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Plant Communities in the Americas Are Highly Bee Dependent Regardless of Biome or Local Bee Diversity

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ABSTRACT

Aim: All bees depend on angiosperms for survival, while many angiosperms depend on bees for reproduction. However, bee and flowering plant species richness do not peak in the same geographical regions of the world, suggesting that the flora in regions where bees are not as diverse, such as the tropics, may be relatively less bee-dependent. We test this assumption by analysing whether local relative bee diversity can predict the proportion of angiosperm species that attract bees (i.e., "bee flowers").

Location: The Americas.

Time Period: Present.

Major Taxa Studied: Bees and angiosperms.

Methods: We map the proportion of bees to angiosperm species using recently available datasets of geographic distribution for both taxa. We then combine data from surveys on pollination systems for 56 floristic communities to estimate the proportion of angiosperm species with bee flowers in different regions. Finally, we test whether the proportion of bee flowers in a community can be predicted by a combination of relative bee species richness and abiotic environmental variables.

Results: Broad distribution maps show that the relative richness of bees in relation to angiosperms decreases in tropical areas; however, there is no evidence that tropical floristic communities are less dependent on bees. Interestingly, the proportion of angiosperm species with bee flowers was almost always found to be around 50% across biomes, with some variation depending on the habitat type and method of data collection.

Main Conclusions: Our results suggest that plant communities can be highly bee-dependent even where bees are relatively less diverse. While lower species richness does not mean lower abundance, and fewer bee species of specific life histories can still provide adequate pollination supply for a large number of angiosperm species, this pattern may impact how bee flowers interact with bees in different areas, and consequently how bees and bee flower specialisations have evolved over time.

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1 | Introduction

Flowering plants (i.e., angiosperms) form the basis of almost every terrestrial ecosystem around the globe. They are also the basis of our diet and important players in the carbon cycle (Stuart Chapin III et al. 2009; Coelho et al. 2023). Given their ecological and economic relevance, there is a general interest in understanding how flowering plants reproduce, specifically in the context of their interaction with pollinators. Most flowering plants are pollinated by animals, with bees being among the most important groups of pollinators (Ollerton et al. 2011; Ollerton 2017). In this mutualistic interaction, bees seek flowers for pollen, nectar, and other resources, and end up transferring gametes between flowers, leading to their fertilisation. Flowering plants attract bees using many signals, including, among other things, floral and inflorescence morphology, colour patterns, and scents (Valenta et al. 2017). As bee-pollinated flowering plants compete for the local supply of bee pollinators, bees in turn compete for floral nectar, pollen, and other floral resources. As a result, bees and other pollinators are thought to drive flowering plant diversification, and vice versa (Neff and Simpson 1993; Cardinal and Danforth 2013; Murray et al. 2018).

Surprisingly, however, the spatial distribution of bee species richness does not positively correlate with that of angiosperms. Bees have an unusual bimodal latitudinal gradient of diversity, with most of their diversity concentrated in drier areas at mid-latitudes in contrast to a more classic latitudinal gradient of diversity observed in flowering plants (Michener 1979; Ollerton 2017; Orr et al. 2021). This mismatch in bee and angiosperm species richness might be explained by the different ecological conditions that are required for each group to thrive. While plants in general succeed in the warm and humid environments typical of lower latitudes, these conditions may be less suitable for most bees. Protecting larval food (pollen) from moisture and spoilage by fungi and bacteria has been pointed out as a major challenge for many solitary bee groups when nesting on the ground in tropical humid environments (Michener 1979); but note that some groups overcome this challenge with specific adaptations to waterproof nests and prevent food spoilage (Wcislo and Cane 1996; Antoine and Forrest 2021). Additionally, the competitive dominance of eusocial bees, which are less diverse but more abundant in tropical forests, may be a key factor limiting the diversity of other bee species in these environments (Michener 1979; Roubik 1992). Among the drivers of bee richness distribution worldwide, angiosperm productivity and richness are only important when tropical forests are excluded (Orr et al. 2021).

The mismatch between bee and angiosperm diversity is especially evident in the Americas, which is also the most data rich continent for both bee and angiosperm occurrence data (Ondo et al. 2024; Dorey et al. 2023), meaning that when taken together these patterns should be relatively robust to undersampling in this region. If this mismatch is real, it might suggest that areas with relatively low bee species richness, such as tropical rainforests (Orr et al. 2021), also have a lower proportion of bee-pollinated plants. This pattern would align with prior findings indicating that bee-pollinated plant lineages often undergo evolutionary transitions to alternative pollination strategies when they expand into regions with lower bee diversity, such as tropical mountains (Dellinger et al. 2023; Nery et al. 2024). The tropics also support a more diverse array of competing animal pollinators, such as beetles, bats and birds (Ollerton 2017) and consequently a higher diversity of pollination systems and syndromes, the latter defined as a set of floral traits associated with the pollination by a specific animal or abiotic agent (Faegri and van der Pijl 1979; Ollerton et al. 2005). In this sense, the prominence of bees as pollinators in these regions could be reduced when compared to other regions and their ecological role filled by other functional groups of pollinators.

Quantifying whether local bee diversity impacts the number of bee-pollinated species in a plant community, and whether certain biomes are more “bee dependent” than others, is crucial to better understand the ecology and evolution of species interactions. For example, in ecosystems where bee diversity is high, such as Mediterranean regions and deserts (Michener 1979; Minckley 2008), a greater reliance on bee pollination might drive floral adaptations that attract specific guilds of bees, creating more specialised systems that are more sensitive to phenological mismatches caused by climate change (Bartomeus et al. 2011). Conversely, if tropical angiosperms rely more on alternative pollinators due to the lower diversity of bees compared to other regions, then their pollination systems may be both more resilient to disruptions affecting bees and more vulnerable to threats targeting other pollinator groups. Understanding whether the floras of certain areas are more dependent on bee pollination can thus help identify conservation priorities and shed light on the broader implications of biodiversity loss on ecosystem functioning (Ollerton 2017).

