Temporal turnover of plant-pollinator interaction networks

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Abstract

Analysing the factors that drive of interaction turnover can provide new insight into the impact of climate change on plant-pollinator networks. Global climate changes result in shifts in flowering timinings, which ead to disruptions of spatial and temporal co-occurrences of flowers and pollinators, thereby indirectly affecting species interactions. However, the extent of the impact of harsher weather conditions on plant-pollinator interactions remain unknown. In this study, I propose a framework for investigating how climatic factors can influence interaction turnover using two datasets collected in the Cerrado and report that month-to-month interaction turnover, β_{int}, is consistently high throughout the year. Moreover, plant turnover, β_{Plant} is a strong driver of β_{int}. Temperature in the wet season is also positively correlated with plant turnover, β_{Plant}, indicating that a rise in temperature may indirectly increase β_{int}.

Contents

Abbreviations

BBG:	Brasília's Botanical Garden Protected Area
IBGE:	Reserva Ecológica do IBGE
βint:	Interaction turnover
βrw:	Interaction rewiring
βst:	Contribution of species turnover to interaction turnover
βS:	Species turnover
βBee:	Bee turnover
$\beta Plant$:	Plant turnover

1 Introduction

Interactions between plants and pollinators contribute significantly towards the diversity of ecosystems by maintaining plant reproduction and communities (Olesen et al., 2008). Moreover, pollination services constitute a major part of our global economy by supporting the crop industry (Allsopp et al., 2008) and has therefore attracted much attention in recent years. In plant-pollinator networks, a link is created between a pollinator and a plant when a pollinator visits the flowers of the plant. The pollinator and plant species are represented by the nodes of the networks, where every link between nodes constitute a pollination event (Olesen et al., 2008; Burkle et al., 2011; Poisot et al., 2012a).

Studies of plant-pollinator networks have provided much insight into the structure of ecosystems and their function. Nonetheless, previous studies have frequently assumed a static picture of plant-pollinator networks and ignored the dynamic nature of interactions and its variation across temporal networks. 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, there remains a lack of interest in temporal networks, which is likely due to the significant amount of sampling effort required to build multiple networks across seasons (Burkle et al., 2011).

Research on temporal plant-pollinator networks have likewise been largely restricted to peak flowering seasons and temperate ecosystems. These research have mainly focused on the robustness, stability and structure of networks over time. Others have aimed their attention at the factors that constrained interactions across time and are generally in agreement that abundance and phenology are the key constraints to the assembly of interaction networks (Basilio et al., 2006; Olesen et al., 2008; CaraDonna et al., 2017). However, relatively little is known about the factors that result in the high temporal variability of interactions (Burkle et al., 2011).

Understanding the drivers of interaction turnover can provide new insight into the impact of climate change on plant-pollinator networks. Increases in global temperature result 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). However, in tropical regions, where

most pollinators are active for periods longer than the flowering timescale of most individual plant species (Biesmeijer and Slaa, 2006), the impact of rising temperatures and harsher weather conditions on pollination services remain unknown (Schweiger et al., 2010; Poisot et al., 2015).

Neotropical habitats are mostly characterised by drastic seasonal changes between dry and rainy seasons that influence the dynamics of species interactions (Kricher, 2011). Seasonally dry forests and savannas of neotropical habitats cover a large region of the tropical and subtropical Americas and are recognised for their species rich fauna and highly diverse flora, which includes many endemic plant species (Myers et al., 2000; Klink and Machado, 2005; Pennington and Ratter, 2010). Understanding the variability of interactions in these habitats is crucial in maintaining pollination interactions in the face of climate change, and thereby ensuring that diversity of plant communities is conserved and protected.

The Brazilian Cerrado is a seasonally dry savanna that consists of a variety of pollinators with bees as its major pollinating agent. Many Cerrado bees are active throughout the year as they live in colonies or produce multiple generations annually. However, seasonal changes in precipitation can constrain dry season flowering in plants with shallow root systems, such as herbs and shrubs (Oliveira, P.E., Gibbs, 2002; Toby Pennington et al., 2006; Gottsberger and Silberbauer-Gottsberger, 2006a).

Besides being a highly seasonal habitat, the Cerrado acts as an important model system for studies on temporal plant-pollinator networks 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 and Machado, 2005).

In this study, I propose a framework for investigating how climatic factors can influence interaction turnover using two dataset collected in the Cerrado (Figure 1). Firstly, differences between subsequent temporal networks, also known as β-diversity, was quantified using a number of β-dissimilarity measures, which reflect interaction, species, plant and bee 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.
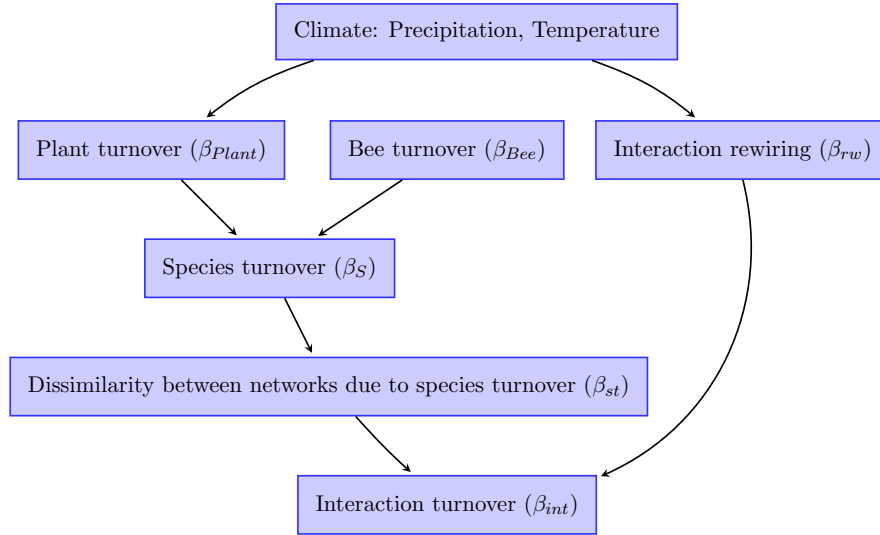

