Title: **Pollen specialisation is associated with later phenology in *Osmia* bees (Hymenoptera: Megachilidae)**

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Published version available here:
https://resjournals.onlinelibrary.wiley.com/doi/abs/10.1111/een.13211

Abstract

1. Species exhibit a range of specialisation in diet and other niche axes, with specialists typically thought to be more efficient in resource use but more vulnerable to extinction than generalists. Among herbivorous insects, dietary specialists seem more likely to lack acceptable host plants during the insect's feeding stage, owing to fluctuations in host-plant abundance or phenology. Like other herbivores, bee species vary in host breadth from pollen specialisation (oligolecty) to generalisation (polylecty).
2. Several studies have shown greater interannual variation in flowering phenology for earlier-flowering plants than later-flowering plants, suggesting that early-season bees may experience substantial year-to-year variation in the floral taxa available to them.
3. We therefore reasoned that, among bees, early phenology could be a more viable strategy for generalists, which can use resources from multiple floral taxa, than for specialists. Consequently, we expected median dates of collection of adult specimens to be earlier for generalist species than for specialists. To test this, we obtained phenology data and pollen diet information on 67 North American species of the bee genus *Osmia*.
4. Controlling for latitude and phylogeny, we find that dietary generalisation is associated with significantly earlier phenology, with generalists active, on average, 11–14 days earlier than specialists.
5. This result is consistent with the generalist strategy being more viable than the specialist strategy for species active in early spring, suggesting that dietary specialisation may constrain the evolution of bee phenology—or vice versa.

Keywords: phenology, *Osmia*, specialisation, oligolecty, polylecty, solitary bees

Introduction

Ecological communities of all kinds include species that are relatively generalised—along niche axes such as habitat requirements, climatic tolerances, or diet breadth—as well as species that are more specialised (Wilson & Yoshimura, 1994; McPeek, 1996; Hanski *et al.*, 2001; Bascompte & Jordano, 2007). Present-day coexistence of specialists and generalists, as well as past evolutionary shifts in dietary niche breadth within lineages (Forister et al. 2012), suggest that both the generalist and specialist strategies have costs and benefits (Wilson & Yoshimura, 1994). Probably the most obvious cost of specialisation is the risk of death or reproductive failure if the specific host organism, food source, or mutualist is unavailable at the time and place when the specialist is active (Quiring, 1992; Minckley *et al.*, 1994; Posledovich *et al.*, 2018). Conversely, the costs of generalisation are thought to involve the need to maintain cognitive, morphological, or physiological traits that allow an organism to interact with different kinds of resources or mutualists (Futuyma & Moreno, 1988; Waser *et al.*, 1996; Bernays, 2001; Praz *et al.*, 2008a, 2008b).

Bees (with few exceptions) obtain all of their food from flowers and exhibit a wide diversity of floral host breadth, presumably because flowers vary greatly in their morphological, chemical, and nutritional characteristics (Wcislo & Cane, 1996). Pollen, in particular, is an essential protein source that many bee species collect from a limited number of host-plants (Wcislo & Cane, 1996). What limits host choice by bees is poorly understood but may include suitability of different pollens for larval development (Praz *et al.*, 2008a) and neurological constraints affecting foraging behaviour (Praz *et al.*, 2008b). Though definitions and thresholds vary across the literature, pollen-specialist (oligolectic) bee species are usually defined as depending on the pollen from a single plant genus, tribe, subfamily, or family (Robertson, 1925; Cane & Sipes, 2006). Pollen-generalist (polylectic) species are usually defined as collecting pollen from multiple plant families.

Several potential benefits have been suggested to explain the existence of pollen specialisation. Specialisation may allow species to escape competition (Robertson 1925; Minckley *et al.* 1994; but see Wcislo & Cane 1996), increase efficiency of pollen harvesting (Strickler, 1979) and digestion (Müller & Kuhlmann, 2008; Praz *et al.*, 2008a), or grant protection against parasites (Spear *et al.*, 2016). Conversely, generalisation may grant access to a fuller spectrum of essential nutrients, thanks to complementarity among different pollens (Requier *et al.*, 2015; Donkersley *et al.*, 2017). Another major advantage of generalisation over specialisation is non-dependance on a single floral host: dietary specialisation must be highly costly when the food source is unavailable, particularly if bees are unwilling or unable to obtain pollen from non-host flowers (e.g. Williams 2003; Praz *et al.* 2008a). Indeed, the availability of floral resources often limits bee reproduction (Roulston & Goodell, 2011) and is an important determinant of bee nesting phenology (Neff *et al.*, 1982; Neff & Simpson, 1990; Cane & Payne, 1993). A pollen specialist's reproductive output can be severely limited if it emerges during a period when its floral host is unavailable (Minckley *et al.*, 1994; Müller *et al.*, 2006). Specialisation can therefore be a risky strategy, with success depending on host flowers being reliably present during the period when the bee is active.