In this study, we aim to assess whether the spatial mismatch between bee and angiosperm species richness impacts the proportion of species with bee-pollinated flowers in plant communities. To that end, we compile occurrence and checklist data to characterise the spatial mismatch between bee and flowering plant diversity across the American continent. We then analyse data on pollination surveys across the Americas and test whether the proportion of plant species with bee-pollinated flowers in a community varies between latitudes and biomes and if it can be predicted by a combination of environmental factors and local bee species richness. We expect that plant communities in areas where the ratio of bee-to-angiosperm species is low will have fewer bee-pollinated angiosperms.

2 | Methods

2.1 | Distribution Data and Mismatch Mapping

To characterise the mismatch between bee and flowering plant diversity across the American continent, we mapped the species richness of both groups using a combination of occurrence data from Dorey et al. (2023) and checklists available from the Plants of the World Online portal for angiosperms (POWO 2024) and the Moure Bee Catalogue (Moure et al. 2024) for bees. For angiosperms, we downloaded the POWO dataset of distribution per Level 3 botanical country and filtered it to include only angiosperm species with native distributions in the Americas, excluding all introduced records and non-angiosperm families. For bees, we used the filtered dataset of Dorey et al. (2023), which combines taxonomically verified occurrence points available through GBIF with checklists (Ascher and Pickering 2024). Because bee occurrence data is strongly biased by spatial sampling, we took additional measures to mitigate the impact of these known biases. To that end, we first cross-checked this list with that available through the Neotropical bee catalogue (Moure et al. 2024), retaining the values from the latter for countries in the Neotropics. This was then updated for countries from the data from Discover Life where DL values were higher than country totals (https://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS). Lastly, the dataset generated in Russell et al. (2024) was used to cross-reference provinces in ArcMap 10.8 (where boundaries overlapped, as different delineations were used in the two analyses) and the higher value of recorded species number was used (though such adjustments were only needed for around 8 provinces). That was an important step because bee occurrence data from tropical countries is generally not digitised and thus not available through GBIF, and so scoring species richness using only these points would underestimate the diversity in these areas. All bee species richness data were also summarised as means by Level 3 botanical countries (Brummitt et al. 2001), so that the same diversity metrics could be applied to both bees and angiosperms.

After mapping species richness for both groups across the American continent, we then divided the values in each botanical country in the map of bees by that of the corresponding polygon for flowering plants to map and visualise areas where the proportion of bee species is particularly high or low compared to those of angiosperms. Higher numbers in the resulting map show areas where the species richness of bees is relatively high in relation to the number of local flowering plant species. Conversely, numbers closer to zero show areas where the richness of bees in relation to the diversity of flowering plants is low. Finally, to assess whether these large-scale geographic patterns of bee–angiosperm richness correspond to local patterns observed in floristic and faunistic surveys (which tend to be more carefully sampled), we compiled species richness data for bees and plants from specific localities. We then conducted a regression analysis between the bee-to–angiosperm proportions from these local surveys and the corresponding botanical country values to test whether they are strongly positively correlated (methodological details in Data S1).

2.2 | Literature Review on Community Surveys

To test whether the mismatch between bee and angiosperm diversity impacts the proportion of bee flowers in plant communities across the Americas, we conducted an extensive literature search in April 2024 to assemble a database on pollination systems in various latitudes and biomes on the continent. The search was focused on community-level studies which assessed the prevalence of all modes of pollination. We searched the Web of Science, Google Scholar, and Scielo platforms to retrieve publications using the keywords: "Pollination syndrome" OR "Pollination systems" OR the variants in Portuguese and Spanish (e.g., Sistema de polinização, Sistemas de polinización). In complementary searches, we associated the former keywords with country names using "AND" for all countries in South America (Argentina, Brazil, Bolivia, Chile, Colombia, Ecuador, Paraguay, Peru, Guianas, Suriname, Venezuela, Uruguay) and North America (Canada, Mexico, United States), as well as region names to cover the entire American continent (Central America, Caribbean, Neotropical). To ensure the completeness of our search, we also searched for backward citation, which means we checked all the referenced papers in each study to assure we were including historical papers, not always retrieved in the database searches. In this search, we only included papers that analysed all possible angiosperm species in a delimited area, considering either morphological traits associated with pollination syndromes (e.g., colour, reward, etc.), observation of flower visitors, or both. Because our search focused on community-based studies where all co-occurring flowering plant species were systematically surveyed, studies focusing on one pollination system (e.g., buzz pollination or hummingbird pollination syndromes), or on a single flowering plant species or lineage, were not considered. We also did not consider interaction network studies since those are focused only on animal-pollinated plants, and we also wanted data on abiotic pollination (e.g., wind and water) to make sure all pollination systems were included.

The literature survey recovered 66 studies and 97 communities among peer-reviewed articles in scientific journals and book chapters. Twenty-five studies and 41 communities were excluded for presenting data only on part of the community (e.g., only insect pollinated plants) or for lumping bee pollination with other systems (e.g., by reporting data only on biotic vs. abiotic pollination), resulting in a total of 41 studies and 56 communities kept in the final community dataset (Table S1). Some papers included sampling in more than one area; therefore, we considered them as distinct communities based on the different coordinates or elevations. Surveys were further classified in terms of the type of data presented as "observation only" (4 studies), i.e., pollination systems retrieved from field-based observation of floral visitors; "syndrome only" (19 studies), i.e., when the authors classified plants in a given community in pollination systems based on the set of traits that characterise each pollination syndrome, mostly following the concept of Faegri and van der Pijl (1979); or "observation + syndrome" (30 studies), i.e., when a combination of floral visitors observation and syndrome defined by floral traits was applied. In those cases, the authors often classify floral morphology following the syndrome concept but assign a likely functional group of pollinators based on field observations. In cases where more than one study investigated the same community (e.g., Opler et al. 1980; Bawa et al. 1985) we kept the study that also performed observations and was not based only on syndromes, following preliminary analyses that showed that syndrome studies tend to recover a higher percentage of the flora as bee visited (pairwise Conover test $p < 0.05$; Figure S1). Geographical information (i.e., latitude and longitude) was recorded from the original study when informed in the paper or retrieved from Google Maps for the approximate centroid when the information was not available. Elevation was recorded from studies when available to accommodate studies along elevational gradients. Missing elevations were gathered from an altitude raster from WorldClim 2.0 at 2.5 min resolution (Fick and Hijmans 2017). Biome type information was retrieved by overlaying coordinates of each community with shapefiles from the World Wildlife Fund (WWF) map of terrestrial biomes and ecoregions (Olson et al. 2001).

