

Seasonal turnover and diet breadth shape long-term occurrence patterns of oil-collecting bees in the Brazilian Cerrado

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Abstract

Ecological traits and seasonality may shape species occurrence and population dynamics, yet their long-term effects remain poorly understood, especially for tropical pollinators. Here, we used six decades of museum records to investigate how diet breadth and seasonality influence occurrence patterns and temporal trends in oil-collecting *Centris* and *Epicharis* bees in the Brazilian Cerrado, a highly seasonal and threatened biodiversity hotspot. We found that oil specialists exhibited lower relative occurrence and more frequently declining population trajectories than oil generalist, suggesting potentially higher vulnerability of the former. In contrast, seasonality did not explain differences in occurrence or population trends. However, we detected contrasting seasonality patterns between *Centris* and *Epicharis*. While both genera peaked during the transition from the dry to the rainy season, *Centris* occurred significantly more frequently during the dry season, whereas *Epicharis* predominated during the rainy season, suggesting temporal niche differentiation and different developmental strategies. Together, our results highlight how trait-mediated responses and seasonal niche partitioning may structure oil-bee communities and shape long-term occurrence patterns, while also informing conservation management by predicting species' responses to ongoing environmental change in the Cerrado.

Introduction

The Cerrado biome in central Brazil is a global biodiversity hotspot¹ and harbours an exceptionally high diversity of plant and animal species, promoted by climatic seasonality, its large spatial extent, its proximity to the Amazonian and Atlantic rainforests, and a high degree of landscape heterogeneity². Bees are among the most diverse and ecologically important insects of the Cerrado^{3–5}, including the highly charismatic oil-collecting bees of the family Apidae⁶. Bees are key pollinators of wild⁷ and cultivated plants⁸, particularly oil-producing plants, which depend strongly on oil-collecting bees for pollination⁹. Floral oils are collected exclusively by female bees for larval provisioning and, in some cases, nest waterproofing^{10–12}. The plant family Malpighiaceae has evolved especially close associations with oil-collecting bees^{13,14}, most notably with *Centris* and *Epicharis*^{9,15}.

The genera *Centris* and *Epicharis* are sister taxa¹⁶ that diverged in South America 110 – 75 Mya¹⁷. All species are solitary and, except four *Centris* species, collect floral oils^{14,18}. *Centris* contains 329 described species¹⁹, ranging from southern Argentina to the southern United States and Caribbean²⁰, whereas *Epicharis* comprises 36 described species¹⁹ ranging from Uruguay and northern Argentina to Mexico²⁰. While *Epicharis* collects floral oil exclusively from Malpighiaceae, several *Centris* species also exploit oil resources from Krameriaceae, Calceolariaceae and/or Plantaginaceae^{14,21}. Those differences in their distribution, diet breadth, and evolutionary history suggest that *Centris* and *Epicharis* may differ in their vulnerability to environmental change.

Despite its high biodiversity, the Cerrado is threatened by human-induced land-use change²², particularly by agricultural expansion converting approximately 46% of the native vegetation into farmland²³.

Additionally, intensive agriculture^{24–26}, introduced species^{27,28} and urbanisation²⁹ negatively affect insect species richness and abundance.

Studies further suggest that ecological traits like diet breadth shape bee eco-evolutionary dynamics and sensitivity to anthropogenic disturbance^{30–32}. Generally, generalist (polylectic) species show higher occurrence and broader distribution range than diet specialists (oligolectic species)³³, likely because specialists are constrained by the availability of suitable host plants, which limits their geographic distribution and population size. As a consequence, generalist species may cope better with environmental pressures^{30,32,34} or climate change³⁵, as they can more readily switch among alternative resources and maintain larger populations. In contrast, dietary specialisation requires a tight synchrony between bee activity and host-plant flowering phenology, and disruptions may reduce fitness and cause population declines³⁶. Because of this synchrony, diet is also inherently linked to a species' seasonal activity.

Flight-period length and timing may likewise influence species' occurrences and sensitivity to environmental disturbances as species with shorter flight periods may show lower occurrence and abundance³⁰. However, for many tropical bees data on flight period length are lacking. Seasonality provides an indication of flight period length and, in tropical insects, is driven primarily by precipitation, i.e. dry vs. rainy season in the Cerrado^{37,38}. Species restricted to one season may therefore show lower occurrence than species active across both seasons, potentially increasing their vulnerability to climate change^{35,39}.

