




## LETTER

# Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions

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### Abstract

Morphology and phenology influence plant–pollinator network structure, but whether they generate more stable pairwise interactions with higher pollination success remains unknown. Here we evaluate the importance of morphological trait matching, phenological overlap and specialisation for the spatio-temporal stability (measured as variability) of plant–pollinator interactions and for pollination success, while controlling for species' abundance. To this end, we combined a 6-year plant–pollinator interaction dataset, with information on species traits, phenologies, specialisation, abundance and pollination success, into structural equation models. Interactions among abundant plants and pollinators with well-matched traits and phenologies formed the stable and functional backbone of the pollination network, whereas poorly matched interactions were variable in time and had lower pollination success. We conclude that phenological overlap could be more useful for predicting changes in species interactions than species abundances, and that non-random extinction of species with well-matched traits could decrease the stability of interactions within communities and reduce their functioning.

### Keywords

Abundance, interaction frequency, pollination success, pollinator impact, spatial variability, specialisation, temporal variability.

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## INTRODUCTION

Understanding the mechanisms that determine species interactions and interaction network patterns is critical for predicting changes in community structure and ecosystem function. Research on networks of species interactions has moved from assessing static interaction patterns towards evaluating the temporal variability of species interactions (Trøjelsgaard & Olesen 2016). For instance, recent studies on plant–pollinator interactions show that interactions frequently vary across space and time (Petanidou *et al.* 2008; Trøjelsgaard *et al.* 2015), and that this variability is underpinned by species turnover and interaction rewiring (Trøjelsgaard *et al.* 2015; Burkle *et al.* 2016; Rabeling *et al.* 2019). However, the mechanisms that make individual plant–pollinator interactions more or less persistent in space and time (i.e. what makes an interaction more stable), and whether the mechanisms determining species interaction frequencies are also responsible for determining the stability of interactions, remain uncertain.

Among the drivers of plant–pollinator interactions, species phenology, morphology and abundance have extremely important roles (Stang *et al.* 2007; Krishna *et al.* 2008; Vázquez *et al.* 2009b). Abundant species, for example, are

more likely to randomly encounter each other and interact (Canard *et al.* 2012, 2014), hence increasing species interaction probability among potentially interacting species. However, if species are abundant at different times (i.e. species have non-overlapping phenologies), then the likelihood of them interacting is likely to decline. Therefore, the influence of species abundance on interactions may be better represented by the phenological overlap of the interacting species (i.e. the amount of time interacting species co-occur), rather than total abundance. Phenological overlap is not just a result of species abundances (abundant species have longer phenologies and hence increase the chances of phenological overlap, Gillespie *et al.* 2017), but also depends on species characteristics (i.e. the timing of phenological stages, Pleasants 1990), and on the interaction between species characteristics and abundance (i.e. changes in the timing of phenological stages induced by changes in species abundance, Wolf *et al.* 2017). Phenological overlap can, therefore, be an extremely important predictor of the occurrence and frequency of species interactions, but could also play an important role in the temporal and spatial dynamics of species interactions. For instance, if a plant and a pollinator species have highly overlapping phenologies across multiple years, it will be more likely that the