2.3 | Pollination Systems and Proportion of Bee Flowers in Each Community

We then retrieved information on pollination systems in each analysed community as a percentage of the total number of angiosperm species in that community presenting each pollination system. As different studies had different approaches to analyse pollination systems of a given plant community and applied different categories, we standardised the most common categories for which we had a reasonable amount of data. The following pollinator categories/groups were considered: bees (Hymenoptera, Apoidea), wasps (Hymenoptera non-Apoidea), flies (Diptera), butterflies (diurnal Lepidoptera), moths (nocturnal Lepidoptera), beetles (Coleoptera), insect generalists (two or more insect orders), birds (Aves), bats (Chiroptera) and wind. As our main question relates to the proportion of flowering plants that depend on bees for pollination in each community, we calculate the proportion of the flora attracting bees as the major floral visitor/pollinator by dividing the number of angiosperm species visited mainly by bees by the total number of angiosperm species in the community. We also recorded the size of the area surveyed for 22 communities from studies where this information was reported to test whether area size may influence our results, under the assumption that smaller communities are more thoroughly surveyed.

The proportion of angiosperm species that were categorised as mainly bee visited in each community is henceforward called "proportion of bee flowers". This includes instances of confirmed bee pollination (i.e., bee visitation associated with higher proportion of fruit set), bee visitation with no confirmed pollination, and floral morphology indicative of a bee pollination syndrome. It is important to differentiate what we call "bee flowers," that is, all plants mainly visited by bees in a given community, from other uses of the term in the literature, which are furtherly explained in Data S2.

2.4 | Spatial Regression Analyses

To test whether angiosperm communities in certain biomes or latitudinal zones tend to be more or less bee dependent, and whether local bee diversity can predict the local proportion of bee flowers in a community, we ran two tests. First, we used the coordinates of each community survey to classify them in terms of their biome type by overlaying the coordinates with the ecoregion shapefiles from WWF (2024). Because other axes of landscape variation could be more explanatory than biome type, we ran additional tests by further transforming biome type into three additional discrete categories: (1) biome type in terms of canopy covering ("open" or "closed"), following the classification of Boyko and Vasconcelos (2024); (2) biome type according to "super-biome" ("arid," "tropical" or "temperate") following the classification of Ramírez-Barahona et al. (2020), and tropicality according to major latitudinal zones ("tropical" if between latitudes −23° and 23° and "temperate" otherwise). To test for significant correlation between biome or habitat type and proportion of bee flowers in a community, we built linear models using the generalised least squares method in the function *gls* from the R package nlme (Pinheiro et al. 2024). To correct for spatial autocorrelation in the data structure, we used a spatial autoregressive model using the argument "corSpher" using a maximum likelihood approach. The proportion of bee flowers in a plant community was set as the response variable in all cases and analyses were run for each biome type as predictors individually. We also considered a "nugget" effect by setting nugget = TRUE in the model, so that additional sources of variation could be captured by the data structure.

Second, we used the community survey coordinates to extract both climatic data and the proportion of bees in relation to flowering plants (henceforward "relative bee diversity") as resulting from our mismatch mapping. For climatic data, we extracted data for nine continuous environmental variables from 2.5 min resolution rasters: the bioclimatic variables from WorldClim 2.0 (Fick and Hijmans 2017) (BIO1) mean annual temperature, (BIO4) temperature seasonality, (BIO5) maximum temperature of warmest month, (BIO6) minimum temperature of coldest month, (BIO12) mean annual precipitation, (BIO15) precipitation seasonality, (BIO16) precipitation of the wettest quarter and (BIO17) precipitation of driest quarter. These climatic variables represent both mean climatologies that are widely used in climate-trait correlation studies (e.g., Boyko et al. 2023), but also variables that represent temperature and precipitation seasonality and extremes. The latter was also included because how temperature and precipitation vary along the year can be more important to predict ecosystem functioning the yearly means. Mean wind speed, solar radiation and potential evapotranspiration (Trabucco and Zomer 2019) were also included in the analysis, as these were shown to be important predictors of subset of bee pollinated species in previous studies (e.g., Russell et al. 2024).

We then built a multi-predictor model based on a generalised least squares analysis corrected for spatial autocorrelation where the combined effect of all 12 environmental variables plus relative local bee diversity was set as predictors of the proportion of bee flowers as an additive model. We combined these variables within the same model because a possibility is that relative bee diversity can only predict the local proportion of bee flowers in some environments, but not in others. Next, we tested which combinations of variables increase the explanatory power of the model, building multivariate regression models with all possible combinations of variables, totalling 4054 possible models, when all combinations of predictors are accounted for. To fit all 4054 models, we used the *dredge* function of the R package MuMin (Barton 2024), which calculates the Akaike Information Criterion (AIC) of all possible combinations of variables in the model. We kept all models with a delta AICc of 2 to the best model and we conducted model averaging to weight the contribution of each variable into the global model, following Burnham and Anderson (Burnham and Anderson 2002, p. 151). The standard error of the effect size of each predictor was also included as a measurement of uncertainty. To assess the relative importance of each variable, we assessed the cumulative AIC weight of models that included