Centris and *Epicharis* both reach their occurrence peaks during transitions between the two seasons^{40,41}. Moreover, a seasonal turnover with *Centris* being more common during the dry season and *Epicharis* predominating during the rainy season has previously been suggested⁷ but remains to be formally tested. Given the substantial overlap in oil-host use, particularly on *Byrsonima* and *Banisteriopsis*⁴², seasonal segregation could facilitate niche partitioning by reducing competition for limited floral oil resources, as documented in other systems^{43–45}.

Here, we use six decades of museum records to test: I) Do diet specialists and species restricted to one season show lower relative occurrence than generalists and seasonally flexible species? (II) Do dietary and seasonal specialisation increase the likelihood of population decline over time? (III) Do *Centris* and *Epicharis* exhibit a seasonal turnover, as previously suggested?

Materials and Methods

Data processing and species richness

Occurrence data were obtained from the entomological collection of the University of Brasília (Brazil). After excluding records without collection date or geographic coordinates and those outside of the

Federal District, our final dataset contained 1,691 records of 50 *Centris* and *Epicharis* species from 1976–2023 (Fig. 1). To account for uneven sampling effort across time and space, we defined each unique combination of collection date and geographic coordinates as a single collection event, resulting in 649 unique collection events. For each event, species presence or absence was recorded. As sampling intensity varied strongly among years ($\bar{x} = 15.5 \pm 18.4$ SD), records were aggregated into six decadal bins, yielding a more even distribution of sampling effort ($\bar{x} = 108.17 \pm 35.05$ SD events per decade; Supplementary Table S1).

Rarefied species richness under Shannon's index was estimated using the R package *vegan* v2.6-10⁴⁶ with data rarefied to the minimum number of specimens per decade. Species accumulation curves were computed across all decades with the function 'specaccum' with 100 permutations. Temporal trends in rarefied species richness (response variable) were tested using a generalised linear model (GLM) with decade as continuous predictor, assuming a gamma error distribution and *log* link.

Relative species occurrence per decade and season

To examine seasonal differences in species occurrence, we calculated the relative occurrence of each species in the dry (April to September) and rainy season (October to March) of each decade as the proportion of collection events in which the species was recorded within a given season-decade combination. We excluded species with fewer than the median number of collection events overall ($n < 6$), per decade ($n < 3$), or per year ($n < 4$) from subsequent analysis to avoid biasing model estimates.

For each remaining species, we fitted a binomial generalised linear effect model (GLMM) with a *logit* link, using relative occurrence per season-decade as the response variable and season (categorical: dry vs rainy) and decade (continuous) as predictors. For *Centris violacea* and *C. rupestris*, recorded exclusively in the dry season, models excluded season as a predictor.

Effect of diet breadth and seasonality on species relative occurrence

To assess whether diet breadth and seasonality influence species occurrence and temporal trends, we compiled data on oil-host usage from the literature (Supplementary Material). Four species were excluded due to lack of information. Because diet breadth in bees is continuous rather than binary¹⁸, and incomplete host-plant records may obscure specialisation levels, we used two complementary approaches to quantify oil specialisation: (1) a discrete classification of oil specialists (one host plant family) versus oil generalists (more than one host family) and (2) a continuous index of diet breadth incorporating the number of host plant families and genera visited within each plant family (Eq. 1):

$$Genscore = \frac{Numberofhostfamilies \times Numberofhostgenera}{(Numberofhostgenera + 1)}$$

(1)

This index assigns higher values to species with broader host spectrum and therefore reflects increasing degrees of dietary generalisation.

We then fitted a binomial GLMM with a *logit* link, using relative species occurrence per season-decade as the response and diet breadth (discrete or continuous) and seasonality (categorical: dry, rainy, or both) as fixed effects, with species identity as a random effect. Post hoc comparisons between seasonality categories were conducted using estimated marginal means (EMMs) calculated with the *emmeans* package⁴⁷. Finally, we used Fisher's exact tests to assess whether dietary (categorical) or seasonal specialisation was disproportionately represented among declining or increasing species.

