Colour polymorphism is prevalent on islands but shows no association with range size in web-building spiders

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Data and codes are available here: 10.5281/zenodo.13765962.

Codes are also available here:

https://github.com/fcsalgado/polymorphism_spider_rangesize/tree/main

Abstract

One of the most evident sources of phenotypic diversity within a population is colouration, as exemplified by colour polymorphism. This is relevant to a greater extent in animals with visually-biased sensory systems. There is substantial evidence suggesting that different colour morphs can access a broader range of habitats or niches, leading to larger geographic range sizes. However, this hypothesis has been tested in few lineages, comprising species where colour is likely to be involved in sexual selection. Furthermore, some available evidence considers geographical variation as polymorphism, thus limiting our comprehension of how sympatric colour polymorphism can influence a species' geographic range. Through an extensive systematic literature review and a comparative analysis, we examined the relationship between colour polymorphism and range size or niche breadth in web-building spiders. We identified 140 colour polymorphic spider species, belonging mainly to the families Araneidae and Theridiidae. We found no evidence that colour polymorphic species differ significantly from non-polymorphic species in terms of range size and niche breadth, after accounting for phylogenetic relationships and other covariates. However, we did observe that colour polymorphic species were more likely to be found on islands compared to non-polymorphic species. Overall, our results indicate that the association between colour polymorphism and geographic range size may not exist among web-building spiders, or be as pronounced as in other lineages. This suggests that the strength of the association between colour polymorphism and ecological success might depend on the ecological role that colouration plays in each clade.

Keywords

Graphical abstract

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Polymorphic · Theridiidae
No information
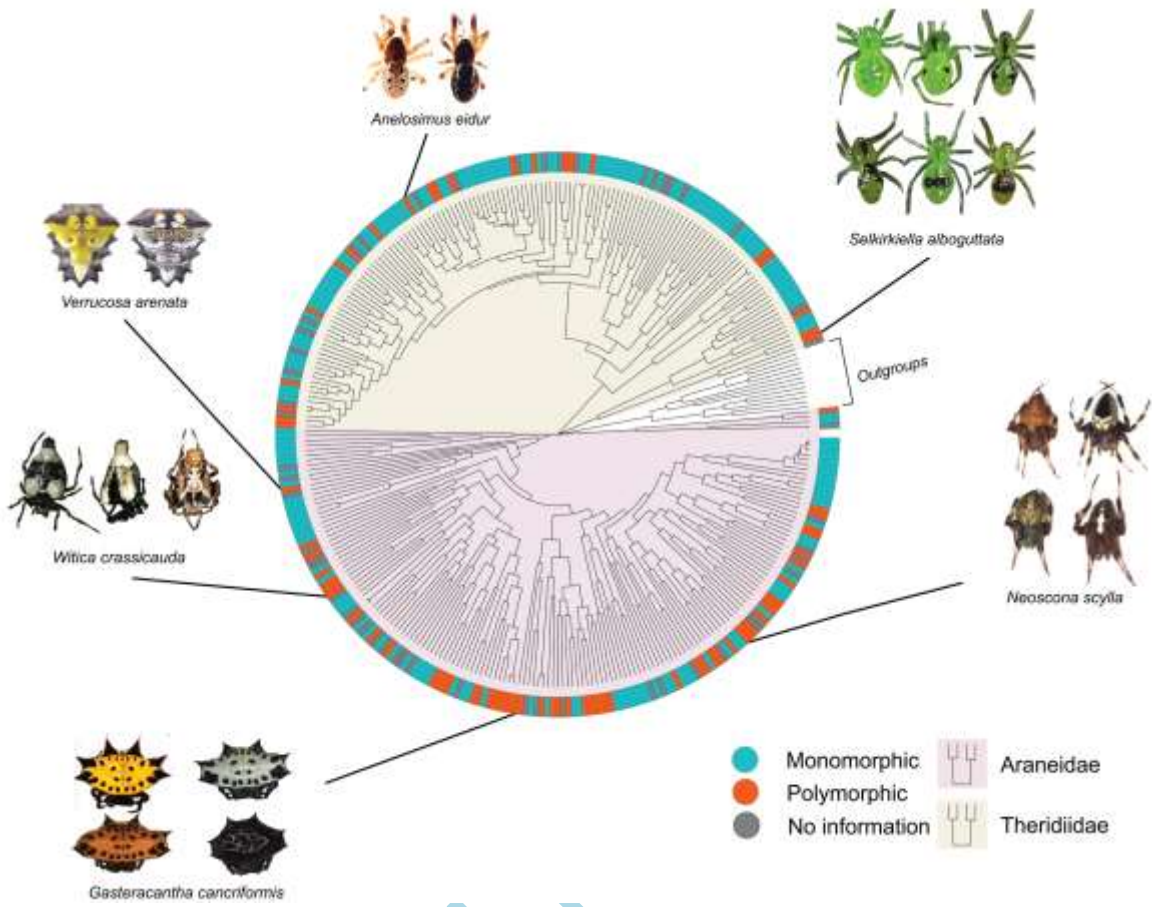
Introduction

Populations with high phenotypic diversity are of great interest because variation is the raw material for evolution. These populations may consist of sets of individuals that are phenotypically specialised to use specific resources or habitats (Van Valen, 1965; Bolnick et al., 2003, 2007; Sexton et al., 2017), leading to an increase of the population or species' niche breadth (Smith, 1987; Smith & Skúlason, 1996; Bolnick et al., 2003). Extended niche breadth can, in turn, increase the geographical area that a population can inhabit (Slatyer et al., 2013; Kambach et al., 2019; Carscadden et al., 2020), but empirical evidence is mixed. Morphological variation has been reported to have a positive correlation with the niche breadth and geographic range size in some cases (Galeotti & Rubolini, 2004; Hsu et al., 2014; Snowberg et al., 2015; Bolnick & Ballare, 2020), while in other cases an increase in niche breadth is not linked to increase in morphological variation, and could be linked to behavioural variation instead (Meiri et al., 2005; Bolnick et al., 2007; Carlson et al., 2021). Therefore, it is difficult to draw generalisations on how phenotypic variation may affect niche breadth and, in turn, the range size of a species.