Across temperate regions, angiosperm flowering phenologies vary widely year to year in response to climatic variables (e.g., CaraDonna et al. 2014). Furthermore, plants with earlier average first flowering dates often show more interannual variability in their first flowering dates, and/or larger changes in flowering phenology over time, than those that flower later. This pattern has been observed in temperate European (Fitter *et al.*, 1995; Menzel *et al.*, 2006) and

North American (Iler *et al.*, 2013; Bertin, 2015) floras, as well as among cherry trees (*Cerasus* and *Prunus* spp.) in Japan (Miller-Rushing *et al.*, 2007). A likely explanation for this pattern is that the flowering phenology of early-blooming plants tends to be more sensitive to temperature than that of late-blooming plants (Miller-Rushing *et al.*, 2007; Miller-Rushing & Inouye, 2009; Mazer *et al.*, 2013; Wolkovich *et al.*, 2013; Lessard-Therrien *et al.*, 2014), and early spring in at least some north-temperate regions tends to exhibit more interannual temperature variation than summer (Chen & Hellström, 1999; Menzel *et al.*, 2006). If this trend for greater phenological variability among early-flowering plants is generally true in temperate regions, we should expect the availability of specific floral hosts during the period of adult bee activity to be more variable, and less dependable, earlier in the season than later. This means that, unless bees are capable of closely matching their emergence phenology to the flowering phenology of their host-plants, an early-emerging specialist risks, in certain years, not having any flowering hosts from which to forage. Generalists, on the other hand, can feed from a broader range of hosts, offsetting the effects of unreliable bloom (Vicens *et al.*, 1994; Kraemer & Favi, 2005; Yourstone *et al.*, 2021). Consequently, we propose that dietary generalisation should be a better strategy than specialisation for bees that are active early in the growing season—in other words, we suggest that early-flying specialists are less likely to persist than late-flying specialists or early-flying generalists. We therefore expect the adult activity period of generalist (polylectic) species to be earlier than that of specialist (oligolectic) species.

Methods

We tested the predicted association between host-breadth and phenology using the primarily Holarctic genus *Osmia* Panzer (Hymenoptera: Megachilidae). This genus of solitary bees contains over 350 species worldwide, around 165 of them in the New World, with varying diet breadth (Rightmyer *et al.*, 2013). Members of this typically univoltine genus overwinter within cocoons and emerge as adults from early spring to mid-summer, depending on the species (Bosch *et al.*, 2001; Forrest & Thomson, 2011). Most *Osmia* species lack an ability to facultatively undergo a prolonged diapause that could buffer populations against occasional poor years (cf. Danforth 1999), so a single year in which emergence is poorly timed relative to floral host availability could be devastating for bees that are entirely dependent on those specific hosts. Species-specific phenologies were inferred from specimen records on GBIF.org (Global Biodiversity Information Facility), and data on host breadths of different species were taken from published literature, as described below.

Phenology

The GBIF network includes over 100 000 records of *Osmia* specimens throughout the world, including dates of capture, coordinates, species names, and more. We downloaded the raw data for all North American *Osmia* bees that occur between the latitudes of 45°N and 35°N and between the longitudes of 125°W and 60°W (70 126 total occurrences) (GBIF, 2021). This geographic range, corresponding to the mid-latitudes of the conterminous United States and small areas of southern Canada (Figures S1 and S2), was chosen to encompass as many species and occurrences as possible while minimizing the latitudinal range (and hence the variation in phenology due to latitude rather than species identity). This latitudinal band largely excludes the hot deserts of North America, a region of exceptional bee diversity (Michener, 1979; Moldenke, 1979). Extreme interannual variability in the occurrence of flowering in these deserts, (Frank & Inouye, 1994) and the greater importance of precipitation cues (rather than temperature) for phenology (Beatley, 1974; Kimball *et al.*, 2010; Crimmins *et al.*, 2011), could lead to different hypotheses about the relationship between specialisation and phenology (e.g. Minckley et al.