Figure 1: Framework demonstrating the effect of climatic factors on the different measures of turnovers.

By applying this framework to two different datasets collected in the tropical Cerrado habitat, I report a strong and positive correlation between interaction turnover, β_{int} and species turnover, β_S. To the best of my knowledge, this is the first study to investigate the effect of climatic factors on temporal β_{int} and β_{Plant}. Temperature in the wet season is positively correlated with plant turnover, β_{Plant} while β_{Plant} drives β_{int} and can be used to estimate β_{int}, indicating that a rise in temperature may indirectly increase β_{int}.

2 Materials and Methods

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 and Silberbauer-Gottsberger, 2006a).

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 (Gottsberger and Silberbauer-Gottsberger, 2006b).

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. (Eiten, 1972).

2.2 Sampling methods and species identification

Bees are the predominant pollinators in the Cerrado ($\sim$70%) followed by moths ($\sim$12%), hummingbirds ($\sim$3%), bats, ($\sim$2%) and beetles ($\sim$2%) (Klink and Moreira, 2002; Gottsberger and Silberbauer-Gottsberger, 2006b; Cappellari, 2011). 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 (Moure, 1962; Silveira et al., 2002; Michener, 2000; Moure et al., 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 4 km apart (Boaventura, 1998). 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. 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 and Silberbauer-Gottsberger, 2006b).

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 (Whittaker, 1960):

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

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 (Poisot et al., 2012a).

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 (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_{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 (Poisot et al., 2012a; CaraDonna et al., 2017).

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 Poisot et al. (2012a).

Measure	Definition	Items	Reference
β_{int}	Dissimiliarity of interactions; Interaction turnover	All interactions	Canard (2011); CaraDonna et al. (2017)
β_{rw}	Dissimilarity of interactions between species present in both networks; Interaction rewiring	Interactions of shared species	Canard (2011); CaraDonna et al. (2017)
β_{st}	Dissimilarity of interactions due to species turnover	Equation 1	Poisot et al. (2012a)
β_{st}/β_{int}	Contribution of species dissimilarity to dissimilarity of interactions		Poisot et al. (2012a)
β_S	Dissimilarity in the species composition of both networks; Species turnover	Species identity	e.g. Koleff et al. (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 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 (Dehmer et al., 2011).