One of the most evident forms of phenotypic variation is colouration. Discrete colour variation within populations is known as colour polymorphism, and has historically attracted the interest of ecologists and evolutionary biologists (Svensson, 2017; Jamie & Meier, 2020). The presence of multiple colour variants in a population might facilitate the use of diverse habitats (Roulin & Wink, 2004; Gray & McKinnon, 2007; White & Kemp, 2015). For instance, colour polymorphism in *Timema* walking sticks is maintained by the presence of multiple and distinct colour backgrounds provided by the host plant. In this species, different colour morphs occupy different ecological niches (e.g., stem and leaves), thereby reducing predation (Nosil et al., 2018; Villoutreix et al., 2023). Similarly, the colour variation of the flowers of *Clarkia xantiana* is linked to different pollinator preferences for the two colour

variants, indicating niche partitioning among specialist pollinators (Eckhart et al., 2006). The

use of different habitats or niches by different colour morphs has, in turn, been linked to

broader habitat use for species overall and wider geographic range sizes (Forsman & Åberg,

2008a; Bolton et al., 2016; Takahashi & Noriyuki, 2019; Forsman et al., 2020). For example,

the presence of female colour polymorphism in *Ischnura* damselflies is positively associated

with geographic range size (Takahashi & Noriyuki, 2019; Blow et al., 2021). This may be

possible because higher phenotypic diversity (colour or non-colour related) increases the

probability of having phenotypes already adapted to new environments (Gamfeldt &

Källström, 2007; Wennersten et al., 2012), or because variable populations exhibit reduced

susceptibility to pathogens, predators, or illnesses (Glanville & Allen, 1997; Bond & Kamil,

1998; Nokelainen et al., 2013; Forsman, 2014).

Current evidence supporting the association of colour polymorphism with broader range

sizes, however, usually does not discriminate between geographic colour variation within a

species and within-population colour variation (polymorphism *sensu stricto*). It is thus

possible that differences in the definition of polymorphism across studies have grouped

different processes. Namely, species with larger ranges are probably more likely to show

geographic variation in phenotype due to local adaptation to geographically variable

environmental conditions, rather than use a wider geographic range due to within-population

variation (Endler, 1977; Amézquita et al., 2009; Corl et al., 2010; McLean et al., 2014). In

consequence, to test the causal association between colour polymorphism and geographical

range size it is important to separate colour polymorphism *sensu stricto* (i.e., within-

population colour variation) from geographic colour variation. Additionally, most of the

studies to date are biased towards vertebrates and a few insects, which not only use colour

in an ecological context (i.e. against predation) but also in sexual signalling (Franzén et al.,

2019; Takahashi & Noriyuki, 2019; Forsman et al., 2020). For example, colour polymorphism

in the butterfly *Heliconius numata* is promoted by two opposite selective forces imposed by

predators and female mate preference at the same time (Chouteau et al., 2017).

Consequently, colour polymorphism in these groups may be linked with sexual selection

(e.g., Nokelainen et al., 2011), resource polymorphism (Smith & Skúlason, 1996) or both

(e.g., Chouteau et al., 2017), making it difficult to interpret any positive correlation between

colour polymorphism and range size.

Web-building spiders provide an opportunity to examine whether within-population colour

variation can influence geographic range size by increasing ecological niche breadth. They

are a widespread group that exhibit great variation in colouration within species, with a

broad-scale literature search identifying that out of 245 species, 44 exhibited colour

polymorphism (White & Kemp, 2015). These predators are characterized by limited dispersal

during the day (i.e., sit-and-wait predators), and hence rely on colouration for multiple

purposes such as thermoregulation (Oxford & Gillespie, 1998; Rao & Mendoza-Cuenca,

2016), prey attraction (Hauber, 2002; I.-M. Tso et al., 2002; I. M. Tso et al., 2006; Nakata &

Shigemiya, 2015), and likely predator avoidance (e.g. aposematism, Ximenes &

Gawryszewski, 2020; Robledo-Ospina & Rao, 2022). Additionally, many web-building

spiders appear to lack colour vision, in contrast to other spider groups like jumping spiders

(Morehouse et al., 2017). This is because most web-building spiders examined to date only

have one photoreceptor (Yamashita, 1985; Tiedemann et al., 1986). Therefore, colour cues

might not play a relevant role in sexual selection, and instead, chemical and vibration signals

could be more important for mate choice (Huber, 2005; Gaskett, 2007; Wignall &

Herberstein, 2013). Despite the ubiquity of colour polymorphism in spiders, we know almost

nothing about the ecological and evolutionary drivers and consequences of such colour

variation.

In this study, we tested whether colour polymorphic spiders exhibit broader range sizes and

wider niches compared to monomorphic spiders. To do this, we systematically reviewed the

literature to collate information on colour polymorphism in web-building spiders and investigated the potential link between colour polymorphism and increased geographical range and niche breadth. To examine this association, we calculated various geographical measures related to range size and the number of ecoregions and climatic zones occupied by each species (as an indirect measure of niche breadth). We controlled for phylogenetic relatedness by reconstructing the phylogenies of the predominant families, while also controlling for other covariates such as body length, number of geographic records and the latitude of the distribution centroid of each species.

