Exploring macroevolutionary drivers in golden orbweavers

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Study aims

Heterogeneity in species diversity is driven by the dynamics of **speciation and extinction**, in turn influenced by **organismal and environmental factors**. We explored macroevolutionary trends on a robust phylogeny of golden orbweaver spiders (Nephilidae), known for conspicuous sexual size dimorphism with gigantic females (Figure 1). We inferred overall dynamics in speciation and extinction and tested two binary factors (climate and landmass type) and two continuous factors (phenotypic extremeness and dispersal propensity) for their potential influence on the observed heterogeneity in taxonomic diversity.

Hypotheses

(i) We predicted higher diversification in tropical vs. subtropical clades, thus revealing the **latitudinal richness gradient** pattern.
(ii) We predicted higher diversification in insular clades due to **island endemism**.
(iii) We predicted highest levels of diversification in clades with **intermediate** dispersal propensity and intermediate phenotypes (Figure 2).
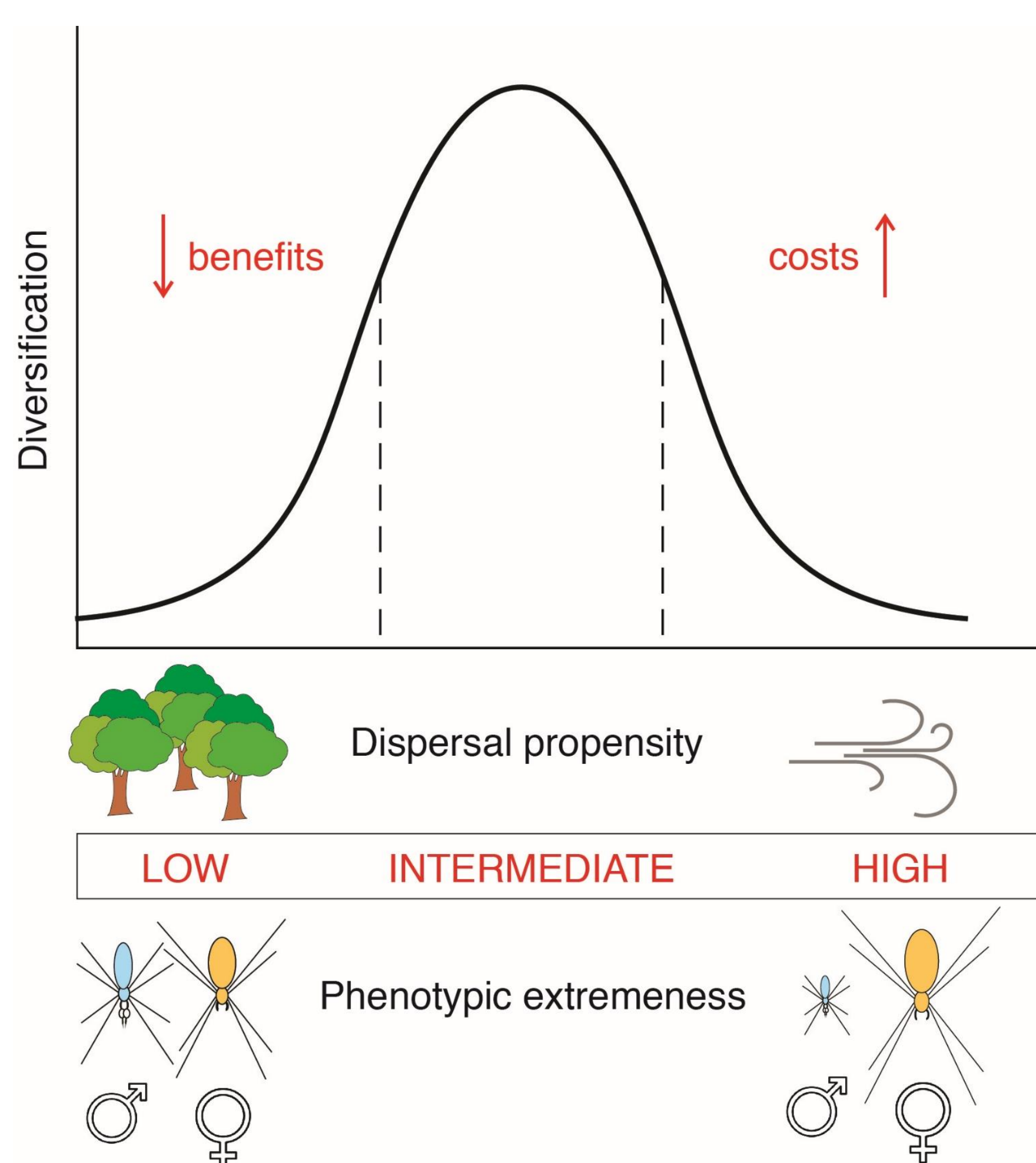

