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Looking for a signal: how well do specialist and generalist bees track preferred host plants over time?

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Abstract

Understanding the factors that signal plant and pollinator phenologies is important for assessing the potential impacts of climate change. However, limited information is available on how well bees track preferred host plants over time and how traits like body size may govern differential responses among species, particularly in xeric areas where floral resources and climate are unpredictable. We studied the nesting phenology of six solitary, cavity-nesting bees that differ in host breadth and body size in the Monte Desert ecosystem, Argentina, over nine consecutive years. We used cross-correlation analysis to assess if the ability of bees to track the flowering phenology of their host plants and abiotic environment, as well as to detect potential differences between specialist and generalist bees. We found that nesting phenology is predicted by multiple flowering and climatic variables regardless of the bees' level of specialization, and that there is a differential pattern in body size. The nesting phenology of smaller bees was predicted by the number of individuals in bloom, indicating some spatial pattern in resource availability. While the nesting phenology of some bees was predicted by flowering variables alone, that of other bees was explained by a combination of flowering and climatic variables. Our study also indicated that the inter-annual variability of nesting was greater in generalist bees than in specialist bees. These results suggest that if phenological decoupling occurs, bees might be able to restore it by detecting multiple environmental signals, and that generalist bees might be more vulnerable than previously expected.

Keywords Pollinators · Climate change · Foraging niche · Plant-bee interactions · Nesting behavior

Introduction

Plant-pollinator relationships are keystone mutualistic interactions due to their role in plant reproduction, ecosystem maintenance, and food security (Klein et al. 2007; Ollerton et al. 2011). Because plants and pollinators might respond differently to changes in climate, these relationships are particularly vulnerable to spatial, temporal, morphological, and recognition mismatches (Visser and Both 2005; Hegland et al. 2009; Willmer 2012; Gérard et al. 2020). For example, while both plants and bees respond to temperature cues for their phenologies (Hegland et al. 2009; Forrest and Thomson 2011), each might react to different aspects of it. Flowering time might be more responsive to average temperatures (Craufurd and Wheeler 2009), while nesting activity of bees might be more responsive to maximum temperatures. Thus, understanding the environmental factors that signal plant and pollinator phenologies is important for assessing the impacts of climate change (Olliff-Yang and Mesler 2018).

Bees are among the most important pollinators of many wild and cultivated plants (Michener 2007; Klein et al. 2007), relying on pollen as the only source of protein to raise their brood. Some bees collect pollen from a single or a few host plants (specialist or oligolectic bees), while others use pollen from a wide range of plants (generalist or polylectic bees). Unlike pollen, bees take nectar (a source of carbohydrates) from either their host plant or many other plants (Müller 1996; Nicolson et al. 2007). Despite flowering plants being nearly 20 times more species-rich than bees, a surprisingly high proportion of bees are specialists,

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particularly in areas with high bee diversity (Linsley 1958; Michener 1974; Vazquez and Aizen 2004; Minckley 2008).

Plants tend to have a generalized pollination system that attracts a wide range of pollinators (Waser et al. 1996; Vazquez and Aizen 2004). Generalist bees might respond to environmental changes by switching between plant resources, likely making them more resilient to climate change. In contrast, specialist bees which have a narrower range of host plants, are at higher risk of extinction under climate change if they are more limited in their phenological response (Bartomeus et al. 2013; Forrest 2015; Gérard et al. 2020). However, even specialist bees may change host plants when floral resources are unavailable (Wcislo and Cane 1996; Vitale et al. 2020), suggesting that if phenological decoupling between bees and their floral hosts occurs, adult bees might detect environmental signals and adjust their phenology to match that of their host plants.

Temporal mismatches between plants and pollinators have been documented (McKinney et al. 2012; Kudo and Ida 2013) but appear to be rare (Iler et al. 2013). Both plants and pollinators tend to keep pace with one another under global warming, as phenological shifts may progress at similar rates (Bartomeus et al 2011; Iler et al. 2013). However, most studies have tracked changes in flowering time and insect emergence (e.g., Forrest and Thomson 2011; Visser and Holleman 2001; Iler et al. 2013) while few works have explored the impacts by tracking other aspects of pollinators' life cycles, such as adult foraging activity and nesting (Olliff-Yang and Mesler 2018). Even if phenological mismatch never occurs, climate change is a reality, and understanding the relationships between wild bee nesting and its environmental triggers, as well as the bee traits that may govern differential responses among species or functional groups, is critical. For example, after adult emergence, it is important to know if pollinators are "looking for environmental signals" to forage, mate, or nest. In this study, we aim to piece together a temporal puzzle that allows us to organize the events experienced by female bees before nesting. Among these events, some are surely more important than others, and understanding this will enable us to identify the best predictors of nesting. However, while some predictors may better explain nesting behavior, it does not mean that the rest of the signals can be ignored. Is it enough for bee survival to simply share time and space with its floral resources? How much of "living together with floral resources" is necessary for bees to survive? Is it just a pollinator-plant issue, or is there much more to it? Based on long-term observations (2006 to 2015), we assessed the effects of flower availability and climatic variables on the nesting activity of six solitary cavity-nesting bee species that differ in host breadth and body size (Table 1) from Monte Desert of Mendoza, Argentina. The Monte Desert, a xeric area in South America, is characterized by plant species of *Larrea* (Zygophyllaceae) and *Prosopis* (Fabaceae), with floral blooming highly variable among years, typically occurring in the spring (Chacoff et al. 2012). All bee species are univoltine and overwinter as immature pre-pupae, emerging as adults in the spring and remaining active through the summer, except for the carpenter bee *Xylocopa atamisquensis* which overwinters as an adult (Vitale et al. 2017; Vitale and Vázquez 2017). The phenological and climatic variables analyzed in this work represent time series and are most likely not independent from each other, as bees depend on abiotic factors and flowers for provisioning their nests and plants depend on temperature and humidity to bloom (Minckley et al. 2013). Thus, we used cross-correlation analyses to explore how one time series may predict or explain another, and how well they match up with each other (Shumway and Stoffer 2017). Specifically, we sought to assess how well bees track the flowering phenology of their host plants and abiotic environment, and to detect potential differences between specialist and generalist bees or between large and small bees.