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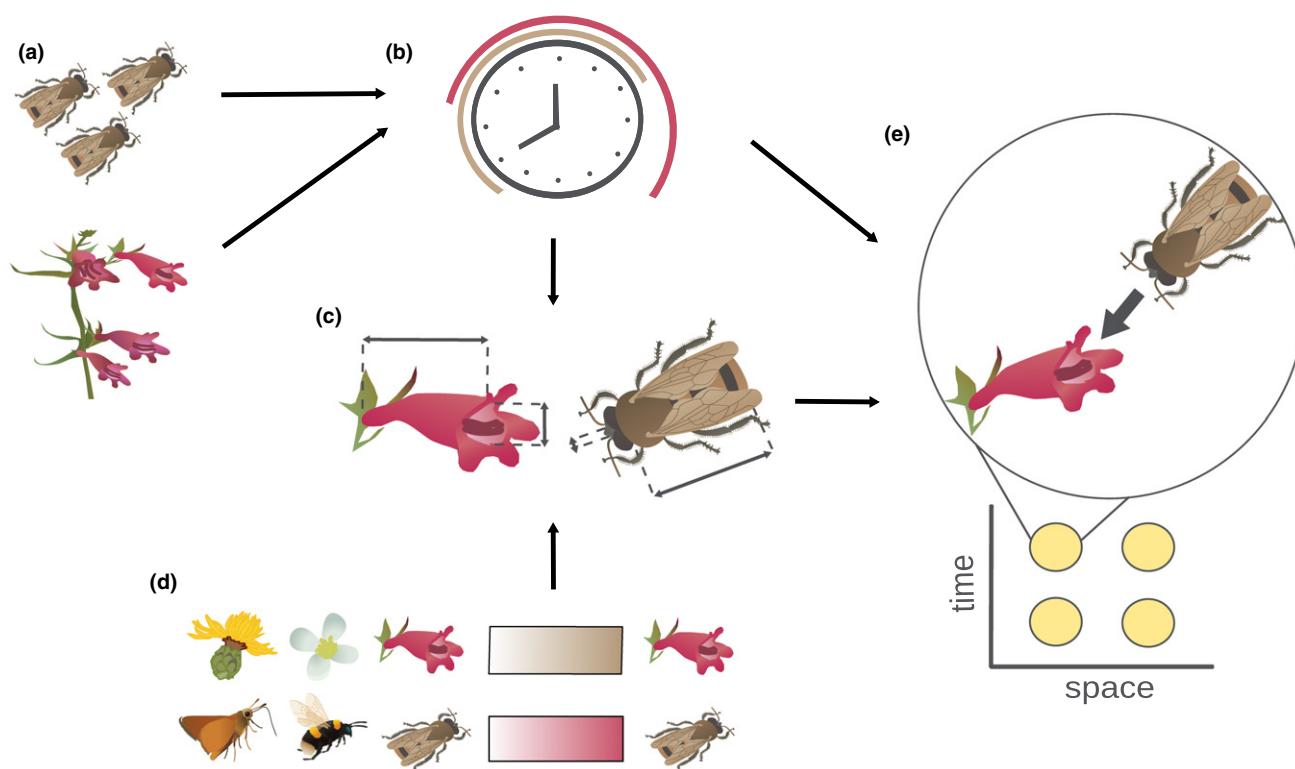
interaction between those two species will occur in multiple years (i.e. will be more stable across time), compared with two interacting species whose phenologies have little overlap (Fig. 1a, b and e).

Phenological overlap between plant and pollinator species can persist over long periods (evolutionary time) and, by allowing species to consistently interact more strongly, it can facilitate evolution of trait matching among interacting species (Lomáscolo *et al.* 2019) (Fig. 1b and c). Furthermore, it has been suggested that trait matching might occur or coevolve to improve efficiency in the removal and deposition of pollen and/or as a way to favour the acquisition of greater rewards. For instance, if a pollinator obtains greater feeding rewards from flowers with traits matching the pollinator's, then the pollinator might preferentially visit that plant species and thus increase the interaction frequency between those species (Klumpers *et al.* 2019). Therefore, trait matching is an important predictor of network architecture and species interactions (Santamaría & Rodríguez-Gironés 2007; Stang *et al.* 2009). In addition, networks may contain a persistent (i.e. occur consistently through time and space) core of well-matched high-reward coevolved interactions, with additional interactions between poorly matched species being more opportunistic and easily disrupted (Tylianakis & Morris 2017; Chacoff *et al.* 2018), and, hence, more variable (Fig. 1c and e).

The evolution of trait matching among plants and pollinators seems to be affected by species' trophic specialisation and

the asymmetries in specialisation among interacting species (Anderson *et al.* 2010; Klumpers *et al.* 2019). For example, if a pollinator forages on different plant species, it may be less likely to match a particular focal plant species than if it were foraging on that species alone (Anderson *et al.* 2010). Hence, specialisation of both interacting partners might indirectly increase the spatial and temporal stability of interactions by promoting trait matching (Fig. 1d, c and e). However, these specialised interactions may be more vulnerable to extinction (Aizen *et al.* 2012), which would make them less stable. Nevertheless, assessing the effect of specialisation on interaction stability requires controlling for the effects of species abundances (Winfree *et al.* 2014), as rare (less abundant) species could present apparent specialisation (Dorado *et al.* 2011).

Trait matching could also play an important role in the functional outcome of plant–pollinator interactions, such as pollination success. For instance, although imperfect trait matching does not imply a complete functional mismatch (Memmott *et al.* 2004; Solís-Montero & Vallejo-Marín 2017), strong trait matching between interacting plant and pollinator species increases pollinator foraging efficiency (Klumpers *et al.* 2019), and can favour fruit set in crop plants (Garibaldi *et al.* 2015). Furthermore, pollination success relies on *per capita* (i.e. per-visit) efficacy of each pollinator species on plant reproduction and interaction frequency (Vázquez *et al.* 2012), both of which could be influenced by trait matching (Klumpers *et al.* 2019). Specifically, if increased trait matching results in a