2000). Additionally, desert-adapted specialist bees may use bet-hedging strategies to cope with variability in availability of their host flowers (Danforth, 1999), which may restrict the applicability of our hypothesis. Of the 70 126 *Osmia* records in our selected geographical area, only 620 were from citizen-science observations, and fewer than 10 other records were from sources that lack preserved specimens, so identification error is unlikely to play a large role in our dataset. In any case, errors in identification, or in the phenology or locality data, would only add noise, and not bias, to the dataset.

We eliminated from the dataset all occurrences without dates or species names and all occurrences preceding the year 1800, and we combined all subspecies into species. All species represented by fewer than 20 occurrences were excluded because this sample size was judged insufficient for characterising phenology. All 20 occurrences of *O. rostrata* Sandhouse were deleted because a suspiciously high proportion of them were from midwinter (6 in January, 4 in December). Following the taxonomic revisions of Rightmyer *et al.* (2013), *O. sladeni* Sandhouse was considered a synonym of *O. nifoata* Cockerell, and *O. physariae* Cockerell a synonym of *O. giliarum* Cockerell. Only three species in our dataset (*O. caerulescens* (L.), *O. cornifrons* (Radoszkowski), and *O. taurus* Smith) are exotic to North America; they were kept in the dataset because, if our hypothesis is correct, introduced early specialists should face the same challenges in establishing and maintaining populations as native early specialists.

Host breadth

We classified species simply as specialist or generalist because this binary classification predominates in the bee literature (e.g., Haider *et al.* 2014; Sheffield *et al.* 2014; Normandin *et al.* 2017; Schenk *et al.* 2017) and gives a simple signal of a species' level of pollen specialisation.

Host-breadth was determined from an exhaustive search of the literature combined with solicitation of expert opinion, all carried out blind to phenology data. Classifications we deemed to be based on biased evidence (i.e., surveys of visitors to single plant taxa) were excluded. Monolectic and oligolectic species were classified as specialists; eclectic oligoleges, mesoleges, and polyleges were classified as generalists since most literature classified any species collecting pollen from more than one botanical family as polylectic. Diet information was first sought in Krombein (1979), then using Google Scholar, typically searching the species name, with and without the word “oligolectic” or “polylectic”. Every article from the first page of results was investigated for species host-breadths, and references cited within these articles were also investigated if they were the source of the host-breadth classification. These searches, along with Fowler (2020b, a) and Fowler & Droege's (2020) online databases of North American specialist bees, literature from our personal database of *Osmia*-related literature assembled over 14 years, and personal communications with V. J. Tepedino, gave the host-breadth classifications of 67 species (see Table S1 for full results).

We found contradictory information on host breadth for 20 species in the dataset. We evaluated all sources for bias and compared them to determine which host-breadth category was best supported for each species. We gave precedence to studies that showed the methodology that led them to certain classifications, or at least gave clear definitions of host-breadth classification, over articles that gave no explanation for their classifications. Three species were unanimously classified as oligoleges in the literature (see references for *O. californica*, *O. coloradensis*, and *O. montana* in Table S1) except for being classified as mesoleges by Cane (2017), who used more nuanced classifications; we kept the specialist classifications that were used in the majority of the literature. Torchio (1990) considered *Osmia ribifloris* an Ericaceae oligolege based on observations of floral visits and cell provisioning of one population, but Rust (1986) classified it as oligolectic on Berberidaceae based on nest pollen data from another location. Based on that disagreement and on Haider's (2013) scopal pollen analysis of 50 individuals from 42 different localities revealing pollen from 8 families, we classified *O. ribifloris* as a generalist. Similarly, *O. inermis* was listed as an Ericaceae specialist by multiple sources (Giles & Ascher, 2006; Wolf & Ascher, 2008), but Müller's (2018) and Hicks's (2009) scopal pollen data showed it to be a probable polylege (or eclectic oligolege with a preference for Ericaceae and Fabaceae), so we listed it as a generalist.