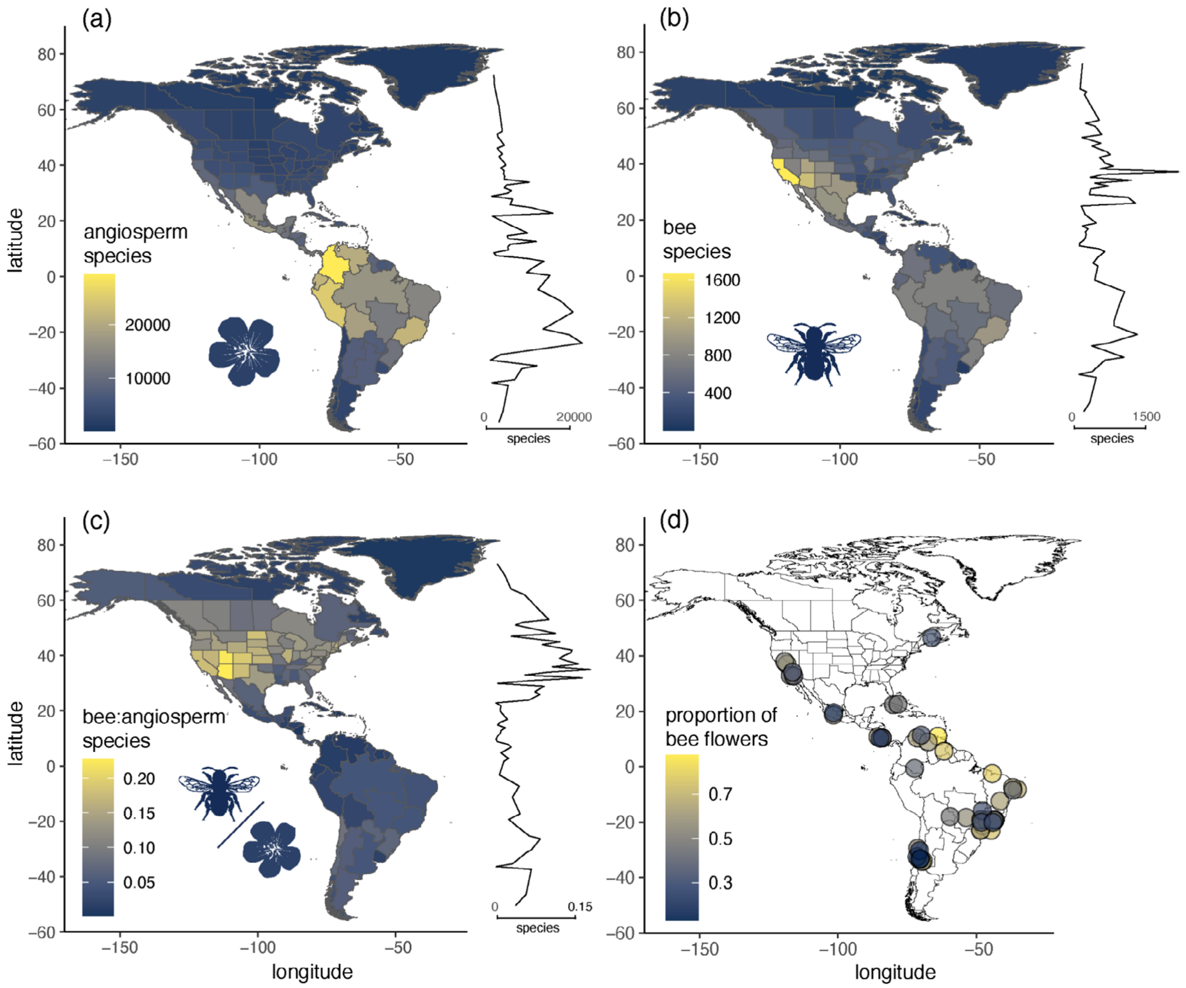

FIGURE 1 | Map of the American continent showing the geographical distribution of (a) angiosperm and (b) bee richness, (c) bee per angiosperm richness mismatch, and (d) proportion of bee flowers in analysed plant communities. (a) Total geographical distribution of angiosperm richness in the Americas according to POWO (2024) by botanical country. (b) Total geographical distribution of bee richness in the Americas according to a combination of occurrence data from Dorey et al. (2023) and Moure et al. (2024) per botanical country. (c) Proportion of bee *per* angiosperm species, where higher values represent a relatively high number of bee species per angiosperm and values close to zero represent areas where the bee richness is relatively low compared to diversity of angiosperms. (d) Geographical distribution of analysed plant communities across the American continent. Each circle represents a plant-pollinator community survey. Line plots in (a–c) represent trends of mean species richness by degree of latitude. Bee and flower silhouettes in a–c were sourced from phylopic.org (public domain).

that variable, in addition to standard *p*-values (Burnham and Anderson 2002). All code used in these analyses can be found at https://doi.org/10.5281/zenodo.14585236.

3 | Results

3.1 | Characterising the Spatial Mismatch Between Bee and Angiosperm Species Richness

Our general angiosperm species richness map recovered a latitudinal gradient of diversity in the Americas, that is, low latitude tropical regions hold a high diversity of angiosperm species that gradually decreases toward the polar regions (Figure 1a). Plant richness is particularly high in the Amazon and North Andean Regions (Figure 1a). Conversely, bee species richness does not peak in tropical regions of the Americas (Figure 1b). There is, however, a bimodal latitudinal gradient from polar regions (zero to low diversity) to mid latitudes (higher diversity) that decreases toward tropical regions as seen in flowering plants. Peaks of bee richness will be found in mid latitudes, especially in arid and semi-arid regions, where California and Arizona stand out as the most speciose regions of the Americas for bees (Figure 1b).