**Figure 1** Conceptual figure showing the potential determinants of plant–pollinator interaction frequency and the spatial and temporal variability of interactions. (a) Abundance of a plant species and a pollinator species; (b) plant–pollinator phenological overlap; (c) plant and pollinator morphological traits, used to estimate trait matching between species; (d) plant and pollinator species specialisation; (e) plant–pollinator interaction frequency and spatio-temporal variability of interactions. Filled circles in (e) represent sampling sites and the arrow between plant and pollinator species represent their interaction frequency.

more efficient interaction (e.g. more efficient pollen deposition) (Nagano *et al.* 2014; Solís-Montero & Vallejo-Marín 2017), it would increase pollination success via the *per capita* effect of pollinator species on pollination success. In addition, specialisation of interacting species could strengthen trait matching (and *vice versa*) via coevolution, thereby increasing interaction frequency and, indirectly, pollination success. Similarly, because phenological overlap influences the frequency of interactions among species, it could indirectly affect interaction-dependent functions, such as pollination success.

Here we use temporal and spatial data on plant and pollinator interactions, traits and pollination success to evaluate the relevance of trait matching and phenological overlap for the spatio-temporal stability (measured as the variability of interaction frequency) and functionality (measured as pollination success, i.e. the number of pollen tubes growing after pollen deposition) of plant–pollinator interactions. Although morphological trait matching among plant and pollinator species has been usually evaluated as a univariate metric (Solís-Montero & Vallejo-Marín 2017; Klumpers *et al.* 2019), for example the match (or mismatch) of the pollinator proboscis length with the floral nectar tube length, species interactions depend on the matching of multiple non-independent traits (Vázquez *et al.* 2009a). Moreover, multiple pollinator traits are known to be important for pollination success (Hoehn *et al.* 2008), such that a trait–interaction–function framework will likely need to incorporate multiple traits. Therefore, we assessed the congruence of multiple traits simultaneously (in multivariate space). Furthermore, because species abundance is an important determinant of interaction frequencies (Vázquez *et al.* 2009b), we incorporated plant and pollinator species abundances in our analyses to assess the effects of trait matching and phenological overlap after controlling for abundance. We hypothesise that: (1) interaction frequency increases with increasing trait matching and phenological overlap between the interacting species; (2) spatio-temporal stability of interactions increases with increasing trait matching and phenological overlap between the interacting species; (3) trait matching between interacting species increases with specialisation, hence increased specialisation indirectly increases the spatio-temporal stability of interactions; (4) pollination success increases with increasing trait matching and phenological overlap between the interacting species.

## METHODS

### Plant–pollinator visitation networks

During 2006–2011 plant–pollinator interactions were recorded in the Monte Desert of Villavicencio Nature Reserve (Mendoza, Argentina, 32°32' S, 68°57' W). The maximum number of sites sampled per year was four (each of 1-ha area) and they were separated by at least 1 km. Vegetation across all sites was *c.* 2 m tall shrubland, dominated by *Larrea divaricata*, *Condalia microphylla*, *Prosopis flexuosa* and *Opuntia sulphurea* (further study site and sampling methodology details can be found in Chacoff *et al.* 2012). In 2006 we sampled four sites (sites 1, 2, 3 and 4), in 2007 three sites (sites 1, 2 and 4) and from 2008 to 2011 we sampled two sites (sites 1 and 4).

We pooled all interactions sampled across sites per year to obtain a plant–pollinator visitation network per year. We combined the 6 years of visitation data to obtain a single plant–pollinator visitation network, and used the total number of flower visits by each pollinator species across the 6 years to represent interaction frequency.

Although the number of sites sampled and sampling effort differed across years, the percentage of links observed (i.e. connectance), interaction evenness, network specialisation and the percent of observed links relative to the estimated total links (estimated by the Chao2 statistic) were not significantly related to sampling effort (Chacoff *et al.* 2018). In addition, the species interaction composition (i.e. the identity and frequency of the pairwise interactions forming the network) did not differ significantly across years, and did not depend on the number of sites sampled each year (Supporting Information, Fig. S1).

### Species abundance

To estimate the abundance of flowers in the sites where species interactions were sampled, we counted the number of flowers per plant species per site using transects and quadrats. In 2006 we sampled forty 2 × 2 m quadrats per site (640 m<sup>2</sup> total area), in 2007 five 50 × 2 m transects (500 m<sup>2</sup> total), and in 2008–2011 two 50 × 2 m transects and four 20 × 8 m quadrats (840 m<sup>2</sup> total per year). We summed the abundance of each flower species across years to obtain an overall measure of flower abundance per plant species: number of flowers per species over the entire sampling period (i.e. 4500 m<sup>2</sup> sampled over the 6 years).

