

## RESEARCH ARTICLE

# Pollinator intraspecific body size variation and sociality influence their interactions with plants

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## Abstract

1. Species morphological and behavioural traits are key determinants of which pollinator species interact with which plant species. However, individuals within species are not identical in their traits and this diversity could help us understand plant–pollinator interaction patterns.
2. Using three independent data sets, we assessed whether bee intraspecific body size variation (ITV) and sociality influenced pollinator interaction specialisation, intraspecific niche partitioning, centrality in the interaction network and phylogenetic diversity of the plants visited.
3. We found that solitary pollinators were more specialised in their interactions with plants and had lower intraspecific niche partitioning compared to social pollinators. Furthermore, solitary pollinators with higher ITV had higher centrality in the network and visited a higher phylogenetic diversity of plants compared to solitary species with lower ITV, whereas the opposite pattern emerged for social pollinators. Pollinator ITV did not differ between social and solitary bee species.
4. Our findings show that the effect of pollinator body size variation on plant–pollinator interactions depends on pollinator species sociality. Specifically, solitary pollinators with higher ITV and social pollinators with lower ITV seem to be the most important contributors to maintaining the evolutionary diversity of the plant community, and also the species with the largest potential to affect (via cascade effects) the entire plant–pollinator network.

## KEYWORDS

bee, intraspecific trait variability, plant phylogeny, plant–pollinator interactions, social, solitary, specialisation, species role

## 1 | INTRODUCTION

Resource use partitioning among species in a community is often driven by differences in morphological traits among species. Therefore, competition should be strong among morphologically similar species co-occurring in the same area, and species with more extreme trait values should occupy empty corners of the niche space. Similarly, individuals

within the same species can vary in their morphological traits (Grass et al., 2021), defining the boundaries of intraspecific trait variation (ITV). Despite the ecological implications ITV can have on populations and communities, its influence on animal species niches has been neglected compared to that of interspecific trait variation (Bolnick et al., 2011).

Species traits influence multiple dimensions of their niches, such as species feeding specialisation (Raiol et al., 2021; Smith, Weinman,

et al., 2019), but whether ITV also influences those niche dimensions is not well understood. For instance, ITV could allow the consumption of a broad range of resources, decreasing species feeding specialisation, by promoting niche partitioning among individuals from the same species. Consequently, increased interaction specialisation of the individuals within a species (Bolnick et al., 2007) can influence their fitness (Soares et al., 2021), and potentially their ecological importance for their interaction partners. Furthermore, ITV may impact evolutionary aspects of communities, by allowing individuals of the same species to interact with partners from different phylogenetic lineages, thereby contributing to the maintenance of the interaction partner's community evolutionary diversity (Dehling et al., 2022).

Species co-occurrence not only depends on resource partitioning but also on a myriad of direct and indirect interactions with other species in the community and with their environment, which are also affected by species traits. This influence of traits on interactions could impact trait or trait variability selection by altering trade-offs between resource competition avoidance and mutualistic interactions with other species (Coux et al., 2016). Therefore, a species interaction network approach, which incorporates information on both direct and indirect interactions in the community, could be useful to understand the link between ITV and species roles (Cirtwill et al., 2018). For instance, species with high ITV might have a higher number of direct and indirect interactions, compared to species with low ITV, therefore occupying central roles in the community and exerting stronger effects on community dynamics. Furthermore, understanding the relationship between ITV and species roles in ecological networks could shed light into whether studies using mean trait values are missing relevant patterns.

Although multiple traits influence species interactions, body size has been identified as a master trait, tightly linked with many physiological and ecological processes (Grula et al., 2021; Peralta et al., 2023). For instance, body size is related to pollinator species foraging ranges, resource consumption and ecosystem functions (Földesi et al., 2021; Goulson et al., 2002; Greenleaf et al., 2007). Hence, intraspecific body size variation could be a useful proxy of ITV with which to understand ITV effects on community-level interaction patterns.