Given that specialist bees depend on a single or few closely related plants, we hypothesize that their adult nesting phenology should respond to cues related to the flower availability of their host plants, rather than climatic cues. For

Table 1 Solitary bees studied in the Monte desert of Mendoza, Argentina

Bee species	Nest abundance	Specialization level	Body size	Population diet
Anthidium andinum Jörgensen	Low	Specialist	Small	*Prosopis flexuosa* (32%) + *Lycium chilensis* (26%) + *Glandularia* sp. (24%) + other 6 spp.
A. decaspilum Moure	Low	Generalist	Small	*Larrea* spp. (51%) + other 19 spp.
A. rubripes Friese	Low	Generalist	Small	*Larrea* spp. (74%) + other 21 spp.
A. vigintipunctatum Friese	High	Specialist	Small	*P. flexuosa* (56%) + *Larrea* spp. (18%) + *L. chilensis* (15%) + other 21 spp.
Trichothurgus laticeps (Friese)	High	Specialist	Large	*Opunthia sulphurea* (90%) > *P. flexuosa* (5%) > *L. chilensis* (5%)
X.atamisquensis Lucia & Abrahamovich	High	Generalist	Large	All plant species available are used

Information on nest abundance, lecty level, body size and host plants (population diet) gathered from Vitale (2017), Vitale et al. (2017, 2020), Vitale and Vázquez (2017) example, flower abundance or density could be more reliable cues for female bees than a particular aspect of temperature or precipitation for nesting. In contrast, because generalist bees can use a wider range of pollen hosts, adult females may rely primarily on abiotic cues or cues that allow them to predict flower availability across the whole plant community. Alternatively, if both specialist and generalist bees co-exist in the same area, they might respond to similar cues, regardless of their pollen specialization level. Finally, the variation in body size among our species provides an opportunity to explore potential differential responses between small and large bees. Body size strongly correlates with physiological, ecological, and life-history traits (Ostwald et al. 2023) including foraging distance (Greenleaf et al. 2007). Larger bees can forage longer distances and collect more floral resources than smaller bees (Kelemen and Rehan 2021), but they also require more resources to survive and reproduce (Müller et al. 2006). Therefore, there is not yet enough information to hypothesize about which signals (if any) might differentially trigger nesting in small or large bees and what impact this could have on populations in ecological time.

Materials and methods

Study area

We conducted this work between 2006 and 2015 in the Central Monte Desert in Mendoza, Villavicencio Private Nature Reserve (Fig. 1A, B), a xeric biome with a high degree of endemism for both plants and animals located in western central Argentina. The study area is characterized by a permanent water deficit, with a mean annual evaporation of 700 mm exceeding the mean annual precipitation of 218.2 mm (Dalmasso et al. 1999). Rainfall is sporadic and localized, generally occurring between October and March. The predominant vegetation of the area is a tall shrubland dominated by some species of *Larrea* (*L. divaricata, L. nitida* and *L. cuneifolia;* Zygophyllaceae) and *Prosopis flexuosa* DC (Fabaceae); other common plants are the cactus *Opuntia sulphurea* Gillies ex Salm-Dyck (Opuntiaceae), and grasses of the genus *Stipa* L. (Poaceae) (Dalmasso et al. 1999; Chacoff et al. 2012). We monitored both flowering and nesting phenologies in two sites that were at least 2.0 km apart and located on the eastern flank of Piedmont, foothills or a low hill at the base of a mountain range, at similar elevations (1261 and 1230 m.a.s.l.). Based on our knowledge of the area, we chose these two sites to represent the local diversity of bees and plants.

Study species and field methods

We followed the nesting phenology of three generalist and three specialist solitary bee species (Table 1). The categorization of these species, as specialists or generalists, follows that of Vitale (2017), Vitale et al. (2017), Vitale and Vázquez (2017), and Vitale et al. (2020), based on the index that considers resource availability, population diet, intra- and inter-individual variability, and behavioral aspects proposed by Roughgarden (1974), Sargeant (2007), Araujo et al. (2008) and Bolnick et al (2002).