Because empirical measures of pollinator abundance (measured independently of interactions) were not available, we estimated them from quantitative interaction data using the mass action principle (Staniczenko *et al.* 2013, 2017). The mass action principle originated in chemistry, and states that the rate of a chemical reaction is proportional to the product of the concentration or mass of the reactants. From an ecological perspective, it is assumed that the frequency of interactions ( $F_{ij}$ ) between species is proportional to the product of the species relative abundances ( $x_i$  = pollinator species  $i$  abundance;  $x_j$  = plant species  $j$  abundance) due to random encounters, but also depends on the interaction preferences between interacting species ( $\gamma_{ij}$ ), that is  $F_{ij} = x_i x_j \gamma_{ij}$ . Therefore, when sufficient species interaction frequencies ( $F_{ij}$ ) data are available (such as in our dataset), it is possible to infer interaction preferences ( $\gamma_{ij}$ ) and then the effective relative abundance of the interacting partners ( $x_i$  and  $x_j$ ) (Staniczenko *et al.* 2013).

**Species traits and trait matching.** We selected plant and pollinator morphological traits that are considered important for the occurrence of plant–pollinator interactions (Eklöf *et al.* 2013; Junker *et al.* 2013; Coux *et al.* 2016; Johnson & Raguso 2016). For plant species, we measured corolla length, corolla aperture and mean flower height (see Supporting Information for more details). We sampled between 3 and 24 flowers per species and calculated the mean value of each trait per species. For pollinators, we measured proboscis length and width, body width, body thickness and body length (see Supporting Information for explanation of how plant and

pollinator traits are related, i.e. matched). We measured up to 10 individuals per species and used the mean value of each trait per species; details of the measured traits can be found in Lomáscolo *et al.* (2019).

We measured traits from 45 (of 59; 76.3%) plant species and 135 (of 196; 68.9%) pollinator species present in the interaction networks. Because some specimens were missing from the collection, we could not measure traits from all species. Therefore, we used only the measured subset of species (and their interactions) in our analyses. This subset represents 73% of the species sampled in the interaction networks, 84% of the binary links (i.e. 881 links) and 97% of all interaction events recorded (i.e. 27 074 interactions). Although species not included in our analyses were rare, their specialisation did not differ systematically from that of the species in our analyses (Supporting Information, Fig. S2). In addition, although the phenology of the species excluded from our analyses tended to be short (between 1–13 weeks and 1–8 weeks for plants and pollinators respectively), plant and pollinator species with similar phenology duration were included in our analyses (i.e. species with short phenologies were represented in the analyses).

As discussed earlier, the linking of traits, interactions and functioning likely requires the inclusion of multiple non-independent traits. For this reason, we used a multivariate trait congruence metric to quantify trait matching, which also accounts for the correlation between traits that occurs within species (Cariveau *et al.* 2016; Melin *et al.* 2019). First we calculated similarity in morphological traits between each pair of plant species (i.e. a plant species trait similarity matrix) and between each pair of pollinator species (i.e. a pollinator species trait similarity matrix) using Gower's similarity coefficient (Gower 1971) and the *vegdist* function from the *vegan* v 2.5-5 R package (Oksanen *et al.* 2019). Then, we performed a Parafit test (Legendre *et al.* 2002) using the plant and pollinator trait similarity matrices and the binary species interaction matrix, using the *parafit* function from the *ape* v 5.1 R package (Paradis *et al.* 2004). The Parafit test quantifies the congruence between two topological trees (one for plants and one for pollinators) defined by the species trait similarity matrices. Parafit tests the null hypothesis that species interact randomly with respect to trait differences at each trophic level, that is that pollinator species with similar traits do not interact with plant species with similar traits more often than expected at random. If the null hypothesis is rejected, that is pollinator species with similar traits interact with plant species with similar traits, there is significant congruence between plant and pollinator traits. Given significant congruence, the contribution of each interaction to this pattern (i.e. how strongly pollinator traits predict their interactions with plants based on their traits) can be estimated. A large contribution to the community trait-matching congruence pattern (as measured by the statistic *ParafitLink1*) therefore provides strong evidence of trait matching for that interaction.

**Pollination success.** To estimate pollination success, we used data on pollen deposition for four of the most abundant plant species, *Larrea divaricata* and *L. nitida* (Zygophyllaceae), *Opuntia sulphurea* (Cactaceae) and *Zuccagnia punctata* (Fabaceae), from a previous study (Vázquez *et al.* 2012).

Pollen deposition on these four plant species was sampled in 2008, at the same sites as plant–pollinator interactions were sampled. Two of these plant species had many flower visitor species (*L. divaricata* had 52 and *Z. punctata* 56 visitor species), whereas the others had fewer flower visitors (*L. nitida* had 24 and *O. sulphurea* 33). We measured pollen deposition by three to seven pollinator species for each plant species (10 pollinator species, 19 different interactions [i.e. links]). We acknowledge that by focusing on plant species with intermediate and large number of flower visitor species we are omitting more specialised plant species. Nevertheless, the plant–pollinator interactions for which we measured pollen deposition span almost the entire range of phenological overlap, trait matching and interaction frequency across all the interactions sampled during the 6 years (Supporting Information, Fig. S3).