The proportion of bees per angiosperm species across the American continent evidences the geographical mismatch in mid-latitudes, especially in the Northern Hemisphere (Figure 1c). Tropical regions, such as the Amazon and Andean regions, present the lowest proportion of bees: angiosperms. A tendency of increasing the proportion of bees per angiosperm with latitude is observed in both the South and Northern Hemisphere approximately between the parallels 30° and 40°, where the gradient becomes inverse and the proportion of bees: angiosperms starts to decrease. The proportion of bees: angiosperms per botanical country ranges from a minimum of 0.0009 bee species per angiosperm species in the Cayman Islands to 0.2278 bee species per angiosperm species in Arizona. The 13 lowest values of bee: angiosperm richness are found in islands, whereas the top nine highest values of bees: angiosperms are either in the great plains or in the west USA (see full list in Table S3). The comparison between these results and those from point locations, where careful angiosperm and bee diversity surveys have been performed, shows a significant and strong positive correlation ($p < 0.001$, $R^2 = 0.44$; Figure S2), suggesting that the pattern that these broad estimates are capturing may be realistic.

3.2 | Proportion of Bee Flowers According to Region and Biome

In total, we collated 56 plant-pollinator community surveys across the Americas encompassing forested and non-forested biomes (Table S1). In spite of our efforts to compile a geographic distribution as wide as possible, the results were relatively geographically clustered, with few to no pollination survey studies that followed our criteria in the Amazon Basin of South America and much of the USA and Canada (Figure 1d; see also Figure S3 for a map of biomes). Nonetheless, the surveys included in the analysis captured a wide latitudinal range (from 48°N to 42°S) and represented more than 30 ecoregions (Table S1). The diversity of plant species analysed in each of the communities in the final dataset ranged from 12 in the least species-rich community (boreal forest of Canada) to 289 in the most species-rich one (Atlantic Forest of Brazil), and the proportion of bee flowers in these communities ranged from 0 (Juan Fernandez Islands; this data point was excluded from further analyses as it likely represents an outlier due to the isolated nature of this island) to 0.88 (coast of Venezuela) (Figure 2), with 31 out of the 56 communities having most of the flora (> 0.5) visited by bees. There is no strong relationship between the area size of the community surveyed and the proportion of bee flowers recovered (spatial gls $p = 0.09$; $p = 0.39$ with outliers removed), suggesting a low impact of bias resulting from area size and sampling effort in the results (Figure S4). Most of the surveys (56.4%) were based on a combination of observation and syndrome data, whereas 36.4% of the surveys were based on syndrome only and 7.2% were based on observation only (Figure S1). The median proportion of bee flowers in a community was highest for studies that scored the proportion of bee flowers based on syndrome only (0.61, vs. 0.30 from observation only and 0.48 from a combination of syndrome and observation data; Figure S1). Conover's pairwise comparison test shows that the difference between the proportion of bee flowers assigned from syndrome studies is significantly higher than those that use a combination of syndrome and observation to score bee flowers (pairwise Conover test $p = 0.046$).

For the analyses of biome type, the median proportion of bee flowers in a floristic community was found to be around 50% in all cases, no matter how biome is categorised (Figure 2). Even though the medians are similar, the distributions are often quite different, and some variations are worth mentioning. Some regions have a high proportion of bee flowers in general, for example, desert areas where the proportion of bee flowers in an area can surpass 80% (Figure 2a). Even in some islands, bees are important, for example, Chamorro in Galapagos, although in others no bee flowers were observed (Juan Fernandez Islands). Montane grasslands, conversely, present a medium to low proportion of bee flowers, with exceedingly low values of less than 0.2 (Figure 2a). Tropical dry forests and temperate conifer forests present surprisingly similar variation in the proportion of bee flowers, with low variation and close to the medium value of 0.5 of bee flowers (Figure 2a). However, it is important to note that these cases involve small sample sizes ($n = 4$ and $n = 2$ respectively), so the pattern may be spurious. Tropical savannas and tropical forests are also relatively similar, with a medium to high proportion of bee flowers. However, tropical savannas are apparently more bee-dependent than tropical forests (Figure 2a), a pattern that reflects the proportion of bee flowers in closed versus open canopy biomes (Figure 2b). When considered as a whole, open canopy biomes present a larger variation in terms of proportion of bee flowers (Figure 2b), probably because they comprise a wider variety of latitudes, climates, and flora. When super-biomes and latitudinal zones are considered, temperate regions seem to vary more and present slightly lower proportions of bee flowers, but overall, all super-biomes and latitudinal zones present medians around 0.5 (Figure 2c,d). However, although some heterogeneity in data distributions exists, no pairwise comparison was found to be significant (spatial gls $p > 0.05$ for all comparisons), meaning that no biome or biome category was found to have a significantly higher or lower proportion of bee flowers. Removing syndrome-only studies from these analyses reduces the sample size of some biomes that tend to rely more on this type of data for inferences of pollination mode (e.g., tropical rainforests), but does not change the main results of these or further analyses (Figures S5–S7).

3.3 | Interaction Between Abiotic Factors and Bee Relative Diversity

Of the 4056 possible multi-predictor models tested, the model structure that best fit the data (i.e., had the lowest AICc) was proportion of bee flowers ~ BIO15 + BIO17 + BIO4 (AICc = −29.49) (respectively: precipitation seasonality, precipitation of the driest quarter and temperature seasonality). Twelve models had a delta AICc < 2, and when averaging the contribution of the variables included in those models according to their AICc, those three variables are the only ones that appear to significantly explain the variation of bee flowers overall (i.e., $p = 0.021$, $p = 0.022$ and $p = 0.029$ respectively). Precipitation Seasonality (BIO15) (weight = 0.75) and Precipitation of the Driest Quarter (BIO17) (weight = 0.56) were the variables that ranked the highest in the averaged global model, meaning that they appear in most well-supported models. All other variables had weights below 0.55, so are less relevant in explaining variation in proportion of bee flowers in plant communities across the Americas. The R^2 values of models with delta AICc < 2 ranged from 0.039 to 0.175; therefore, explaining up to 17.5% of the variation in proportion of bee flowers. The effect size of the most important variables on the proportion of bee flowers was negative, that is, increments in the variable lead to a negative correlation with the proportion of bee flowers. For example, the higher the precipitation seasonality, the lower the proportion of bee flowers in the community. Importantly, bees: angiosperms ratio, although included in the global model, was not included in any of the most explanatory models, suggesting that local bee diversity does not significantly explain variation in the proportion of bee flowers.