Traditionally, ecologists have viewed the niche as a property of the species or population. However, no species is a strictly pollen generalist or pollen specialist, as individuals exhibit these traits at varying levels (Bolnick et al. 2002). Although we use a dichotomous categorical grouping in this work (specialist or generalist), it simplifies the fact that we observed a specialist-generalist gradient among the species in our study. *Trichothurgus laticeps* is considered a specialist species, meaning it has a narrow population diet and exhibits specialization at the individual level; *Anthidium andinum* and *A. vigintipunctatum* are almost specialist species, with

Fig. 1 Study area and sampling methods. **A** Study sites (gray dots) in Villavicencio Nature Reserve, Mendoza, Argentina. Insert shows map of Argentina with the province of Mendoza in black and the study area in red. **B** Flowering time (late spring, November) in Villavicencio. **C** Metal pole with its two sets of trap-nests in the field

a broader population diet achieved through the aggregation of narrow individual diets. For both species we observed a clear pattern in pollen use despite inter annual variability in resource availability and the use of plant species that were not uniform in spatial scale, indicating an active search for resources. *Anthidium decaspilum, A. rubripes,* and *X. atamisquensis* are generalist species, with broad diets at both population and individual levels. These three generalist species collect pollen from all blooming plant species without any particular pattern based on availability. The dominant presence of *Larrea* spp. pollen in the larval provisions reflects the abundance of this shrub in the landscape. This shrub is dominant in the plant community, offering significant pollen and nectar resources.

Body size is a common functional trait used in bee ecological studies and the variation in body size among our species allows us to explore if this trait influences differential responses to nesting. We classified body size categorically with a subjective reference to a size standard: small (similar to or smaller than the size of the European honey bee) and large, (much bigger than the size of the European honey bee).

Because all species are cavity-nesters, they readily nest in trap-nests (Fig. 1C). Trap nests consisted of wooden blocks with pre-drilled tunnels of varying diameter placed in the field (Krombein 1967). No paper straws or similar materials were used to line the drilled tunnels. At each study site, we set up a rectangular plot of 200 × 100 m and installed pairs of metal poles supporting groups of trap nests every 100 m (six pairs of trap nest poles in total), with each pole in a pair placed 10 m apart (ESM 1 Fig. S1). Each pole supported three sets of trap nests (8 trap nests per set) of varying lengths and diameters (14 cm × 0.5 cm; 14 cm × 0.8 cm; 28 cm × 1.1 cm), which were positioned on a pole 40 cm (shortest trap nests) and 70 cm (remaining trap nests) above the ground. Once nest construction was concluded, as indicated by the presence of a nest plug, or once adult female nest activity had ended, we took the nest to the laboratory and replaced it with a new trap nest of the same diameter.

We recorded the phenology of the following six plants, which are the main pollen hosts of the selected bee species (Vitale 2017; Vitale et al. 2017; Vitale and Vázquez 2017): the shrubs *Larrea divaricata* (Zygophyllaceae)*, P. flexuosa* (Fabaceae)*, Lycium chilense* Bertero (Solanaceae)*,* and *O. sulphurea* (Opuntiaceae); and the herbaceous plants *Helenium donianum* (Hook. & Arn.) Seckt (Asteraceae), and *Glandularia* sp. (Verbenaceae). In addition, we tracked the phenology of all plants at the study sites because the plant community exhibits high inter-annual variability in the number of species and individuals in bloom. For example, as few as five species were in bloom during the worst season (2014), and as many as 44 species were in the best seasons (2008 and 2010). To monitor flowering phenology, we established four 20 × 8 m quadrats, one at each corner of the plot, and two 50 × 2 m transects about 60 m apart located in the center of the plot. Thus, we monitored flowering phenology in a total area of 840 m^2 per plot (ESM 1 Fig. S1). We visited each site weekly from August to January and recorded the number of open flowers per species for all species and for each individual plant for shrubs (number of flowers to record pollen abundance and number of flowers by individuals to capture spatial availability). For each bee species, we recorded the number of nests and the number of brood cells per nest (the number of nests as an indicator of nesting behavior and the number of cells to record contribution to the next generation), as described in Vitale et al. (2017) and Vitale and Vázquez (2017). We used two nesting and six flowering variables as proxies of phenological response in our study (Table 2).

Climatic data

We used climatic data from the meteorological station Plumerillo (1980 to 2015 time series) of the National Meteorological Service of Argentina, which is located about 40 km from our study sites (Las Heras, Mendoza). Climatic data from this station is representative of the climatic variations at the study sites, as evidenced in Vitale (2017) by linear models obtained for the climate variables between Villavicencio (in situ sensors) and the Plumerillo data, which explained more than 75% of the observed variance. For analyses, we used five climatic variables as proxies which represent climatic variability and season features (Table 2).

Data analyses

We performed all analyses in R version 3.2.0 (R CoreTeam 2015) and used the packages stats (R CoreTeam 2015), and astsa (Stoffer 2014) to create plots. We analyzed all 13 proxy variables in a time series analysis using the ts (Time Series) and stl (Seasonal Decomposition of Time Series by Loess) functions in the R packages stats and astsa. We analyzed all variables weekly, starting on June 1, 2006, and ending on May 31, 2015 ($n = 52$ weeks per year). We used cross correlations (cross-correlation function estimation, astsa) to identify which of the climatic and plant phenology variables predict or explain bees' nesting phenology, as well as which climatic variables explain plant phenology. We chose R_h as the statistical coefficient of cross-correlation ($R_\mathrm{h} = C_0/C_\mathrm{h}$, covariance functions coefficient/variance functions coefficient; Venables and Ripley 2013). Cross-correlation is the correlation between two time series, both in simultaneous time and delayed over time. This analysis is useful for assessing the joint pattern of two stationary series whose behavior may be related in some unspecified way. Even though cross-correlation is not a causal effect model, it allows us to track

