

Temporal turnover of plant-pollinator interaction networks

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Abstract

Plant-pollinator interactions are ecologically significant and economically important. Although it is widely agreed that climate affects plant physiology and flowering phenophases, little is known about how or if these responses influence plant-pollinator interactions. Most temporal network studies have focused on the impact of the climate on network structure and robustness but have failed to draw a clear link between climate change and species interactions. In this study, I develop a framework for investigating the influence of climatic factors on interaction turnover using two datasets collected in the Cerrado and present evidence that month-to-month interaction turnover is surprisingly and consistently high. Moreover, this study shows that temperature positively correlates with plant turnover during wet seasons in the Cerrado. Furthermore, plant turnover is a strong predictor of interaction turnover, hence suggesting that elevated global temperatures may drive an increase in temporal interaction turnover.

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Abbreviations

BBG:	Brasília's Botanical Garden Protected Area
IBGE:	Reserva Ecológica do IBGE
β_{int} :	Interaction turnover
β_{rw} :	Interaction rewiring
β_{st} :	Contribution of species turnover to interaction turnover
β_S :	Species turnover
β_{Bee} :	Bee turnover
β_{Plant} :	Plant turnover

1 Introduction

Plant-pollinator interactions contribute significantly towards the diversity of ecosystems by maintaining species-level fitness and community composition in plants (Olesen *et al.*, 2008). Moreover, pollination services constitute a major part of our global economy by supporting the crop industry and contributing towards food security. This field of study has therefore attracted much attention in recent years (Allsopp *et al.*, 2008).

Studies of plant-pollinator networks have provided much insight into the structure of ecosystems and their function. In these networks, a link is created between a pollinator and a plant when a pollinator visits the flowers of the plant. Both species are represented by the nodes of the networks, where every link between nodes constitutes a pollination event (Poisot *et al.*, 2012a).

Nonetheless, previous studies have typically depended upon a static picture of plant-pollinator networks and ignored the dynamic nature of interactions. Recently, compelling evidence has surfaced, demonstrating that interaction networks vary between days, weeks, within seasons and even across decades or centuries (Olesen *et al.*, 2008; Burkle *et al.*, 2013; Yeakel *et al.*, 2014; CaraDonna *et al.*, 2017). However, the significant amount of sampling effort required to build multiple networks has resulted in insufficient studies on temporal networks (Burkle *et al.*, 2011).

Research on temporal plant-pollinator networks has likewise been largely restricted to peak flowering seasons and temperate ecosystems. These studies have mainly focused on the robustness, stability and structure of temporal networks and the factors that constrained interactions across time (Basilio *et al.*, 2006; Olesen *et al.*, 2008; CaraDonna *et al.*, 2017). Nonetheless, relatively little is known about the drivers of high temporal variability of interactions (Burkle *et al.*, 2011).

Understanding the factors that drive interaction turnover can provide new insight into the impact of climate change on plant-pollinator networks. Elevated global temperature results in drastic shifts in flowering, which can lead to disruptions of spatial and temporal co-occurrences of flowers and pollinators in temperature regions (Schweiger *et al.*, 2010). Moreover, even if climate change causes subtle differences in plant or pollinator phenology, these minute changes could affect each other, eventually significantly influencing interaction networks. For example, changes

in plant physiology could lead to reduced pollinator reproduction, which could indirectly cause reduced pollination visits in a positive feedback loop, hence resulting in an amplified effect of climate change on plant-pollinator interactions (Scaven & Rafferty, 2013).

In the tropics, most pollinators are active for periods longer than the flowering periods of most plants (Biesmeijer & Slaa, 2006). Plant phenology shifts may hence not have the same impact on species interactions as in the temperate regions, where most interaction network studies have been conducted. Thus, the direct influence of rising temperatures and harsher weather conditions on plant-pollinator interactions in tropical regions remains unclear (Schweiger *et al.*, 2010).

The greatest biodiversity in the world can be found in the tropics (Brown, 2014). Understanding the variability of interactions in these habitats is hence crucial in maintaining plant-pollinator interactions and species richness in the tropics. Here, I focus on temporal interaction networks in the Cerrado; a neotropical habitat characterised by drastic seasonal changes between dry and rainy seasons (Kricher, 2011).

Besides being a highly seasonal habitat, the Cerrado acts as an important model system for interaction network studies as it sustains a significant percentage of the Neotropical angiosperm diversity. The Cerrado is the second largest tropical biome in South America and is viewed as one of the most threatened tropical ecosystems due to excessive deforestation and poor conservation policies, which have already caused more than 50% of its area to be degraded. Unfortunately, data of the region is scarce and the ecological networks of this region are poorly understood (Myers *et al.*, 2000; Klink & Machado, 2005). Thus, a better understanding of the interaction networks of this region will significantly help conservation efforts in the Cerrado.

In this study, two different datasets collected in the tropical Cerrado habitat were used to investigate temporal interaction turnover. To the best of my knowledge, this is the first study to investigate the effect of climatic factors on temporal interaction turnover. Here, I report that temporal interaction turnover is surprisingly high and consistently high in the Cerrado. Moreover, plant turnover is a strong driver of interaction turnover. Temperature in the wet season is also positively correlated with plant turnover, indicating that a rise in temperature may indirectly increase interaction turnover.

2 Materials and Methods

To address the questions stated above, I develop a framework for investigating the influence of climatic factors on interaction turnover (Figure 1). Firstly, differences between subsequent temporal networks, also known as β -diversity, were quantified using a number of β -dissimilarity measures. These measures reflect interaction, species, plant and bee species changes over time. Correlations between β -dissimilarity measures were then investigated and compared to theoretical and previously published trends. Lastly, to provide a macroscopic view, relationships between climatic factors and temporal dissimilarity in plant communities were examined.

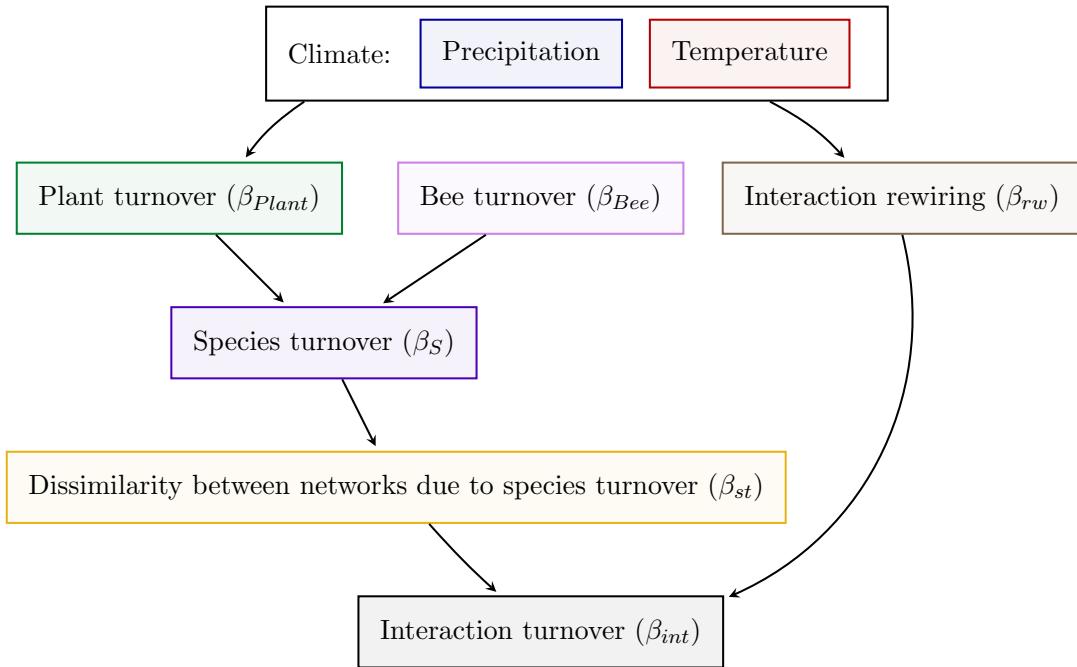


Figure 1: Framework demonstrating the effect of the climate on the different measures of turnovers. Changes in temperature or precipitation can lead to modifications in plant phenology, which may result in an elevated plant turnover. A higher plant turnover can lead to a higher dissimilarity between interaction networks due to species turnover, resulting in a higher interaction turnover. Colours correspond with those used to represent measures in later figures.

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 (Gottsberger & Silberbauer-Gottsberger, 2006) 

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'). Both 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 wet summer season that lasts from November until March followed by a dry winter period that extends from May until September (Gottsberger & Silberbauer-Gottsberger, 2006) 

The IBGE site consisted of a 8-hectare plot covered with mainly grasses mixed with herbaceous plants and shrubs, with a sparse distribution of lianas and trees. In contrast, the BBG site comprised of a denser type of vegetation with a predominance of large shrubs, lianas, and trees (Eiten, 1972).

