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#### NOT KNOWING WHAT YOU DON'T KNOW: GEOGRAPHY AND DISPERSAL IN LEPIDOPTERA BIOGEOGRAPHY

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#### Not knowing what you don't know: Geography and dispersal in Lepidoptera biogeography

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"No botanist should be expected to locate on the spot 'S. rawa' [Rawas River], 'Sampit', and the like, but a botanist having received basic instruction in scientific biogeography (not its substitutes, of course) could not completely ignore where are situated the Langkawi Islands, and what Atjeh [Ache] in Sumatra normally stands for. Thus prepared, a botanist could at least sense on the spot the importance of these two records. As a matter of fact, they are a perfect instance of vicariant [allopatric] tracks (see fig. 1) of interest to Malaya, Sumatra, and Borneo alike." (Croizat 1968: 6)

#### Abstract

An inferred trans-oceanic dispersal of Painted Lady butterflies was recently presented as evidence for chance dispersal being responsible for allopatric distributions of taxa in support of the belief that the biogeographic distributions and phylogenetic histories of many insects could not otherwise be explained. The six studies cited as providing evidence for chance dispersal origins are shown to share assumptions about molecular divergence estimates, chance dispersal, centers of origin, and ancestral areas computations that render their findings highly problematic, if not invalid. The approach used in these studies exemplifies the absence of geographic distribution as a direct subject of comparative biogeographic analysis. The analytical significance of this absence is illustrated for *Arhuaco* butterflies in Central America where the origin of a disjunct species was attributed to Pleistocene chance dispersal based on an assumption of recent divergence. Comparison of *Arhuaco* distribution with other taxa suggests its location and differentiation was affected by geological displacement between the Romeral and Polochic-Motagua fault zones in late Mesozoic time. This tectonic context is made visible when directly comparing the distributions of different taxa, but lost to view when subordinated to *a priori* area units in ancestral-area methods.

**Keywords** Arhuaco Center of origin, Choreutidae Croizat, Junonia Papilio Sapayoa Schistocerca tectonics, vicariance.

#### Introduction

One of the first principles in biogeography is the need for a broad knowledge of biogeography – the localities of taxa (Croizat 1968). Even if one is not familiar with geography in all detail, at least have some familiarity with localities or regions that stand out as relevant to the distributions of animals and plants in general. In this way, biogeographers aim to be as 'well read' as possible. It may not be possible to always retain a full breadth of biogeographic knowledge about distributions and localities, but it is possible to appreciate that biodiversity does have a coherent global biogeographic structure – in effect the evolutionary glue that holds biodiversity together is manifest in the distributions and phylogenetic relationships of taxa (Heads 2017, Grehan 2021).

Croizat (1968) emphasized the desirability of being familiar with at least the principle features of geography and its biogeographic structure. In sharp contrast, Lepidopteran

biogeography based on centers of origin and chance dispersal methods portrays global biodiversity as a rather chaotic assemblage of organisms. While allowing for some vicariance when taxa are considered old enough, most Lepidoptera studies treat each taxon as having its own unique history of chance dispersal. Through the implementation of ancestral areas programs, the origin of allopatric differentiation is attributed to the biogeographic equivalent of throwing dice.

Recognizing geography as informative about the origins of distribution requires a comparative approach to biogeography. The geographic structure of any distribution can be individually evaluated with respect to patterns of spatial differentiation such as disjunction, allopatry, sympatry, tectonics etc., but to assess their evolutionary significance requires comparison. For example, oblique disjunctions of a taxon either side of the Alpine Fault in New Zealand may represent transform movement along the fault. In the context of hundreds of animal and plant taxa with similar displacement or disjunction, including marine forms, and both sessile and aerial organisms, the individual case contributes to a high degree of confidence in a historical relationship between the distributions and the evolutionary history of the Alpine Fault (Heads & Craw 2004, Heads 2017).

#### Geography as an active player in evolution

Absence of geographic distribution is characteristic of center of origin-chance dispersal (CODC) approaches to Lepidoptera biogeography. CODC focuses on combining fossil or island calibrated molecular divergence ages with vicariance-dispersal programs for a few (usually less than 15) *a priori* areas. In this approach the fossil calibrated ages are treated as actual or maximal, even though fossils provide information on the minimum age of taxa only. There is no comparison of geographic distribution and phylogeny represented by multiple groups or their possible tectonic correlation (Grehan & Nielsen 2024). The need for geographic comparison is minimized when the presumed ability of organisms to move about to new localities is seen as the foundation for biogeographic study. This emphasis was presented in a recent report on butterfly dispersal by Suchan *et al.* (2024) who asserted that "The biogeographic distributions and phylogenetic histories of many insects could hardly be explained without long-range transoceanic dispersal" based on six studies they cite in support. Each of these studies are, however, deficient in the way various assumptions are made about biogeographic origins and biogeographic methods:

1. *Molecular phylogenetics of Schistocerca* (Lovejoy *et al.* 2006). A sister group relationship between the single Old World species and a diverse New World clade of *Schistocerca* was portrayed as consistent with an African center of origin followed by a single chance dispersal crossing of the Atlantic by the ancestor of the Old World *S. gregaria* (Forskål, 1775). Gondwana vicariance was precluded by the belief that a gondwanic ancestry would require other members of the Cyrtacanthacridinae (that includes the Old World *Schistocerca*) to also be present in Africa and the Americas (since they were part of Gondwana). The oldest acridid fossils were noted to all be post-Cretaceous, and the 3-4% mtDNA divergence of *S. gregaria* and the New World clade was seen too low to be consistent with a gondwanic origin.