Besides morphological traits, behavioural characteristics, such as species sociality, can also influence species interactions (Smolla et al., 2016). Compared to solitary species, social species tend to have higher abundances, longer activity periods and foraging ranges (Grüter & Hayes, 2022; Michener, 2007), which may promote interactions with a larger array of interaction partners (Fort et al., 2016; Olesen et al., 2008). Furthermore, consuming a wider variety of resources could result in larger morphological variation among social species offspring, compared to solitary species, as body size variation is influenced by nutrition during early stages (Nicholls et al., 2021). In addition, individuals from the same social species can have morphological differences that may promote ITV, such as different castes in social pollinators. However, whether the effects of species sociality on species interactions are related to, or coupled with, trait variability is still unclear, despite the considerable

intraspecific trait variation present both in social and solitary species (Chole et al., 2019). Therefore, understanding the potentially interactive effects species sociality and ITV have on species interactions, could help us untangle the drivers of species interaction patterns at the community level.

Here, we assessed the relationship between pollinator ITV, social behaviour and pollinator interactions with plants. Specifically, we first evaluated whether pollinator intraspecific body size variation was related to their social nesting behaviour. We then assessed whether pollinator intraspecific body size variation and pollinator species sociality influence pollinator specialisation, intraspecific niche partitioning, the phylogenetic diversity of plants visited by pollinators and pollinator species centrality in the plant–pollinator interaction network. To accomplish this, we used three data sets, sampled in a replicated manner, that contained information on plant–bee interactions and bee body size measurements taken at the individual level.

## 2 | MATERIALS AND METHODS

To assess the effects of pollinator ITV and sociality on their interactions with plants, we used three data sets from Western North America, sampled in mixed grass prairie rangelands (Alberta, Canada; Worthy et al., 2023a), subalpine meadows (Colorado, USA; Resasco et al., 2021) and conifer forests (Western Montana, USA; Burkle et al., 2019). Each data set contained plant–bee interactions (observations of bees touching the reproductive parts of the flower) sampled at the community level in a spatially and temporally replicated manner (Supporting Information). The use of these three data sets, sampled in different environments, allowed us to assess the generality of the studied relationships. Furthermore, these data sets have a variety of species and body sizes representing the major families of bees Apidae, Megachilidae, Halictidae, Andrenidae and Colletidae.

We focused on plant–bee interactions because bees were the common group across all data sets and because doing so allowed us to incorporate sociality in our analyses as a behavioural variable of interest. We built a meta-network for each data set by combining all plant–bee interactions across all the spatially and temporally replicated networks within each data set (Figures S1–S3). We used the total number of bee individuals per species observed in each meta-network as estimates of pollinator species abundances, which was positively related to species phenology (Supporting Information).

### 2.1 | Bee body size, body size variation and sociality

We measured bee body size as intertegular distance or body width (see Supporting Information for a description of how body size was measured on each data set) as this morphological trait is related to species ability to interact with plant partners (Peralta et al., 2023) and is correlated with other morphological traits related to resource

consumption (Cariveau et al., 2016). We measured body size from all the flower visitors collected, regardless of the cast they belonged to. Each data set had measurements of bee body size for at least 10 individuals per species for more than 10 species per data set (Burkle, 2024; Resasco & Manning, 2024; Worthy et al., 2023b), from which we estimated ITV. To estimate bee ITV, we calculated the coefficient of variation ( $CV = \text{standard deviation}/\text{mean}$ ) of the body size of 10 randomly selected bee individuals per species. High CV values indicate high variation in body size among individuals of a species, whereas low CV values indicate similar body sizes of individuals within a species. The number of species from which we could estimate ITV values, and hence used in our analyses, represented 22%, 13% and 23% of the bee species in the Alberta, Colorado and Montana data set, respectively.