Analysis

All analyses were conducted with R version 4.0.2 (R Core Team, 2020). The species that occurred in the GBIF database but for which we lacked host-breadth information were excluded from the analysis. Visual inspection of distributions of day of year of specimen collection (DOY) revealed a normal distribution for almost every species, with few outliers. Median DOY and median latitude were calculated for each species. The following linear model was tested: median DOY ~ host breadth + median latitude. Latitude was included in the model because bee emergence timing is highly positively correlated to latitude (Bartomeus *et al.*, 2011; Skandalis *et al.*, 2011), even over the limited (10°) latitudinal range we considered. Altitude could not be included as a factor because altitudes were only available for 11% of records in the raw GBIF data.

To control for the lack of independence among related species, we also conducted a phylogenetic generalised least-squares regression (PGLS) (Symonds & Blomberg, 2014) using the most recent phylogeny of *Osmia*. Phylogenetic information was only available for a subset of the species for which we had data, so the PGLS was used to test the assumption of independence among those species. If the assumption of independence among related species is not violated, we can use the non-phylogenetic linear model to test the central prediction with the full dataset, which has the advantage of a larger sample size. Using the R package *ape* (Paradis *et al.*, 2004), we manually wrote Rightmyer *et al.*'s (2013) *Osmia* phylogeny, which they inferred from three nuclear genes and the mitochondrial COI gene, into Newick format. Branch length data could not be obtained directly, so we used WebPlotDigitizer (Rohatgi, 2020) to extract branch lengths from Figure 2 of Rightmyer *et al.* (2013). Due to the limits of the measurement tool, several very short branches were measured as having a length of 0. For these, we used an arbitrarily small value of 0.0001. The tree used for the PGLS regression was pruned to only include the species in the Rightmyer *et al.* (2013) phylogeny for which we had phenology data and host-breadth classifications, and the phylogenetic analysis was restricted to that subset of our data.

Pagel’s λ is a value ranging from 0 to 1 indicating the magnitude of phylogenetic signal in a variable, with 0 indicating no phylogenetic signal and 1 indicating maximum phylogenetic signal (corresponding to a model of trait evolution by Brownian motion). With the R package *nlme* (Pinheiro *et al.*, 2013), we ran a PGLS regression with Pagel correlation structure to determine the best-fit Pagel’s λ with the following model: median DOY ~ host breadth + median latitude. We also ran the same model twice more, with λ fixed at 0 and 1, and compared AIC values and log-likelihoods of all three models to determine which correlation structure (λ value) was best supported. R^2_{pred} (Ives, 2019) was determined using the R package rr2 (Ives & Helmus, 2011) for the three phylogenetic models.

Results

The final non-phylogenetic dataset included 67 *Osmia* species with known host-breadths, collectively represented by 34 098 occurrences from the GBIF dataset (Table S1). Number of occurrences per species ranged from 20 (*O. nanula*) to 5091 (*O. pumila*) and median dates of occurrence ranged from 12 April (*O. liogastra*) to 22 July (*O. chalybea*). Twenty-eight species were classified as specialists and 39 as generalists (see Figures S1 and S2 for geographic distribution of data). Among specialists, twelve species were specialists on Fabaceae, nine on Asteraceae, five on Plantaginaceae, one on Ericaceae, and one on Boraginaceae.

The subset of the data used for the phylogenetic analysis included 43 *Osmia* species (19 986 occurrences from the GBIF dataset), of which 18 were specialists and 25 were generalists (Figure 1). Number of occurrences per species ranged from 26 (*O. cyaneonitens* and *O. nigriventris*) to 4285 (*O. lignaria*) and median dates of occurrence ranged from 12 April (*O. liogastra*) to 13 July (*O. juxta*). Among specialist species, seven were specialists on Fabaceae, five on Asteraceae, five on Plantaginaceae, and one on Boraginaceae.

In the non-phylogenetic model that included all 67 species, generalist species exhibited a 13.9-day earlier median date (95% CI: 3.3, 24.5 days) than specialist species, with every additional degree of median latitude being associated with a 7.7-day later median date (95% CI: 5.0, 10.4 days) (Figure 2, Table 1).