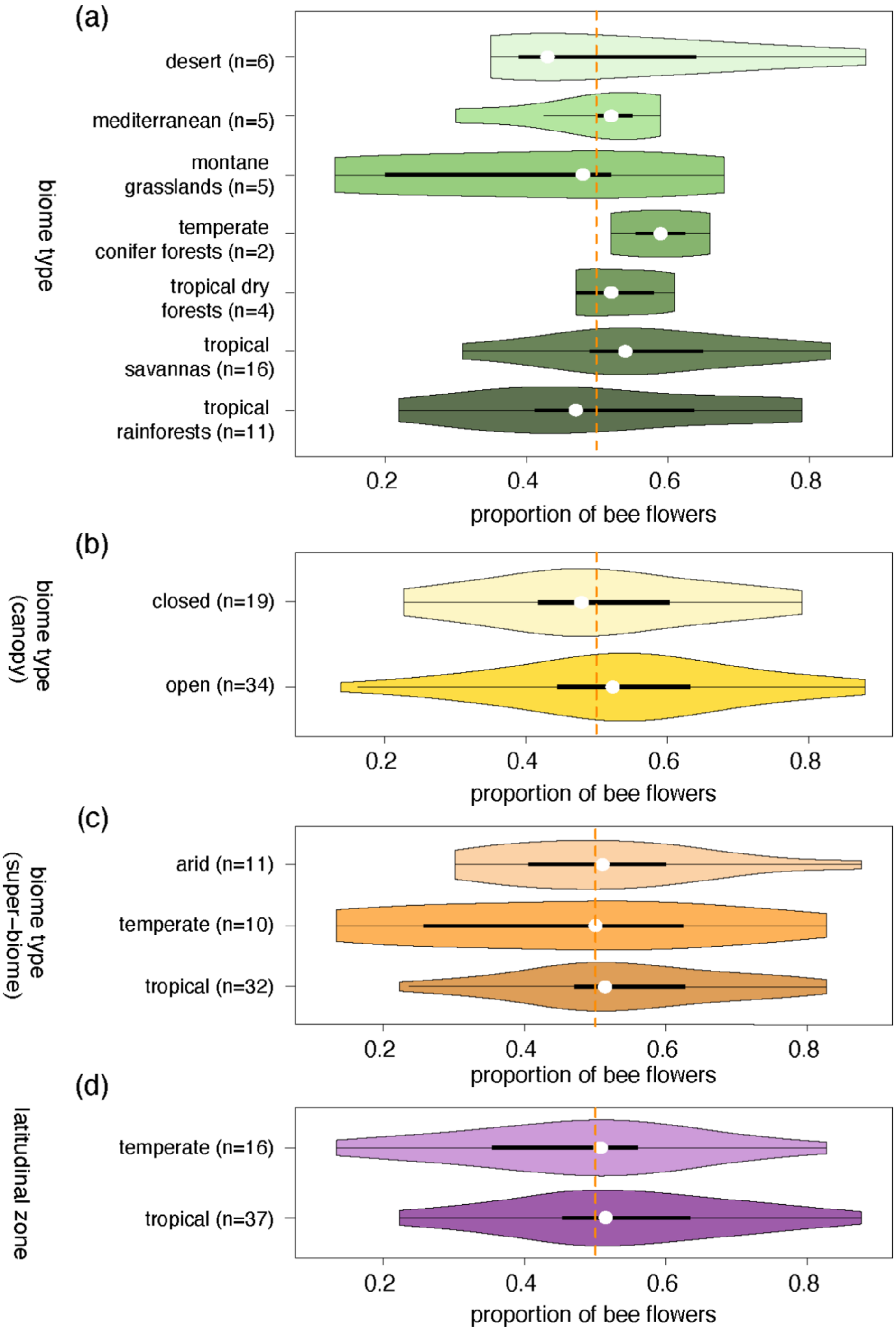

FIGURE 2 | Distribution of the proportion of bee flowers among the plant-pollinator community studies according to different geographic zones: (a) biome type (b) canopy cover (c) super-biomes and (d) latitudinal zone. Density curves indicate the distribution of studies presenting different proportions of bee-flowers, where larger zones indicate a larger number of studies presenting that proportion of bee-flowers. White dots represent median values and thicker black lines the interval between the upper and the lower quartile in the distribution of the data. Values in parenthesis indicate the number of studies in each geographic zone. Orange dashed line marks 0.5 proportion of bee flowers, meaning that white dots to the right of this line indicate biomes that are mainly composed of bee-flowers.

4 | Discussion

4.1 | New World Floras Are Highly Bee Dependent Regardless of Latitude and Biome

The diversity of pollinators is thought to be correlated with the proportion of angiosperms in an area (Ollerton 2017). Surprisingly, an exception to this pattern is one of the most important groups of pollinators, the bees. The large-scale geographical distribution maps demonstrate a spatial mismatch that had been indirectly inferred by previous studies, where bee and plant species richness were shown not to peak in the same areas (e.g., Brown 2014; Eiserhardt et al. 2017 for angiosperms; Michener 1979; Orr et al. 2021 for bees). The reasons for the