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%) (Oliveira, P.S. & Marquis, R.J., 2002; Gottsberger & Silberbauer-Gottsberger, 2006b; Cappellari, 2011). Hence, this study focused only on bee-flower interactions. Data analysed in this research were collected during studies by M. C. Boaventura and S.C. Rabeling in the Cerrado. Further details on the sampling methods can be found in Boaventura (1998) and Cappellari (2011).

During surveys, a plant or pollinator species was included 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). At 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 (Michener, 2000; Moure & Melo, 2012) 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 4km apart (Boaventura, 1998). Sampling in this site totalled 125 days over 25 months (mean = 5 days/month). Interactions involving the introduced honey bee (*Apis mellifera*) were not included in BBG surveys. 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. Sampling totalled 47 days over 12 months (mean = 3.91 days/month) (Cappellari, 2011). 

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 made available.

Monthly precipitation sum from June 1995 to June 1997 ranged from 0mm to 358mm while median temperatures varied between 18.4°C to 23.5°C. From October 2008 until September 2009, monthly precipitation sum ranged from 0mm to 270.6mm with median temperatures of 18°C to 24°C (Table S2). For analytical purposes, the interactions recorded in the transitional months of April and October were assigned to the dry and rainy seasons respectively. Turnovers between networks of September and October and those between networks of March and April were similarly designated to the dry and rainy seasons respectively. Periods specified for each season are in concordance with patterns reported for other Cerrado areas (Gottsberger & Silberbauer-Gottsberger, 2006b).

2.4 Data analysis

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

2.4.1 Month-to-month turnover

Bee-flower interaction turnover is calculated using the Whittaker's presence-based dissimilarity measure (Whittaker, 1960):

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

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 present in each of the networks respectively (Poisot *et al.*, 2012a)(Figure S1).

The Whittaker's index was chosen as it is most commonly used for presence-absence data. Moreover, it does not require additional information such as the abundance of species in the Cerrado, of which data is scarce, and is relatively more robust than other β -dissimilarity indexes when dealing with heterogeneous dataset sizes (Koleff *et al.*, 2003; Poisot *et al.*, 2012a).

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

$$\beta_{int} = \beta_{st} + \beta_{rw} \quad (2)$$

In theory, β_{int} and β_{st} , but not β_{rw} , covary with species turnover, β_S , where β_S reflects the differences between species composition of two networks (Poisot *et al.*, 2012a). In this study, β_S can be driven by either plant turnover (β_{Plant}) or bee turnover (β_{Bee}).

β_{rw} , β_S , β_{Bee} and β_{Plant} are calculated using Equation 1, where a refers to the number of elements present in both networks and b and c refer to the number of unique elements present in each of the two networks; elements refer to interactions common to both networks, species, bee species and plant species respectively (Table 1, Figure S1). 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 elements in common (Poisot *et al.*, 2012a; CaraDonna *et al.*, 2017).

Table 1: **Measures of network dissimilarity.**

Dissimilarity measures are calculated using the respective elements and Equation 1.

Measure	Definition	Elements	Reference
β_{int}	Dissimilarity of interactions; Interaction turnover	All interactions	Poisot <i>et al.</i> (2012a); CaraDonna <i>et al.</i> (2017)
β_{rw}	Dissimilarity of interactions between species present in both networks; Interaction rewiring	Interactions of shared species	Poisot <i>et al.</i> (2012a); CaraDonna <i>et al.</i> (2017)
β_{st}	Dissimilarity of interactions due to species turnover		Poisot <i>et al.</i> (2012a)
β_S	Dissimilarity in the species composition of both networks; Species turnover	Species identity	e.g. Koleff <i>et al.</i> (2003)
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 Correlations

As turnover measures are not normally distributed, 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 Spearman's correlation coefficient, r_s , of 1 indicates that both factors are positively correlated by a monotonic function while a negative r_s value indicates that variables are negatively correlated. A zero value of r_s suggests that there is no tendency for one variable to change as the other variable increases (Dehmer *et al.*, 2011).

A Monte Carlo procedure was then used to generate p-values for correlation tests. p-values of Spearman's test, p_s , deviate away from actual p-values due to turnovers being non-independent variables (Table S3). For example, if the interaction network of April was altered, this would affect both March-April and April-May plant and interaction turnover, resulting in non-independence of turnover measures.

Hence, randomised sets of bees and plants were drawn across the dataset to form 10^5 simulated networks for each month. Correlation coefficients between turnover measures for each simulation were thereafter calculated. This generates a null distribution of r_s values between turnover measures of interaction networks undergoing random rewiring. Number of bees, plants

and interactions as well as connectance of each simulated monthly network were kept constant. p-values were thereafter obtained by dividing the total number of simulations with a r_s value higher than the r_s value obtained in either the BBG or IBGE dataset by 10^5 .

2.4.3 Climate

The two seasons exhibit different temperature and precipitation ranges (Table S2, Figure 2, Figure S5), resulting in seasonal interactions (Figure S2). To investigate whether precipitation and/or temperature affects turnovers, two climate-turnover models were utilised in this study.

The first model uses the differences between climatic factors of two subsequent months as the explanatory variable of turnover (hereafter known as the difference model) (Figure 2). In this study, the differences between the precipitation sums or median temperatures of two subsequent monthly networks were utilised. The alternative hypothesis of the difference model assumes that networks at a particular temperature and precipitation level are stable 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 is zero. Interaction turnover increases as the temperature or precipitation level difference between networks increases.

The second model uses the average of precipitation sums or median temperatures of two subsequent months as the explanatory variable of turnovers (hereafter known as the average model) (Figure 2). 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 climate-turnover models, linear regression was used to fit β_{Plant} and β_{int} against precipitation, temperature, season and their interactions. Due to its small sample size, the IBGE dataset was not utilised in model fitting to prevent overfitting. The more explanatory model was thereafter used to fit turnovers against climatic factors within seasons to prevent overfitting and to minimise multicollinearity.