The PGLS model with best-fit λ also showed host breadth to be significantly associated with phenology (Table 1). Specifically, generalisation was associated with an 11-day earlier median (95% CI: 0.5, 21.6 days) occurrence date with a model-estimated λ of 0.183, indicating moderate phylogenetic signal (Table 1). Both fixed-λ models showed host breadth to be only marginally associated with phenology (Table 1). The model with fitted λ had the highest log-likelihood but fit the data little better than the model with $\lambda = 0$, which was the best-supported model based on AIC. Latitude was a highly significant predictor of phenology in all models ($t = 5.9$–6.8, $p < 0.0001$), with median occurrences 9.4–9.7 days later per degree northward (95% CI: 6.3–6.9, 12.3–12.5 days). Phylogenetic models including both predictors (host breadth and latitude) explained >45% of the variation in *Osmia* species phenology (Table 1).

Discussion

Association between host breadth and phenology

Our results show that generalist (polylectic) *Osmia* species are active on average 14 days earlier than specialist (oligolectic) species, which is consistent with pollen specialisation being less compatible than generalisation with early phenology. The lack of detectable phylogenetic signal in the PGLS regression suggests that species' relatedness is not responsible for the relationship between host breadth and phenology; we are therefore reasonably confident in the significant association we detected using the non-phylogenetic regression. Though the phylogenetic regression shows only a marginally significant relationship between host breadth and phenology, its smaller sample size compared to the non-phylogenetic regression makes it less reliable. These results are consistent with our expectation that greater unpredictability of early-season flowering makes a specialist diet less tenable for early-season bees.

The pattern of generalists having a long-term fitness advantage over specialists in temporally variable environments has been well established (Futuyma & Moreno, 1988; Waser *et al.*, 1996; Kassen, 2002; Overington *et al.*, 2008); our finding suggests that this advantage can lead to seasonal trends in the prevalence of generalisation. Higher late-season competition for pollen resources (e.g. Mizunaga & Kudo, 2017) may lead to a pattern of seasonal increase in the proportion of specialists, which are generally held to be stronger competitors than generalists (Futuyma & Moreno, 1988), but, to our knowledge, that has yet to be demonstrated.

An alternative explanation for our results could be that angiosperm traits that are conducive to bee specialisation, such as highly specialised floral structures or well defended pollen, are also associated with later floral phenology, leading their bee associates to have later phenology. For example, the characteristically late-flowering Asteraceae family (Kochmer & Handel, 1986), which may have defended pollen (Müller & Kuhlmann, 2008; McAulay *et al.*, 2021) and supports numerous specialist bees in multiple genera (Müller, 1996; Larkin *et al.*, 2008; Müller & Kuhlmann, 2008), was host to nine specialist *Osmia* species in our dataset. However, 19 of our 28 specialist species are associated with early- to mid-season flowering families (Ericaceae, Boraginaceae, Fabaceae, Plantaginaceae) (Kochmer & Handel, 1986), and another specialist-hosting plant family with apparently defended pollen (Ranunculaceae; Sedivy et al. 2008, Eckhardt et al. 2013) also typically flowers early (Kochmer and Handel 1986). Consequently, the later phenology we observed among specialists is unlikely to be explained by an association with late-flowering families, though host-plant phenology certainly impacts bee phenology (Neff *et al.*, 1982; Neff & Simpson, 1990; Cane & Payne, 1993; Minckley *et al.*, 1994).

Phenological matching

Some bees, like other herbivorous insects, can adjust their emergence timing in such a way that they remain more or less synchronised with their host-plants, despite spatial or interannual variation in host-plant phenology (Minckley *et al.*, 1994; Danforth, 1999; Van Asch & Visser, 2007; Posledovich *et al.*, 2018). This may be common in warm desert-adapted bee species (e.g. Danforth, 1999; Minckley *et al.*, 2013); our sampling range mostly avoided the warm deserts of

North America. Precise and reliable phenological tracking would negate the disadvantage of variable host-plant phenology; however, synchronisation of insects and host-plants is often imperfect (e.g. Visser & Holleman 2001; Uelmen Jr. *et al.* 2016; Posledovich *et al.* 2018). Though the phenologies of many specialist species such as *Osmia iridis* (a Fabaceae specialist) are correlated with those of their host-plants, the phenologies of plant and bee may respond to different environmental cues, making it difficult for the bees to adjust precisely to interannual variation in the plant's phenology (Forrest & Thomson, 2011). Therefore, variability in the timing of host-plant bloom could still make early emergence a risky strategy for pollen specialists.