Table 2 Variables used in the analyses

Variable	Description
(a) Climatic variables	
T_{mean} (mean temperature)	Weekly mean temperature (°C)
T_{min} (minimal temperature)	Weekly mean minimum temperature (°C)
T_{max} (maximal temperature)	Weekly mean maximum temperature (°C)
Precipitation	Weekly cumulative rains (mm)
Spring rains	Weekly cumulative precipitation (mm) recorded from October to December each year
(b) Nesting phenology	
Nests	Number of nests established by each bee species per week
Cells	Number of brood cells built by each bee species per week
(c) Floral phenology	
F_f (flower number)	Number of flowers of each target species per week per 100 m^2
I_f (individual in bloom)	Number of individuals in bloom of each target species per week per 100 m^2
S_{Tot} (flower richness)	Number of plant species in bloom in the community per week per 100 m^2
I_{Tot} (total individual in bloom)	Number of individuals in bloom of all species in the community per week per 100 m^2
F_{Tot} (flower abundance)	Total number of flowers across all plant species in the community per week per 100 m^2
FAnom (Anomaly)	Proportion of the weekly number of flowers per species divided by the historical mean number (across all nine years) of flowers by species

if some independent variable triggers behavioral responses in the dependent variable, which is relevant in biological research. This type of analysis also allows us to assess how well the time series match up with each other. The lag indicates how far the series are offset and thus how long it takes the effect to propagate from one variable to the other; its sign determines which series is shifted (Shumway and Stoffer 2017). In the analyses of the bee nesting phenology, both climate and floral resources could model bee nesting behavior, but never the other way around. Thus, we considered the proxies for nesting phenology (nests and cells) as response variables and the proxies for floral resources or climate as possible triggers of bee nesting behavior. Consequently, we analyzed just negative lag for all results. For analyses of the climate- floral resource relationships, we used proxies of floral resources as response variables and those of climate as possible signals. One requirement of cross-correlation is the time series must be stationary (to avoid the effect of temporal lag and trends), as it ensures the independence of the data, which is an essential assumption in this type of analysis (Diaz 2014). All biological variables represent stationary series, and we did not standardize them. In contrast, we standardized climatic variables because they failed to pass the test assumptions. Thus, for each climate variable, we calculated the annual deviation from the historical average (First differences $= X_{observed} - X_{historical\ 1980–2015}$); time series of climatic variables shown in ESM1 Fig. S2.

To visualize the results of each cross-correlation, we used cross-correlograms where the coefficient R_h is plotted against the fraction of a lag corresponding to a week ($0.0192 = 1$ week/52 weeks per year). In these cross-correlograms, each vertical line indicates the value of the coefficient R_h for each pair of variables per week; the values on the x axis are negative because we analyzed just negatives lag for all results (i.e., how many weeks before nest construction a given flowering or climatic variable produces a response). Fig. S5 in EMS1 shows examples of cross-correlations with no signal, negative signal, and long- and short-term positive signals, terms we used when describing the results below. We also mentioned a few cross-correlations that were marginally significant but that displayed a pattern or trend in the data worth mentioning in the context of the study. In these cases, we referred to them as "diffuse signals."

Our complete analysis resulted in 332 cross-correlations (60 bee-climate cross-correlations: 2 nesting variables × 5 climatic variables × 6 bee species; 144 bee-floral resources cross-correlations: 2 nesting variables × 2 flowering variables × 6 bee species × 6 plant species; 48 bee- plant community cross-correlations: 4 plant community variables × 2 nesting variables × 6 bee species; 60 plant-climate cross-correlations: 2 flowering variables × 6 plant species × 5 climatic variables; 20 plant community-climate cross-correlations: 4 plant community variables × 5 climatic variables), of which 73.5% showed no significant signal (details of all cross-correlations are in ESM1 Tables S1–S6, Figs. S6–S12). Due to the large number of cross-correlation tests, type I error is inflated, and caution is needed regarding the statistical approach. Even so, this is an exploratory study, and we aim to gain a better understanding of the plant-bee-climate relationship in the Monte desert. To avoid the problem of spurious regressions, we present only significant results and discuss those with high biological significance. However, this study represents just one small step, and we hope it will inspire new ideas and approaches to understanding the complexity of this phenomenon.

Results

Bees exhibited inter-annual variation in their nesting phenologies, as indicated by the number of nests and brood cells across years (ESM 1). However, unlike specialist bees that built nests inside the trap nests almost every year throughout the entire study period, generalist bees showed a more erratic behavior and established nests in some years only. Plant resources at the study sites, both at the individual and community level, also varied among years. *Glandularia* sp. and *H. donianum* did not bloom in some years and sometimes exhibited more than one blooming event per season. Remaining host pollen plants bloomed every year, albeit with variations in the number of individuals in bloom, as well as the number of flowers (ESM 1 Fig. S3).