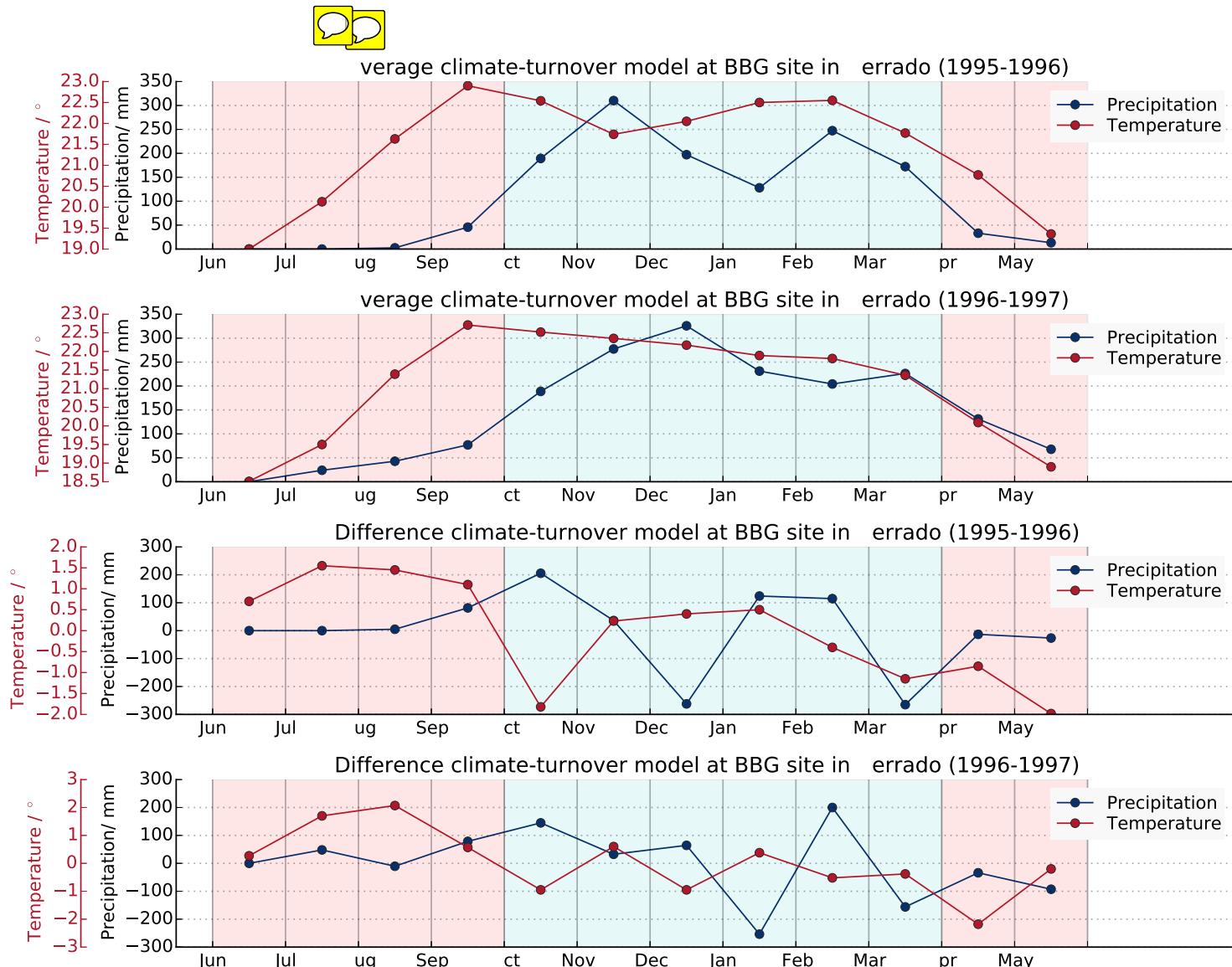


Figure 2: **Time series plot of climatic factors from Jun 1995 to Jun 1997 (BBG site).** Climatic factors in the average model show a different trend across time when compared to climatic factors in the difference model. (Average model: average of precipitation sums/median temperatures of two subsequent months; Difference model: difference between precipitation sums/median temperatures of two subsequent months)

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 (Pinheiro-Machado *et al.*, 2002) with Apidae being the richest group (77 spp.) followed by Halictidae (19 spp.), Megachilidae (13 spp.), Andrenidae (1 sp.), and Colletidae (1 sp.). Plant species recorded at this site consisted of mainly herbs and shrubs and belonged to 24 families, with 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 dataset, Fabaceae was the most species rich group in this area (31 spp.), followed 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, Figure S3, Figure S4). Surprisingly, only 8.19% and 4.83% of all unique interactions appeared in three or more monthly networks at the BBG and IBGE site respectively (Figure 3).

As expected, β_{int} is positively correlated with β_S (BBG: Spearman's test, $r_s = 0.698$, $p = 0.0308$; IBGE: $r_s = 0.809$, $p = 0.0123$) (Figure 5) as an increase in species turnover, β_S , will result in an elevated β_{int} (Poisot *et al.*, 2012a).

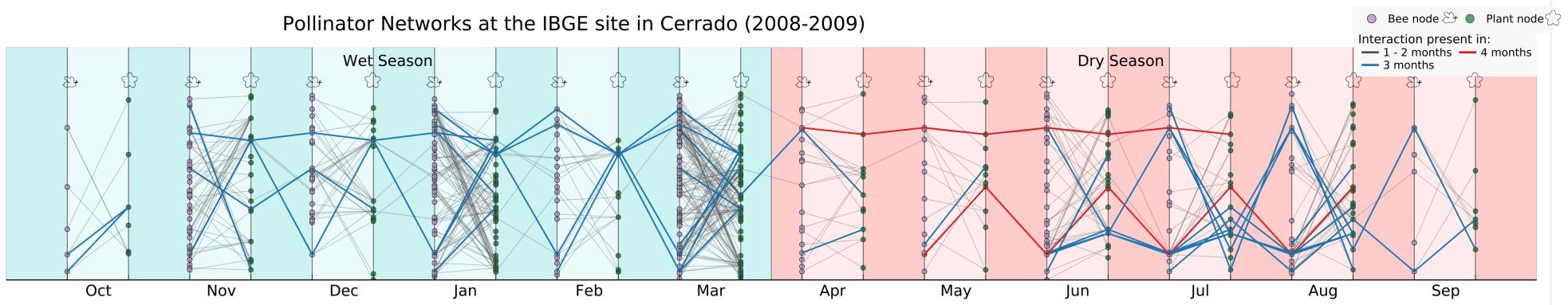
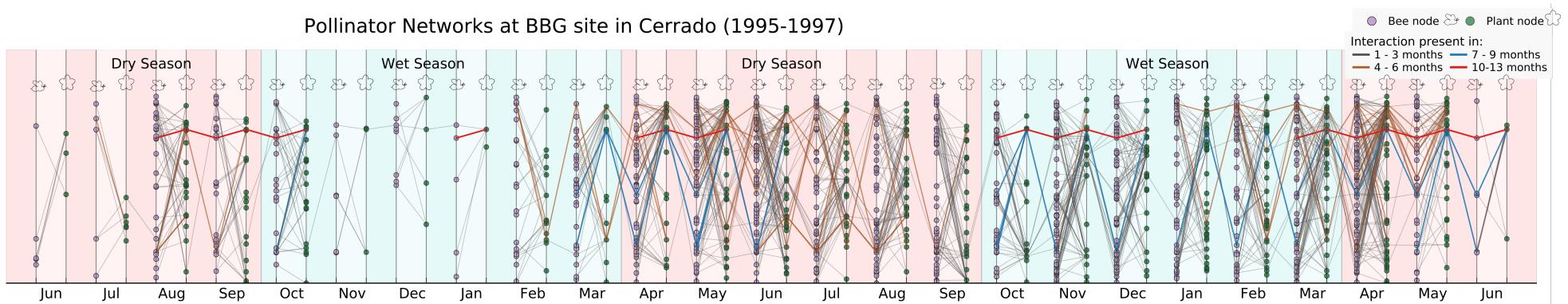


Figure 3: **Hover in monthly bee-plant networks from Jun 1995 to Jun 1997 (BBG site) and from Oct 2008 to Sep 2009 (IBGE site).** Every node in a monthly network represents a distinct plant or bee species. Each link between plant and bee nodes represent a unique pollination visit in the corresponding month. Links between monthly networks show interactions recorded in both monthly networks. Background of plot is colour-coded to reflect the seasons: blue - wet season; red - dry season. Lighter shaded areas demarcate the pollinator networks of each month, while darker areas demarcate the links present between monthly networks. Colour of links represent the number of monthly networks in which the interaction was found. (BBG: Total no. of unique interactions: 1050, No. of interactions present in 4-6 months: 20, 7-9 months: 3, 10-13 months: 1; IBGE: Total no. of unique interactions: 434, No. of interactions present in 1-2 months: 414, 3 months: 18, 4 months: 2)

At both sites, correlation between interaction turnover, β_{int} , and plant turnover, β_{Plant} , did not occur by chance (random rewiring), implying that β_{Plant} has a significant and strong positive correlation with interaction turnover due to non-random rewiring wherein certain bees preferentially visit certain, newly-available plants (BBG: $r_s = 0.822$, $p = 0.00008$; IBGE: $r_s = 0.773$, $p = 0.0118$) (Figure 4). Hence, β_{Plant} drives β_{int} and is a strong predictor of β_{int} .

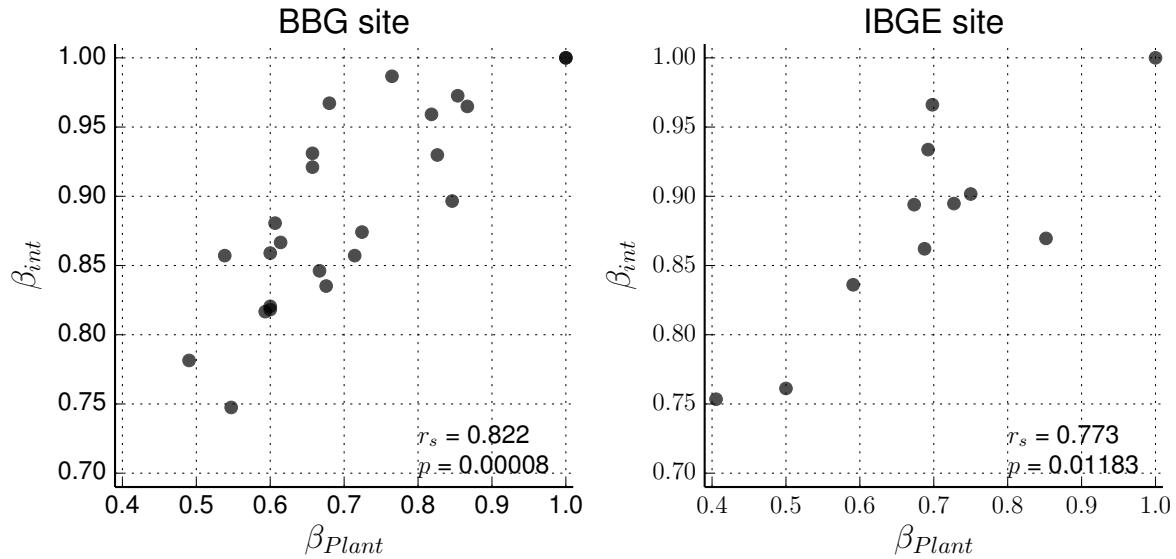


Figure 4: **Plant turnover (β_{Plant}) drives interaction turnover (β_{int}).**

A high β_{Plant} and/or β_{int} indicates a high dissimilarity between interactions and/or plant communities of two networks. (r_s : Spearman's rank correlation coefficient; p : p-values generated using Monte Carlo simulations.)