METHODS

Data collection of polymorphic lineages

We compiled a list of colour-variable web-building spiders based on abdomen colouration. We focused on this body part because it is usually larger and more noticeable than other segments of the body. Additionally, it has been empirically associated with multiple ecological functions (White & Kemp, 2015; Robledo-Ospina & Rao, 2022). We first conducted a systematic literature search (January 2022) on Web of Science (www.webofscience.com) using the following search terms: *((Araneae OR Araneidae OR Theridiidae) AND (color* OR colour*) AND (polymorph* OR intraspecific variation OR variation OR morph))*. We supplemented the obtained list by searching for descriptions of colour variation in the literature published by Herbert W. Levi, who extensively studied web-building spiders (Leibensperger, 2016). The final list was checked and compared with a previous compilation of spider species with colour variation (White & Kemp, 2015).

Because the final list might include colour-variable species that are not strictly colour polymorphic (e.g., species with distinct geographical colour morphs), we narrowed down this

list to include only colour-polymorphic species. To accomplish this, we excluded those species without any explicit description of within-population variation or without evidence of multiple colour morphs in a single population based on literature or research-grade records from iNaturalist. For the iNaturalist check, we first explored whether the species had reported "subspecies" that were in sympatry, because this taxonomical category has often been misused in arachnology to describe within-population variation (Nentwig et al., 2019). For species that were not categorized as polymorphic in the previous step, we selected at least 10 geographical areas with high density of reports to explore if there were multiple colour phenotypes. In cases where this occurred in at least inone area, we narrowed down the geographical scale to confirm whether reports of different morphs were within 100 km to categorize the species as colour polymorphic.

Phylogenetic reconstruction

To account for phylogenetic relationships in further analyses, we reconstructed the phylogenies for Araneidae and Theridiidae, which are the families with the highest number of colour polymorphic web-building species. This was done based one five loci (28S, 18S, COI, H3, and 16S) used in previous publications (Scharff et al. 2020 & Liu et al. 2016). We successfully reconstructed the phylogenies for both families (Figure 1, and Supplementary figures 1 and 2; Details about the phylogenetic reconstruction are in the supplementary material), obtaining identical or highly similar results to those already published, but with the additional polymorphic species incorporated. In other words, we found support for the monophyletic clades previously described in the literature (Scharff et al. 2020 & Liu et al. 2016).

Geographical distribution data

For the species included in the phylogenies and those described as colour polymorphic, we validated their currently accepted taxonomy and obtained their geographic distribution information (names of countries or geographical regions) using the R package *arakno v1.3* (Cardoso & Pekár, 2022), which provides access to information from the World Spider Catalog (WSC; wsc.nmbe.ch). The WSC is an online curated database of spider taxonomy that includes the current and past nomenclature for each species and general descriptions of their geographical distribution (i.e., countries where they are found). To calculate different measures of geographical range and niche breadth, we downloaded the geographical records available on the Global Biodiversity Information Facility (GBIF) for each species (GBIF.Org User, 2023) using the R package *rgbif v3.7.8* (Chamberlain & Boettiger, 2017). Since a high proportion of these records can be potentially erroneous (Maldonado et al., 2015), we applied automated cleaning using the R package *coordinatecleaner v3.0* (Zizka et al., 2019), which removed empty records, records on the sea, and outliers. We compared GBIF record information with information from the WSC, and discarded records that were not within the geographic distribution as reported in the WSC. We also excluded the geographical areas where some species have been introduced by humans, as this might introduce noise to the data and lead to an overestimation of the range size in only some species.

Using filtered occurrence data, we employed R packages *raster v3.6* (Hijmans, 2020) and *rgdal v1.6* (Bivand et al., 2019) to calculate various geographical measurements for each species. We determined each species' range size by computing the minimum convex polygon area from points downloaded from GBIF (after confirming with WSC information and filtering). Additionally, we calculated the latitudinal range by finding the difference between the highest and lowest latitudinal distribution records. To assess climatic niche breadth

differences between colour polymorphic and monomorphic species, we explored the number of climatic zones occupied by each species. For this we counted the number of climatic zones occupied for each species overlapping their geographical records and minimum convex polygon with a 1-km^2 climatic zones layer (Beck et al., 2018). In addition, considering that colour polymorphic lineages may use a higher number of habitats (Roulin & Wink, 2004; Gray & McKinnon, 2007), we calculated the number of habitats where the species were present by intersecting their minimum convex polygon and geographical records with the most recent layer of ecoregions (Dinerstein et al., 2017). This is an approach that has captured differences between species at large-scale (Cooper & Purvis, 2010; Martins et al., 2022). All the six variables that measure range size were positively correlated with each other (minimum Pearson's r = 0.25, maximum Pearson's r =0.79; Supplementary Figure 3), and were also correlated to the number of ecoregions occupied and climatic zones (Supplementary Figure 3).

Considering that the presence on islands can be an indicator of range expansion (Paulay, 1994), we also determined whether species were distributed on islands by overlaying the occurrences with the global shoreline vector from the islands database (Sayre et al., 2019). To confirm the presence of each species on islands, we further overlaid their distribution, as described in the WSC, with the same islands database (Sayre et al., 2019). This allowed us to categorize, with greater confidence, whether species were present or absent on islands, particularly those with limited publicly available geographical records in databases.