Figure 2: The hypothesised bell-shaped relationship between diversification and two tested continuous factors, dispersal propensity and sexual size dimorphism. Low dispersal propensity prevents colonization of new space (and thus speciation), while high dispersal propensity prevents speciation by maintaining gene flow among populations. On the other hand, phenotypic extremeness, like female gigantism, provides certain fitness advantages (e.g. increased fecundity), potentially promoting diversification, but necessarily also implies fitness costs, inhibiting the evolution of new species.

Methods

We inferred overall speciation and extinction dynamics and potential shifts in their rates with both a Bayesian method, **BAMM** (Bayesian Analysis of Macroevolutionary Mixtures; Rabosky et al., 2014), and a maximum-likelihood method, **MEDUSA** (Alfaro et al., 2009).

To test if candidate organismal and environmental factors indeed influence nephilid diversification, we used **SSE-class models**. For the two binary characters (island vs continental and tropical vs subtropical distribution), we used BiSSE (Binary-state Speciation and Extinction; Maddison et al., 2007).

For the two quantitative traits, dispersal propensity and phenotypic extremeness, we used QuaSSE (Quantitative-state Speciation and Extinction; FitzJohn, 2010). We used the species' estimated areas of occupancy (from own and IUCN Red List data) as a proxy for dispersal propensity, while phenotypic extremeness was represented by the ratio between mean female and mean male body length.

Figure 1: Extreme sexual size dimorphism: giant female and small male of *Nephila pilipes* (photo: M. Kuntner).