Moreover, there is a relatively weak and non-significant correlation between interaction rewiring, β_{rw} , and species turnover, β_S (BBG: $r_s = -0.444$, $p = 0.176$; IBGE: $r_s = 0.629$, $p = 0.359$) (Figure 5), indicating that factors driving β_{rw} are different from those that drive β_S (Poisot *et al.*, 2012a).

Although there is a high correlation value between bee turnover, β_{Bee} , and plant turnover, β_{Plant} , both trends occur by chance (Table S3). At the BBG site, neither β_{Bee} nor β_{Plant} drives β_S (Table S3). However, β_S has a strong and non-random positive correlation with β_{Plant} at the IBGE site ($r_s = 0.964$, $p = 0.0021$), suggesting that plants are the main driver of β_S at this site.

Surprisingly, dissimilarity of interactions due to species turnover, β_{st} , does not associate with species turnover, β_S , at both sites (Table S1)(Figure 5). 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 climatic conditions, interactions were unequally sampled across time, resulting in inflated interaction rewiring, β_{rw} , values (Figure 3). 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 . Thus, β_{rw} and β_{st} will hereafter not be used for further analysis. Nonetheless, β_{int} , β_S , β_{Plant} and β_{Bee} accumulate less error than β_{rw} and are more robust to sampling efforts (Poisot *et al.*, 2012a). β_{int} and β_{Plant} measures are hence utilised for the climate-turnover models.

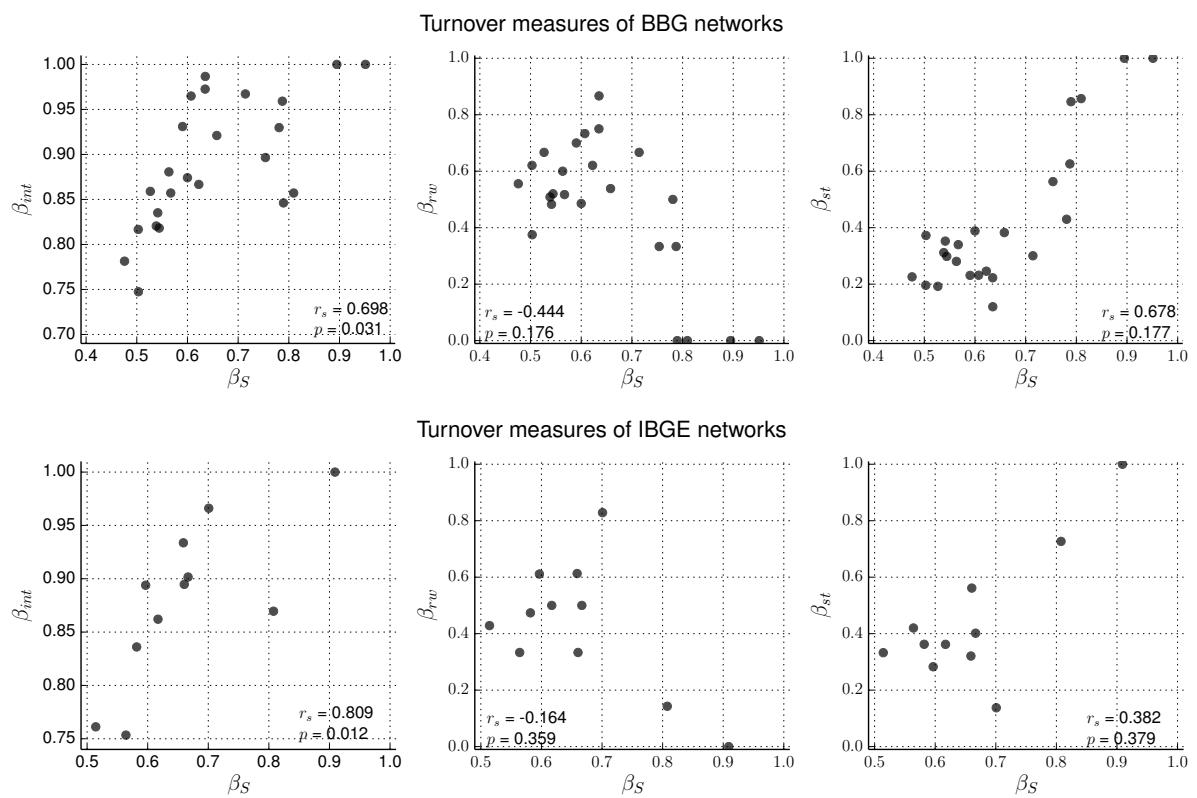


Figure 5: Trends between species turnover (β_S) and interaction turnover (β_{int}), interaction rewiring (β_{rw}) and network dissimilarity due to β_S (β_{st}). β_S has a strong and non-random positive correlation with β_{int} at both sites while β_{st} and β_{rw} do not associate with β_S . (r_s : Spearman's correlation coefficient; p: p-values generated using Monte Carlo simulations)

3.3 Effect of climatic factors on plant and interaction turnover

Spearman's correlation coefficients indicate that there exists a seasonal effect on the trends between climatic factors and plant turnover, β_{Plant} , and interaction turnover, β_{int} (Table S4). Hence, a linear regression model was used to predict β_{Plant} using temperature, precipitation, season and their interactions. Median temperature difference and precipitation sum difference between months  do not explain β_{Plant} as the null model  was obtained after minimising the linear regression model (intercept = 0.706 ± 0.0284 , $p < 0.0001$, $df = 23$, res.s.e. = 0.139).

By contrast, under the average model, networks experience a lower β_{Plant} during the wet season and β_{Plant} increases as average median temperature increases during the wet season ($adj.r^2 = 0.122$, $F_{3,20} = 2.07$, $p = 0.137$) (Table S5). This indicates that the average model is a better model for β_{Plant} than the difference model  Nonetheless, the variation inflation factor (VIF) for variables in this minimal model exceeds the recommended value of 3 (Zuur *et al.*, 2010). β_{Plant} was hence fitted against average median temperature and average precipitation sum within seasons to reduce multicollinearity.

Within the dry season, average  temperature and precipitation levels do not explain β_{Plant} as the null model was acquired as the minimal model  (intercept = 0.700 ± 0.0447 , $p < 0.0001$, $df = 11$, res.s.e. = 0.155). However, within the wet season, minimal model shows that average temperature explains significant variation in β_{Plant} ($adj.r^2 = 0.504$, $F_{1,10} = 12.18$, $p = 0.00583$) and β_{Plant} increases as average temperature increases (intercept = -4.57 , s.e. = 1.51, $p = 0.0129$; slope = 0.239, s.e. = 0.0685, $p = 0.00583$).

Under both models, the null model was obtained as the minimal model when using temperature, precipitation, season and their interactions to explain β_{int} (intercept = 0.891 ± 0.0146 , $p < 0.0001$, $df = 23$, res.s.e. = 0.0714). As expected from previous results, β_{Plant} explains significant variation in β_{int} ($adj.r^2 = 0.653$, $F_{1,22} = 44.35$, $p < 0.0001$). β_{Plant} increases as β_{int} increases  (intercept = 0.594, s.e. = 0.0453, $p < 0.0001$; slope = 0.421, s.e. = 0.0631, $p < 0.0001$).

4 Discussion

Previous studies have mainly focused on static ecological networks, leading to species interactions being largely ignored in the past (Poisot *et al.*, 2015). However, this study demonstrates, in agreement with previous studies on temporal networks, that dissimilarity between monthly interaction networks is consistently high (Olesen *et al.*, 2008; Burkle *et al.*, 2013; CaraDonna *et al.*, 2017). Nonetheless, there are surprisingly no apparent differences between turnover values within seasons and between seasons¹, despite the Cerrado being a highly seasonal habitat (Kricher, 2011)(Table S1, Figure S3, Figure S4).

In the Cerrado, interaction turnover, β_{int} , was higher than previously reported week-to-week and year-to-year β_{int} values² (CaraDonna *et al.*, 2017)(Table S1). In CaraDonna *et al.* (2017), sampling only took place during the flowering period as the area is mostly covered by snow for the rest of the year. β_{int} values could therefore be relatively low³ due to climatic factors remaining relatively similar throughout the flowering season in the temperate region. As plants can only be pollinated during a short timeframe annually, temperate plant communities have a longer mean flowering time than those in the tropics (Bawa, 1990), resulting in a lower plant turnover, β_{Plant} . Lower β_{Plant} values could thereafter lead to lower β_{int} values. However, as no month-to-month β_{int} or β_{Plant} values were made available, no direct comparison of β -diversity between temperate and tropical regions can be made (CaraDonna *et al.*, 2017).