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

The two seasons exhibit different temperature and precipitation ranges, resulting in seasonal interactions. To investigate whether precipitation and/or temperature affects turnovers, 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 β_{Plant} and β_{rw} against precipitation, temperature and season and their interactions. Due to its small size, the IBGE dataset was not utilised in model fitting. The more explanatory model was thereafter used to fit turnovers against climatic factors 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 (Silveira and Campos, 1995; 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 (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.), 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 S2, Figure S4). Surprisingly, only 8.19% of all unique interactions appeared in three or more monthly networks (Figure 2).
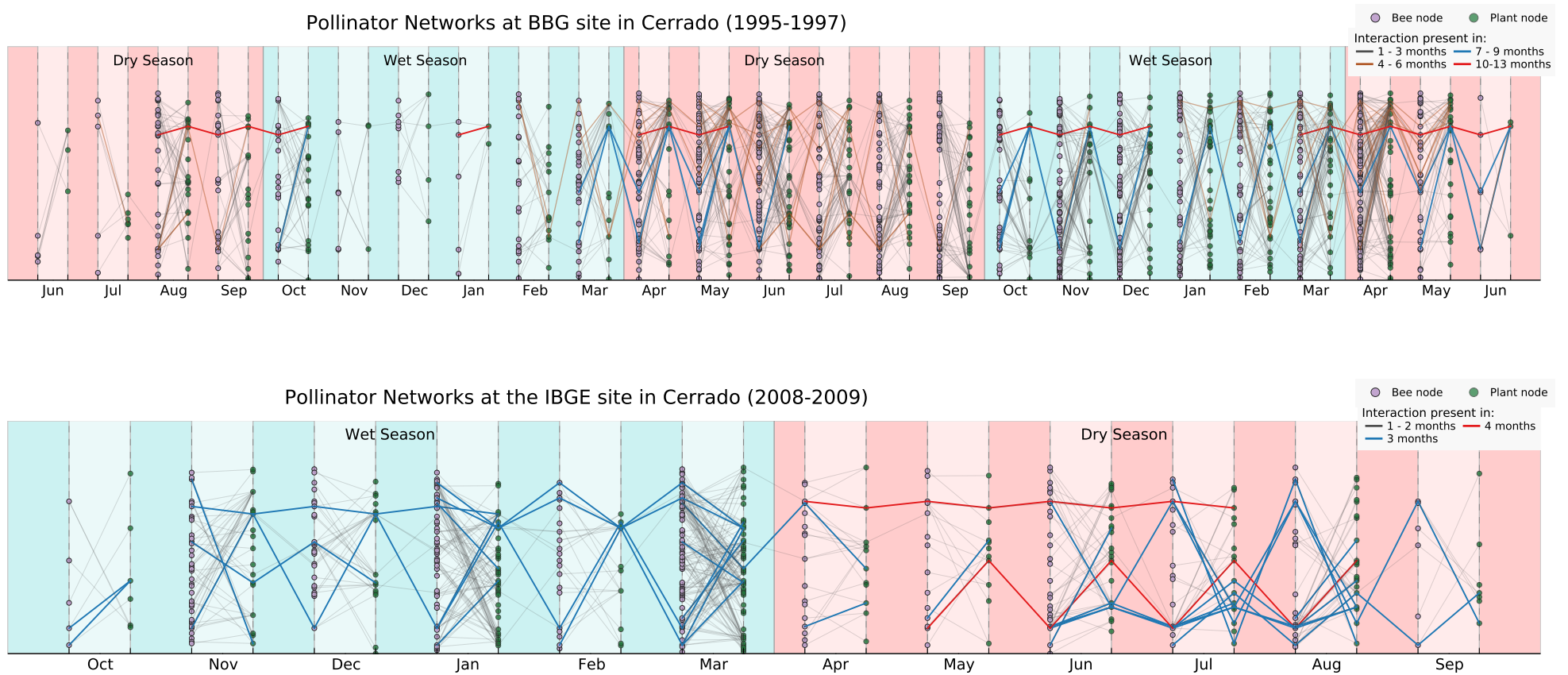
Figure 2: Monthly bee pollinator networks from Jun 1995 to Jun 1997 (BBG site) and from Oct 2008 to Sep 2009 (IBGE site).

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. Colour of links represent the number of monthly networks the link 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)

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)(Figure 4) 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} (Figure 3).
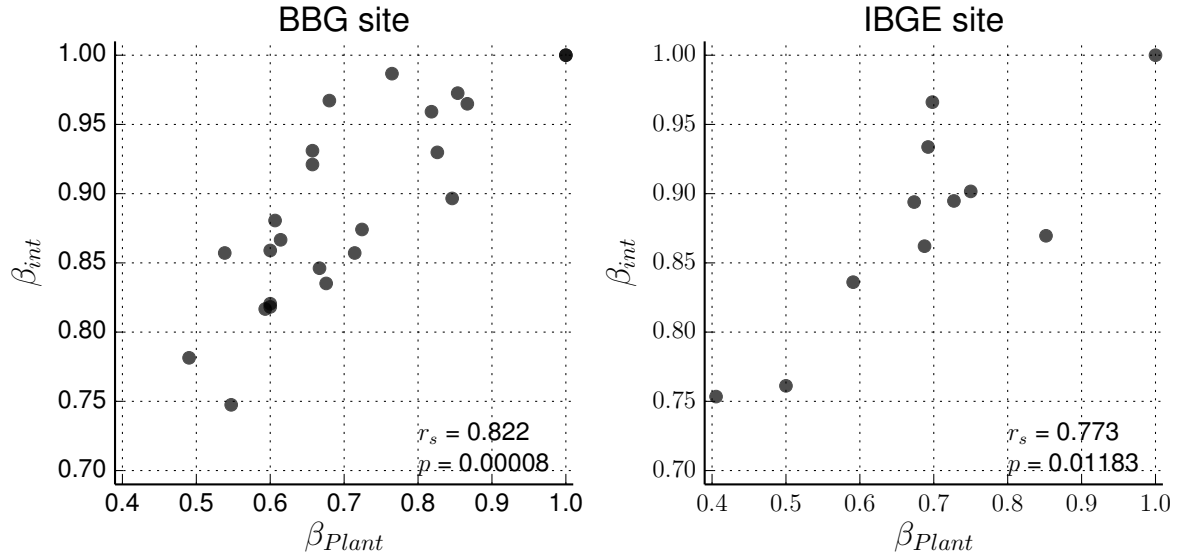

Figure 3: Plant turnover (β_{Plant}) drives interaction turnover (β_{int}).
A high β_{Plant} and/or β_{int} indicates a high dissimilarity between interactions and/or plant communities of two networks. (r_s: Spearman's rank correlation coefficient; p: values generated using Monte Carlo simulations.)