We also classified bee species based on their nesting habits into social (including eusocial behaviour or species presumed to be eusocial) or solitary. Social bee species are those for which individuals live together in colonies regardless of labour division. Conversely, we considered solitary bee species as those whose individual females build a nest and provision for their offspring alone. To classify the species according to their social nesting habits, we consulted the literature, taxonomic experts and the Bees of Canada Royal Saskatchewan Museum website.

## 2.2 | Bee species specialisation, intraspecific niche partitioning and species centrality

To describe bee species specialisation, intraspecific niche partitioning and bee species centrality within the plant–pollinator interaction network, we used bee species normalised degree, species specificity and closeness centrality metrics, respectively. Normalised degree was estimated as the number of links per bee species scaled by the number of possible plant partners, with lower values representing specialist pollinators and higher values representing generalist pollinators. Species specificity was measured as Shannon's entropy, which quantifies the evenness in a bee species' interactions within its range of partners. Shannon's entropy varies between 0 and 1, with 0 indicating that the interactions of bee individuals of a given species are distributed evenly across plant species (indicating higher intraspecific niche partitioning) and 1 indicating perfect specialisation among individuals (indicating lower intraspecific niche partitioning) (Schug et al., 2005). Lastly, closeness centrality (hereafter 'centrality') represents the distance of each bee species to all the other species in the network via their shortest path lengths. Higher centrality values indicate bee species are highly connected to other species in the interaction network, and hence can have a stronger impact on community dynamics. All metrics were calculated from the plant–bee meta-network of each data set. Indices were obtained using the species level and CC functions from the bipartite v 2.17 R package (Dormann et al., 2008), except for bee specificity, which was estimated using the getspe function from the ESM v 2.0.3–02 R package (Poisot, 2011).

## 2.3 | Phylogenetic diversity of plants visited

To estimate the evolutionary diversity of the plants visited by each bee species, we first constructed one plant phylogeny for each data set using the phylo.maker function from the V.PhylMaker v 0.1.0 R package (Jin & Qian, 2019). This R function derives phylogenies based on available mega-trees (Smith & Brown, 2018; Zanne et al., 2014) generated based on molecular data. We then estimated the phylogenetic diversity of plants visited by bees as the sum of the plant phylogeny branch lengths that connect the plant species interacting with each bee species (Dehling et al., 2022) of each meta-network, using the phylo\_niche function (Dehling et al., 2022).

## 2.4 | Replication statement

To understand how pollinator intraspecific trait variation (ITV) and social behaviour (social vs. solitary) affect their interactions with plants, we estimated ITV from 22 social and 51 solitary pollinator species. The scale of inference is, hence, the species level. The variables of interest are ITV (continuous variable) and social/solitary behaviour (factor), both of which differ at the scale of species. The unit of replication at the appropriate level is 22 and 51 for each factor level.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Species	22 social, 51 solitary

## 2.5 | Analyses

To assess whether bee ITV was related to species sociality, we used a linear mixed effects model, with bee species ITV as the response variable and species sociality (social vs. solitary) as the predictor variable. We also included bee species abundance as a covariate, to control for potential differences in trait variation due to abundance, and data set and species ID as random factors to account for lack of independence of bee species from the same data set (i.e. cannot be directly compared with species from other data sets) and of species that appear across different data sets. We log-transformed the response variable to fulfil the normality and homoscedasticity assumptions of the linear model.

To determine whether bee species specialisation, specificity (as an estimate of intraspecific niche partitioning), centrality and phylogenetic diversity of plants visited were influenced by bee ITV and sociality, we used four linear mixed effects models. In the first model, we included bee species specialisation (normalised degree) as the response variable and bee species ITV and sociality (social vs. solitary) as predictor variables. We also included an interaction term between the predictor variables to assess whether the effect of ITV on specialisation changed