Bee nesting- climate relationships

We obtained 13 significant signals out of 60 cross-correlation analyses among bees' nesting phenologies and climatic variables (ESM1 Table S1, Fig. S5). None of the variables we included predicted nesting activity in the specialist bee *A. andinum* and the generalist bee *A. decaspilum*. The nesting phenology of two specialist bees (*A. vigintipunctatum* and *T. laticeps,* Fig. 2) was predicted by both temperature and precipitation (spring rains) variables, whereas those of two of generalists (*A. rubripes* and *X. atamisquensis*) by precipitation only (Fig. 2, and more details in ESM1 Table S1 and Fig. S6). For the small body-sized specialist bee *A. vigintipunctatum*, we observed a medium-term (delay around 8 weeks) diffuse negative signal in maximal temperature (T_{max}), whereas for the large body-sized specialist bee *T. laticeps* a short-term (2–3 weeks) positive signal in mean and minimal temperature (T_{mean} and T_{min}). We found a positive signal between bee nesting phenology and spring rains, but the response time (lag) differed among species (ESM1 Table S1). In small body-sized species of *Anthidium* it was short, while in the two large body-sized bees, *T. laticeps*

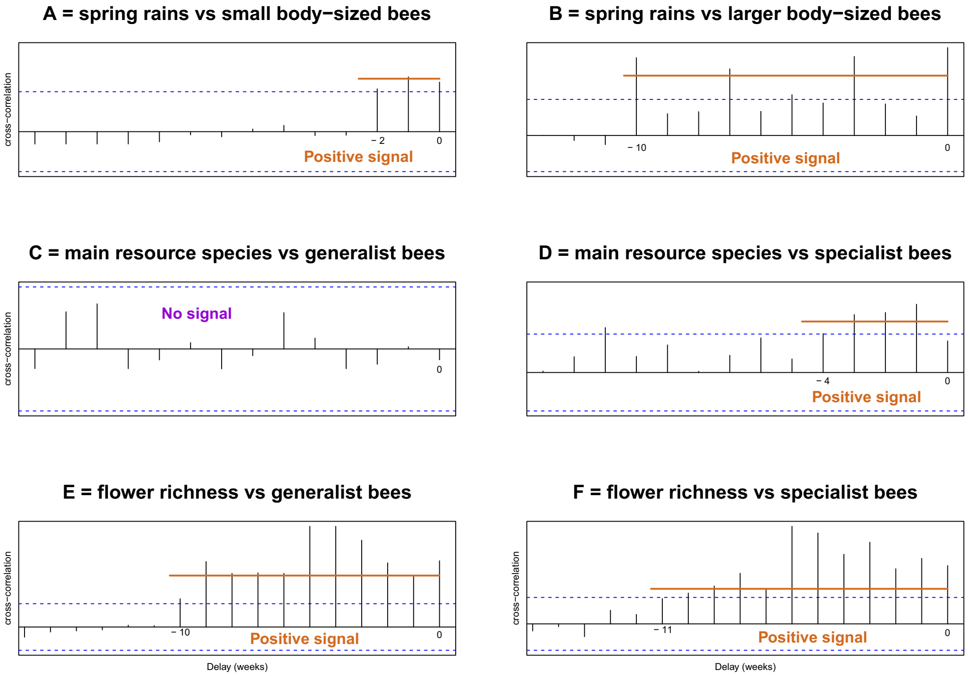


Fig. 2 Summary of cross-correlation illustrating some differential responses of bees to the same environmental variable. Top and bottom figures show similar positive responses with different delays while middle figures show no signal and a positive signal. Bee species and environment signals showed here: *A. rubripes* (generalist small bee in **A**, **C** and **E**); *A. vigintipunctatum* (specialist small body-size bee in **D** and **F**); *T. laticeps* (specialist larger bee in **B**); spring rains (**A** and **B**); *P. flexuosa* (number of individuals in bloom in **C** and **D**); number of plant species in bloom in the community (S_{Tot}, flower richness in **E** and **F**). All completed cross-correlation results (observed for each bee species) are in electronic supplemental material, Tables S1–S5, Figs. S5–S11. Blue broken lines indicate range of significance ($\alpha = 0.05$). This figure aims to improve cross-correlation understanding for readers not familiar with this approach, we try to show just the most relevant aspects of this statistical tool; for example, to avoid an excess of information, and we remove some axes values

and *X. atamisquensis*, it was long and continuous (October–December; Fig. 2).

