involving the introduced honey bee (*Apis mellifera*) were not included in the BBG data set. The IBGE study site was sampled by S.C. Rabeling by walking transects covering the entire area for a full day (0800h to 1700h) at a weekly basis from November 2008 to October 2009. In total, there were 47 sampling days over a 12-month period (mean = 3.91 days/month).

2.3 Climate information

Data from the IBGE's weather station was used to obtain monthly median temperature and precipitation sum for the past 30 years (1980 - 2010). Median temperature was adopted as monthly distributions of daily average temperatures were skewed. Humidity was not considered as only relative humidity data of IBGE was available.

Monthly precipitation sum from June 1995 to June 1997 ranged from 0 mm to 358 mm while median temperatures varied between 18.4°C to 23.5°C (Table S2). From October 2008 until September 2009, monthly precipitation sum ranged from 0 mm to 270.6 mm with median temperatures of 18°C to 24°C. For analytical purposes, the interactions recorded in the transitional months of April and October were assigned to the dry and rainy seasons respectively. Periods specified for each season are in concordance with patterns reported for other Cerrado areas (**?**).

2.4 Data analysis

Due to temporal and spatial differences between the BBG and IBGE datasets, the two datasets were hence analysed separately.

2.4.1 Month-to-month turnover

Bee-flower interaction turnover is calculated using the Whittaker's presence-based dissimilarity measure (**?**):

$$\beta_{int} = \frac{a+b+c}{(2a+b+c)/2} - 1 \tag{1}$$

where interaction turnover (i.e. interaction dissimilarity or interaction β-diversity; β_{int}) reflects the differences, or dissimilarity, of interactions between two successive monthly networks. a represents the number of interactions present in both networks while b and c are the number of unique interactions in each of the two networks respectively (**?**).

β_{int} can be partitioned into two components; network dissimilarity due to species turnover (β_{st}) and interaction rewiring between shared species of networks (β_{rw}):

$$\beta_{int} = \beta_{st} + \beta_{rw} \tag{2}$$

In theory, β_{int} and β_{st}, but not β_{rw}, covary with species turnover, where species turnover reflects the differences between species composition of two networks; β_S. In this study, β_S can be driven by either plant turnover (β_{Plant}) or bee turnover (β_{Bee}).

β_{rw}, β_S, β_{Plant} and β_{Bee} are calculated using Equation 1, where a refers to the number of items present in both networks and b and c refer to the number of unique items present in each of the two networks (Table 1). β_{st} is obtained by subtracting β_{rw} from β_{int} (Equation 2). The dissimilarity measure takes the value of 0 when two networks are identical and the value of 1 when two networks do not share any items in common (**??**).

Table 1: Measures of network dissimilarity.

The contribution of species turnover to interaction turnover is illustrated indirectly by the fraction of interaction turnover due to species turnover alone (β_{st}). Dissimilarity measures are calculated using the respective items and Equation 1. Modified from **?**.

Measure	Definition	Items	Reference
β_{int}	Dissimiliarity of interactions; Interaction turnover	All interactions	**?**; **?**
β_{rw}	Dissimilarity of interactions between species present in both networks; Interaction rewiring	Interactions of shared species	**?**; **?**
β_{st}	Dissimilarity of interactions due to species turnover	Equation 1	**?**
β_{st}/β_{int}	Contribution of species dissimilarity to dissimilarity of interactions		**?**
β_S	Dissimilarity in the species composition of both networks; Species turnover	Species identity	e.g. **?**
β_{Bee}	Dissimilarity in the bee composition of both networks; Bee turnover	Bee identity	This study
β_{Plant}	Dissimilarity in the plant composition of both networks; Plant turnover	Plant identity	This study

2.4.2 Correlation

As turnover measures are dependent variables, the non-parametric Spearman's rank correlation test from the python package SciPy was utilised to investigate the relationships between the different dissimilarity measures as well as the associations of climatic factors and dissimilarity measures (**?**).