depending on species sociality. We incorporated bee species abundance as a covariate to account for the fact that less abundant species tend to be more specialised (Fort et al., 2016), and data set and bee species ID as random factors. In the subsequent models, we entered bee specificity, centrality and phylogenetic diversity of the plants visited as the response variables, respectively, and used the same fixed, random and covariate variables as in the first model. To fulfil the normality and homoscedasticity assumptions of the linear models, we squared-root transformed normalised degree, centrality and phylogenetic diversity of the plants visited response variables. In addition, we removed an observation in the centrality model to fulfil the heteroscedasticity assumption, though keeping this data point did not qualitatively affect the results. We checked the normality and homoscedasticity assumptions of the linear models by visually inspecting the residuals, using Q-Q plots and residual versus fitted value plots. We used the lmer function from the lme4 v 1.1–29 (Bates & Maechler, 2009) and lmerTest v 3.1–3 (Kuznetsova et al., 2017) R packages to fit the models. All analyses were conducted in R v 4.2.0 (R Core Team, 2022).

### 3 | RESULTS

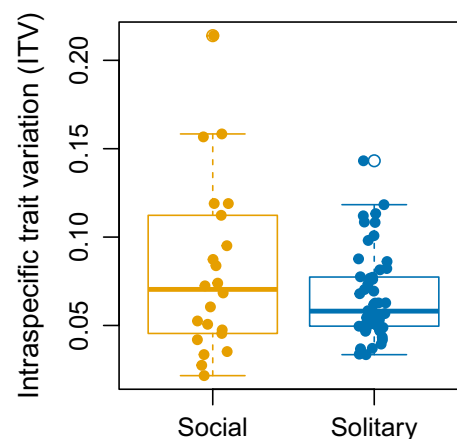
The Alberta plant-bee data set registered 865 plant-bee interactions (between 33 plant species and 72 bee species), the Colorado data set registered 1007 plant-bee interactions (between 34 plant species and 103 bee species), and the Western Montana data set registered 2579 plant-bee interactions (between 111 plant species and 191 bee species). We estimated intraspecific body size variation (ITV) for 16, 13 and 44 bee species in each data set (Figures S1–S3, respectively), finding ITV ranges (min–max) of 0.05–0.16, 0.03–0.21 and 0.02–0.14, respectively. We did not find any significant relationship between bee species ITV and sociality ( $t = -0.426$ ,  $p = 0.672$ , Figure 1) or bee abundance ( $t = 0.462$ ,  $p = 0.646$ ).

We found no effect of bee ITV on bee specialisation ( $t = -0.671$ ,  $p = 0.505$ ) and specificity ( $t = 0.686$ ,  $p = 0.505$ ), but found significant effects of sociality on bee specialisation and specificity. Specifically, solitary species were more specialised (had lower normalised degree,  $t = -2.487$ ,  $p = 0.016$ ) and had higher specificity (i.e. lower niche partitioning) within species ( $t = 3.500$ ,  $p = 0.001$ ) compared to social species (Table S1; Figure 2).

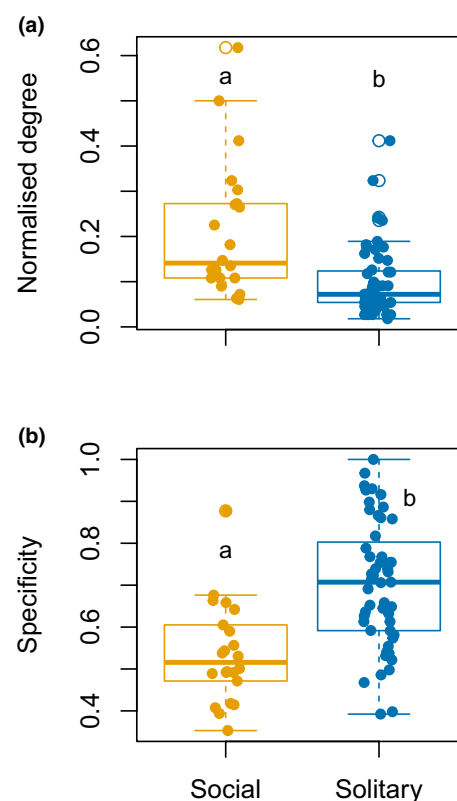
Finally, we found a significant interaction between bee ITV and sociality when assessing their effects on bee centrality and phylogenetic diversity of plants visited by bees (ITV  $\times$  sociality interaction term:  $t = 2.180$ ,  $p = 0.043$  and  $t = 2.148$ ,  $p = 0.040$ , respectively). In particular, bee ITV had a positive effect on bee centrality and the phylogenetic diversity of plants visited by solitary species, whereas the opposite was observed for social species (Table S1; Figure 3).