Floral resource-climate relationships

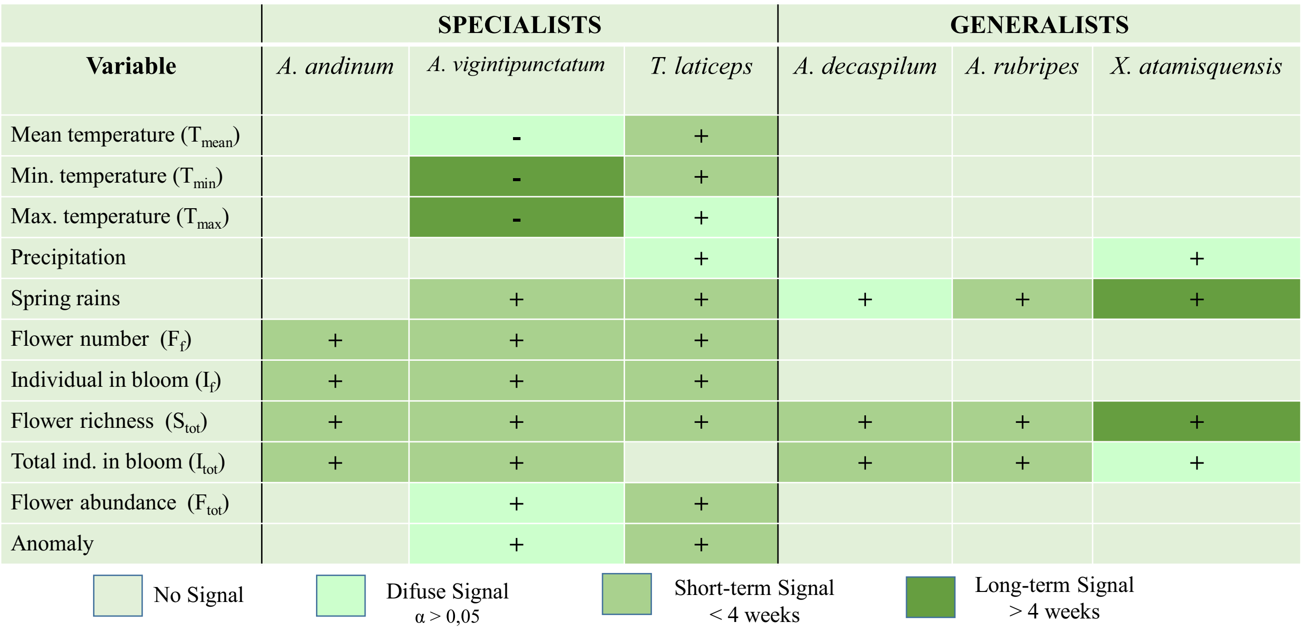
Only 9 out of the 60 cross-correlation analyses among the host plant phenologies and climatic variables were significant, all of them related to *L. divaricata*, *P. flexuosa*, and *O. sulphurea* (ESM1 Table S4, Fig. S11). The flowering phenology of *L. divaricata* and *P. flexuosa* responded negatively to mean, maximal and minimal temperature (T_{mean}, T_{min}, and T_{max}). Additionally, the blooming of *L. divaricata* and *O. sulphurea* showed a positive response to spring rains. Phenological responses at the community level were independent of temperature, but both precipitation variables had a positive, significant effect (4 out of 20 cross-correlation analyses were significant). Flower richness (S_{Tot}) responded immediately to both precipitation variables, whereas flower abundance and total individual in bloom (F_{Tot} and F_{Anom}) responded to spring rains, mainly at the beginning of the season with a delay of 4 weeks (ESM1 Table S5, Fig. S12).

Bee nesting-floral resources relationships

We obtained 38 significant signals out of 144 cross-correlation analyses among bees' nesting phenologies and the two proxy variables flower number and individual in bloom (F_f and I_f) related to the phenology of the target plant species (ESM1 Table S2, Figs. S6–S7). The nesting phenologies of specialist bees (*A. andinum, A. vigintipunctatum, T. laticeps*) showed significant positive signals to the phenology of each main flower resources (like *L. divaricata, P. flexuosa, L. chilense,* or *O. sulphurea*; Figs. 2, 3 and more details in ESM1 Table S2, Figs. S7–S8). The nesting phenology of the specialist bee *A. andinum* showed an immediate response to the blooming of *L. divaricata* and *P. flexuosa* and a delayed signal of around 6 weeks for *L. chilense.*

The nesting phenology of the specialist bee *A. vigintipunctatum* exhibited a similar pattern to that of *A. andinum*, but the delayed response to *L. chilense* was shorter (around 4 weeks). The nesting phenology of the specialist bee *T. laticeps* showed an immediate response to that of *O. sulphurea* (1 week), its main host plant, and a delayed response of 4 weeks to the other two host plants (*L. divaricata* and *P. flexuosa*).

We obtained 24 significant signals out of 48 cross-correlation analyses among bees' nesting phenologies and the four community-level proxy variables of floral resources (flower richness, total individual in bloom, flower abundance and anomaly. ESM1 Table S3, Figs. S9–S10). Bee responses varied among variables. The nesting phenology of all bee species showed a positive signal to the total number of plant species in bloom (S_{Tot}), differing only in their response time (Figs. 2 and 3). Such response was as short as from 0 to



	SPECIALISTS			GENERALISTS		
Variable	*A. andinum*	*A. vigintipunctatum*	*T. laticeps*	*A. decaspilum*	*A. rubripes*	*X. atamisquensis*
Mean temperature (T_{mean})		-	+			
Min. temperature (T_{min})		-	+			
Max. temperature (T_{max})		-	+			
Precipitation			+			+
Spring rains		+	+	+	+	+
Flower number (F_f)	+	+	+			
Individual in bloom (I_f)	+	+	+			
Flower richness (S_{tot})	+	+	+	+	+	+
Total ind. in bloom (I_{tot})	+	+		+	+	+
Flower abundance (F_{tot})		+	+			
Anomaly		+	+			

No Signal

Difuse Signal $\alpha > 0,05$

Short-term Signal < 4 weeks

Long-term Signal > 4 weeks

Fig. 3 Summary of results from bee nesting-climate and bee nesting-resources cross-correlation analyses. Symbols (+ or −) indicate direction of response, which was immediate (short-term signal < 4 weeks) or delayed (medium/long-term signal > 4 weeks). "No Signal" indicates no response, while "Diffuse Signal" indicates a response that is not statistically significant. For further explanations of each variable, refer to Table 2. All cross-correlation results are provided in the electronic supplemental material, including Tables S1–S5 and Figs. S5–S11

5 weeks in *A. vigintipunctatum* to as long as 6 to 15 weeks in *X. atamisquensis* (ESM1 Table S6, Figs. S9–S10). Except for the large body-sized *T. laticeps* and *X. atamisquensis*, the nesting phenology of remaining small body-sized bees showed a positive signal and short delay (1 or 2 weeks) to the total number of individual shrubs in bloom (I_{Tot}). Only the nesting phenology of *T. laticeps* showed a positive and short delay to flower abundance and anomaly community-level proxy variables, 1 week delay for the total number of flowers (F_{Tot}) and 4 weeks for anomaly (F_{Anom}).