Seasonal turnover

To test for a seasonal turnover in occurrence between *Centris* and *Epicharis*, we fitted a GLMM with a binomial error distribution and a *logit* link, using relative species occurrence per season-decade as the response and genus (*Centris* vs. *Epicharis*), season (dry vs. rainy), and their interaction as fixed effects, with species identity as a random effect. Estimated marginal means and predicted probabilities for each genus–season combination were obtained using *emmeans*⁴⁷. Bee community composition was further compared between seasons with permutational multivariate analyses of variance (PERMANOVA) based on Jaccard dissimilarity, implemented with the *adonis2* function in *vegan*⁴⁶ and 999 permutations. Homogeneity of multivariate dispersions was tested before, using the function *betadisper*. Community dissimilarity between seasons was visualised using non-metric multidimensional scaling (NMDS).

All mixed effect models were fitted using *glmmTMB*⁴⁸ and the distribution of response variables was evaluated using *fitdistrplus* v1.2-2⁴⁹. Model assumptions and fit were assessed by visually inspecting residual dispersion, uniformity and potential outliers using *DHARMa* v0.4.7⁵⁰. When models included more than one fixed factor, collinearity was assessed using variance inflation factors computed in *performance* v0.13⁵¹. To assess the robustness of our results to temporal aggregation, we repeated all analyses aggregating the data into five-year bins rather than decadal bins, resulting in ten instead of six bins (Supplementary Table S2). Because results were largely congruent, we present results based on decadal bins in the main text as they show a lower variation of sampling effort among bins (coefficient of variation: 32% vs. 76% for 5-year bins) and report five-year bin analyses in the Supplementary Methods.

Results

Species recorded and species richness

In total, 45 species were recorded in the Federal District, comprising 35 *Centris* species and ten *Epicharis* species (Supplementary Table S3). Rarefied species richness ranged between 20 species in the 2000's to 26 species in the 1990's ($\bar{x} = 22.84 \pm 2.28$ SD; Supplementary Fig. S1) but did not vary significantly across time (GLM: $\beta = 0.01$; $t = 0.45$; $p > 0.1$). Despite relatively stable species richness across decades, species accumulation curves did not plateau (Supplementary Fig. S1). Analyses based on five-year bins yielded similar results, with no significant effect of time on rarefied species richness (GLM: $\beta = 0.01$; $t = 0.81$; $p > 0.1$; Supplementary Fig. S1).

Species seasonality

Seasonal and temporal trends could be estimated for 23 species using decadal bins (24 species using five-year bins). Only two species were recorded exclusively in a single season; *C. rupestris* and *C. violacea* in the dry season (Supplementary Fig. S2). Three additional *Centris* species (*C. fuscata*, *C. machadoi* and *C. trigonoides*) showed significantly higher relative occurrence during the dry season (GLM; $p < 0.05$), whereas *C. mocsaryi*, *C. nitens*, *E. analis*, *E. bicolor*, *E. cockerelli*, *E. flava* and *E. iheringi* were significantly more common during the rainy season (Fig. 2; Supplementary Tables S4 and S5). Notably, all species with a higher relative occurrence in the dry season belonged to the genus *Centris*, while all *Epicharis* species showed a significantly higher relative occurrence during the rainy season, supporting contrasting seasonality between the two taxa. Results based on five-year bins were highly congruent with those findings (Supplementary Table S6).

Species occurrence and the impact of diet breadth and seasonality

Overall, *E. flava*, *C. fuscata*, *C. tarsata* and *C. aenea* exhibited the highest mean relative occurrence (Supplementary Table S1). While the species *C. aenea*, *C. lutea*, *C. spilopoda*, *E. analis*, *E. bicolor*, and *E. iheringi* increased significantly over time, *C. collaris*, *C. dorsata*, *C. fuscata* (marginally), *C. violacea*, and *E. flava* decreased significantly (Fig. 2; Supplementary Tables S4 and S5). Analyses based on five-year bins largely supported those trends (Supplementary Table S6).

Diet breadth was strongly associated with species occurrence. When diet was treated as a continuous variable, species with broader oil-host use exhibited significantly higher relative occurrence than specialised species (GLMM: $\beta = 0.42$; z-score = 2.68; $p < 0.01$; Fig. 3a, Supplementary Tables S7 and S8). The same pattern was observed for diet as a discrete variable, although the effect was not statistically significant (GLMM: $\beta = 0.54$; z-score = 1.74; $p > 0.05$; Fig. 3c, Supplementary Table S7 and S8). In contrast, seasonality did not significantly affect species occurrence in either the continuous or discrete diet model (Figs. 3b and 3d; and Supplementary Tables S7 and S8). Consistent outcomes were obtained using five-year bins (GLMM with diet as continuous: $\beta = 0.54$; z-score = 1.74; $p > 0.05$; GLMM with diet as discrete: $\beta = 0.42$; z-score = 2.68; $p < 0.01$).