A Monte Carlo process was then used to generate p-values for correlation tests. p-values of Spearman's test deviate away from actual p-values due to turnovers being dependent variables (Table S3). Randomised sets of bees and plants were drawn across the dataset to form 100000 simulated networks for each month. Correlation coefficients between turnover measures for each simulation were thereafter calculated. Number of bees, plants and interactions as well as connectance of each monthly network in simulations were kept constant. p-values were obtained by dividing the total number of simulations with a correlation coefficient higher than the value obtained in either the BBG or IBGE dataset by 100000.

2.4.3 Climate

Two climatic models were utilised in this study. The first model uses the differences between precipitations or temperatures of two subsequent months as the explanatory variable of turnovers (hereafter known as the difference model). The alternative hypothesis of the difference model assumes that networks at a particular temperature and precipitation level are static and do not experience changes as long as climatic factors remain constant. When two networks are at the same temperature and precipitation level, interaction turnover equals to zero. Interaction turnover increases as the temperature or precipitation level difference between networks increases.

The second model uses the average of precipitations or temperatures of two subsequent months as the explanatory variable of turnovers (hereafter known as the average model). The average model postulates that two networks with identical climatic factors will yield a particular turnover rate. Interaction turnover increases as the temperature or precipitation level of networks increases.

To compare the two climatic models, linear regression was used to fit precipitation, temperature and season against β_{Plant} and β_{rw} values of the BBG dataset. Model fitting was not carried out for the smaller IBGE dataset. The more explanatory model was thereafter used to fit climatic factors against turnovers within seasons to prevent overfitting and to minimise multicollinearity.

3 Results

3.1 Community composition

111 species of bees and 93 species of plants were recorded over the 12-month study period at IBGE. In total, 968 bee-flower interactions, which comprised of 434 unique interactions, were observed. The bee community composition in IBGE was similar to those previously observed in other Cerrado areas (**??**) with Apidae being the richest group (77 spp.) followed by Halictidae (19 spp.), Megachilidae (13 spp.), Andrenidae (1 sp.), and Colletidae (1sp.). Plant species recorded at this site consisted of mainly herbs and shrubs, and belonged to 24 families, the most species rich group being Fabaceae (18 spp.).

Between June 1995 and June 1997, 1050 unique interactions and 1616 visitation events between 203 bee species and 182 plant were recorded in the *cerrado sensu strictu* area of BBG. Although the BBG area contained a more species rich pollinator community, bee families were present in comparable proportions as those observed in IBGE: Apidae (115 spp.), Halictidae (38 spp.), Megachilidae (27 spp.), Colletidae (3 spp.), and Andrenidae (1 sp.). Plants recorded in BBG represented 41 families, consisting of mostly shrubs, some trees, and a few herbs. Similar to IBGE, Fabaceae was the most species rich group in this area (31 spp.), followered by Asteraceae (20 spp.) and Malpighiaceae (17 spp.).

3.2 Month-to-month turnover

Interaction turnover, β_{int}, is consistently high, ranging from 0.747 to 1 (Table S1). As expected, β_{int} is positively correlated with β_S (BBG: r_s=0.698, p=0.0308; IBGE: r_s=0.809, p=0.0123) as an increase in species turnover, β_S, will drive an increase in β_{int}. At both sites, β_{int} is significantly and positively correlated with β_{Plant} (BBG: r_s=0.822, p=0.00008; IBGE: r_s=0.773, p=0.0118), suggesting that β_{Plant} drives β_{int}.

Moreover, there is a relatively weak and non-significant correlation between interaction rewiring, β_{rw}, and β_S (BBG: r_s=-0.444, p=0.176; IBGE: r_s=0.629, p=0.359), indicating that factors driving β_{rw} are different from those that drive β_S.

Although there is a high correlation value between bee turnover, β_{Bee}, and plant turnover, β_{Plant}, both trends occur by chance and are statistically non-significant. At the BBG site, neither β_{Bee} nor β_{Plant} drives β_S (Table S1). However, β_S has a strong and significant positive correlation with β_{Plant} at the IBGE site (r_s=0.964, p=0.0021), suggesting that plants are the main driver of species turnover, β_S, at this site.