Pollination success was estimated as the impact that each pollinator species has on plant reproduction relative to the impact of all pollinator species (Vázquez *et al.* 2012). Pollinator species impact depends on the *per capita* pollinator's effect (per-visit effect) and the frequency of interaction between the plant and pollinator species (Vázquez *et al.* 2005; Wootton & Emmerson 2005). Therefore, a pollinator species' impact on plant reproduction ( $t_{ij}$ ) was calculated as  $t_{ij} = P_{ij} I_{ij} / T_i$ , where  $P_{ij}$  is the *per capita* pollinator's effect;  $I_{ij}$  is the frequency of interaction (number of visits) of pollinator species  $j$  to plant species  $i$  across the entire sampling period (6 years); and  $T_i$  the impact of all pollinator species to plant  $j$  reproductive success ( $T_i = \sum I_{ij} | P_{ij}$ ). As an estimate of the *per capita* pollinator's effect ( $P_{ij}$ ), we counted the number of pollen tubes growing below the tip of the pistil (as a measure of plant reproductive success) resulting from pollen deposited by each pollinator species on the stigma of each plant species in one visit, relative to the pollen deposited by all pollinator species (Vázquez *et al.* 2012).

## STATISTICAL ANALYSES

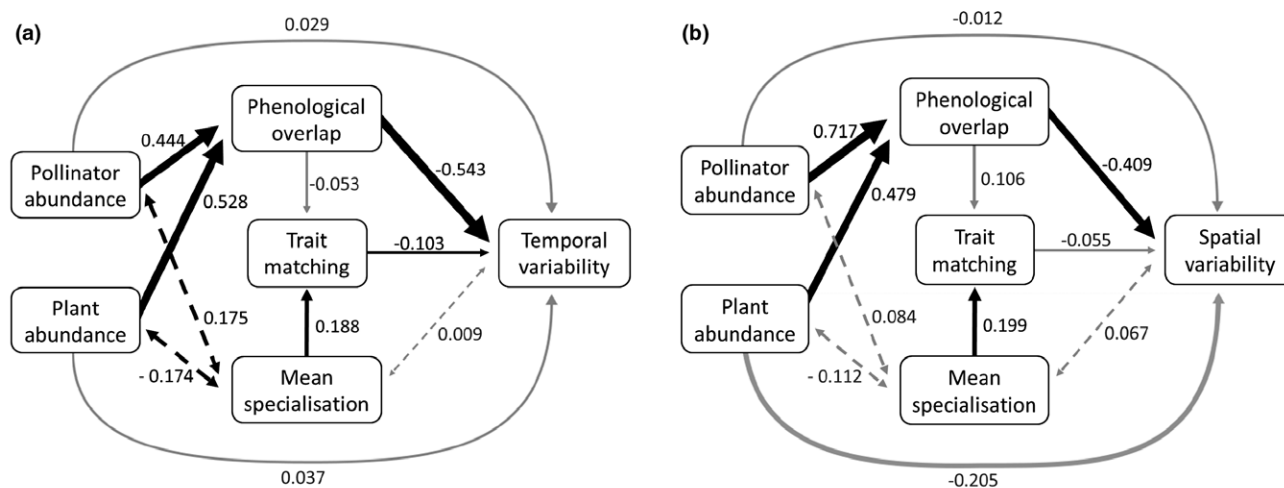
To assess the effects of trait matching and phenological overlap on interaction frequency, pollination success, and the temporal and spatial variability of interactions, after controlling for species abundance effects, we used generalised multilevel path models (Shipley 2009), a form of structural equation model (SEM) fitted through separate component models. Each SEM used to assess changes in interaction frequencies, or the temporal and spatial variability of interactions, consisted of three linear mixed effects models (LMMs). The first LMM consisted of plant and pollinator species abundances, trait matching and phenological overlap as predictor variables and interaction frequencies, temporal variability of interactions or spatial variability of interactions as response variables on each of the three SEMs respectively. The second LMM in each SEM included phenological overlap as a response variable and plant and pollinator species abundances as predictor variables. The third LMM included trait matching as a response variable and phenological overlap and mean specialisation of the interacting partners ( $d'$ ) as predictors. All LMMs included plant and pollinator identities as random factors to account for the non-independence of interactions sharing one