Furthermore, only 8.19% and 4.83% of all unique interactions appeared in three or more monthly networks at the BBG and IBGE site respectively (Figure 3, Results 3.2). Although this low percentage may have been in part due to insufficient sampling efforts, another plausible cause is the high biodiversity levels found in the tropics⁴. 111 pollinators and 45 flowering plants were observed over 3 years of study in CaraDonna *et al.* (2017). Comparatively, within the 1-year study period at IBGE, 111 species of bees and 93 species of plants were already recorded (Section 3) and yet, it is apparent that there still exist many missing interactions⁵. β_{Plant} values may hence be higher in the tropics than in the temperate regions due to the species richness found in tropical biomes. Nonetheless, due to the lack of temporal network data in the tropics, there is no support for this hypothesis yet.⁶

Moreover, this study shows that β_{Plant} is a major contributor of β_{int} and is a good predictor of β_{int} (Results 3.2). Alarcón *et al.* (2008), the Bray-Curtis dissimilarity index along with a different approach were utilised to compare species turnover to plant-pollinator interaction turnover in a montane meadow system in California, United States. Unexpectedly, the study has likewise demonstrated that the degree of similarity between flowering plant compositions of two weekly networks mirrors the extent of similarity between the two corresponding interaction networks (Alarcón *et al.*, 2008).

In contrast, Poisot *et al.* (2015) and CaraDonna *et al.* (2017) argue that interaction rewiring, β_{rw} , is indispensable in estimating interaction turnover, β_{int} . CaraDonna *et al.* (2017) postulates that dissimilarity of interactions due to species turnover, β_{st} , only coincides with β_{int} when both values are elevated at seasonal transitions. Within seasons, β_{st} falls while β_{rw} rises (CaraDonna *et al.*, 2017). Due to inflated β_{st} values, the presence of such a trend in the Cerrado datasets cannot be determined. Nonetheless, randomising networks using the Monte Carlo procedure has illustrated that the strong collinearity between β_{Plant} and β_{int} did not occur by chance. β_{Plant} has a strong positive correlation with interaction turnover, β_{int} , due to non-random rewiring, indicating that particular bees preferentially visit particular, newly-available plants (Results 3.2). Hence, this further strengthens the case that β_{Plant} is a major driver of β_{int} .

To date, to the best of my knowledge, there has been no research investigating the effect of climatic factors on temporal plant-pollinator interaction turnover (Burkle *et al.*, 2011; Scaven & Rafferty, 2013). Although it is widely agreed that the climate affects the physiology of plants and in certain cases, even bees, little is known about how or if these responses do influence plant-pollinator interactions (Hughes, 2000; Parmesan & Yohe, 2003). Most temporal network studies have focused on how the climate can affect network structure, species richness or abundance and even possible mismatches between plant flowering and insect emergence (Basilio *et al.*, 2006; Alarcón *et al.*, 2008; González *et al.*, 2009; Schweiger *et al.*, 2010). However, although climate change may not have a direct harmful impact on species, it could have a greater effect on plant-pollinator interactions due to positive feedback loops (Hegland *et al.*, 2009; Scaven & Rafferty, 2013).

Furthermore, plant-pollinator interactions are ecologically significant and economically important. Pollination visits drive plant diversity and maintain plant reproduction and lifecycles (Olesen *et al.*, 2008). Being at the bottom of the food chain, changes in the stability of plant communities can have rippling effects across entire ecosystems (Scaven & Rafferty, 2013). Moreover, pollination services contribute annually an estimated \$220 billion worldwide to the global economy (Gallai *et al.*, 2009). Hence, there is an urgent need to study the impact of climate change on interaction networks (Scaven & Rafferty, 2013).

To address the above question, two contrasting climate-turnover models were used. Average climatic values of two subsequent months proved to be a better explanatory variable of plant turnover, β_{Plant} , than the use of differences between climatic values of two subsequent monthly networks. This further supports the average model with the alternative hypothesis that two networks experiencing the same climate will still yield a positive interaction turnover, β_{int} . This is a logical scenario as networks constantly experience changes over time even if temperature, precipitation and all other climatic factors were kept constant (Results 3.3). 

Although both precipitation and temperature do not explain the variation in β_{int} , β_{int} is driven by species turnover, β_S , and plant turnover, β_{Plant} .   β_{Plant} has a weaker correlation with β_S as compared to its relationship with β_{Plant} . This could be due to the correlation between bee turnover, β_{Bee} , and β_{Plant} occurring by chance (Results 3.3), indicating that different factors drive the turnover of the two different species. 

Indeed, climatic changes can have a significant impact on plants, and especially on flowers. Plants living under higher temperatures have been shown to produce fewer flowers as temperature elevates, resulting in a higher β_{Plant} (Scaven & Rafferty, 2013), hence explaining the positive correlation between β_{Plant} and temperature during the wet season (Results 3.3). Nevertheless, this is surprising as the range of temperatures of the BBG dataset is less than 5°C (Figure 2), and thus further illustrates the extent of sensitivity of plants to the climate. In the Cerrado, dry season flowering is restricted in species with shallow root systems (Oliveira, P.S. & Marquis, R.J., 2002; Gottsberger & Silberbauer-Gottsbeger, 2006a) and therefore, flowering plants may not respond to temperature changes during the dry season as no flowering has occurred. 

accounting for the lack of an association between β_{Plant} and temperature during this season. Although β_{int} is consistently high throughout the year, there appears to be a seasonal difference in factors that drive turnover (Results 3.2)  

Unexpectedly, despite the drastic difference between the precipitation level of dry and wet seasons, precipitation was a insignificant factor in explaining β_{Pla}  (Results 3.3). Plants in the Cerrado have evolved mechanisms to survive cycles of extreme drought and may therefore be less sensitive to changes in precipitation (Oliveira, P.S. & Marquis, R.J., 2002; Gottsberger & Silberbauer-Gottsbeger, 2006a). Nonetheless, precipitation may account for the seasonal effect that temperature has on β_{Plant} , but more complex models and data will be required to support this hypothesis.

Lastly, β_{Plant} drives β_S at the IBGE site but not at the BBG site (Results 3.2). The IBGE survey site is covered with sparse distribution of plants, consisting mainly of grasses and shrubs. In contrast, the BBG community comprises of mainly large shrubs, lianas and trees which have a longer lifespan (Eiten, 1972), and hence, BBG communities may experience a lower β_{Plant} than IBGE communities. The higher β_{Plant} of the IBGE communities may hence contribute to β_S to a larger extent, resulting in a positive correlation. Further analysis is required to explore this relationship. However, due to time constraints, this line of investigation was not pursued.

4.1 Limitations

Past studies of temporal plant-pollinator networks utilise one of the other 23 β -diversity measures, making it highly difficult for any direct comparisons (Basilio *et al.*, 2006; Alarcón *et al.*, 2008; Olesen *et al.*, 2008; Burkle *et al.*, 2013). Little consensus has yet been reached as to which β -dissimilarity measure best reflects temporal and spatial β -diversity, resulting in a large number of different approaches and contradictory results (Koleff *et al.*, 2003; Poisot *et al.*, 2015).

Insufficient sampling is yet another problem,  which can lead to inflated β_{rw} values, as networks falsely appear to be more dissimilar than in reality due to missing interactions (Vázquez, Melián, Williamns, Bluthgen, Krasnov, 2007; Dormann *et al.*, 2009; Poisot *et al.*, 2012b). This problem is sometimes unavoidable due to existing weather conditions and can be illustrated

by the abnormally high β_{st} and β_{int} between the months of November 1995 to January 1996 at the BBG site (Table S1, Figure S3). Removing these data points would have significantly reduced the sample size of the BBG dataset. As β_{int} , β_S , β_{plant} and β_{bee} are more robust to sampling error, these data points were included and tests which are robust to outliers, such as the Spearman correlation coefficient test was used.

4.2 Conclusion and Future Research

Understanding temporal interaction networks is crucial in the conservation of ecosystems as protecting or restoring an ecosystem requires approaches that restore its interactions and functions for its long term stability. Climate change has already influenced plant phenology, resulting in plants blooming earlier than ever before (Cleland *et al.*, 2007; Miller-Rushing & Primack, 2008). Hence, there is an urgent need to investigate and validate the drivers of dissimilarity of temporal interaction networks, in order to understand the extent to which climate and plant phenology can affect species interaction. A decrease in pollination visits globally will result in decreased plant diversity and stability of plant communities. In return, this will adversely affect our ecosystems and food security (Schweiger *et al.*, 2010; Burkle *et al.*, 2011).