### 4 | DISCUSSION

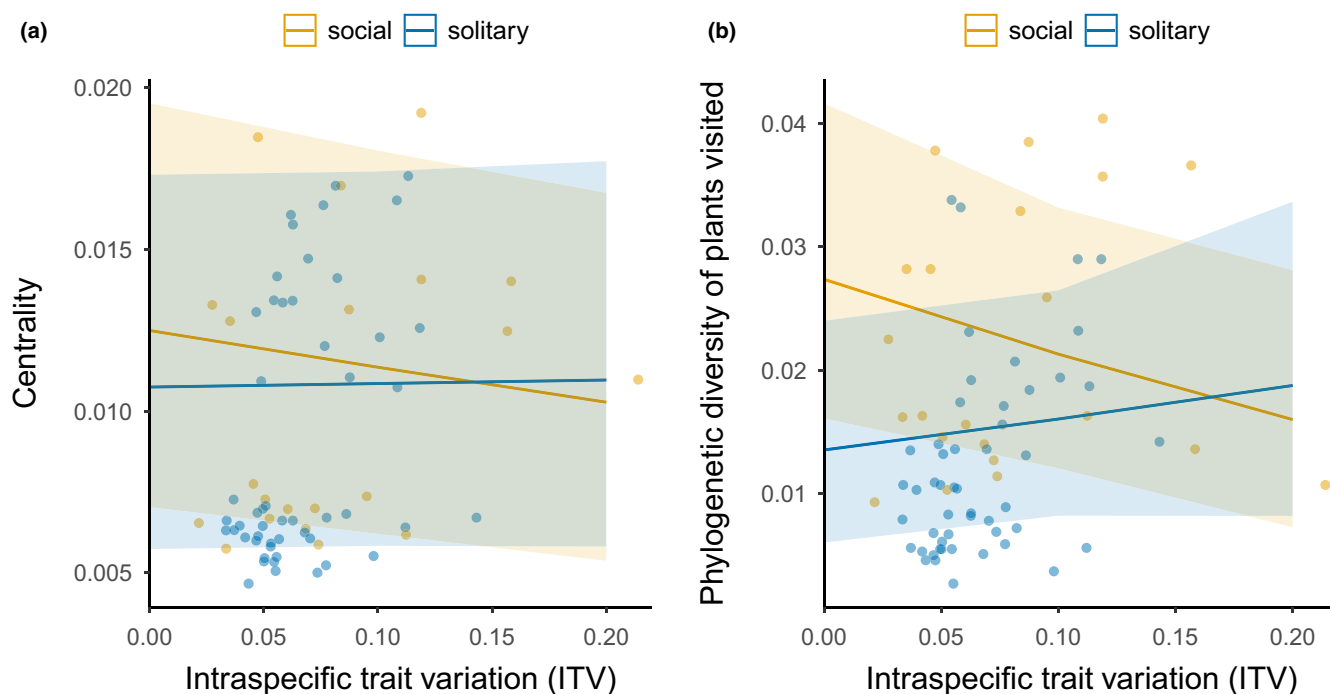
Pollinator individuals within species are morphologically variable (Dellicour et al., 2017; Gavini et al., 2020), but whether this variation



**FIGURE 1** Intraspecific trait (body size) variation (measured as coefficient of variation) for social and solitary bee species. In each box plot, the middle line indicates the median; bottom and top box limits are the first and third quartiles, respectively. Whiskers indicate the most extreme points 1.5 times the interquartile range, and open circles indicate outliers. Data points are displayed using the jitter method.



