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Diversification dynamics and transoceanic Eurasian-Australian disjunction in the genus *Picris* (Compositae) induced by the interplay of shifts in intrinsic/extrinsic traits and paleoclimatic oscillations

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ABSTRACT

Understanding transcontinental biogeographic patterns has been one of the main foci of the field of biogeography. While multiple explanations for transcontinental disjunctions have been proposed, little is still known about the relative importance of intrinsic and extrinsic traits for the diversification dynamics of disjunct taxa. Here, we study the evolutionary history of the genus *Picris* L. (Compositae), a great model for investigating the diversification dynamics of transoceanic bipolar disjunct organisms. Ancestral state reconstructions indicate that the most recent common ancestor (MRCA) of *Picris* was a semelparous and heterocarpic herb that lived in unpredictable environments of North Africa and West Asia. Diversification analyses suggest a significant shift in speciation ca. 1 million years ago, likely associated with the onset of the mid-Pleistocene revolution. Longevity characters are correlated with the evolution of particular fruit types and with environmental conditions. Heterocarpic species are mostly semelparous herbs strongly linked with unpredictable habitats, while homocarpic taxa are mostly iteroparous plants occurring in predictable environments. Binary-state speciation and extinction analyses suggest that homocarpy, iteroparity, and habitats predictability accelerate diversification. Although the combination of homocarpy and iteroparity evolved in several lineages, only members of the *P. hieracioides* group were able to colonise Eurasia and expand to Australia by transoceanic dispersal. Those findings indicate that large-scale colonisation events depend on a complex interplay of intrinsic and extrinsic factors.

1. Introduction

Transcontinental disjunctions represent one of the most fascinating aspects of biogeography (Raven and Axelrod, 1974; Thorne, 1972), with bipolar transcontinental disjunctions constituting the most remarkable and extreme type of organismal disjunction (e.g., Crame, 1993; Drummond et al., 2012; Gussarova et al., 2008; Thorne, 1972; Winkworth et al., 2002). Two competing hypotheses claim to explain the origin of disjunctions: (i) the vicariance scenario, generally related to plate tectonics, and (ii) the dispersal scenario, which considers the colonisation of novel habitats across pre-existing barriers. Migrations across continents and via historical or recent land bridges are also plausible alternatives (Givnish and Renner, 2004; Sanmartín, 2003; Xiang et al., 1998, 2000).

The colonisation of novel habitats is often linked with adaptation to novel niches, which is commonly accompanied by speciation. Rapid diversification associated with the adaptation to disparate ecological niches (i.e., adaptive radiation) has been extensively documented in the literature (e.g., Gavrilets and Losos, 2009; Losos, 2010; Schluter, 2000). Adaptive radiation is traditionally attributed to ecological opportunity, availability of abundant and underutilised resources or the evolution of novel traits, all of which can lead to more efficient interactions with novel environments (Gavrilets and Losos, 2009; Schluter, 2000). The geotemporal patterns of adaptive radiations, the evolution of adaptive forms, the association between net diversification rates and intrinsic and/or extrinsic traits are topics of great interest to evolutionary