Nonetheless, correlation of variables does not relate to causation. Experimental approaches are therefore required to test out these predictions on artificially manipulated ecosystems. If the spatial and temporal scale of experiments are not large enough to significantly affect network turnover, available datasets across diverse habitats with varying climates can be compared to support these predictions (Burkle & Irwin, 2009; Burkle *et al.*, 2011). In fact, spatial network studies which utilises natural gradients of climatic factors have already provided several insights. In the West Indies, plant species become increasingly specialised with elevated precipitation levels and decreased temperatures (González *et al.*, 2009). Hence, research on spatial networks are necessary to further support the predictions found in studies of temporal interaction networks.

Moreover, before further progress can be made in this field of study, it is crucial to establish a definition and measure of β -diversity that most researchers can come to a consensus to. Alternatively, future research should either utilise more than one measure of β -diversity, publish their original datasets or release the a , b and c values commonly used for most β -dissimilarity measures.

This will enable comparison of results across different datasets and reveal more insights into the characteristics of interaction turnover. Collecting temporal network data is time-consuming and require large amounts of sampling to prevent inflated values of network dissimilarity (Koleff *et al.*, 2003; Burkle *et al.*, 2011; Poisot *et al.*, 2015). Hence, compiling available data and comparing networks in both the temperate and tropical regions will be necessary to paint a clearer picture of interaction networks.

With better β -diversity measures, drivers of temporal interaction turnover can be better understood. For example, sensitivity of interactions to the climate, predictors of interaction turnover and the significance of phenology in interaction networks are fascinating and essential topics in which we currently lack an understanding of (Poisot *et al.*, 2012a). Furthermore, current datasets of temporal networks are sorely lacking in both resolution and length of study. Currently, the best dataset available originates from a four year study of a Phryganic community in Greece (Petanidou, 1991). Additional long-term studies across different ecosystems are crucial to further our understanding of the temporal variability of interactions (Burkle *et al.*, 2011).

In conclusion, this study presents evidence that month-to-month interaction networks are highly dissimilar from each other and is the first of its kind to study temporal networks in the Cerrado as well as to directly link climatic changes to temporal plant turnover and thereafter, temporal interaction turnover. Future studies on temporal networks of finer resolutions will be able to greatly improve our understanding of interaction networks and allow us to better protect our ecosystems in the face of climate change.

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5 Supplementary Figures

Figure S1: Example of calculating turnover measures of the networks of April and May 2009. Each number represents a bee or plant species and is represented by a node in Figure 3 and Figure S2. Unique interactions of both networks are shown here (April 2009: 21; May 2009: 17). Boxes are color coded to show bee and plant species common to both networks.

April 2009		May 2009	
Bee	Plant	Bee	Plant
6	132	49	147
22	132	65	147
32	148	109	178
90	155	91	185
72	164	28	117
57	166	16	159
57	168	22	169
71	168	90	185
84	168	17	159
91	205	90	159
102	205	6	165
91	147	106	201
41	138	90	117
17	138	90	139
91	164	70	159
9	166	37	161
13	166	84	168
76	166		
91	185		
101	185		
30	118		

Whittaker's dissimilarity measure:

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

Interaction turnover:

$$\beta_{int} = \frac{2 + 19 + 15}{(2 * (2) + 19 + 15)/2} - 1 = 0.895$$

Interaction rewiring:

$$\beta_{rw} = \frac{2 + 1 + 1}{(2 * (2) + 1 + 1)/2} - 1 = 0.333$$

Dissimilarity of interactions due to β_S :

$$\beta_{st} = 0.89474 - 0.33333 = 0.561$$

Species turnover:

$$\beta_S = \frac{9 + 19 + 16}{(2 * (9) + 19 + 16)/2} - 1 = 0.660$$

Bee turnover:

$$\beta_{Bee} = \frac{6 + 11 + 8}{(2 * (6) + 11 + 8)/2} - 1 = 0.613$$

Plant turnover:

$$\beta_{Plant} = \frac{3 + 8 + 8}{(2 * (3) + 8 + 8)/2} - 1 = 0.727$$

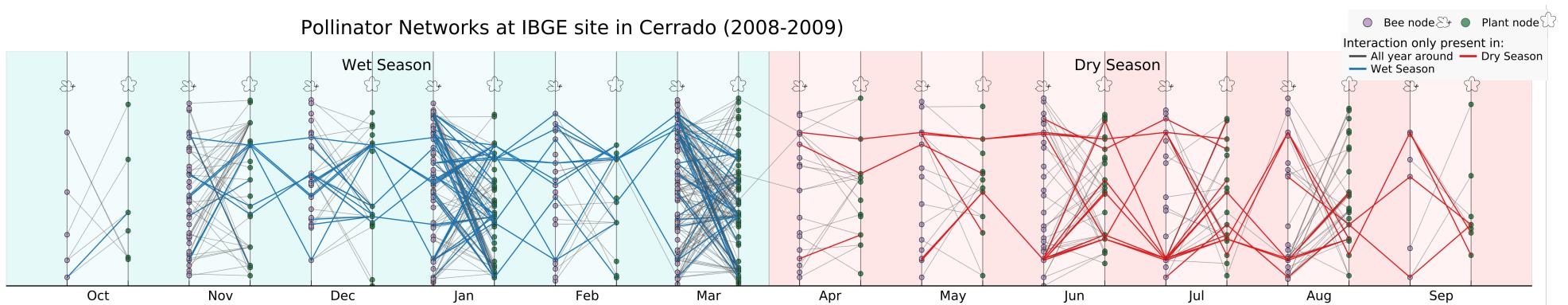
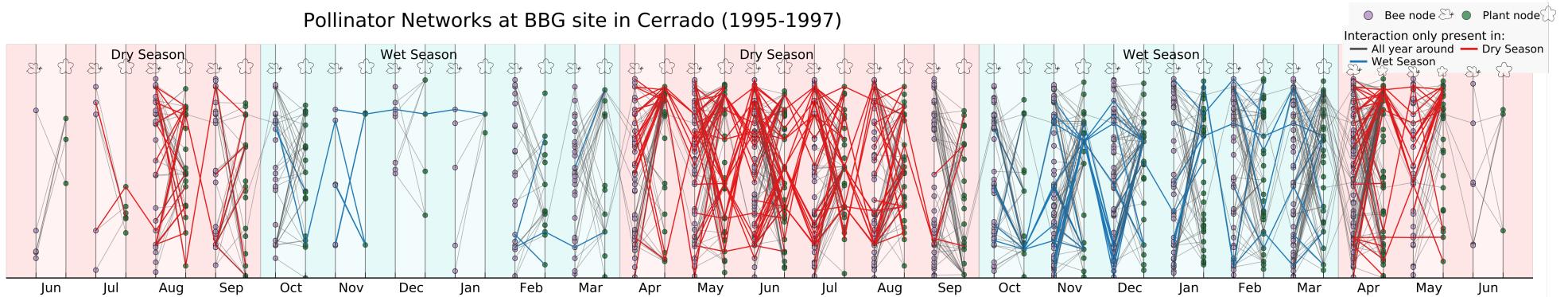


Figure S2: Turnover in monthly bee pollinator networks from Jun 1995 to Jun 1997 (BBG site) and from Oct 2008 to Sep 2009 (IBGE site). Every node in a monthly network represents a distinct plant or bee species. Each link between plant and bee nodes represent a unique pollination visit in the corresponding month. Links between monthly networks show interactions recorded in both monthly networks. Background of plot is colour-coded to reflect the seasons: blue - wet season; red - dry season. Lighter shaded areas demarcate the pollinator networks of each month, while darker areas demarcate the links present between monthly networks. Each link is colour-coded to reflect its period of activity: blue - only present during the wet season; red - only present during the dry season; black: present in both seasons.