Variables used in all SEMs were scaled (to make their effect sizes comparable) by subtracting the mean and dividing by the s.d., and a Gaussian error distribution was used in all linear mixed effects models (normality and homoscedasticity assumptions were checked). All statistical analyses were performed in the R environment v 3.6.1 (R Core Team 2019). We used the lme4 v 1.1-21 package (Bates *et al.* 2015) for the LMMs and piecewiseSEM v 2.0.2 package (Lefcheck 2016) to fit the SEMs. We evaluated model fit by performing a d-separation test of each SEM (Shipley 2009). The d-separation test estimates a Fisher's  $C$  statistic and performs a chi-squared test

Figure 1: Path diagram of the structural equation model. The model includes five variables: Pollinator abundance, Plant abundance, Phenological overlap, Trait matching, and Mean specialisation. Path coefficients are: Pollinator abundance to Phenological overlap (0.444), Pollinator abundance to Trait matching (0.528), Plant abundance to Phenological overlap (0.175), Plant abundance to Trait matching (-0.174), Phenological overlap to Trait matching (-0.053), Phenological overlap to Interaction frequency (0.219), Trait matching to Interaction frequency (0.072), and Mean specialisation to Trait matching (0.188). Correlations are: Pollinator abundance and Plant abundance (0.234), and Phenological overlap and Mean specialisation (0.035).

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**Figure 3** Structural equation models evaluating the effects of trait matching and phenological overlap on plant–pollinator interaction temporal (a) and spatial (b) variability. Specialisation was measured as  $d'$ . Other conventions as in Fig. 2. Both models were a good fit to the data (temporal variability model: Fisher  $C$  statistic = 4.644, d.f. = 6,  $P$  = 0.59; spatial variability model: Fisher  $C$  statistic = 5.714, d.f. = 6,  $P$  = 0.456)

We calculated the mean specialisation of each pair of interacting plant and pollinator species and refer, hereafter, to this variable as mean specialisation of the interacting partners. We also estimated phenological overlap between any pair of interacting plant and pollinator species as the number of weeks (across the entire 6-year sampling period) when these species co-occur.

### SPATIO-TEMPORAL STABILITY OF PLANT–POLLINATOR INTERACTIONS

As a measure of the spatial and temporal stability of plant–pollinator interactions, we used the coefficient of variation of interaction frequency (lower coefficients of variation indicate higher stability of interactions). The temporal coefficient of variation of interactions was obtained by dividing the standard deviation (SD) of the frequency of each interaction sampled across the 6 years by its mean. Similarly, the spatial coefficient of variation of interactions was obtained by dividing the SD of the frequency of each interaction sampled across the four sites sampled in 2006 (year in which the highest number of sites were sampled) by the mean interaction frequency of those interactions sampled on those sites that year. The spatial stability was estimated only for those interactions that occurred at least once in 2006 (i.e. 150 links).

### RESULTS

High trait matching and phenological overlap made interactions more frequent and stable, and indirectly improved pollination success. Interaction frequency was positively and directly affected by trait matching, phenological overlap and pollinator abundance, and indirectly by the mean specialisation of the interacting partners ( $d'$ ) and the interacting partners' abundances (Fig. 2, Table S1). The importance of abundance was emphasised by the direct effect of pollinator abundance on interaction frequency and of plant and pollinator abundance

on phenological overlap (which, in turn, influenced interaction frequency). Nevertheless, because the method we used to estimate pollinator abundance involved interaction frequencies, there could be some correlation between pollinator abundance and interaction frequency and hence we remain cautious about this particular result (i.e. the direct effect of pollinator abundance on interaction frequency).

Trait matching and phenological overlap independently stabilised mutualistic interactions in time (i.e. they decreased the temporal variability of interactions; Fig. 3a, Table S4), even after controlling for the effects of interaction frequency on interaction variability (Table S7). The temporal variability of interactions was indirectly negatively affected by the abundance of plants and pollinators and the mean specialisation ( $d'$ ) of the interacting partners (Fig. 3a, Table S4). On the other hand, the spatial variability of interactions was only directly affected by phenological overlap, and indirectly negatively affected by the interacting species' abundance (Fig. 3b, Table S8).

The impact of pollinator species on plant reproduction was directly affected by both the *per capita* pollinator effect and interaction frequency, because both variables were used to calculate pollinator impact. More importantly, interactions in which pollinators and plants had matching traits and overlapping phenologies were more frequent, and therefore associated with stronger pollinator impacts ( $t_{ij}$ ), even though the pollinator's *per capita* effect was not significantly affected by trait matching (Fig. 4, Table S11). Combined with the previous SEM showing the effects of abundance and mean specialisation on interaction frequency, we can conclude that these variables also indirectly influence pollination impact via interaction frequency.