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)(Figure 4), 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)(Figure 4). 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. Thus, 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 (Poisot et al., 2012a). These measures are hence utilised for further analysis.
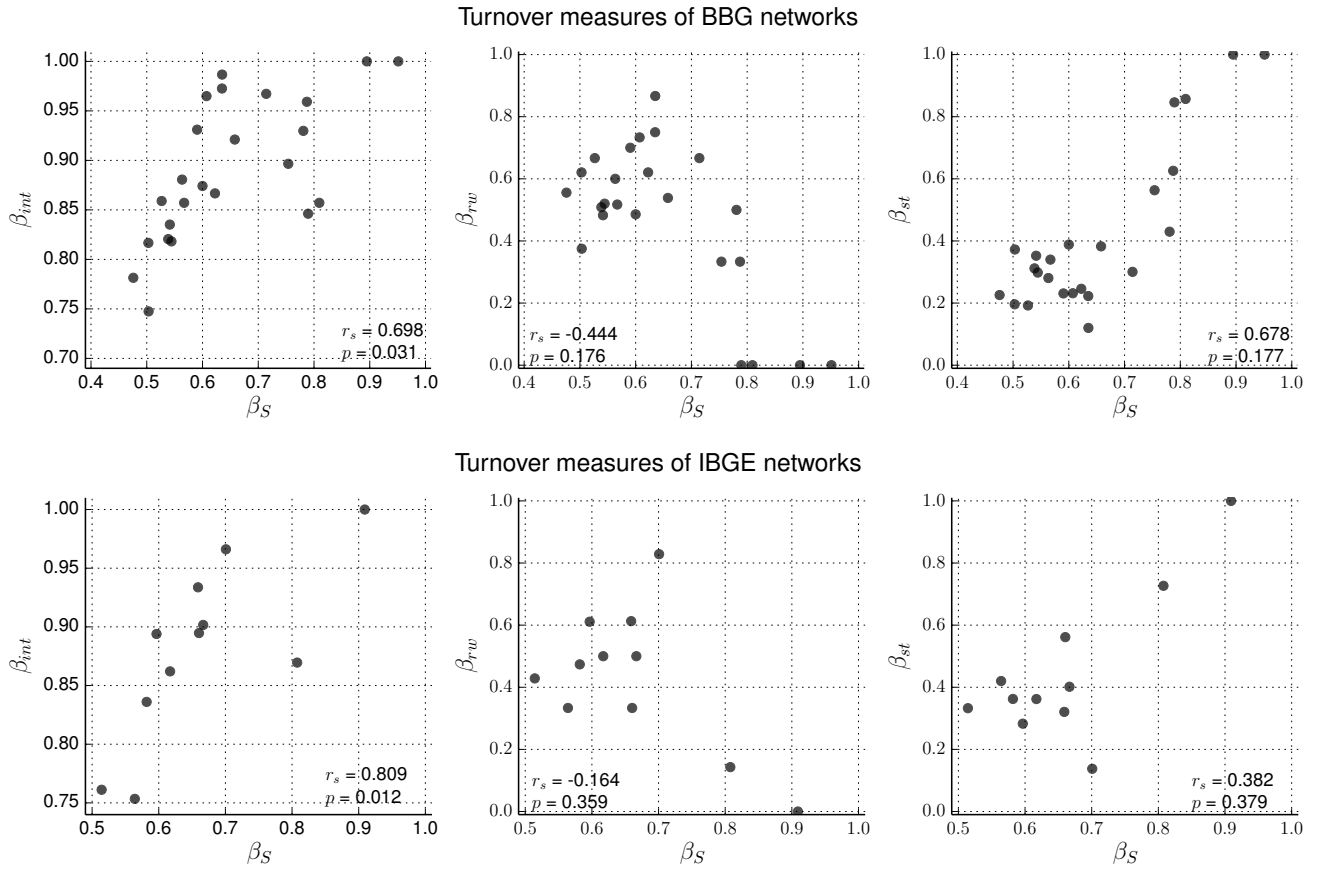

Figure 4: Trends between species turnover (β_S) and interaction turnover (β_{int}), interaction rewiring (β_{rw}) and network dissimilarity due to β_S (β_{st}).
(r_s: Spearman's rank correlation coefficient; p: values generated using Monte Carlo simulations.)

3.3 Climatic factors influence turnover

Spearman's correlation coefficients indicate that there exist a seasonal effect on the trends between climatic factors and β_{Plant} and β_{int} (Table S4). Hence, a linear regression model was used to predict β_{Plant} using temperature, precipitation, season and their interactions. Temperature

difference and precipitation 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 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 temperature and precipitation within seasons to reduce multicollinearity.

Within the dry season, average temperature and average 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

Ecological networks have previously been assumed to be invariant across long time periods, leading to species interactions being largely ignored (Poisot et al., 2015). However, this study demonstrates, in agreement with previous studies on temporal networks, that dissimilarity between monthly networks is consistently high (Olesen et al., 2008; Burkle et al., 2013; CaraDonna et al., 2017). Surprisingly, there are no apparent differences between turnover values within seasons and between seasons (Table S1, Figure S2, Figure S4).

Furthermore, this study shows that β_{Plant} is a major contributor of β_{int} and can be used to estimate β_{int} (subsection 3.2). Alarcón et al. (2008) utilised the Bray-Curtis dissimilarity index and used a different approach to compare species turnover to plant?pollinator interactions 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 is indispensable in estimating interaction turnover. CaraDonna et al. (2017) postulates that 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 process has illustrated that the strong collinearity between β_{Plant} and β_{int} did not occur by chance and strengthens the case that β_{Plant} is a major driver of β_{int} (subsection 3.2).