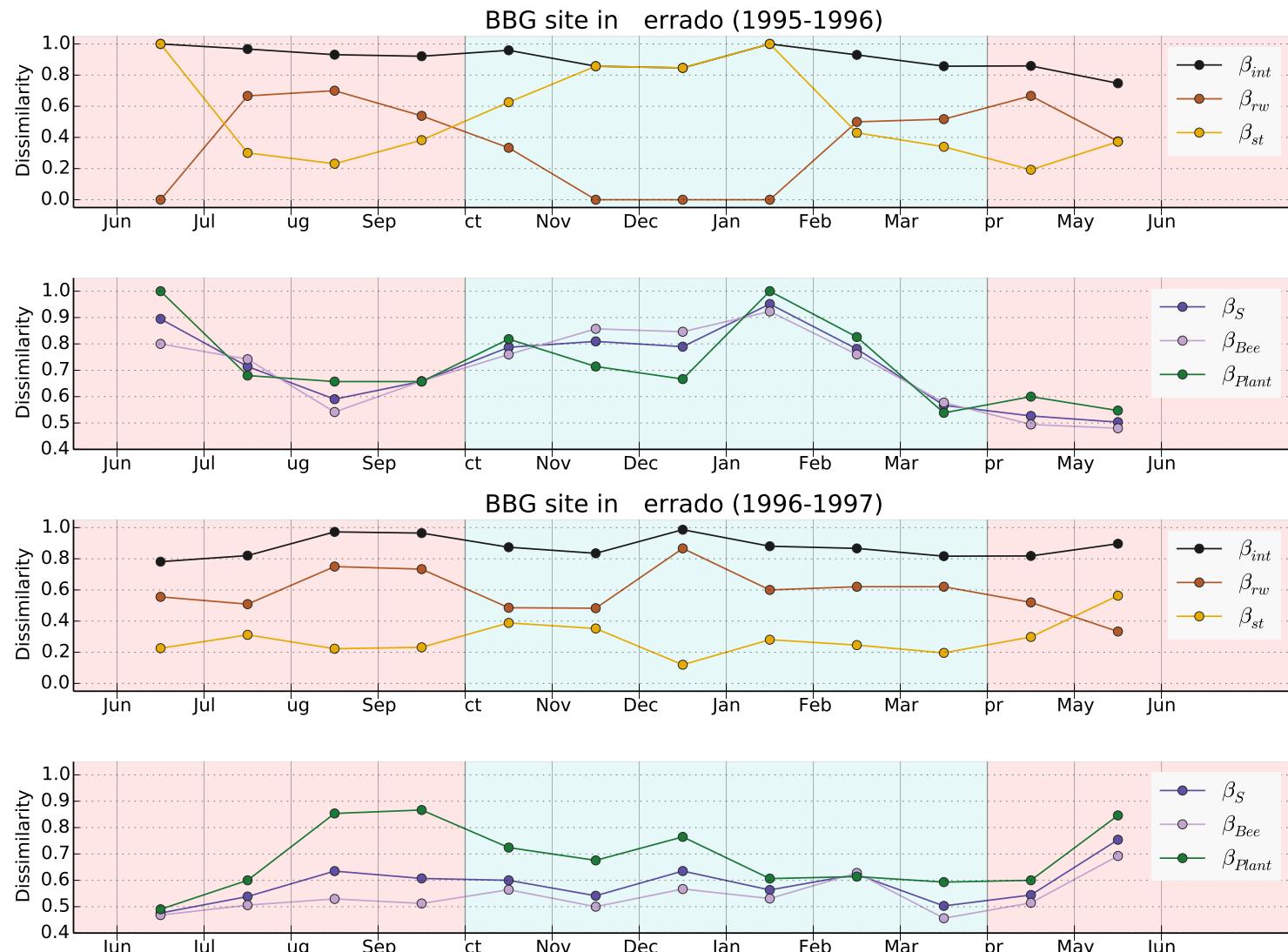


Figure S3: **Time series plot of turnover measures from Jun 1995 to Jun 1997 (BBG site).** Interaction turnover, β_{int} , is surprisingly and consistently high in the Cerrado and is driven by both species turnover, β_S , and plant turnover, β_{Plant} . (β_{st} : Dissimilarity of interactions due to species turnover; β_{rw} : Dissimilarity of interactions between species present in both networks; β_{Bee} : Bee turnover)

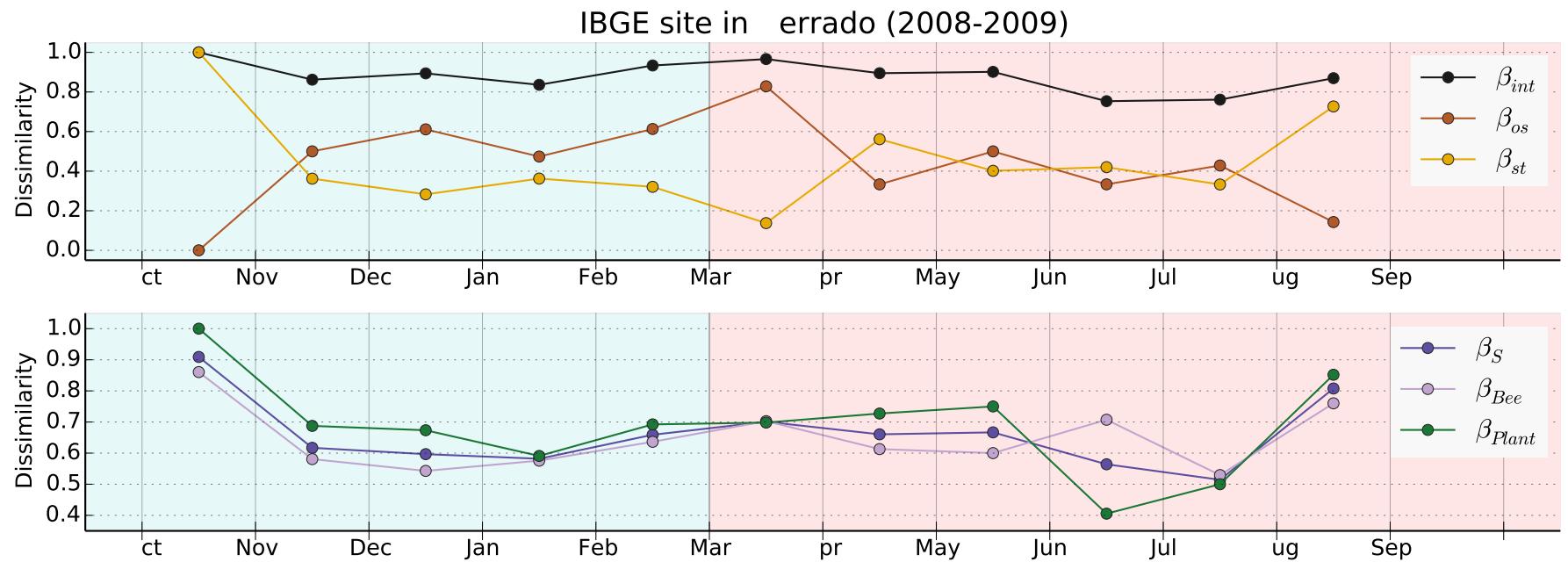


Figure S4: Time series plot of turnover measures from Oct 2008 to Sep 2009 (IBGE site).

Interaction turnover, β_{int} , is surprisingly and consistently high in the Cerrado and is driven by both species turnover, β_S , and plant turnover, β_{Plant} . (β_{st} : Dissimilarity of interactions due to species turnover; β_{rw} : Dissimilarity of interactions between species present in both networks; β_{Bee} : Bee turnover)

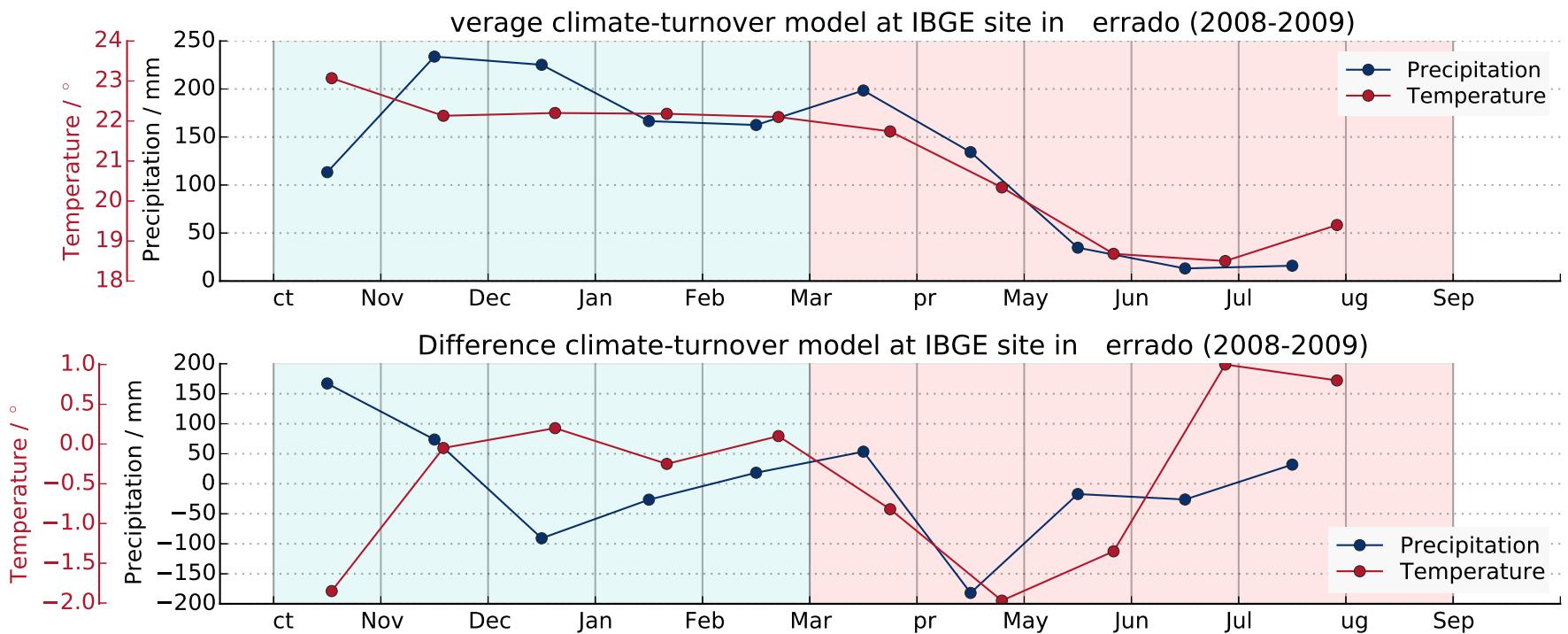


Figure S5: Time series plot of climatic factors from Oct 2008 to Sep 2009 (IBGE site). Climatic factors in the average model show a different trend across time when compared to climatic factors in the difference model. (Average model: average of precipitation sums/median temperatures of two subsequent months; Difference model: difference between precipitation sums/median temperatures of two subsequent months)