Discussion

Our study represents a unique and valuable long-term investigation of nesting phenology across multiple solitary bee species in an understudied ecosystem. We found that nesting phenology is influenced by various flowering and climatic variables, regardless of the bee species' level of specialization. While some bee species had their nesting phenology predicted solely by flowering variables, others were influenced by a combination of flowering and climatic factors. Body size emerged as a critical trait in explaining differential nesting responses, with variations in body size resulting in different short- or long-term responses. Furthermore, our study revealed that generalist bee species exhibited greater inter-annual variability in nesting compared to specialist bee species, thus suggesting that generalist bee species may be more vulnerable to phenological mismatches than previously thought.

Our analyses suggested that bees' nesting phenology may be predicted by several flowering and climatic variables regardless bees' level of specialization. While the nesting phenology of two specialist bees followed the phenology of their host plants and the flower richness (total number of plant species in bloom, S_{Tot}), we also observed significant signal to both temperature and precipitation (spring rains), except for the nesting phenology of the specialist bee *A. andinum* that was independent of climatic signals. The nesting phenology of two generalist bees responded to local floral resources (flower richness S_{Tot} and total individual in bloom I_{Tot}), as well as to precipitation (spring rains). The generalist bee *A. decaspilum* also did not respond to any climatic signals (Fig. 3). Thus, these results are only partially consistent with our expectations that the nesting phenology of specialist bees is predicted by the flowering phenology of their host plants, whereas that of generalist bees is predicted mostly by abiotic cues that allow them to track flower availability across the whole plant community.

It is important to remember that our analyses only allow us to identify which of the time series used as proxies of the flowering phenology and climate are best at predicting or explaining bees' nesting phenology, as well as how well they match up with each other. The results from these cross-correlations analyses are not evidence that nesting cues exist, in the same manner that environmental cues are required for adult emergence in bees and other insects (e.g., Danforth 1999; Beer el al. 2019). However, we do not rule out this possibility entirely, as there are observations of specialist bees delaying nesting activity following emergence until their primary host is available or using a different host (Minckley et al. 2013). In addition, some behavioral decisions by females are likely necessary prior to nest building and provisioning. For instance, females must be able to correctly interpret environmental signals when deciding to start searching for suitable nesting sites, nectar, and pollen for their own nourishment, or gathering nesting materials (petals, oil, plant fibers, etc.). The influence of abiotic factors in these activities has been documented for some species (e.g., Forrest and Chisholm 2017; Straka et al. 2014) and this aspect is doubtless worth exploring.

Body size is a recognized biological trait that affects bees' foraging behavior. Larger bees are not only able to forage longer distances but also to fly at lower temperatures than small body-sized bees (Greenleaf et al. 2007). Regardless of the specialization level, the nesting phenology of only small body-sized bees in our study (all species of *Anthidium*) was predicted by the number of individuals in bloom (I_{Tot}). This is probably because small bees are limited to nearby resources in comparison to larger body-sized bees (*X. atamisquensis* and *T. laticeps*), which can forage longer distances from their nesting sites when local resources are limited. Although we did not measure bees' foraging distances, available data indicates that some species of *Anthidium* forage within a few hundred meters from their nests, whereas carpenter bees can forage up to 6 km from their nests (Pasquet et al. 2008; Zurbuchen et al. 2010). The large body-sized bee *T. laticeps* was the only species whose nesting phenology responded positively to the total number of flowers in the community (flower number F_{Tot}, anomaly F_{Anom}). This bee relies on the cactus *O. sulphurea* but it also occasionally visits other plants (Chacoff et al. 2012; Vitale and Vázquez 2017). Thus, a greater availability of flowers across the whole plant community during the spring promotes the construction of nests because it provides access to a wide range of nectar resources.

Bees' nesting phenologies also responded differently to different aspects of the same biotic and abiotic variables (Fig. 3; ESM1 Table S6). For example, the nesting phenology of *A. vigintipunctatum* responded negatively to maximal temperature (T_{max}), particularly if these temperatures occurred during the winter, which led to a low number of nests built during the late spring. In contrast, the nesting phenology of *T. laticeps* responded positively to mean and minimal temperature (T_{mean} and T_{min}), which promoted the construction of nests. All bees studied here overwinter as a pre-pupae, and not all emerged every season (Vitale et al. 2017, 2020; Vitale and Vázquez 2017), except for *X. atamisquensis*, which as in other carpenter bees, overwinters as an adult (Michener 1990; N. Vitale unpublished data). Thus, variation in temperature could influence immatures' diapause or survivorship for these species. However, knowledge of the thermal biology of bees is limited, particularly in their immature stages (Cane and Neff 2011).