Last but not least, to the best of my knowledge, this is the first study to investigate the effect of climatic factors on temporal β_{int} and β_{Plant}. Previous studies have mainly focused on how temperature affects shifts and lengths of flowering times and have thereafter indirectly linked the effect to the uncoupling of interactions (Hegland et al., 2009; González et al., 2009; Schweiger et al., 2010).

Average climatic values of two subsequent months proved to be a better explanatory variable of β_{Plant} than the use of differences between climatic values of two networks. This further sup-

ports the hypothesis that two networks experiencing the same climate will still yield a positive β_{int}. This is a logical scenario as networks constantly experience turnover across time even if temperature and all other climatic factors were kept constant (subsection 3.3).

Unexpectedly, despite the drastic difference between the precipitation level of dry and wet seasons, precipitation was an insignificant factor in explaining β_{Plant} (subsection 3.3). This could be due to the adaptation of organisms in the Cerrado to extreme seasonal rain changes. As a result, plants have evolved mechanisms to survive cycles of extreme drought and are less sensitive to changes in precipitation (Pennington and Ratter, 2010). In contrast, despite the range of temperatures being less than 5°C, temperature explains significant variance in β_{Plant} during the wet season (subsection 3.2). Although β_{int} is consistently high throughout the year, there appears to be a seasonal difference in factors that drive turnover.

4.1   Limitations

β_{int} in the Cerrado was higher than previously reported week-to-week and year-to-year β_{int} values (CaraDonna et al., 2017). 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 lower due to climatic factors remaining relatively similar throughout the flowering season in the temperate region. As plants can only be pollinated during the three short months annually, temperate plant communities have a longer mean flowering time than those in the tropics, resulting in a lower β_{Plant}. A smaller β_{Plant} will thereafter lead to a smaller β_{int} (Bawa, 1990). However, as no month-to-month β_{int} values or β_{Plant} were made available, no direct comparison of β-diversity between temperate and tropic regions can be made (CaraDonna et al., 2017).

Moreover, other studies of temporal plant-pollinator networks utilises 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 S2). Removing these datapoints 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, I decided to include these points as the Spearman correlation coefficient test is robust against outliers. Monte Carlo simulation was thereafter carried out to reduce sampling bias.

8.19% and 4.61% of all unique interactions appeared in three or more monthly networks at the BBG and IBGE sites respectively (Figure 2). Although this may have been in part due to insufficient sampling efforts, another plausible cause is the high levels of biodiversity found in the tropics. 45 flowering plants and 74 pollinators were observed over 3 years of study in CaraDonna et al. (2017). Comparatively, within the 12-month study period at IBGE, 111 species of bees and 93 species of plants were already recorded and yet it is apparent that there exist many missing interactions. β_{int} values may hence be higher in the tropics than in the temperate regions due to the species richness found in the tropical biome. Due to the lack of temporal network data in the tropics, there is no support for this hypothesis yet.

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 restores its interaction 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 and Primack, 2008). Hence, there is an urgent need to investigate and validate the drivers of dissimilarity of temporal 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).

Moreover, correlation of variables does not relate to causation. To determine the factors driving dissimilarity of temporal networks, experimental approaches are required to test out these predictions on small artificially manipulated ecosystems. If the spatial and temporal scale of experiments are not large enough to significantly affect network turnover, available datasets across different ecosystems with varying climates can be compared to support these predictions (Burkle and Irwin, 2009; Burkle et al., 2011).

Lastly, before considerable 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 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, gathering all available data and resources is the next step forward in understanding interaction networks.