Although the specialists in our dataset had later phenologies on average than the generalists, the range of phenologies was similar between specialist and generalist *Osmia* species (Figure 2). This suggests that the later season presents no major disadvantages for generalists, and that an early flight season is not completely incompatible with specialisation. In fact, one specialist species, *Osmia liogastra* (a legume specialist native to the southwestern U.S.A.), had the earliest phenology of any species in our dataset. This species is one of a minority in our dataset to nest in soil (Cane *et al.*, 2007); it may therefore be capable of detecting the environmental cues such as soil temperature and snow cover that trigger the onset of flowering in many temperate-region herbaceous plants (Holway & Ward, 1965; Dahlgren *et al.*, 2007; Jánosi *et al.*, 2020), and thus adjust its phenology annually to match that of its host-plant. This species might therefore be more tolerant of early-season variation in phenology than its above-ground, cavity-nesting congeners. More information on the climatic determinants of the phenologies of bee emergence and host-plant flowering will be needed to evaluate this explanation.

Potential impacts of climate change

Though phenological shifts vary widely among species, angiosperm first-flowering dates are advancing overall in response to increased temperatures caused by climate change (Calinger *et al.*, 2013; Bock *et al.*, 2014; CaraDonna *et al.*, 2014; Szabó *et al.*, 2016), paralleling the general advance of springtime phenology in plants (Jeong *et al.*, 2011). Phenology of many generalist bee species is following the same trend, with early-emerging bees advancing their phenology faster than later-emerging bees (Bartomeus *et al.*, 2011) and demonstrating high sensitivity to varying temperatures (Stemkovski *et al.*, 2022). This extension of spring could entail a greater lengthening of the potential foraging and nesting season for generalist bees than for specialists. Additionally, exotic plants have been shown to shift their flowering phenology in response to climate change more readily than native plants (Wolkovich *et al.*, 2013). Since exotic flora are more likely to be exploited by generalist bees than by specialists (Stout & Morales, 2009), this might provide additional support to generalists in the early season, adding to other evidence suggesting that climate change may disadvantage specialists more than generalists (Packer *et al.*, 2005; Davey *et al.*, 2012; Gough *et al.*, 2015). However, our conclusion also implies that specialist bees may not be particularly vulnerable to climate-change-induced phenological mismatch with their host-plants, as a result of their later-season phenology. It is also encouraging—for bees and for other organisms that depend on specific hosts being available at the right time—that climate change does not seem to be increasing interannual phenological variability in a broad sample of taxa (Stemkovski *et al.*, 2022).

Recommendations for future work

If early-spring phenology is broadly associated with dietary generalisation in bees, we would expect to see this pattern in bee genera other than Osmia as well—at least among those taxa that share its predominantly temperate distribution and its relatively early-season phenology (e.g., Andrena). Future work could test whether the association between early phenology and generalisation holds across a greater taxonomic and geographic range. However, a more direct test of our hypothesis would be to investigate whether, across a range of plant taxa, interannual variability in flowering phenology predicts the number (or proportion) of specialist pollinator lineages supported by that taxon. More information on the extent to which bees and their floral host-plants share cues for emergence and flowering would also reveal whether specialists are in fact vulnerable to emerging when no suitable flowers are available.

Acknowledgements

We are grateful to Vince Tepedino for assistance beyond the call of duty in determining or confirming floral-host associations for several *Osmia* species. We also thank Julien Martin for statistical advice (though any remaining errors are our responsibility), Jack Neff for comments on our hypothesis, Emmanuelle Fréchette for help with ArcMap, and Heather Kharouba and two anonymous reviewers for comments on an earlier draft of the manuscript.

Contribution of authors

The project was conceived by JF. Data collection was carried out by DP. Both authors contributed equally to analysis and writing.

Conflict of interest

There is no conflict of interest.