Data analysis

To reduce any bias caused by including species with a low number of geographical records, we calculated the mean and its 95% confidence interval (CI) for the number of geographical records available for all the species. We excluded species from the subsequent analyses that fell outside the lower CI (i.e., species with extremely few records, < 43 records). With

the remaining species, we double-checked their colour polymorphism status by reviewing

the literature available on the WSC. Because species exclusively located on islands may

influence the estimations of our response variables due to their restricted geographical

distribution, we excluded them from the analyses of geographical range size. To facilitate

convergence in the models, we transformed the latitudinal range and range size by

calculating the square root of their values, which increased the normality of the variables.

Additionally, considering that the scale of our study is global, it is possible that response

variables like latitudinal range and range size are affected by other factors such as

geographical location of the species (Rapoport, 1982; Pie et al., 2021) or the species' body

size (Gaston & Blackburn, 1996; Alzate & Onstein, 2022), rather than by colour

polymorphism. To control for this effect, we included the absolute value of the latitude of the

distribution centroid of each species and the maximum body length of the females (applying

the logarithm) as covariates in all our models. The latter data was obtained from the

literature available for each species on the WSC. We explored the presence of collinearity

between the predictors using the function *check_collinearity* from the R package

performance v0.10 (Lüdecke et al., 2021).

To test whether the geographical range of the species can be predicted by the presence of

colour polymorphism (treated as binary: monomorphic or polymorphic), we employed a

Bayesian phylogenetic multilevel models using the R package *brms v2.20* (Bürkner, 2017).

We used default priors and ran the models with four chains with a burn-in of 10,000

iterations followed by 20,000 sampling iterations, thinned every 10 steps. We confirmed

chain convergence by examining the diagnostic plots. We implemented models with a

Gaussian distribution including the geographical range as response variable (area of the

polygon or latitudinal range) and the polymorphism category as a predictor (polymorphic or

monomorphic), while controlling for body length and the latitude of the centroid (covariates).

If the model presented divergent transitions, low effective sizes, or the predicted values did

not fit the original distribution of the data, we implemented a skew-normal distribution instead of a Gaussian distribution.

We tested whether the colour monomorphic and polymorphic spiders differ in their niche breadth with the same Bayesian approach described above. However, in this case, we used the number of ecoregions or climatic zones occupied by each species as response variables. Since these variables are count variables, we ran the models with a Poisson family using the polymorphism category as a predictor (polymorphic or monomorphic) with body length and the latitude of the distribution centroid as covariates. If the model showed divergent transitions, low effective sizes, or the predicted values did not fit the original distribution of the data, we used a Negative Binomial distribution instead of a Poisson distribution.

Because false statistical associations could be caused by sampling bias in the record data, we repeated the analyses using a more conservative dataset and a complementary dataset. The conservative dataset was derived by applying a linear regression between the number of geographical records and the geographical area of the regions described in the WSC (a positive relationship), discarding species outside the 50% predictive confidence interval, which corresponds to species with low number of records relative to the regions described in the WSC (Supplementary figure 4). The complementary dataset included all original species and six colour polymorphic species that did not have available genetic data but with substantial geographical records from public databases. Details about these datasets are available in the supplementary material. Additionally, to explore the effect of including geographically variable species in our dataset, we decided performed the analyses above but either excluded these species or treated them as colour polymorphic.

Finally, to test whether polymorphic species are more likely to be present on islands (a binary response variable), we built a Bayesian Phylogenetic Multilevel Model with the R

package *brms* (Bürkner, 2017). To increase the number of species in our analysis, we ran the same model including the species with few geographic records. This was possible because we verified the presence on islands using the WSC information and not exclusively the geographical records. This expansion allowed us to double the number of colour monomorphic and polymorphic species (N = 125, N = 61, respectively). We executed a model with the Bernoulli family and default priors, including the presence on islands as a response variable (present or absent) and the polymorphism category as a predictor (polymorphic or monomorphic) controlling by body length (covariate). We used the same running parameter as before confirming chain convergence by examining the diagnostic plots. We also ran the same analysis with the conservative dataset that included only species with adequate geographic records.

RESULTS

Colour polymorphic species

In our literature search, we identified 140 colour polymorphic species in 58 genera of web-building spiders (Supplementary table 1), primarily belonging to the families Araneidae (71%) and Theridiidae (27%). The majority of these species exhibit only colour polymorphic females (78%), while the presence of colour polymorphism in both sexes (20%) or exclusively in males (2%) was less frequent (Supplementary table 1). Although we acknowledge that relying solely on qualitative descriptions may not provide the most comprehensive understanding of colour variation, we observed a common pattern where colour polymorphism descriptions often involved black and light morphs (31%) or white and yellow colour morphs (15%). Very few species included morphs of other colours such as black and orange (4.2%), black and silver (3.5%) or green and brown (2.8%). Regarding the number of colour morphs within a single population, in our dataset around half of the

descriptions correspond to species with two colour morphs (53%), 18% to three, and 28% to more than three colour morphs.

Colour polymorphism, range size and niche breadth

After applying filters to remove species with insufficient geographical or phylogenetic information, our dataset comprised a total of 59 monomorphic species (5 with geographical variation in colouration) and 33 polymorphic species, including three that were endemic to islands. Among these species, 80 have occurrences on islands (48 monomorphic and 32 polymorphic), while 12 are exclusively found on the mainland (11 monomorphic and 1 polymorphic). The regions with the highest number of reported polymorphic species were North America, Europe, and northeastern Australia (Supplementary Figure 5). In this dataset, the mean latitudinal range was 30.58 degrees (standard error (SE) = 1.76), occupying an average area of 7,271,573 km^2 (SE= 812,457.7 km^2), 30.76 (SE=3.23) ecoregions and 8.29 (SE=0.38) climatic zones when calculated using the geographical records.