**FIGURE 2** Normalised degree (A) and specificity (B) for social and solitary bee species. Different letters represent significant differences ( $\alpha = 0.05$ ). In each box plot, the middle line indicates the median; bottom and top box limits are the first and third quartiles, respectively. Whiskers indicate the most extreme points 1.5 times the interquartile range, and open circles indicate outliers. Data points are displayed using the jitter method.



**FIGURE 3** Relationship between bee intraspecific trait (body size) variation and (a) centrality and (b) the phylogenetic diversity of plants visited by bees in the plant–bee interaction network for social and solitary species. Shaded areas represent the 90% confidence intervals.

is associated with species sociality, and whether such factors influence their interaction patterns remains largely unexplored. We found that intraspecific body size variation (ITV) in bee pollinators did not differ between social and solitary species, nor did it affect species feeding specialisation. However, pollinator ITV affected their centrality in the plant–pollinator network and the phylogenetic diversity of the plant partners with which they interacted, and these effects of ITV differed between social and solitary pollinator species. Furthermore, pollinator feeding specialisation and niche partitioning differed between social and solitary pollinator species.

Variation in body size within species was similar between social and solitary bees, despite the fact that social insect species can have different castes with associated body size variation, and hence suggesting these species could have higher intraspecific variation compared to solitary species. For example, bumble bee species include queens, female workers and male drones, which exhibit size variation, and even workers within the same colony may vary widely in their body size (Chole et al., 2019; Couvillon & Dornhaus, 2009). These particular species may explain the highest ITV values being reached by social species in some of our data sets, though trait variation can differ considerably among social species (Couvillon & Dornhaus, 2010; Peat et al., 2005; Roulston & Cane, 2000). The nesting environment of social pollinators regulates micro-environmental aspects of their nests that impact brood development and body size (Chole et al., 2019), potentially limiting the variation in traits of most species. Conversely, each individual from a solitary pollinator species has its own nest, and hence, the species as a whole could be subjected to higher environmental variability and seasonal fluctuations impacting

larval development and trait variation (Gerard et al., 2018; Scriven et al., 2016). Therefore, the amount of trait variation generated by the presence of different castes in social pollinators and due to different nest environments in solitary pollinators could contribute to make trait variation more similar among pollinators with different behaviour.

Although bee species specialisation and niche partitioning were not affected by ITV, these species attributes differed between bees with different social behaviour. Specifically, social species had higher feeding generalism and lower specificity, compared to solitary species. Social bees are known to have larger foraging ranges than solitary bees (Grüter & Hayes, 2022), which may allow social species to disperse longer distances, reaching a larger variety of resources. Furthermore, social species tend to be more abundant and have longer activity periods than solitary species, which may contribute to phenological overlap with a larger number of potential plant partners and, hence, increasing their feeding generalism. Conversely, solitary bee species' reproductive success seems to be favoured when bees can forage in nearby areas (Peterson et al., 2006; Zurbuchen et al., 2010), limiting the number of resources available. In addition, social species, such as honey bees, share information among the individuals of the same colony about resource location (Nürnberg et al., 2019), which could explain the fact that social species had interactions distributed evenly across plant species (i.e. higher niche partitioning among individuals of the same species).