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_S	β_{Bee}	β_{Plant}	Site
1995	Jun-Jul	1	0	1	0.895	0.8	1	BBG
1995	Jul-Aug	0.967	0.667	0.301	0.714	0.742	0.680	BBG
1995	Aug-Sep	0.931	0.7	0.231	0.59	0.542	0.657	BBG
1995	Sep-Oct	0.921	0.538	0.383	0.658	0.659	0.657	BBG
1995	Oct-Nov	0.959	0.333	0.626	0.787	0.760	0.818	BBG
1995	Nov-Dec	0.857	0	0.857	0.81	0.857	0.714	BBG
1995	Dec-Jan	0.846	0	0.846	0.789	0.846	0.667	BBG
1996	Jan-Feb	1	0	1	0.951	0.923	1	BBG
1996	Feb-Mar	0.930	0.5	0.430	0.781	0.760	0.826	BBG
1996	Mar-Apr	0.857	0.517	0.340	0.567	0.577	0.538	BBG
1996	Apr-May	0.859	0.667	0.192	0.527	0.495	0.6	BBG
1996	May-Jun	0.747	0.375	0.372	0.503	0.480	0.547	BBG
1996	Jun-Jul	0.781	0.556	0.226	0.476	0.468	0.490	BBG
1996	Jul-Aug	0.821	0.509	0.312	0.538	0.506	0.6	BBG
1996	Aug-Sep	0.973	0.75	0.223	0.635	0.529	0.854	BBG
1996	Sep-Oct	0.965	0.733	0.232	0.607	0.512	0.867	BBG
1996	Oct-Nov	0.874	0.486	0.388	0.6	0.564	0.724	BBG
1996	Nov-Dec	0.835	0.483	0.352	0.541	0.5	0.676	BBG
1996	Dec-Jan	0.987	0.867	0.120	0.635	0.567	0.765	BBG
1997	Jan-Feb	0.881	0.6	0.281	0.563	0.531	0.607	BBG
1997	Feb-Mar	0.867	0.621	0.246	0.622	0.628	0.614	BBG
1997	Mar-Apr	0.817	0.621	0.196	0.503	0.456	0.593	BBG
1997	Apr-May	0.818	0.520	0.298	0.544	0.515	0.6	BBG
1997	May-Jun	0.897	0.333	0.563	0.754	0.692	0.846	BBG
2008	Oct-Nov	1	0	1	0.909	0.860	1	IBGE
2008	Nov-Dec	0.862	0.5	0.362	0.617	0.581	0.688	IBGE
2008	Dec-Jan	0.894	0.611	0.283	0.597	0.543	0.673	IBGE
2009	Jan-Feb	0.836	0.474	0.362	0.582	0.576	0.591	IBGE
2009	Feb-Mar	0.934	0.613	0.321	0.659	0.636	0.692	IBGE
2009	Mar-Apr	0.966	0.829	0.138	0.701	0.703	0.698	IBGE
2009	Apr-May	0.895	0.333	0.561	0.660	0.613	0.727	IBGE
2009	May-Jun	0.902	0.5	0.402	0.667	0.6	0.75	IBGE
2009	Jun-Jul	0.753	0.333	0.420	0.564	0.707	0.405	IBGE
2009	Jul-Aug	0.761	0.429	0.333	0.514	0.529	0.5	IBGE
2009	Aug-Sep	0.87	0.143	0.727	0.808	0.760	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: generated using 10^5 randomised networks for each month)

BBG site, Cerrado (1995-1997)					IBGE site, Cerrado (2008-2009)				
Measures		r_s	p_s	p-value	Measures		r_s	p_s	p-value
β_{int}	β_{st}	0.140	0.514	0.145	β_{int}	β_{st}	-0.027	0.937	0.037
β_{int}	β_{rw}	0.156	0.468	0.509	β_{int}	β_{rw}	0.228	0.500	0.844
β_{int}	β_S	0.698	0	0.031	β_{int}	β_S	0.809	0.003	0.012
β_{int}	β_{Bee}	0.568	0.004	0.150	β_{int}	β_{Bee}	0.436	0.180	0.364
β_{int}	β_{Plant}	0.822	0	0.0001	β_{int}	β_{Plant}	0.773	0.005	0.012
β_{st}	β_S	0.678	0.0003	0.177	β_{st}	β_S	0.382	0.247	0.379
β_{st}	β_{Bee}	0.732	0.0001	0.056	β_{st}	β_{Bee}	0.555	0.077	0.158
β_{st}	β_{Plant}	0.425	0.038	0.640	β_{st}	β_{Plant}	0.473	0.142	0.191
β_S	β_{Bee}	0.955	0	0.097	β_S	β_{Bee}	0.7	0.016	0.873
β_S	β_{Plant}	0.791	0	0.391	β_S	β_{Plant}	0.964	0	0.002
β_{Plant}	β_{Bee}	0.610	0.002	0.242	β_{Plant}	β_{Bee}	0.582	0.060	0.116

Table 4: Relationships between turnover measures and climatic factors.

(r_s : Spearman's correlation coefficient; p_s : p-value of Spearman's test)

Average Model (BBG site)							
Turnover	Climatic Factor (Average of two months)	Dry Season		Wet Season		Aseasonal	
		r_s	p_s	r_s	p_s	r_s	p_s
β_{int}	Temperature	0.399	0.199	0.613	0.034	0.362	0.082
β_{int}	Precipitation	-0.120	0.711	-0.144	0.656	-0.076	0.723
β_{Plant}	Temperature	0.296	0.350	0.797	0.002	0.378	0.068
β_{Plant}	Precipitation	0.146	0.652	0.014	0.966	0.107	0.620
Difference Model (BBG site)							
Turnover	Climatic Factor (Difference between two months)	Dry Season		Wet Season		Aseasonal	
		r_s	p_s	r_s	p_s	r_s	p_s
β_{int}	Temperature	0.622	0.031	-0.281	0.377	0.349	0.094
β_{int}	Precipitation	0.324	0.304	0.571	0.053	0.409	0.047
β_{Plant}	Temperature	0.413	0.182	0.011	0.974	0.302	0.152
β_{Plant}	Precipitation	0.188	0.558	0.671	0.017	0.455	0.026
Average Model (IBGE site)							
Turnover	Climatic Factor (Average of two months)	Dry Season		Wet Season		Aseasonal	
		r_s	p_s	r_s	p_s	r_s	p_s
β_{int}	Temperature	0.3	0.624	0.029	0.957	0.391	0.235
β_{int}	Precipitation	0.9	0.037	-0.543	0.266	0.309	0.355
β_{Plant}	Temperature	0.7	0.188	-0.086	0.872	0.209	0.537
β_{Plant}	Precipitation	0.6	0.285	-0.486	0.329	0.018	0.958
Difference Model (IBGE site)							
Turnover	Climatic Factor (Difference between two months)	Dry Season		Wet Season		Aseasonal	
		r_s	p_s	r_s	p_s	r_s	p_s
β_{int}	Temperature	-0.6	0.285	-0.486	0.329	-0.636	0.035
β_{int}	Precipitation	-0.2	0.747	0.543	0.266	0.327	0.326
β_{Plant}	Temperature	0.1	0.873	-0.6	0.208	-0.491	0.125
β_{Plant}	Precipitation	0.2	0.747	0.771	0.072	0.273	0.417

Table 5: Coefficients from a linear regression model of temperature and season as predictors of plant turnover, β_{Plant} .

	Estimate	Std. Error	t value	p
(Intercept)	0.375	0.543	0.691	0.497
Average Temperature	0.016	0.027	0.600	0.555
Season (wet)	-4.945	2.262	-2.186	0.041
Average Temperature : Season (wet)	0.223	0.103	2.170	0.042