We found that polymorphic species do not have more geographical records than monomorphic species (0.55 [95% CI 0.0-1.12]; R^2: 0.04). Polymorphic and monomorphic species did not differ in the latitude of the centroid of their distributions (-4.90 [95% CI -12.52 – 2.66]; R^2: 0.017) or their body length (0.16 [95% CI -0.11 – 0.43]; R^2: 0.015). We found a slight positive association between the presence of colour polymorphism and greater latitudinal range (0.67 [95% CI 0.06 – 1.27]; Figure 2; Supplementary table 2 & 3). Nevertheless, we did not observe differences between colour monomorphic and colour polymorphic species in their geographical range when calculated with the area of the minimum convex polygon (371.37 [95% CI -114.24 – 866.03]); Figure 2; Supplementary table 2). When we explored whether there were differences in the niche breadth of colour

polymorphic and monomorphic species, we found a small effect supporting that polymorphic species occupy more ecoregions when using the geographical records (0.42 [95% CI 0.01 – 0.84]) or the distribution polygon (0.44 [95% CI 0.01 – 0.86]). However, we did not find any differences between polymorphic and monomorphic species in the number of climatic zones occupied (Figure 2; Supplementary Table 2). When we applied the same statistical models to the two additional datasets, designed to account for potential false associations due to sampling bias, we obtained qualitatively similar results (Supplementary Table 3 and 4). However, with these datasets latitudinal range and number of occupied ecoregions did not show any statistical association with the presence of colour polymorphism (Supplementary Table 3 and 4). There was also no link observed when we treated geographical colour variable species as polymorphic, or when we excluded them from the analyses (Supplementary Table 5 and 6).

We identified several significant relationships between our measures of geographic range and covariates other than the presence of colour polymorphism. For example, species with centred temperate distributions have smaller latitudinal ranges (i.e. species with tropical centred distributions have larger latitudinal ranges) when calculated with the geographic records (-0.03 [95% CI -0.05 – -0.02]). Likewise, we found that larger species occupied a greater number of climatic zones, when the latter was calculated using geographical records (0.32 [95% CI 0.15 – 0.48]). Larger species were also present in more ecoregions when this association was calculated with geographical records (0.54 [95% CI 0.10 – 0.99]) and polygon (0.57 [95% CI 0.11 – 1.03]).

We used a larger dataset consisting of 129 colour monomorphic species (70 present on islands and 59 exclusive to the mainland) and 61 colour polymorphic species (50 present on islands and 11 exclusive to the mainland) to test whether polymorphic species are more

likely to be present on islands, considering the presence on islands as an indicator of range expansion while controlling for the effect of body size. Indeed, we found that colour polymorphic species were more likely to be found on islands than monomorphic species (3.39 [95% CI 0.17 – 16.54]; Figure 3; Supplementary Table 4). We obtained an equivalent result when we reran the analyses with the conservative dataset that included only species with a high number of geographic records (Supplementary Table 2).

Discussion

Our literature search revealed that colour polymorphism is a common, widely-distributed phenomenon in web-building spiders, especially in species of the family Theridiidae and Araneidae (Fig. 1). This pattern of colour variation seems to be more prevalent in females than in males, and in at least half of the cases involved black and light morphs or white and yellow colour morphs. Contrary to our expectations, our statistical models suggest that colour polymorphic and monomorphic species have similar range sizes and niche breadths, and this is consistent across most measures. However, we found that colour polymorphic species had a higher probability of being present on islands compared to colour monomorphic species.

Our results contrast with previous findings in vertebrates and a few insect groups that support a positive correlation between range size and colour polymorphism (Forsman & Åberg, 2008b; Forsman et al., 2008; Franzén et al., 2019; Takahashi & Noriyuki, 2019; Blow et al., 2021). This discrepancy might be due to different reasons. First, some studies (Franzén et al., 2019; Takahashi & Noriyuki, 2019) do not distinguish between within-population colour variation and geographical colour differences for some lineages. This means that species with larger ranges have multiple colour phenotypes, but this might be a result of local adaptation to geographically distant habitats (Endler, 1977; Amézquita et al., 2009; Corl et al., 2010; Wittkopp et al., 2011; McLean et al., 2014), rather than having large

distributions due to within-population colour variation. Another possibility is that the role of colouration in each system may influence its association with geographic expansion. For instance, in *Ischnura* damselflies colour polymorphism is linked with broader ranges, but colour variation is maintained by frequency-dependent sexual conflict (Gosden & Svensson, 2009), a phenomenon that becomes more pronounced at higher population densities. It is possible that in that system colour polymorphism is linked to larger ranges because these species also have larger population sizes where there is more male mating harassment (Blow et al., 2021). In other systems, it has been found that anti-predator strategies such as camouflage are linked with higher intra-specific variation in colouration (Nokelainen et al, 2024). In our system, colour polymorphism is unlikely to be driven by sexual selection because unlike jumping spiders, colour discrimination in web-building spiders appears to be limited or absent (Yamashita & Tateda, 1978; Yamashita, 1985; Tiedemann et al., 1986). While it is possible that web-building spiders could use achromatic differentiation of pattern in mate assessment, other ecological processes, such as camouflage, aposematism, or prey capture, are more likely to explain colour polymorphism in web-building spiders (White & Kemp, 2015). The causal association of these ecological functions with the link between colour polymorphism and range size needs to be further explored.

Although most of our predictors did not have statistical support linking the presence of colour with broader range sizes, colour polymorphic species presented greater mean values in all of the variables evaluated (Supplementary tables 2-4). This suggests that we cannot rule out the possibility that our lack of significant results is influenced by the available geographical information used, or the number of species included in this study. However, our analyses would have detected any large differences in the range size or niche breadth between monomorphic and polymorphic species, so any differences that might exist are likely to be small. Even though we utilized different sources of geographic information (geographic records and World spider catalogue), arachnids are one of the taxonomic groups that require

more representation in public databases, considering the number of geographic records available relative to their high species diversity (Troudet et al., 2017; Hughes et al., 2021).