Finally, the number of species declining or increasing did not differ among seasonality categories (Fisher's exact test: odds ratio = 0.97, one-tailed $p > 0.1$ for declines; odds ratio = 0.56, one-tailed $p > 0.1$ for increases) or between dietary specialists and generalists (odds ratio = 3.73, one-tailed $p > 0.1$ for declines; odds ratio = 1.12, one-tailed $p > 0.1$ for increases). Five-year bins supported these findings.

Seasonal turnover between *Centris* and *Epicharis*

October, November and June were the months with highest number of records, respectively (Supplementary Fig. S3). Of the 624 *Centris* records 383 were from the dry season and 241 from the rainy season, while of the 224 *Epicharis* records, 68 derived from the dry season and 156 from the rainy season. GLMMs also suggested a seasonal turnover between the two genera. *Centris* exhibited a significantly higher probability of occurrence in the dry (0.05) than rainy season (0.03; $p < 0.001$; Fig. 4), whereas *Epicharis* showed the opposite pattern (dry: 0.03 vs. rainy: 0.09, $p < 0.001$; Fig. 4). Analyses based on five-year bins supported qualitatively identical results (*Centris*: dry 0.04 vs. rainy 0.03, $p < 0.001$; *Epicharis*: dry 0.03 vs. rainy 0.09, $p < 0.001$).

Community-level analyses provided partial support for seasonal differentiation in species composition. Season did not significantly explain community dissimilarity using decadal bins (PERMANOVA, $R^2 = 0.05$; $p > 0.1$; betadisper $p > 0.1$) but explained a significant proportion of variation in community composition using five-year bins (PERMANOVA, $R^2 = 0.13$; $p = 0.001$, betadisper $p > 0.1$), indicating detectable seasonal structuring at finer temporal resolution (Supplementary Fig. S4).

Discussion

The Cerrado region analysed in this study harbours a high diversity of oil-collecting bees, underscoring its importance as a core area for the conservation of *Centris* and *Epicharis*¹⁹. The 45 oil bee species recorded here exceed the species richness reported in most other Cerrado studies^{52,53} (but see⁴¹). Moreover, species accumulation curves did not reach a plateau, suggesting that additional species remain undetected. This high richness in an area approximately 40 times smaller than the state of São Paulo is remarkable and likely promoted by multiple factors, including its position as a transition zone between the Amazonian and Atlantic rainforests², high environmental heterogeneity^{2,54}, and high plant richness⁵⁵, particularly of oil-producing species⁵⁶.

Despite extensive anthropogenic change, rarefied species richness remained relatively stable across the six decades analysed, potentially reflecting compensatory community dynamics rather than an absence of biodiversity loss. Habitat loss, fragmentation, and altered fire regimes can change floral and nesting resource availability^{57,58}, causing local species extinctions while allowing other species to colonise or increase in abundance. Such turnover could maintain overall species richness while masking shifts in species composition. Consistent with this interpretation, bee assemblages differed between seasons, when analysed at finer temporal resolution, with partial species overlap between seasons suggesting nestedness in species composition. This pattern aligns with our finding that most species occurred

across both seasons, indicating that changes in temperature and precipitation may reshape bee communities primarily by altering relative occurrence and seasonal dominance rather than by causing abrupt species losses of species.

Our results support a partial seasonal turnover between *Centris* and *Epicharis*, with *Centris* dominating in the dry season and *Epicharis* in the rainy season. Although both genera peak in occurrence during the dry–rainy transition in October, coinciding with peak flowering^{41,53,59}, their pronounced seasonal difference indicates that temporal niche partitioning plays an important role in structuring oil-bee communities in the Cerrado. One potential explanation for this seasonal segregation might be *Centris* capacity to use multiple oil-hosts, whereas *Epicharis* depends on Malpighiaceae⁶⁰, a family comprising of numerous species that flower during the rainy season. However, variation in Malpighiaceae flowering periods^{61–63} suggests that host-plant phenology alone cannot explained the seasonal turnover.