Acknowledgements

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5   Supplementary Figures
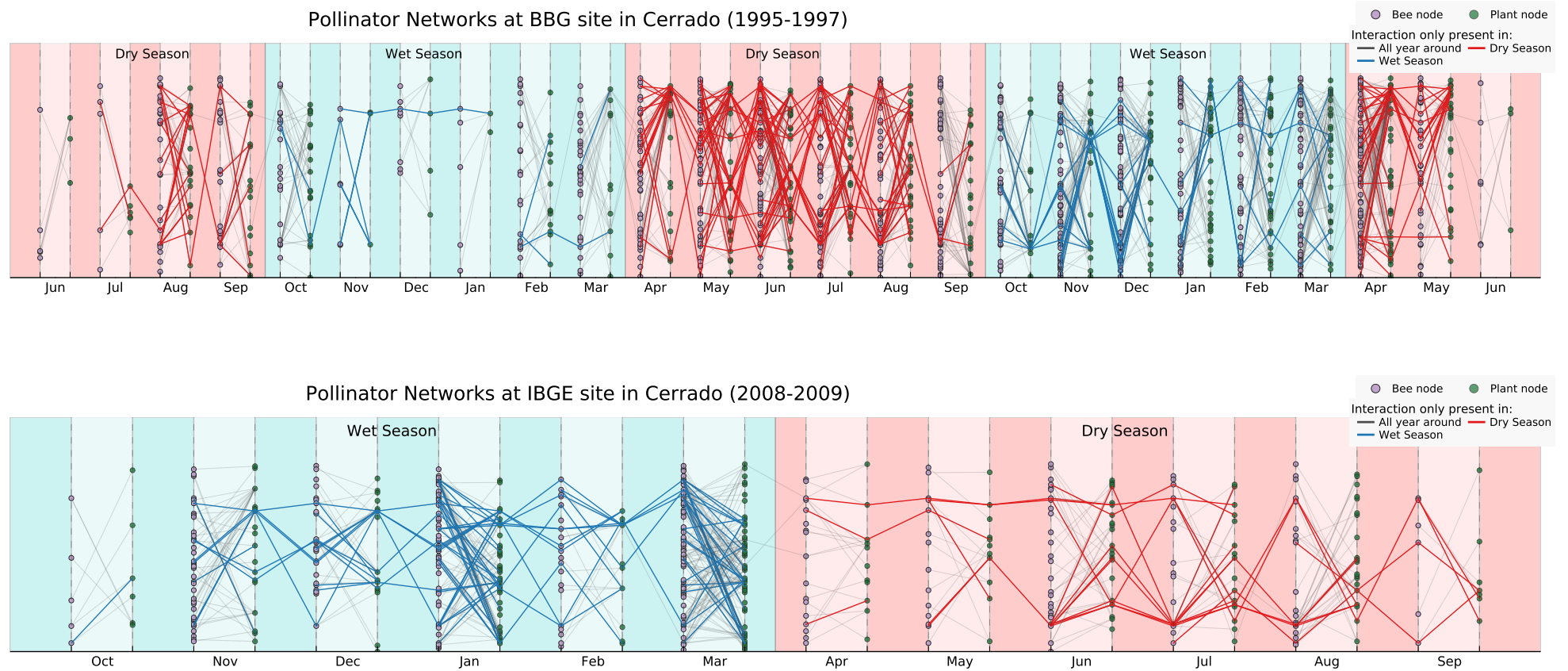
Figure S1: Monthly bee pollinator networks from Jun 1995 to Jun 1997 (BBG site) and from Oct 2008 to Sep 2009 (IBGE site). Every node in a monthly network represents a distinct plant or bee species. Each link between plant and bee nodes represent a unique pollination visit in the corresponding month. 