Our results also indicate that the range size of the species might be affected by other factors. We found that species with larger bodies tended occupied more climatic zones and ecoregions, a pattern that is common for multiple taxa (Gaston & Blackburn, 1996; Gaston, 2003). We also discovered that species with a more tropical centred distribution had larger latitudinal ranges. Hence, there is no support for the hypothesis that tropical species have smaller range sizes compared to temperate species (Rapoport, 1982). This hypothesis has similarly found no support in marine species, some birds and scorpions (Rahbek, 1997; Pie et al., 2021; Lira et al., 2023). We note that our aim was not to test all the factors affecting the geographical distribution of web-building spiders, so the trends we report and their mechanistic link with dispersal need to be formally tested.

Although none of our variables show a clear association between within-population colour variation and range size, we discovered that colour polymorphic spiders have a higher prevalence on islands than monomorphic spiders. In fact, 19.6% of the colour polymorphic species that we report are only present on islands. This agrees with previous reports of a higher probability of presence and establishment on islands for colour polymorphic moths and butterflies when compared to non-variable species (Franzén et al., 2019). The result that colour polymorphism was associated with presence on islands but not with range size is somewhat counterintuitive, considering that both factors might be linked to dispersal capacity (Whittaker et al., 2017; Alzate & Onstein, 2022). This could be because the variable of presence/absence on islands is less affected by the number of geographical records compared to range size.

A higher prevalence of colour polymorphic species on islands could be a cause or a consequence of island colonisation. Greater phenotypic diversity of the colour polymorphic species may enhance the possibility of having traits already well suited to new environments (Gamfeldt & Källström, 2007; Wennersten et al., 2012) or reduced vulnerability to environmental changes, pathogens, or predators (Glanville & Allen, 1997; Bond & Kamil, 1998; Nokelainen et al., 2013; Forsman, 2014). Alternatively, a monomorphic population that reaches a new environment with a lower number of competitors/predators (i.e. relaxed selection) and more ecological opportunities may expand its niche breadth via greater among-individual variation (niche variation hypothesis). An increase in within-population colour variation has been observed in island populations compared to mainland populations in various taxa, such as snails, lizards, and mammals (Hayashi & Chiba, 2004; Raia et al., 2010; Runemark et al., 2014; van der Geer, 2019). However, specific tests of the niche variation hypothesis have provided mixed support, though few of these studies used colouration as a measure of among-individual variation (Meiri et al., 2005; Svanbäck & Bolnick, 2006; Bolnick et al., 2007; Parent et al., 2014; Jones & Post, 2016).

The list of colour polymorphic spiders that we report here opens a range of possibilities for testing other hypotheses regarding how island colonization and colouration might be linked. For example, birds found on islands tend to be less bright than continental birds (Doutrelant et al., 2016), and more colourful when insular predators decrease (Bliard et al., 2020). We still do not know the prevalence of these patterns in insular arthropods, and it would be interesting to explore which colour morphs of the polymorphic spider species are present on islands vs. continents.

Overall, while multiple studies support the positive correlation between colour polymorphism and species range, we found no support for this hypothesis in spiders. In fact, the causes of

such relationship in other taxa remain unknown (Takahashi & Noriyuki, 2019). We still need more information about the significance of colouration in shaping the niche breadth of understudied lineages, where colour plays multiple ecological roles. Our study is a first step towards this, and our dataset of polymorphic species in spiders provides a valuable resource that can be used to explore multiple ecological and evolutionary questions with colouration as a phenotypic marker.