Surprisingly, β_{st} does not associate with β_S at both sites (Table S1). β_{st} indirectly reflects the contribution of β_S to β_{int} and will theoretically increase as β_S increases. However, due to insufficient sampling and climate conditions, interactions were unequally sampled across time, resulting in inflated β_{rw} values. As β_{st} is obtained by subtracting β_{rw} from β_{int}, this results in β_{st} values being underestimated and the lack of relationship between β_{st} and β_S. Hence, β_{rw} and β_{st} will hereafter not be used for analysis. Nonetheless, β_{int}, β_S, β_{Plant} and β_{Bee} accumulate less error than β_{rw} and are more robust to sampling efforts, allowing these measures to be appropriate for further analysis (**?**).

3.3 Climatic factors influence turnover

4 Discussion

Discuss results, why climatic factor would explain turnover

Limitations: Correlation does not relate to causation, but diff to conduct such experiments,

Future Research: more data, artic temperature comparisons

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5 Supplementary Figures

Table 1: Month-to-month turnover values for all dissimilarity measures at both the Brasília's Botanical Garden Protected Area (BBG) and Reserva Ecológica do IBGE (IBGE) sites.

Year	Months	β_{int}	β_{rw}	β_{st}	β_{rw}/β_{int}	β_{st}/β_{int}	β_S	β_{Plant}	β_{Bee}	Site
1995	Jun-Jul	1	0	1	0	1	0.895	0.8	1	BBG
1995	Jul-Aug	0.967	0.667	0.301	0.689	0.311	0.714	0.742	0.68	BBG
1995	Aug-Sep	0.931	0.7	0.231	0.752	0.248	0.59	0.542	0.657	BBG
1995	Sep-Oct	0.921	0.538	0.383	0.585	0.415	0.658	0.659	0.657	BBG
1995	Oct-Nov	0.959	0.333	0.626	0.348	0.652	0.787	0.76	0.818	BBG
1995	Nov-Dec	0.857	0	0.857	0	1	0.81	0.857	0.714	BBG
1995	Dec-Jan	0.846	0	0.846	0	1	0.789	0.846	0.667	BBG
1996	Jan-Feb	1	0	1	0	1	0.951	0.923	1	BBG
1996	Feb-Mar	0.93	0.5	0.43	0.538	0.462	0.781	0.76	0.826	BBG
1996	Mar-Apr	0.857	0.517	0.34	0.603	0.397	0.567	0.577	0.538	BBG
1996	Apr-May	0.859	0.667	0.192	0.776	0.224	0.527	0.495	0.6	BBG
1996	May-Jun	0.747	0.375	0.372	0.502	0.498	0.503	0.48	0.547	BBG
1996	Jun-Jul	0.781	0.556	0.226	0.711	0.289	0.476	0.468	0.49	BBG
1996	Jul-Aug	0.821	0.509	0.312	0.62	0.38	0.538	0.506	0.6	BBG
1996	Aug-Sep	0.973	0.75	0.223	0.771	0.229	0.635	0.529	0.854	BBG
1996	Sep-Oct	0.965	0.733	0.232	0.76	0.24	0.607	0.512	0.867	BBG
1996	Oct-Nov	0.874	0.486	0.388	0.556	0.444	0.6	0.564	0.724	BBG
1996	Nov-Dec	0.835	0.483	0.352	0.578	0.422	0.541	0.5	0.676	BBG
1996	Dec-Jan	0.987	0.867	0.12	0.878	0.122	0.635	0.567	0.765	BBG
1997	Jan-Feb	0.881	0.6	0.281	0.681	0.319	0.563	0.531	0.607	BBG
1997	Feb-Mar	0.867	0.621	0.246	0.716	0.284	0.622	0.628	0.614	BBG
1997	Mar-Apr	0.817	0.621	0.196	0.76	0.24	0.503	0.456	0.593	BBG
1997	Apr-May	0.818	0.52	0.298	0.636	0.364	0.544	0.515	0.6	BBG
1997	May-Jun	0.897	0.333	0.563	0.372	0.628	0.754	0.692	0.846	BBG
2008	Oct-Nov	1	0	1	0	1	0.909	0.86	1	IBGE
2008	Nov-Dec	0.862	0.5	0.362	0.58	0.42	0.617	0.581	0.688	IBGE
2008	Dec-Jan	0.894	0.611	0.283	0.684	0.316	0.597	0.543	0.673	IBGE
2009	Jan-Feb	0.836	0.474	0.362	0.567	0.433	0.582	0.576	0.591	IBGE
2009	Feb-Mar	0.934	0.613	0.321	0.656	0.344	0.659	0.636	0.692	IBGE
2009	Mar-Apr	0.966	0.829	0.138	0.858	0.142	0.701	0.703	0.698	IBGE
2009	Apr-May	0.895	0.333	0.561	0.373	0.627	0.66	0.613	0.727	IBGE
2009	May-Jun	0.902	0.5	0.402	0.555	0.445	0.667	0.6	0.75	IBGE
2009	Jun-Jul	0.753	0.333	0.42	0.442	0.558	0.564	0.707	0.405	IBGE
2009	Jul-Aug	0.761	0.429	0.333	0.563	0.437	0.514	0.529	0.5	IBGE
2009	Aug-Sep	0.87	0.143	0.727	0.164	0.836	0.808	0.76	0.852	IBGE