We also found that the nesting phenology of specialist bees is highly synchronized with that of their host plants and is more regular than that of generalist bees, as the latter exhibited greater inter-annual variation. Thus, our results support previous observations indicating that phenological matching with floral resources is the main adaptive strategy for specialist bees (Wcislo and Cane 1996; Minckley et al. 2000). Our results also suggest that generalist bees could be more vulnerable to climate change than previously suspected. Having access to flower hosts does not always guarantee successful nesting behavior, as we did not detect generalist bees nesting in some years and in some places. The absence of nesting activity may suggest other limiting factors that could significantly impact long-term nesting success, such as an insufficient number of new individuals for generation replacement.

Although several studies highlight the vulnerability of specialist bees to climate change (Bartomeus et al. 2013; Mathiasson and Rehan 2020), this might not apply to all bee communities in all ecosystems. For example, Minckley et al. (2013) suggested that under climate change, specialist bees might dominate the warm deserts of North America (an ecosystem very similar to the Monte desert). This is because in that community, the phenological match determines bee survival, and both specialist and generalist bees emerge from diapause despite a drought if they use plants that are able to bloom independently of rainfall by using subterranean water. But, if plant species required rainfall for flowering, the specialist bees are able to undergo long-term facultative diapause, emerging only in response to adequate rain when their host plant blooms. Thus, when underground water is no longer available for plants to bloom, generalist bees are more vulnerable to phenological mismatch than specialist bees because the former are unable to predict when bloom is poor or absent. Although our study focused on the bees' nesting phenology, which occurred after bees have emerged, fed, mated, and built nests, it supports the vulnerability of generalist bees to climate change. Apparently, the strength of specialist species lies in their ability to optimize the use of one or a few resources to provision the nest and predict their availability. On the other hand, although generalist species can switch pollen sources, they may make suboptimal use of available resources, coupled with the inability to anticipate the decrease or absence of resources, which could explain the absence of nests in some years. Further studies could assess the vulnerability of bees to climate change by targeting specific ecosystems or bee communities.

We have a limited understanding of the phenological cues that plants in our study area follow. Plants cue to a wide range of environmental signals that include temperature, photoperiod, precipitation, soil humidity, and snow coverage (Price and Waser 1998; Visser and Holleman 2001; Inouye et al. 2003). Understanding the signals that trigger plant phenology in our study area was beyond the scope of this work. However, based on the climatic variables analyzed, three of the six host plants responded to climatic cues. *Larrea divaricata* and *P. flexuosa* responded negatively to temperature several weeks before it bloomed. An increase in temperature during the winter resulted in a low number of flowers in the spring, a pattern that is consistent with a study in a different ecosystem (Aldridge et al. 2011). Like most plants in the community, *O. sulphurea* and *L. divaricata* responded positively and immediately to spring rains, which is an expected response for plants in a desert biome (Bowers and Dimmitt 1994). Models of climate change in our area predict an increase in temperature and precipitation during the summer months (Boninsegna 2014), which according to our observations, may affect both plants' and bees' nesting phenologies. Model prediction (Boninsegna 2014; Pizarro et al. 2013) suggests an increase in the minimum temperature for the study area. Our work evidenced that the anomaly of the minimum temperature during autumn–winter is a positive signal for the floral richness of each year, and possibly, this signal positively impacts the nesting of bees (floral richness being a signal of nesting). In the Monte of Mendoza, our study location, an increase in precipitation is also expected throughout the year, especially in the summer; a higher incidence of storms represents very rainy days with extreme precipitation (Boninsegna 2014; Argerich et al. 2013). Precipitation occurring during spring–summer was identified in this study as a critical environmental feature influencing the bee-resource assemblage, and the anticipated changes may negatively impact nest construction and floral resource availability. The bee species studied are adapted to inter-annual climatic variability; even the most specialist bees are resilient to this variability due the assemblage with their main resources (e.g., *T. laticeps–O. sulphurea* or *Anthidium* bees and *P. flexuosa*, plants that bloomed every years and offered a lot of floral resources); however, further studies are needed as it is unknown which environmental signals trigger other phenological events in the studied bees (e.g., adult emergence) and what consequences climate changes may entail.

Conclusion

Our study revealed that the nesting phenology of the six solitary bees is predicted by multiple flowering and climatic variables, which is partially consistent with our expectations related to differences in bees' specialization level. Surprisingly, body size showed a differential pattern between small and large bees, with smaller bees exhibiting a lag in response to climatic signals. Nesting of smaller bees was predicted by the number of individual plants in bloom, indicating some spatial pattern in resource availability. Given that the nesting phenologies of both specialist and generalist bees positively responded to the flowering phenology of the entire community, and small-bodied bees were affected by spatial resource availability, efforts to mitigate the effects of climate change on bees should emphasize the conservation of plant communities as a whole, rather than focusing on individual species. Finally, our study supports previous observations on desert bee communities that suggest a greater vulnerability of generalist bees to climate change than current dogma surmises.

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Author contributions NV conceived the study, collected and analyzed data, and wrote the manuscript; VHG participated in data interpretation and analysis, and wrote the manuscript. Both authors gave final approval for publication and agree to be held accountable for the work.

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Data availability The biological datasets supporting this article are available as part of electronic supplementary material (ESM2). Statistical representations of the climate were generated from the database of the National Meteorological Service of Argentina (SMN) authorized by Centro de Información Meteorologica—SMN—SCTYPD—Ministerio de Defensa—República Argentina, for our exclusive scientific use and prevent shared it without permission.

Declarations

Conflict of interest The authors have no conflict of interest. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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