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Table 1. Results of the non-phylogenetic linear model and three PGLS models of the effect of host breadth on median date of occurrence (median latitude included as a covariate). Coefficients indicate the effect of generalisation (polylecty) on median day-of-year. Significant p-values ($\alpha = 0.05$), the highest log-likelihood, and the lowest AIC value are indicated in bold. R^2 for the phylogenetic models represents R^2_{pred} (Ives, 2019).

Model	**n**	**Pagel's λ**	**logLik**	**AIC**	**d.f.**	**t**	***b***	**Std. error**	**p**	**R^2**
Non-phylogenetic	67	N/A	not comparable	not comparable	64	−2.6	−13.9	5.3	**0.011**	0.34
Best-fit λ	43	0.183	**-174.5**	359.0	5	−2.1	−11.0	5.4	**0.047**	0.53
λ fixed as 0	43	0	-174.8	**357.5**	4	−1.9	−10.1	5.2	0.061	0.54
λ fixed as 1	43	1	-181.8	371.6	4	−1.9	−10.1	5.4	0.066	0.47

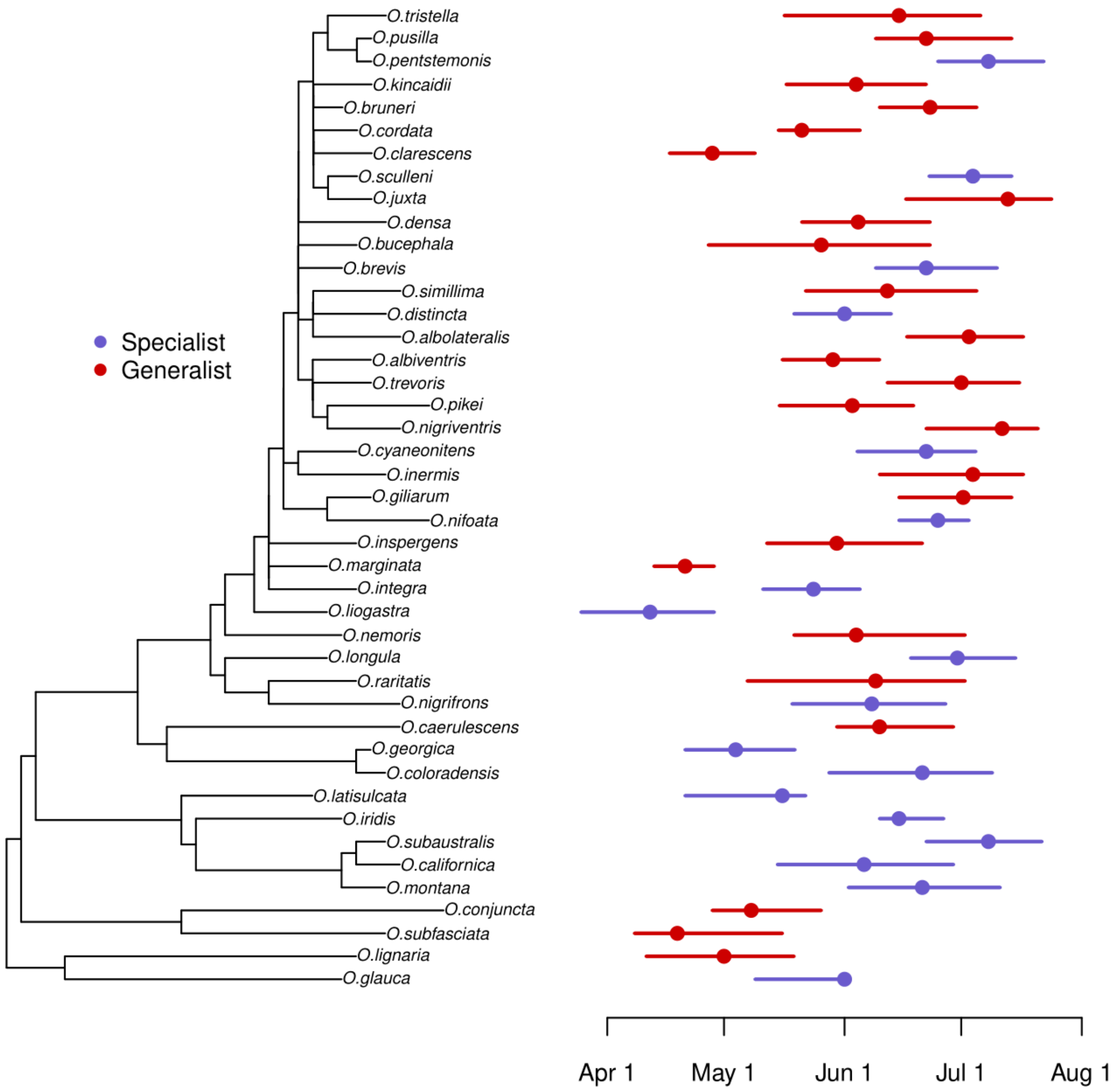