### DISCUSSION

Morphology, phenology and abundance have been identified as the main drivers of plant–pollinator interaction network structure (Vázquez *et al.* 2009b; Olesen *et al.* 2011; Encinas-

Viso *et al.* 2012; Morente-López *et al.* 2018), but their effects on functionality and stability of interactions (measured as interaction variability) were previously unresolved. Here, we demonstrate that plant–pollinator interactions among species with well-matched traits and higher phenological overlap are stable in time and increase pollination success by affecting interaction frequency, independent of the effect of plant or pollinator abundance. In addition, interactions among specialised species had higher trait matching, such that specialisation indirectly favours interaction stability. These results suggest that the non-random extinction of interactions among specialists (Aizen *et al.* 2012) and biotic invasion (with invaders typically being generalists, Aizen *et al.* 2008, Frost *et al.* 2019, and promoters of interaction rewiring, Arroyo-Correa *et al.* 2020), can disproportionately increase the variability of interaction frequencies within communities, increasing ecological network variability and making more difficult the prediction of interaction networks. Furthermore, we show that the strong positive effects of species abundance on the spatio-temporal stability of interactions are mediated by phenological overlap, such that temporal co-occurrence, rather than abundance itself, appears to be stabilising.

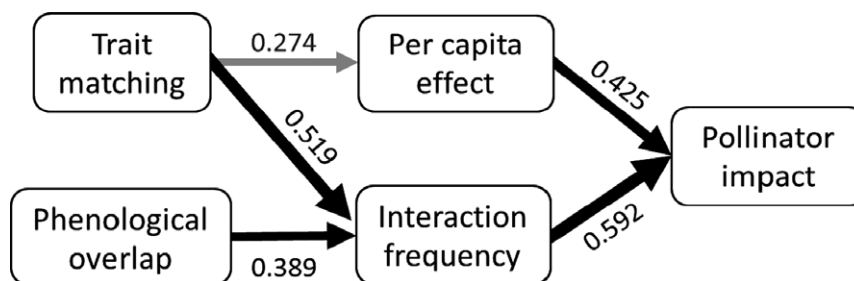
The relevance of phenological overlap for species coexistence (Rudolf 2019) and for species interaction variability, as shown here, reflects the importance of phenologies for community dynamics and for determining the robustness of communities to environmental change (Encinas-Viso *et al.* 2012; Ramos-Jiliberto *et al.* 2018). Furthermore, phenological shifts (mismatches) induced by global environmental changes have been identified as potential drivers of the extinction of plant–pollinator interactions (Memmott *et al.* 2007), which could be initiated by a decrease in interaction frequency, as shown here. Phenological overlap and abundance explain a substantial fraction of species interactions in the system we consider (Vázquez *et al.* 2009b). Furthermore, as we show here, species abundance effects on the spatio-temporal stability of interactions were completely mediated by phenological overlap. Therefore, the quantification of phenological overlap among interacting species could be even more effective than species abundance data for predicting changes in species interactions. The key role of phenological overlap suggests that measuring phenological overlap, that is species temporal co-occurrence,

could be an effective and simpler alternative to measuring the abundance of each species in the community.

Although phenological overlap had direct effects on interaction frequency and the stability of interactions, it did not favour trait matching among interacting partners as we had expected. Despite using a 6-year dataset to estimate phenological overlap, it is likely that a longer time span needs to be considered in the estimation of phenological overlap to capture coevolutionary changes in species morphology (Thompson 1998).

Morphological traits and rewards influence the array of flower visitors a plant receives (Bosch *et al.* 1997; Stang *et al.* 2006), making trait matching between plants and pollinators a key driver of the occurrence and frequency of interactions among these partners. Even though trait matching is an important determinant of plant–pollinator interactions, to our knowledge, its contribution to the stability of interactions has been overlooked. Previous studies have explained spatial and temporal variability of plant–pollinator interactions in terms of changes in species composition (species turnover) and interaction rewiring (Carstensen *et al.* 2014; Trøjelsgaard *et al.* 2015; CaraDonna *et al.* 2017), but without including species morphological dependencies. Here, we took a step forward and showed that trait matching influences not only the temporal stability (i.e. inverse of temporal variability) of interaction frequency, but also the stability of pollination success. Although trait matching had no significant effect on the spatial variability of plant–pollinator interactions, it is possible that the smaller sample size used in this particular analysis (we only used interactions sampled in 2006 for which we had spatial variability data) did not allow us to detect such an effect. It is also possible that, because of the limited spatial extent of our study, not enough variability in interactions was captured across space (spatial variability was lower than temporal variability of interactions) to detect the effects of trait matching on interaction spatial variability.