The absence of cocoons during *Epicharis* pupation, and its presence in *Centris* species⁶⁴ offers an alternative explanation. Cocoons have been shown to provide protection against fungal infections in Hymenoptera larvae⁶⁵. A lack of cocoons in *Epicharis* may therefore favour larval development during the dry season, when less fungal activity is expected, followed by adult emergence during the rainy season. Larval development during dry season in order to avoid fungus infestations as also been suggested for the tropical bee *Ptilothrix plumate*⁶⁶.

Given substantial overlap in oil-host use between *Centris* and *Epicharis*, particularly on *Byrsonima* and *Banisteriopsis* species⁴², a seasonal turnover may also be a strategy to reduce interspecific competition for limited floral oil resources. This may be especially important for *Epicharis*, which are more specialised than *Centris*, and likely less able to switch to alternative resources. Indeed, temporal resource partitioning has been shown to facilitate coexistence among closely related taxa in other insect systems^{43–45}. Reduced competition pressure during the rainy season may also contribute to an overall more positive trends in *Epicharis*. Notwithstanding, we found intraspecific variability in seasonal activity of both genera, which has already been noted in previous studies^{67,68}. This flexibility could enhance resilience to environmental change by allowing species to adjust emergence timing in response to shifting climatic or floral cues.

Our results also indicate that generalists exhibited higher relative occurrence than specialists, consistent with reports of larger population sizes and broader distribution ranges in generalists as they may be less constrained by the availability of specific host plants^{33,69,70}. Higher occurrence may buffer generalists against environmental stochasticity and anthropogenic changes^{30,34,35,39,71}. Yet, the number of declining species did not differ statistically between specialists and generalists, which might be due to a lack of statistical power. In contrast, seasonality did not significantly influence overall species occurrence or population trends. Species exhibiting declining trajectories spanned the full range of seasonal strategies, suggesting that seasonal restriction alone does not increase oil bee vulnerability at the temporal and spatial scales captured here.

Interestingly, despite greater dietary and seasonal specialisation, *Epicharis* activity showed predominantly stable or increasing occurrence trends, with three of five species increasing significantly, compared with only three of 18 *Centris* species. One possible explanation is that species dominating during the rainy season, such as *Epicharis*, may experience comparatively lower climatic stress, as climate projections for the Cerrado suggest disproportionate reductions in precipitation during the dry season, intensifying droughts and reducing floral resource⁷².

Finally, we acknowledge that museum-based data are subject to inherent limitations. Although we accounted for uneven sampling effort and tested alternative temporal binning schemes, non-standardised collection methods may obscure subtle population changes. Nonetheless, concordance between inferred trends and independent genetic studies for several species^{73–75} support the validity of our main conclusions.

Conclusions

Using six decades of museum records, our study provides new insights into how ecological traits and seasonality shape occurrence patterns and population trends of oil-collecting bees in the Brazilian Cerrado. We show that diet breadth, but not seasonality, is a key determinant of species occurrence, with oil generalists showing higher relative occurrence than specialists, underscoring the role of diet breadth in structuring bee communities. We also provide evidence for a partial seasonal turnover between *Centris* and *Epicharis*, likely reducing interspecific competition for limited floral oil resources. Interestingly, despite a higher degree of specialisation most *Epicharis* showed stable or increasing trends, highlighting that specialisation does not inevitably translate into decline. In a biome undergoing rapid environmental change, understanding how diet breadth, seasonality, and niche partitioning interact is essential for forecasting species' responses to future disturbance and for designing conservation strategies that safeguard both pollinators and their specialised plant partners in the Cerrado.

Declarations

Competing Interests

The authors declare no competing interests.

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Author Contribution

P.M.S.: conceptualization, methodology, formal analysis, visualization, investigation, writing- original draft. A.S.: data curation, investigation. G.D.: data curation, investigation. A.J.C.A: data curation, resources, supervision, writing- review & editing. P.T.: supervision, methodology, writing- review & editing. A.C.M.: supervision, writing- review & editing. B.K.: conceptualization, project administration, supervision, writing- review & editing.