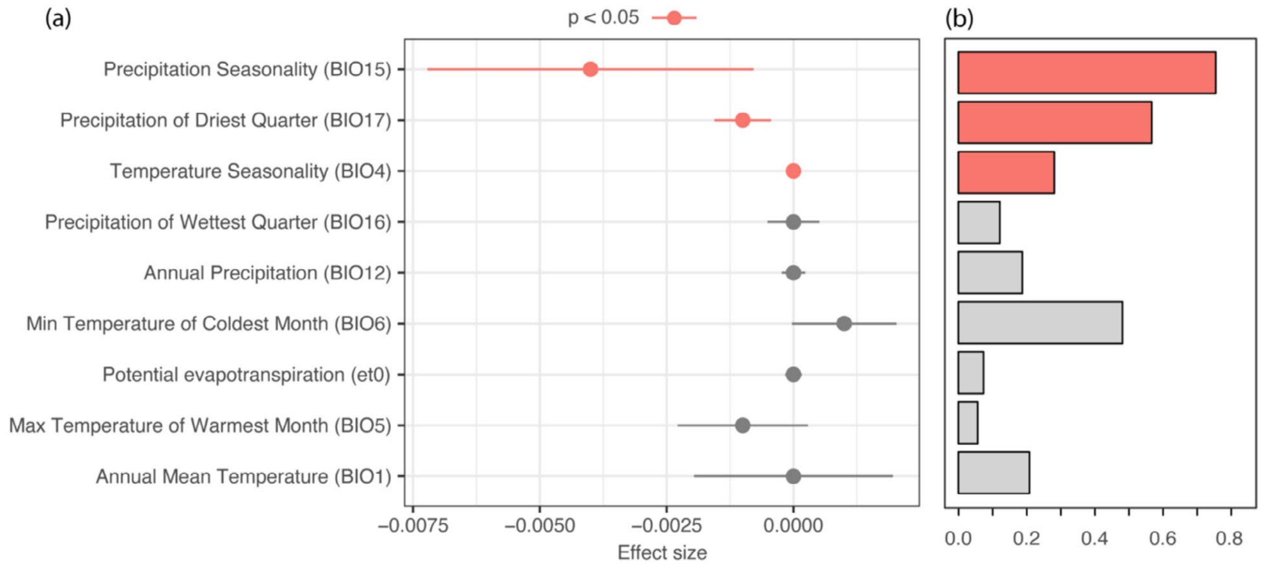

FIGURE 3 | Standardised regression coefficients of Generalised Least Square Models (GLS) for proportion of bee flowers according to bioclimatic variables from WorldClim 2.0 (Fick and Hijmans 2017). (a) Variables are ranked according to their *p* values (lowest to highest). Horizontal bars indicate 95% confidence intervals. (b) Importance value of each variable in the averaged global model; that is how often that variable is included as predictors in the best fitted models.

mismatch may vary in different areas. In one extreme, areas like North Dakota in North America rank high because of the poor floristic diversity compared to relatively high bee species richness. In the other extreme, Colombia in South America ranks particularly low because of its extremely rich flora in contrast to relatively poor local bee diversity (see also Ondo et al. 2024). Islands rank the lowest, likely due to a combination of higher dispersal abilities of flowering plants in comparison to the limited dispersal ability of bees, combined with greater stochasticity in community structure (Pennington et al. 2006; Michener 2007).

Even though we found a relatively lower diversity of bees in the tropics, we did not find evidence that the floras in these regions are less bee dependent. In fact, the proportion of bee flowers in communities across analysed studies was surprisingly similar, regardless of how biomes are grouped together (Figure 2). These results are also supported by local pollination studies that, due to our criteria, were excluded from our community survey search, including studies that sampled woody plants only (Kang and Bawa 2003; Martins and Batalha 2006) and studies focused on the pollination of native edible plants only (Paz et al. 2021). Interestingly, our results also show that local bee diversity is not a good predictor of the proportion of bee flowers in a floristic community (Figure 3), further supporting the idea that flowering plant communities of areas where bee diversity is low are not necessarily less bee dependent.

4.2 | Are Syndrome-Only Studies Overestimating the Proportion of Bee-Pollinated Species?

An unforeseen result of our analyses was the significantly higher proportion of bee-flowers recovered in community surveys based solely on the pollination syndrome concept (following Faegri and van der Pijl 1979). There is ongoing debate about whether pollination syndromes can reliably predict the main functional group of pollinators of a plant species, with arguments both supporting their utility (Fenster et al. 2004; Rosas-Guerrero et al. 2014) and advising caution (Ollerton et al. 2009; see also Dellinger 2020 for a recent review on the syndrome concept). Though the exploratory removal of studies based only on syndromes did not change our main results (Figures S5–S7), the disparity in the proportion of bee-flowers recovered by studies using different methodologies may support either side of this debate. Initially, one may think that studies based on syndrome only may be overestimating the total number of bee-flowers in a community, perhaps because generalist flowers are mistakenly categorised as bee-flowers (Ollerton et al. 2009). Although this possibility cannot be discarded, it can also be argued that pollination syndromes result from successful interactions between flowers and effective pollinators that often play out through large evolutionary timescales, and these interactions may be missed by point field observations, especially those that do not test for effective pollination. In this sense, we echo Dellinger (2020) in calling for more studies that combine both pollination syndromes and direct observations of potential pollinations in the field, as well as studies that effectively test pollination success in the field by measuring reproductive outcomes such as seed set.

4.3 | Bee Life History Traits Might Explain Observed Spatial Patterns of Bee Flower Diversity

If local bee diversity and biome type are not good predictors of the proportion of bee flowers in a community, other predictors might be put forward to explain variation (or lack thereof) in the proportion of bee flower species in a community. In our results, the most consistent predictor of the proportion of bee flowers in a community in both significance and effect size was precipitation seasonality (Figure 3). If a higher proportion of bee flowers is found in areas with lower precipitation seasonality, we might infer that either more seasonal environments preclude the establishment of bee flowers or that less seasonal environments benefit the establishment of bee flowers. In the specific context of our data, precipitation seasonality is lowest in plant communities from tropical rainforests (Figure S8). An explanation for this pattern might be related to the potential correlation between precipitation seasonality and two key bee life history traits: sociality and floral-specialisation. The consistent availability of floral resources in tropical rainforests may have facilitated the dominance of eusocial bee species, which forage year-round to sustain their large, perennial colonies, in contrast to solitary bees which often have more constrained phenologies (Michener 2007; Danforth et al. 2019). This may lead to more generalised bee–flower interactions, as individual bee species tend to visit a wider variety of plant species (Roubik 1992; Schleuning et al. 2012; e.g., Martins et al. 2023).