Table 2: Climate information obtained from IBGE's weather station.
Daily average temperature was calculated using the minimum and maximum temperature of each day. The median value of daily temperatures was then obtained for each month and used for data analysis. Precipitation values were acquired by adding together total amount of rainfall that occurred throughout the month.

Year	Month	Precipitation / mm	Temperature / °C
1995	Jun	0	18.7
1995	Jul	0	19.4
1995	Aug	0	20.9
1995	Sep	5	22.4
1995	Oct	86.5	23.5
1995	Nov	292.1	21.6
1995	Dec	328.3	21.9
1996	Jan	66	22.3
1996	Feb	190	22.3
1996	Mar	304.7	22.4
1996	Apr	39.7	21.2
1996	May	26.5	20.4
1996	Jun	0	18.4
1996	Jul	0	18.7
1996	Aug	48	20.4
1996	Sep	37.6	22.4
1996	Oct	116.3	23
1996	Nov	261.2	22.1
1996	Dec	293.6	22.7
1997	Jan	358	21.7
1997	Feb	104.3	22.1
1997	Mar	304.2	21.6
1997	Apr	148.1	21.2
1997	May	114.2	19
1997	Jun	21.4	18.8
2008	Oct	29.8	24
2008	Nov	196.9	22.2
2008	Dec	270.6	22.1
2009	Jan	179.8	22.3
2009	Feb	153.3	22.1
2009	Mar	171.7	22.2
2009	Apr	225.2	21.3
2009	May	43.3	19.4
2009	Jun	26.2	18
2009	Jul	0	19
2009	Aug	31.9	19.8
2009	Sep	36.2	22.9

Table 3: Relationships between turnover measures.
(r_s: Spearman's correlation coefficient; p_s: p-value of Spearman's test; p-value: value generated using 100000 randomised networks for each month)

BBG site, Cerrado (1995-1997)				
Measures		r_s	p_s	p-value
β_{int}	β_{st}	0.140	0.514	0.145
β_{int}	β_{rw}	0.156	0.468	0.509
β_{int}	β_S	0.698	0	0.031
β_{int}	β_{Bee}	0.568	0.004	0.150
β_{int}	β_{Plant}	0.822	0	0.0001
β_{st}	β_S	0.678	0.0003	0.177
β_{st}	β_{Bee}	0.732	0.0001	0.056
β_{st}	β_{Plant}	0.425	0.038	0.640
β_S	β_{Bee}	0.955	0	0.097
β_S	β_{Plant}	0.791	0	0.391
β_{Plant}	β_{Bee}	0.610	0.002	0.242

IBGE site, Cerrado (2008-2009)				
Measures		r_s	p_s	p-value
β_{int}	β_{st}	0.140	0.514	0.037
β_{int}	β_{rw}	0.156	0.468	0.844
β_{int}	β_S	0.698	0.000	0.012
β_{int}	β_{Bee}	0.568	0.004	0.364
β_{int}	β_{Plant}	0.822	0	0.012
β_{st}	β_S	0.678	0.0003	0.379
β_{st}	β_{Bee}	0.732	0.0001	0.158
β_{st}	β_{Plant}	0.425	0.038	0.191
β_S	β_{Bee}	0.955	0	0.873
β_S	β_{Plant}	0.791	0	0.002
β_{Plant}	β_{Bee}	0.610	0.002	0.116