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Data Availability

Museum records are deposited in the University of Brasília, Zoology Department and are accessible upon permission of the curator (Antonio Aguiar). Curated data records will be available on GBIF. Data used in this manuscript, as well as scripts, are available from Figshare:

<https://doi.org/10.6084/m9.figshare.31182274>

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Figures

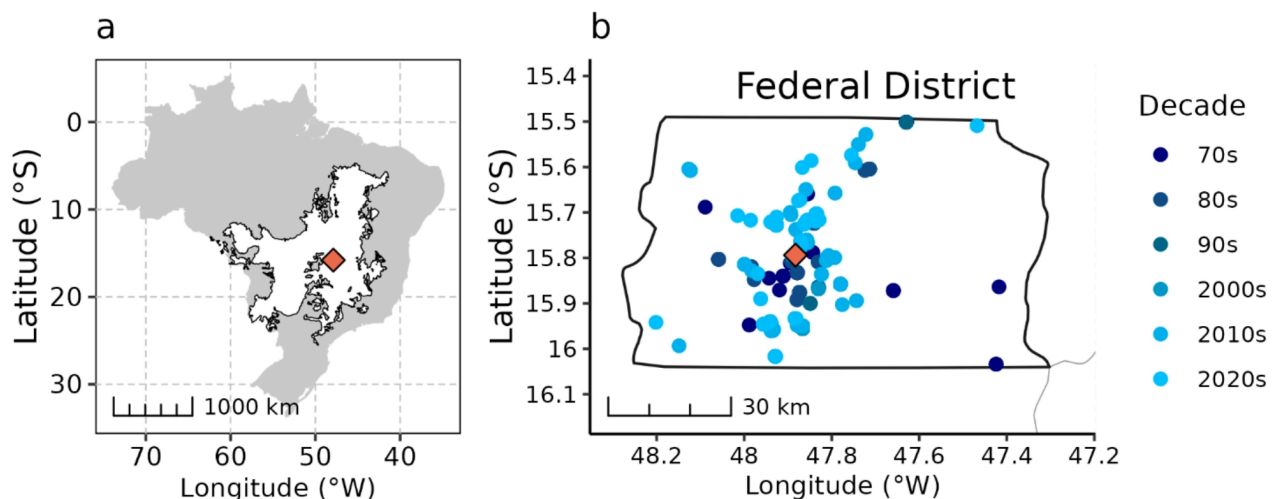


Figure 1

(a) Map of Brazil (grey) showing the Cerrado biome (white) and the capital Brasília (red diamond). **(b)** Spatial distribution of the occurrence records analysed within the Federal District. Record age is indicated by a colour gradient, with lighter blue tones representing more recent records. Solid black lines delineate the boundaries of the Federal District and the red diamond denoting the city of Brasília. Maps were generated in R using open-source shapefiles from Natural Earth (<https://www.naturalearthdata.com/>) in R.