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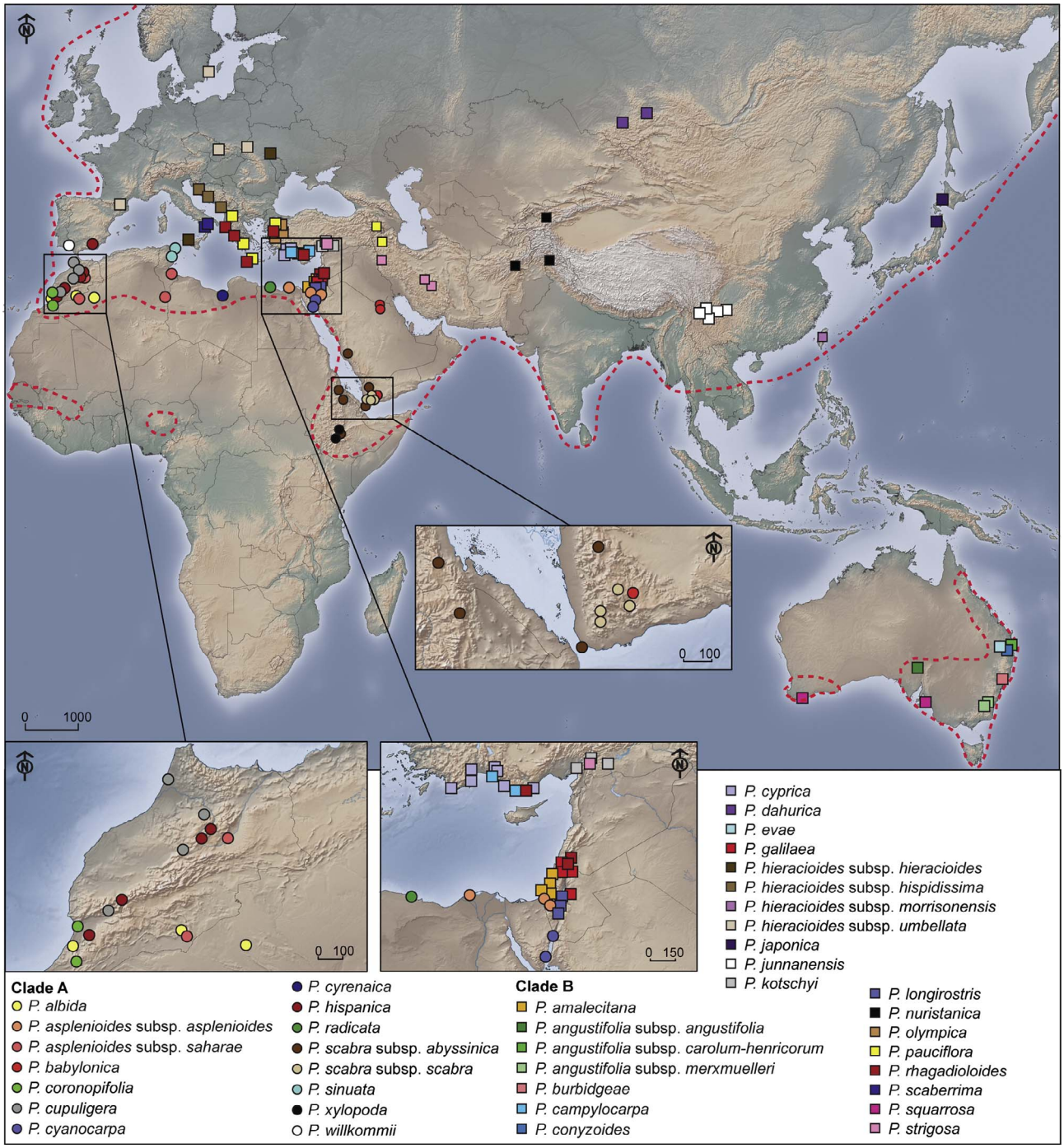

Fig. 1. Geographical distribution of the *Picris* taxa analysed. Red dashed line marks the distribution of the genus *Picris*. Circles represent members of the *Picris* clade A, while squares members of the clade B. For details about sample sites, see Supplementary Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

biology and biogeography (e.g., Drummond et al., 2012; Gavrilets and Losos, 2009; Guzmán et al., 2009; Lagomarsino et al., 2016; Losos, 2010; Madriñán et al., 2013; Ramsey et al., 2008).

The genus *Picris* L. (Compositae) represents an exciting model for investigating the role of intrinsic and extrinsic traits in the diversification dynamics of transcontinental disjunct taxa (e.g., Holzapfel, 1994, 2015; Lack, 1974, 1979; Smalla, 2000). This genus encompasses about fifty taxa distributed in Eurasia, Africa, and Australia. It is characterised by variation in intrinsic traits (longevity characters and fruit morphology) that might play an important role in diversification and colonisation of novel niches (cf. Gibson and Tomlinson, 2002; Imbert, 2002; Brändel, 2007; Cruz-Mazo et al., 2009, 2010). *Picris* species are morphologically variable herbs, characterised by a slender to erect branched habit, 2- to 4-hooked anchor-shaped indumentum, mostly yellow ligulas and achenes accompanied by a plumose pappus. *Picris* achenes can be morphologically and functionally variable (Lack, 1974; Smalla, 2000). Capitula of homocarpic species bear morphologically and functionally identical achenes accompanied by the plumose pappus. These achenes are dispersed by wind. In contrast, heterocarpic species have two types of achenes, i.e., central achenes equipped by the pappus and located in the centre of the capitulum as well as peripheral achenes lacking pappus and enclosed by phylaries. Peripheral achenes