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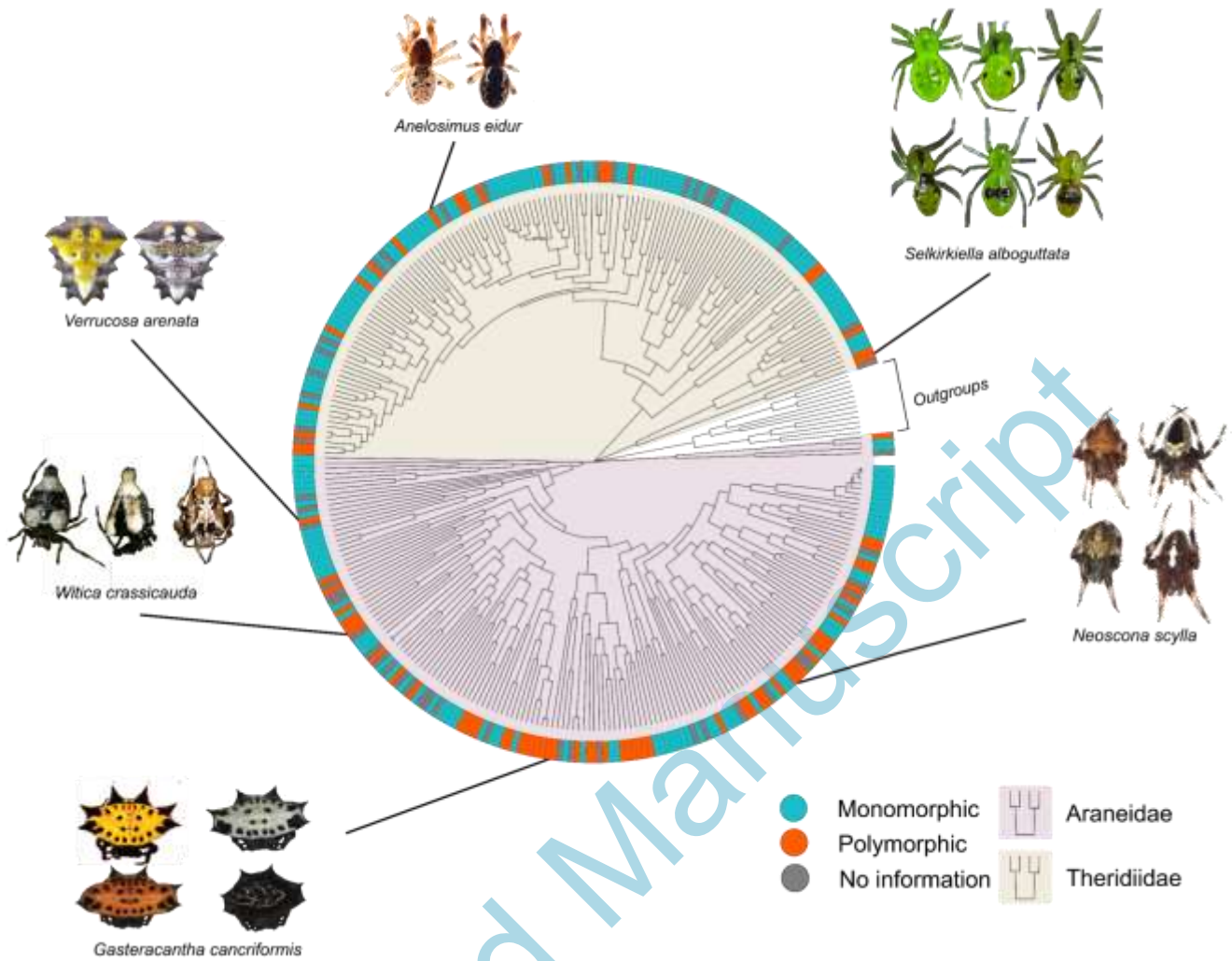
Figure 1. Phylogenetic relationships of colour polymorphic and monomorphic lineages from Araneidae and Theridiidae. Colour tips represent the presence or absence of polymorphism. Details about the species relationships are available in the supplementary figure 1 & 2. Photos credit: *Gasteracantha cancriformis*: Fabian C. Salgado-Roa, *Witica crassicauda*: iNaturalist, *Verrucosa arenata*: Rao et al., 2015, *Anelosimus eidur*: Agnarsson & Zhang, 2006, *Selkirkiella alboguttata*: Cotoras et al., 2017, *Neoscona scylla*: Baba & Tanikawa, 2015
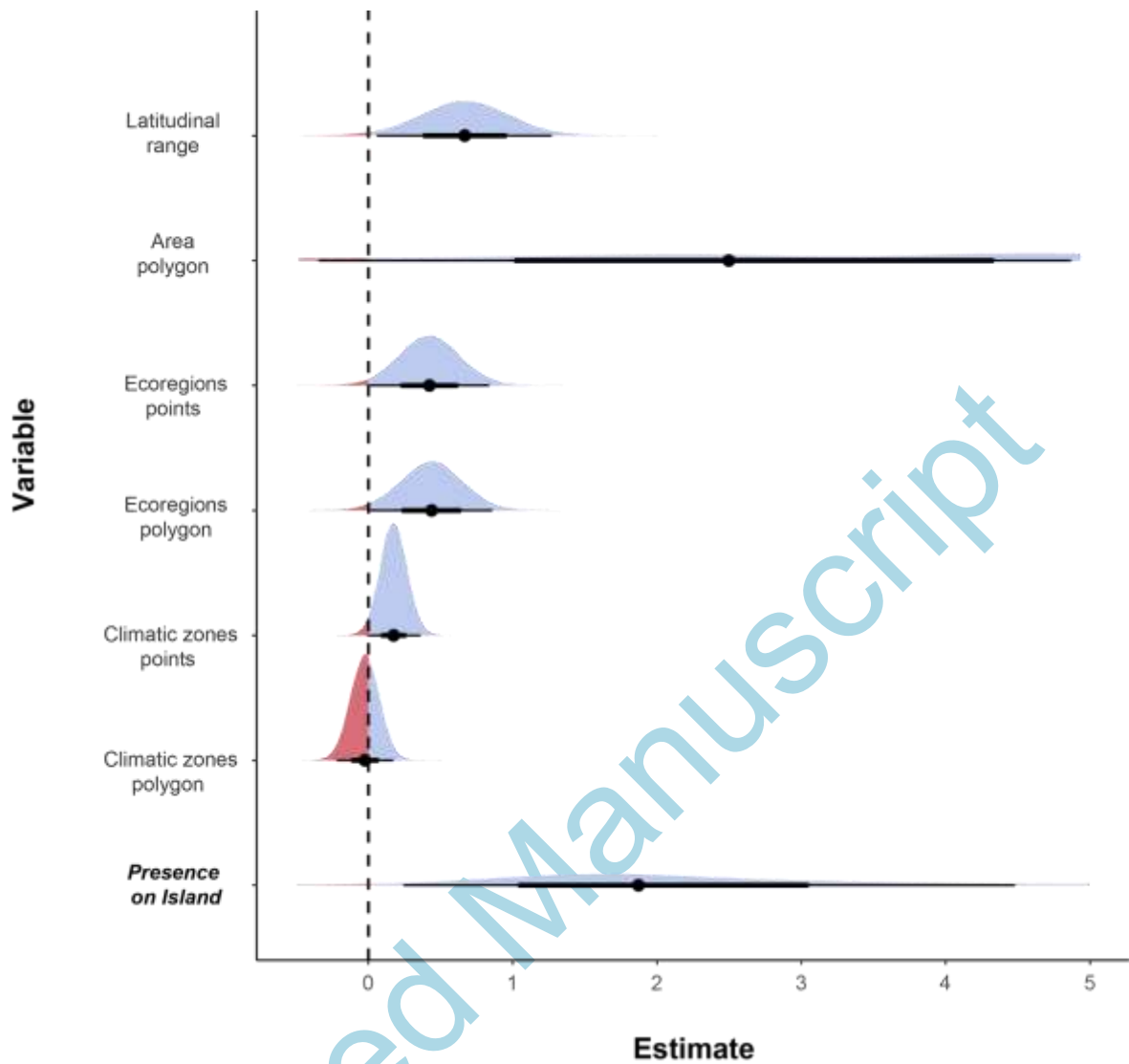
Figure 2. Forest plot of the posterior mean estimate for all the response variables in the different models and their corresponding density distributions when considering the filtered data. Positive estimates shaded in purple and negative estimates shaded in red. Dots represent the mean estimate for each