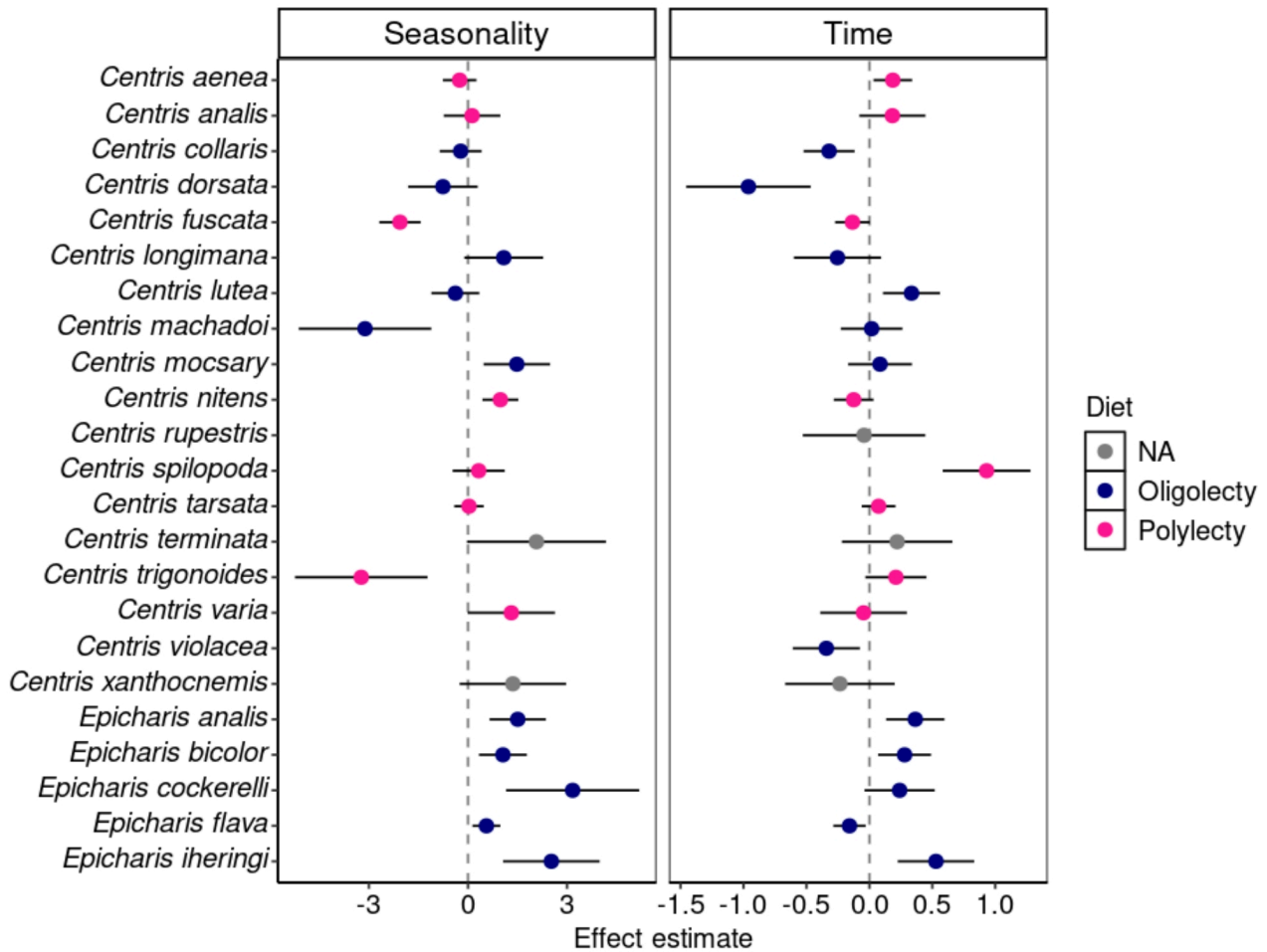


Figure 2

Effect of time and season on species' relative occurrence. For each species the model output testing the effect of time (in decades) and season on relative occurrence is shown. Points represent the effect estimate and bars the 95% confidence intervals. Bars that do not overlap with the dashed line correspond to a significant ($p < 0.05$) effect of the predictor. On the "Seasonality" panel the left side corresponds to the dry season and the right to the rainy season. On the "Time" panel the left side corresponds to recent declining trajectories and the right side to recent increasing trajectories. Polylectic species are shown in pink, whereas oligolectic species are shown in dark blue. Species for which no information regarding oil-plant hosts was available are shown in grey.