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. 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.
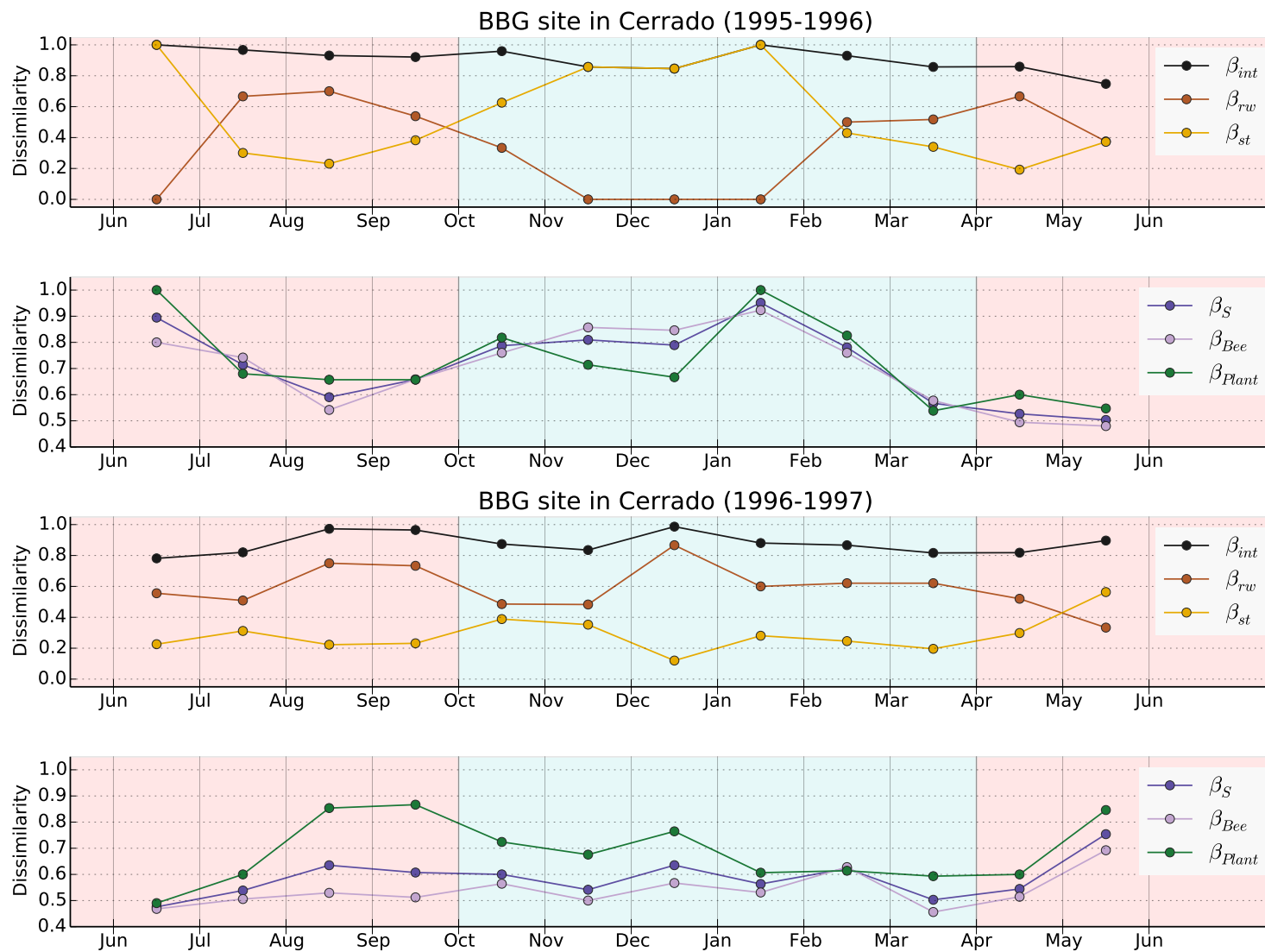
Figure S2: Time series plot of turnover measures from Jun 1995 to Jun 1997 (BBG site).
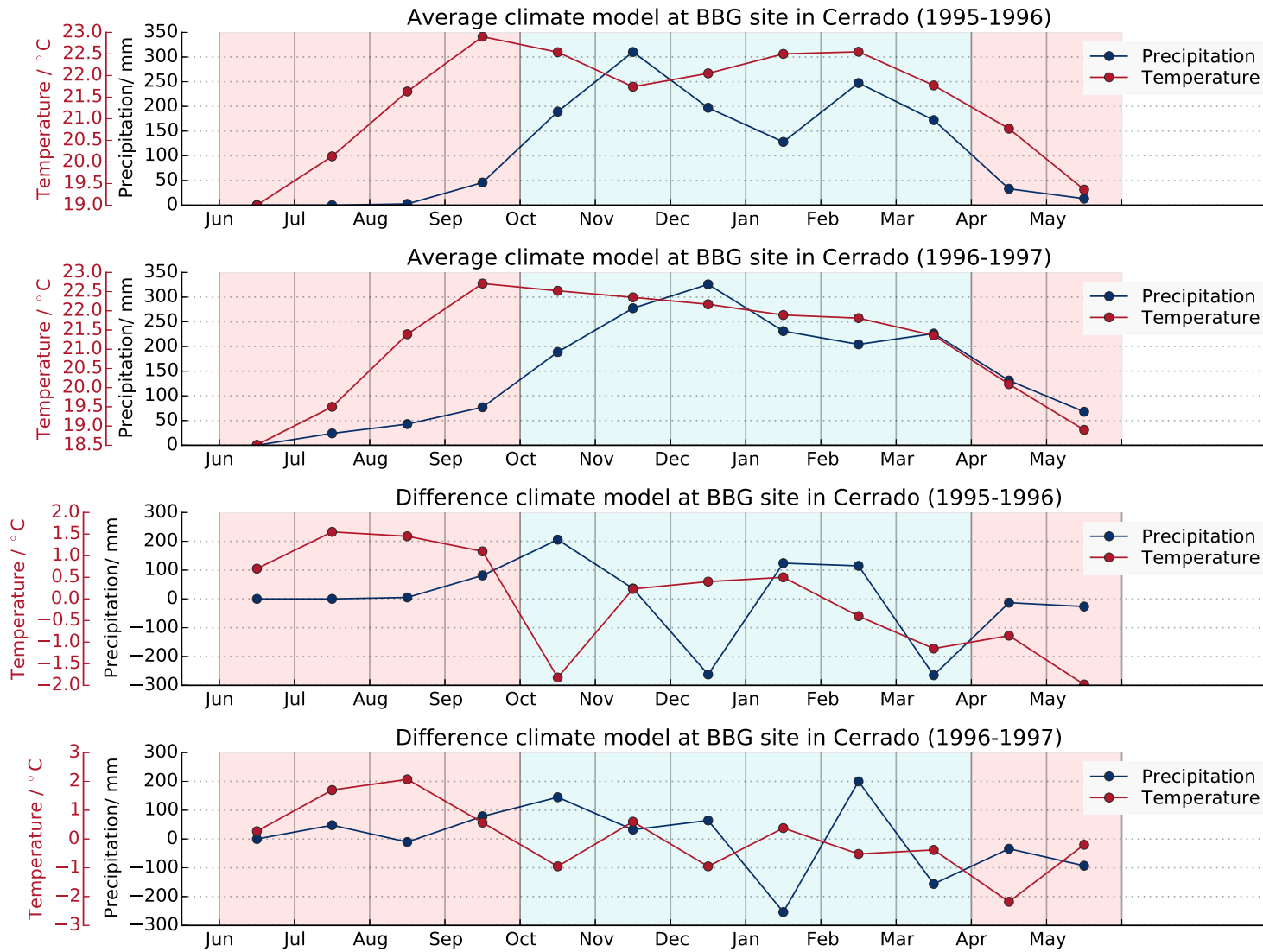
Figure S3: Time series plot of climatic factors from Jun 1995 to Jun 1997 (BBG site).