Figure 1. Partial phylogeny of the genus *Osmia* from Rightmyer *et al.* (2013), including only the 43 species used in the PGLS regression. At right are shown the median occurrence dates and interquartile ranges for each species. The 18 pollen-specialist (oligolectic) species are shown in blue, the 25 pollen-generalist (polylectic) species in red. Branch lengths were extracted from Figure 2 of Rightmyer *et al.* (2013) using WebPlotDigitizer (Rohatgi, 2020).

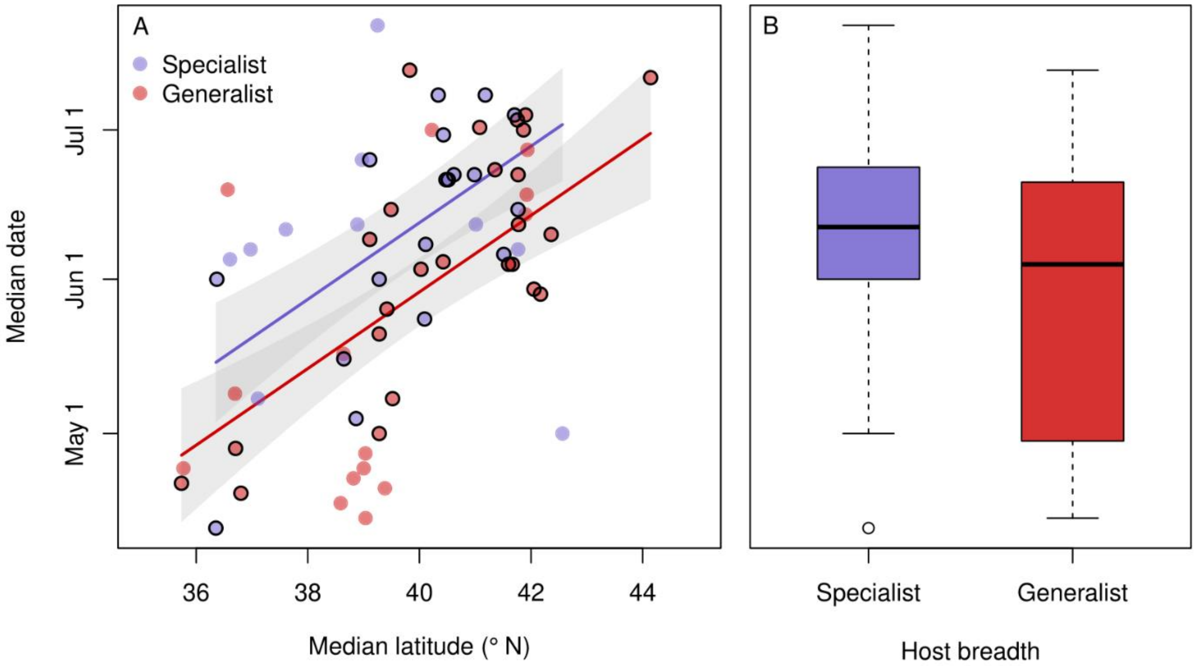

Figure 2. Median dates of occurrence for 28 pollen-specialist (oligolectic) and 39 pollen-generalist (polylectic) *Osmia* species (A) as a function of median latitude and (B) as a function of host breadth. Black outlines on datapoints in (A) indicate the subset of species included in the dataset used for the PGLS regression. Lines represent non-phylogenetic additive model (median date ~ median latitude + host breadth) predictions with 95% confidence intervals. In (B), the thick black line represents the median, hinges represent first and third quartiles, and whiskers extend to earliest and latest dates no more than 1.5× the inter-quartile range.