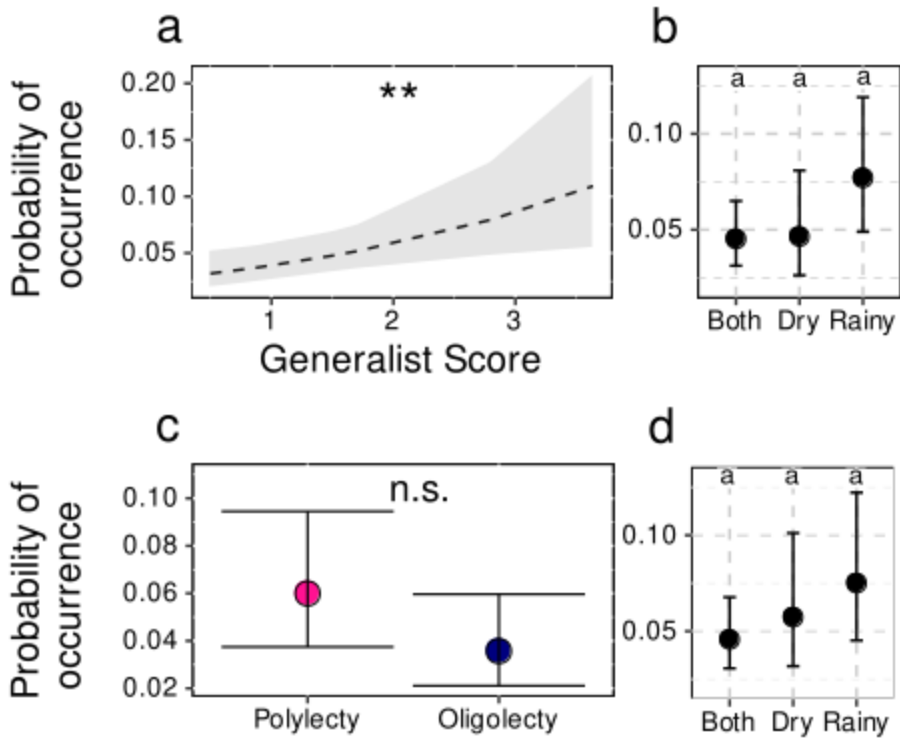


Figure 3

Effects of diet breadth and seasonality on relative species occurrence based on two diet classification approaches (discrete vs continuous). The y-axis shows the model-predicted probability of occurrence. For the continuous diet classification model (higher values indicate a broader oil-host range), **(a)** shows the effect of diet breadth and **(b)** the effect of seasonality on relative occurrence. For the discrete diet model **(c)** shows the effect of diet category (polylectic vs. oligolectic) and **(d)** the effect of seasonality. In **(a)**, the shaded grey area represents the 95% confidence interval and the dashed line indicates the model slope (** p < 0.001). In **(b)** and **(d)**, points represent estimated marginal means for each seasonality category and black bars indicate 95% confidence intervals; different letters denote significant differences between categories (p < 0.05). In **(c)**, coloured points represent estimated marginal means for each diet category (pink = polylectic, dark blue = oligolectic), with black bars showing 95% confidence intervals; n.s. indicates a non-significant effect (p > 0.05).

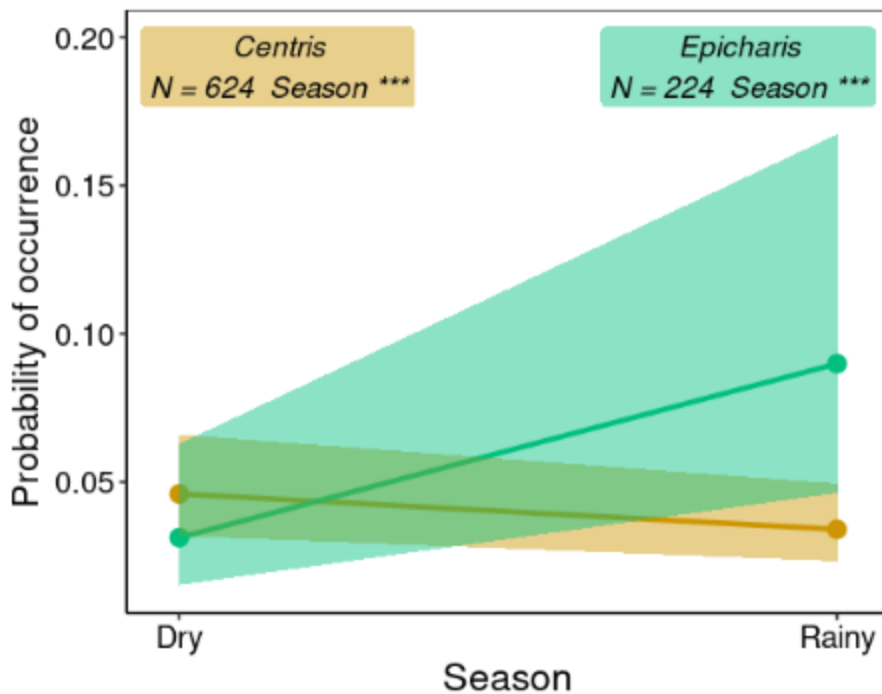


Figure 4

Seasonal turnover of *Centris* (yellow) and *Epicharis* (green).. The y-axis shows the model-predicted probability of occurrence. Points represent estimated marginal means for each season (points for the same genus are connected through line of same color) and colored shaded areas the 95% confidence intervals. Numbers above each boxplot indicate the total number of presence records for each genus. Model-based significance values for the relationship between genus-level occurrence and seasonality are given (***) $p < 0.001$).

Supplementary Files

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