From the angiosperm standpoint, a more generalised bee-flower system may translate into greater flexibility to evolve a broader suite of floral strategies that can attract bee pollinators, consistent with the idea that a higher proportion of plant species are bee-pollinated in those areas. Besides eusocial bees, other bee functional guilds, such as orchid bees and oil-collecting bees, are also more diverse in neotropical regions (Michener 2007; Ascher and Pickering 2024). This means that even though these areas are not as rich in absolute number of bee species as deserts in mid-latitudes, the functional diversity of bees might be similar or even higher, again leading to a potentially broader range of floral strategies that are compatible with bee pollination. It is also important to consider that diversity and abundance are not necessarily linked, and a species-poor pollinator pool may still be abundant enough to provide adequate pollination service to a floristic community. This is especially important when we consider that tropical areas have a larger proportion of eusocial bee species, whose colonies can harbour millions of individuals willing to visit a broad number of floral resources (Michener 2007; Grüter 2020). Although some of these explanations are speculative at this point, they provide a foundation for further studies that aim at investigating how co-occurring bee species partition their foraging preferences throughout the year may help clarify whether the dynamics of bee-floral interaction are spatially variable.

4.4 | Sampling Biases and Other Caveats

Although we took precautions to reduce the impact of sampling biases in bee diversity estimates in the tropics (e.g., by merging data from GBIF with data from species lists), it is still likely that these numbers are underestimated. The magnitude of this underestimation is, however, unclear. Bee species richness is negatively associated with forest cover at the global scale (Orr et al. 2021). However, canopies may be undersampled, and patterns may vary between bee families (Russell et al. 2024). Depending on the group and its foraging behaviour, the canopy can be preferred over the understory (Dorey et al. 2023). However, active canopy sampling is rarely implemented in tropical forests (Prado et al. 2017). Finally, bee collections in the global south are largely not digitised (Bartomeus et al. 2019), which may also lead to diversity underestimation in these areas. We believe that the general trend of relative bee diversity across the Americas will remain consistent even once these biases are corrected; however, because angiosperm species richness is still much higher in tropical forests than in temperate regions (Eiserhardt et al. 2017), and because the hotspots of bee species under-description are all predicted to be in xeric or temperate environments (Orr et al. 2021). Tropical forests and savannas also have a relatively larger diversity of other animal pollination groups when compared to other regions (Ollerton 2017). Butterflies, bats, moths, hummingbirds, and other bird pollinators have increased diversity in the tropics (Ollerton 2017), potentially enabling a more diverse plethora of pollination systems. We acknowledge that the majority of the community surveys that we used in our calculations consider only pollination observations performed during the day. Therefore, the surveys might underestimate nocturnal pollination systems (e.g., bats, hawkmoths, and nocturnal bees). Bats, for instance, usually represent around 4% of the total pollination visitation in the Neotropics; however, this figure may be underestimated due to the difficulties of observing pollinators in the forest canopy at night (e.g., Aguiar et al. 2024).

We also likely have a non-ideal account of the proportion of species that do not depend on pollinators at all (selfing and apomictic) and those pollinated by abiotic factors in the studies surveyed. Given that the diversity of grasses, the largest clade to be almost completely pollinated by wind (Linder et al. 2018), peaks in open areas in the tropics, we believe that, at least in these biomes, the proportion of wind-pollinated species is probably underestimated. Even when considering the same area, the proportion of plant species in each pollination system can vary temporarily, for example, by changes in the amount of disturbance such as fire (Deus and Oliveira 2016) and at relatively small spatial scales, for example, along an elevation transect in the same site, and these might also be sources of noise in our analyses. Finally, it is important to consider that, in most cases, these studies are utilising proxies for bee pollination—usually a combination of floral visitation and morphology—rather than pollination per se, which would also require measuring fruit set and stigmatic contact. We also did not account for the impact of introduced bee species such as the honeybee *Apis mellifera*, which was recorded in several of the community surveys and can potentially drive the number of bee-pollinated species up in some instances (see also Iwasaki and Hogendoorn 2022). They have been shown to dominate the pollination networks in biome-wide analysis (Aguiar et al. 2024), competing with and displacing native bees for resources (Pasquali et al. 2025).

5 | Conclusions

Here, we show that local relative bee diversity does not explain the variation in the proportion of bee-pollinated flowers in plant communities across the Americas, and that around half of the species in plant communities across the Americas may depend on bees for pollination. In the tropics, we hypothesise that lower bee diversity may be compensated for by the high abundance of eusocial bees, whose perennial nests are favoured in conditions of low seasonality. If tropical regions are highly bee dependent despite low local bee diversity, this could result in more generalised bee-flower interactions, with many angiosperm species relying on a smaller number of bee species. These dynamics could have consequences for the reproductive biology of tropical plants, including the timing of flowering, rates of interspecific pollen deposition, mechanisms maintaining genetic barriers, and hybridisation rates. However, the potential effects of poor bee sampling in tropical rainforests remain a significant gap that needs to be addressed before this pattern can be fully understood. To fully understand these interactions, it is crucial to improve our knowledge of tropical bee diversity, especially in poorly sampled regions like canopies of tropical rainforests that are under intense anthropogenic pressure. Similar studies should be performed in other areas to assess whether this pattern is exclusive to the American continent or a global trend.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data, results and analytical R codes used in our analysis are deposited at https://doi.org/10.5281/zenodo.14585236.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70101-sup-0001-DataS1.docx. **Data S2:** geb70101-sup-0002-DataS2.xlsx.