Specialisation of both interacting partners indirectly increased the temporal stability of interactions by promoting trait matching. The idea that interactions among specialist species are more temporally stable, at least in a 6-year period, could be somewhat counter-intuitive, as previous studies have shown that specialised species (Burkle *et al.* 2013) and their interactions (Aizen *et al.* 2012) are the most sensitive to



**Figure 4** Structural equation model evaluating the effects of trait matching and phenological overlap on each pollinator's impact on plant reproduction ( $t_{ij}$ ), as an estimate of pollination success. Pollination success is hence determined by *per capita* pollinator species effects and interaction frequency effects. *Per capita* (per visit) pollinator effects were estimated by measuring plant reproductive success (number of pollen tubes growing from pollen deposited by each pollinator species on the stigma of each plant species in one visit, relative to the pollen deposited by all pollinator species). Other conventions as in Fig. 2. The model was a good fit to the data (Fisher  $C$  statistic = 11.875, d.f. = 8,  $P$  = 0.157)

habitat changes, and to the loss of climatic suitability (Schleuning *et al.* 2016). However, specialised interactions (i.e. those among species with few interacting partners) could be stable and fragile (i.e. vulnerable to rapid change) at the same time. In part this discrepancy may occur because the characteristics of the species that succeed within a given environment could differ from those that succeed in a changing environment. Moreover, studies forecasting the susceptibility of specialised interactions do not consider the effects of species abundance, which suggests that the survival of the most abundant species could confound the effects of species specialisation (Winfree *et al.* 2014). This difficulty in teasing apart the effects of abundance vs. interacting partner specialisation raises the question of whether the persistent core of plant–pollinator networks is formed by interactions among generalist species (Bascompte *et al.* 2003; Bascompte & Jordano 2007) or by the most abundant species that tend to show lower specialisation (Fort *et al.* 2016). For instance Winfree *et al.* (2014) showed that once the positive effect of abundance is accounted for, specialised species are more persistent than generalist species. This trend is clearly observed in our results, where the indirect effects of plant and pollinator abundance on the temporal stability of interactions is more than 13-times larger than the indirect effects of specialisation on temporal stability. Therefore, once the effects of abundance are separated from specialisation, the positive indirect effect of specialisation on interaction stability becomes apparent.

Previous studies have shown that trait matching can influence the accuracy of pollen deposition by pollinators (Poblete Palacios *et al.* 2019) or the amount of pollen deposited (Nagano *et al.* 2014; Solís-Montero & Vallejo-Marín 2017), potentially favouring plant reproduction. However, our results show that interactions among species with matching traits had higher pollination success because of an increase in interaction frequency, but not due to an increase in the pollinator's *per capita* effect on plant reproduction. It is possible that only some of the traits considered here would be extremely important for influencing the pollinator's *per capita* effect on plant reproduction, and using a multivariate metric of trait matching (i.e. simultaneously considering the multiple traits that determine interactions) dilutes the positive relationship between those specific traits and pollinator's *per capita* effect. Another potential explanation for the lack of relationship between trait matching and a pollinator's *per capita* effect is that we assessed pollination success only for generalist plant species. It is possible that including specialised interactions (i.e. interactions among specialised plants and specialised pollinators, with a stronger trait matching signal) could strengthen the trait matching – pollinator's *per capita* effect relationship. Finally, pollination success increased with phenological overlap between interacting species, which supports the idea that phenological mismatches affect species reproductive success and survival (Visser & Gienapp 2019).

Plant and pollinator morphology and phenology are important determinants of their interaction network structure and extinction risk (Stang *et al.* 2007; Vázquez *et al.* 2009b; Morante-López *et al.* 2018). In this study we demonstrate that interactions with well-matched traits and phenologies are temporally and spatially more stable. Moreover, the effects of

species abundance on interactions and their stability are largely mediated by phenological overlap, and the importance of phenological overlap for the stability of plant–pollinator interactions largely surpasses the effects of trait matching. Furthermore, our results reinforce the idea that trait matching (Garibaldi *et al.* 2015) and phenological overlap are extremely important for pollination success by increasing species interaction frequencies. Therefore, the systematic loss of well-matched interactions, alongside the proliferation of less well-matched interactions (e.g. invasive species), and the phenological shifts and mismatches induced by global environmental changes (Memmott *et al.* 2007), could alter interaction stability and ecosystem functions, and further impair our ability to predict changes in species interactions.

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## COMPETING INTERESTS

The authors declare no competing interests.

## AUTHORSHIP

JMT, DPV and GLWP conceived the idea and secured funding. GP and JMT further developed the idea. DPV, NPC and SBL collected data. GP performed analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

## DATA AVAILABILITY STATEMENT

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## SUPPORTING INFORMATION

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

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