variable, while thick bars represent their 66% corresponding confidence intervals (CI) and thin bars their 95% CI. Variables in both italic and bold indicate the presence statistical evidence, meaning that the 95% doesn't overlap with 0. Although most variables show a tendency towards a positive association, this pattern is not significant and becomes even weaker when using other datasets (Supplementary tables 3 & 4).
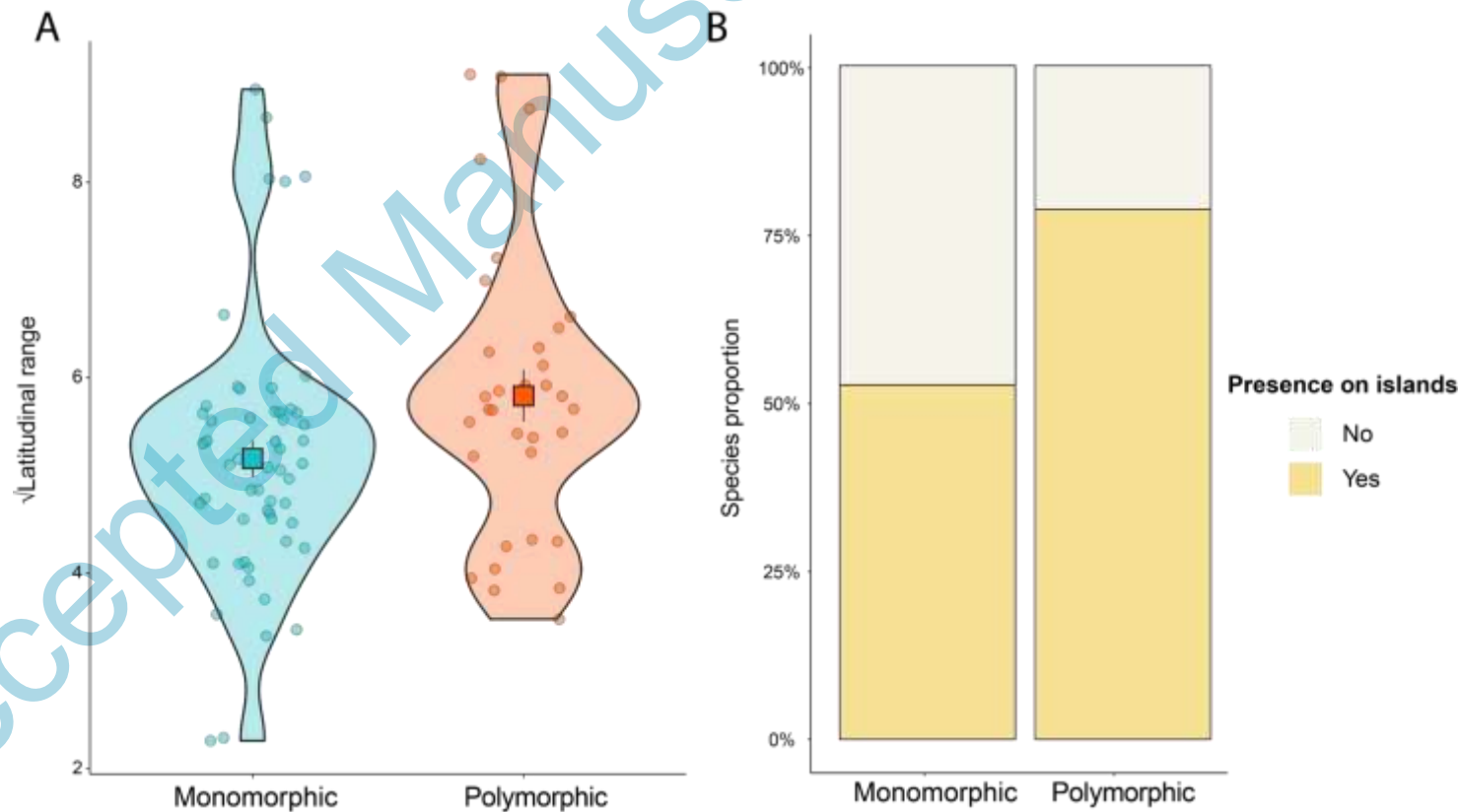
Figure 3. Graphical visualization of the variables that showed statistical support for the difference between colour polymorphic and

monomorphic species. A. The left panel corresponds to the squared root of the latitudinal range, the dots represent species values, and the

squares and bars represent the mean ± standard error of the predicted values from the Bayesian phylogenetic multilevel models. The right

panel shows the proportion of species that have presence on islands or are exclusively in continental land.