(Average model: average of precipitation/temperature of two subsequent months; Difference model: difference between precipitation/temperature of two subsequent months)
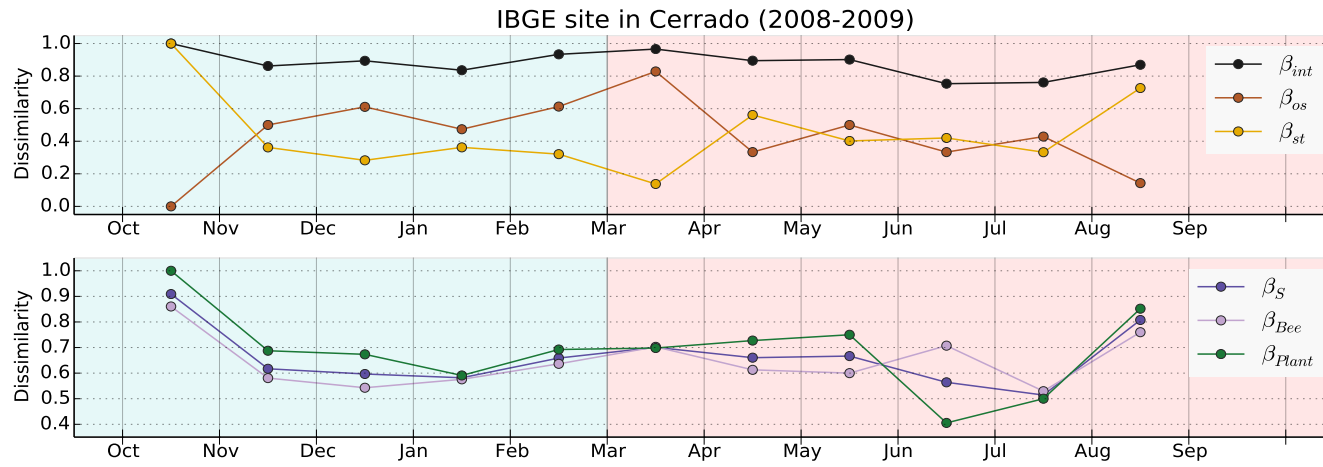
Figure S4: Time series plot of turnover measures from Oct 2008 to Sep 2009 (IBGE site).
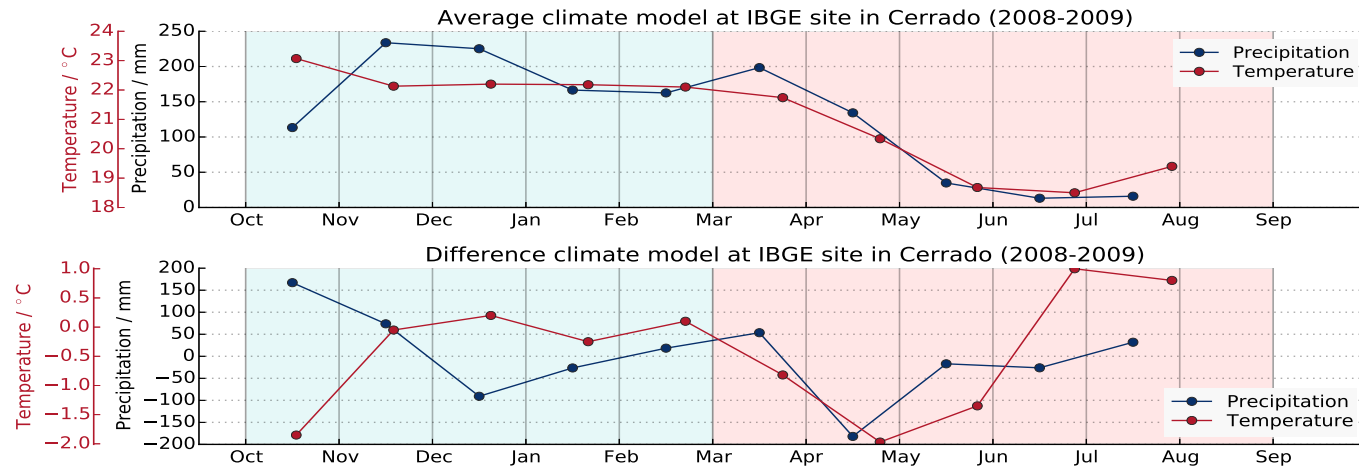
Figure S5: Time series plot of climatic factors from Oct 2008 to Sep 2009 (IBGE site).
(Average model: average of precipitation/temperature of two subsequent months; Difference model: difference between precipitation/temperature of two subsequent months)

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_{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}	-0.027	0.937	0.037
β_{int}	β_{rw}	0.228	0.500	0.844
β_{int}	β_S	0.809	0.003	0.012
β_{int}	β_{Bee}	0.436	0.180	0.364
β_{int}	β_{Plant}	0.773	0.005	0.012
β_{st}	β_S	0.382	0.247	0.379
β_{st}	β_{Bee}	0.555	0.077	0.158
β_{st}	β_{Plant}	0.473	0.142	0.191
β_S	β_{Bee}	0.7	0.016	0.873
β_S	β_{Plant}	0.964	0	0.002
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	Dry Season		Wet Season		Aseasonal	
	(Average of two months)	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	Dry Season		Wet Season		Aseasonal	
	(Difference between two months)	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	Dry Season		Wet Season		Aseasonal	
	(Average of two months)	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	Dry Season		Wet Season		Aseasonal	
	(Difference between two months)	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