The influence of ITV on the phylogenetic diversity of plants visited by bees and on bee species centrality in the interaction network depended on species sociality. In particular, solitary species with higher ITV interacted with a more diverse phylogenetic range of partners and,



consequently, were more connected with other species in the community compared to solitary species with lower ITV. By contrast, social species with higher ITV tended to interact with plants representing a narrower range of phylogenetic diversity and have lower centrality in the network compared to social species with low ITV. Because high ITV could help species to adapt to environmental changes (Henn et al., 2018), the fact that social species with high ITV interacted with a smaller pool of phylogenetically diverse plant species suggests these pollinators could be more susceptible to changes in fewer plant lineages compared to social pollinators with lower ITV. Nevertheless, the high feeding generalism of social species compared to solitary species indicates social bees have a larger number of plant species to switch from in the search for resources. Finally, assuming visitation to floral reproductive organs represents pollination events (Peralta et al., 2020; Vázquez et al., 2005), solitary pollinators with higher ITV and social pollinators with lower ITV are the most important partners from the plant community perspective. Also, changes in their population dynamics have the largest potential to transmit faster throughout the plant–pollinator network (Martín González et al., 2010; Memmott et al., 2004).

Previous research has highlighted the prominent role social pollinator species have in interaction networks compared to solitary species (Maia et al., 2019; Pires et al., 2022). Our findings reflect that a large number of solitary species tend to have lower centrality values, though those solitary species that do have more central roles in the networks had high ITV. This indicates that changes in the population dynamics of solitary pollinators with high ITV, due to environmental and/or seasonal fluctuations, can rapidly spread throughout the community. Nevertheless, it remains to be assessed whether solitary pollinators with high ITV are less susceptible to environmental changes and whether this has contributed through their evolutionary history to increase the phylogenetic diversity of the plants with which they interact.

Because we estimated ITV based on one trait only (body size), we cannot rule out that other traits could influence species feeding specialisation. However, body size tends to be correlated with other traits also related to feeding, such as proboscis length and home ranges (Cariveau et al., 2016; Greenleaf et al., 2007). Assessing the influence of ITV on other niche dimensions of species (e.g. nesting places, phenology, etc.) may provide useful information on species responses to environmental changes. Furthermore, behaviour and morphological traits related to sex-specific resource use may also contribute to explain niche breadth and niche overlap within species (Maglianesi et al., 2022), as females tend to gather different resources from flowers compared to males (Smith et al., 2022; Smith, Bronstein, et al., 2019). Evaluating whether sex differences in ITV contribute to explain such patterns remains to be tested.

Intraspecific trait variation and behaviour represent important adaptations for the survival of species as they can influence species' ability to adjust to diverse abiotic and biotic conditions. We showed that social and solitary pollinators had similar ITV, though they differed in their degree of specialisation across and within species. Furthermore, beyond the known central role social pollinators play in

plant–pollinator communities (Maia et al., 2019; Pires et al., 2022), solitary pollinators can also play prominent roles in the community, especially those species with high ITV. This reinforces the idea that solitary pollinators not only are important contributors to ecosystem functions (Bänsch et al., 2021; Garibaldi et al., 2013) but also that changes in their population dynamics can rapidly spread through the community. Understanding the influence of behavioural and morphological traits, as well as their variation, in species interaction patterns will allow us to predict changes in interaction networks and community dynamics.

## AUTHOR CONTRIBUTIONS

GP conceived the idea with input from LC; LAB, JR, SW, CMF, ATG, IM collected the data; GP curated the data sets and performed the analyses; GP wrote the first draft of the manuscript with input from LB; all authors contributed substantially to revisions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data sets used in this paper are available from <https://doi.org/10.5061/dryad.1vhmgqzg> (Worthy et al., 2023b), <https://doi.org/10.5061/dryad.rfj6q579h> (Resasco et al., 2021), <https://figshare.com/s/1f8fafef4e5441a199dc> (Resasco & Manning, 2024), <https://doi.org/10.5061/dryad.stjq2c4m> (Burkle et al., 2022), [https://figshare.com/articles/dataset/Pollinator\\_intertegular\\_distance/25008425/1](https://figshare.com/articles/dataset/Pollinator_intertegular_distance/25008425/1) (Burkle, 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Dataset description and supplementary figures, analysis and table.

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