Results

- BAMM analyses detected **no distinct shifts** in speciation or extinction rate dynamics, but with **differences in rate dynamics** across the phylogeny (Figure 3): The highest rate of speciation was recovered in *Herennia*, a derived genus with arboricolous webs and pronounced island endemism, while strongly accelerated extinction was recovered in the species poor genus *Nephila*.
- MEDUSA detected a **shift in diversification** rate at the base of *Herennia* (Figure 3), exhibiting significantly higher diversification than the background rate.
- A **marginal effect** on speciation was detected for **tropical** vs subtropical distribution (p=0.06) with higher speciation rates in tropically distributed lineages.
- **No effect** on speciation or extinction was detected for **island** vs continental distribution.
- Against prediction (Figure 2), **neither dispersal propensity nor phenotypic extremeness** were found to be related to diversification in nephilids.
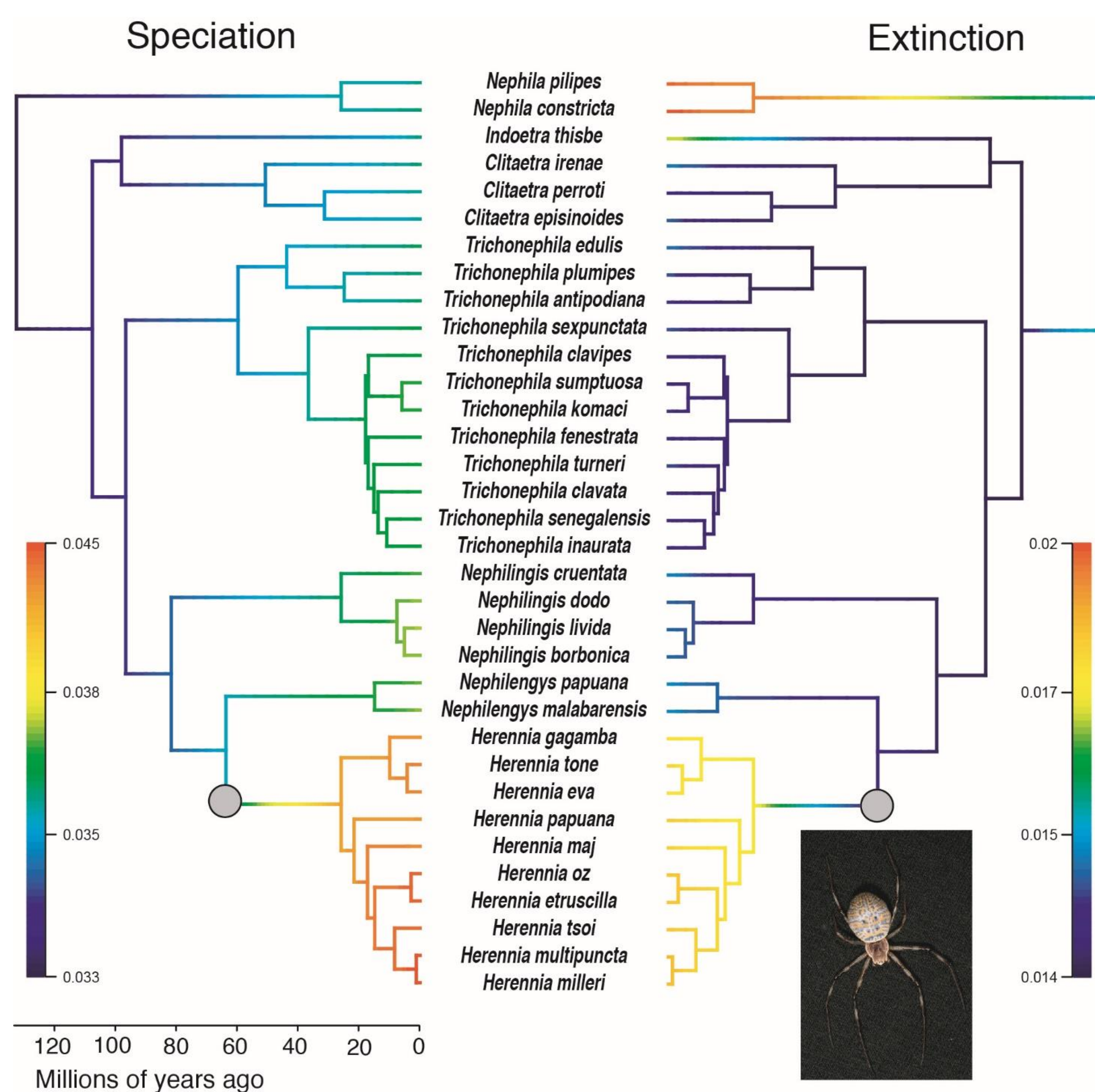

Figure 3: Macroevolutionary rate inference using two methods. BAMM phylorate plots show speciation and extinction rate dynamics in the nephilid phylogeny. Colours denote relative intensity of speciation and extinction along branches. Grey dots signify the location of a shift in diversification rate, inferred by MEDUSA. It detected increased diversification in the genus *Herennia* (visually presented by *H. eva*; photo: M. Kuntner) relative to the rest of the phylogeny.

Limitations in methodology

Despite recent advancements in molecular phylogenetics and macroevolutionary rate estimation methods, there is still **no clear consensus** on how and when macroevolutionary rates should be estimated, if at all. All methods applied here have been criticised.

Another **limitation of our study** is the relatively small size of the phylogeny, which limits the statistical power and accuracy. Hence, the predictions from our hypotheses would best be tested on larger phylogenies.

Conclusions

Using a suite of different approaches to inferring diversification dynamics, we find no clear support for the hypothesized influence of habitat type, extreme phenotypes and dispersal propensity on diversification of golden orb weavers.

While biotic and abiotic factors plausibly influence diversification, species emergence, persistence and demise are complex processes, requiring the right conditions at the right time to unfold.

A **universal pattern of diversification** (Diaz et al. 2019) might explain the lack of correlation between the tested traits and diversification – it is simply not as dependent on organismal and environmental traits as predicted.

Considering the same patterns of diversification are found across the tree of life, results of studies like ours might be best explained in the simplest way possible.

Literature:
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