This study provides no empirical evidence for the existence of a center of origin, let alone one being in Africa. No explanation is given to explain why ancestral gondwanan taxa have to be cosmopolitan. There are numerous examples of extant taxa that do not range throughout the continent/s they occupy. And since the fossil record provides minimum ages only, this measure cannot empirically constrain the upper limits of molecular phylogenetic age. Although a global map is presented for *S. gregaria* and the New World clade ranges,

distribution details of the New Word genera and species are lacking, and there is no comparison with plant and animal distributions in general.

2. Global cockroach distributions (Bourguignon et al. 2018). These authors state that most cockroach taxa have fossil calibrated molecular divergence ages coincident with, or earlier than, proposed continental fragmentation, whereas the African-Madagascar Oxyhaloinae, and several Australian-Indo-Malaya genera "must have acquired their distribution through chance dispersal". The divergence estimates given are empirically minimum ages. The possibility of vicariance is correctly attributed to taxa with minimum ages coincident or earlier than continental fragmentation. But cockroach taxa that were assigned younger ages are also minimum estimates and do not therefore support the necessity of chance dispersal.

3. Choreutidae moths (Rota et al. 2016). The origin of many genera found to have relatively young ages were attributed to chance dispersal that crossed oceans many times. A center of origin was unresolved. The presence of Choreutidae on oceanic islands was presented as evidence for successful long distance [chance] dispersal, and observations of small insects being transported by high-altitude air currents (ecological dispersal) was seen to provide evidence for origin of oceanic island endemics by chance dispersal.

The vicariance-dispersal analysis used Wallacean areas without explanation of their validity as natural biogeographic units. The divergence estimates are fossil calibrated and do not preclude any earlier origins. The center of origin, chance dispersal, and vicariance results are all artifacts of how a vicariance-dispersal algorithm defines area relationships for a particular phylogenetic pattern. The presence of Choreutidae on oceanic islands is not evidence of long distance chance dispersal as these inhabitants may represent old biota with ancestors occupying 'oceanic' regions along with continental areas (Heads 2012).

4. Spodoptera moths (Kergoat et al. 2012). A Middle Miocene age was estimated for *Spodptera* Guenée in 1852 using fossil calibration. A vicariance-chance dispersal program generated an Afrotropical-Oriental center of origin followed by chance dispersal between the Old and New Worlds. This analysis is subject to the same problems as described above for other studies.

5. Junonia butterflies (Kodandaramaiah & Wahlberg). These butterflies occur in the Old World and New Worlds. Fossil calibrations applied derived from other groups limited the molecular phylogenetic age of *Junonia* to about 20 Ma. A vicariance-dispersal program assigned an African center of origin followed by dispersal into Asia then Australasia (but somehow not New Zealand) and to the New World in the north. Again, the analysis suffers the same problems as described above.

6. Biogeographic origins of butterflies (Kawahara *et al.* 2023). Divergence ages were fossil calibrated, and a vicariance-dispersal analysis of 14 *a priori* areas was used to estimate butterfly dispersal from the center of origin. From a proposed New World center of origin  $\sim$ 100 Ma, butterflies dispersed across Beringia to the Old World where diversification in the palaeotropics soon after the Cretaceous Thermal Maximum. These findings are all problematic due to the same methodological constraints described above.

#### Comparative geography of Arhuaco butterflies

Every taxon has a place and time of origin. The forgoing studies all assume that the ancestral 'place' for a group of allopatric taxa is a localized region (center of origin) within the

combined range of the allopatric descendants. This belief goes back to Darwin (1859): "Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle." From that time his idea took hold for most biogeographers. Even when vicariance was considered (such as with the fragmentation of continents), a center of origin followed by chance dispersal was still accepted. The other prominent characteristic of these studies is the absence of comparative biogeographic analysis. Each analysis is restricted to the dispersal of each taxon, with no consideration of individual distribution patterns or those of life in general.

The historical significance of comparative geography and phylogeny is illustrated by a recent study of the butterfly genus *Arhuaco* with two species: *A. dryadina* (Schaus, 1913) at 2,950-3,000 m in Costa Rica–western Panama, and *A. ica* (Adams & Bernard, 1977) at 1,700-2,400 m in northern Colombia (Fig. 1a). An explanation for this distribution was considered by Pyrcz *et al.* (2018) to be challenging from a biogeographical and evolutionary perspective because a vicariance scenario implied a wide ancestral distribution followed by extinction within the range, and it implied that *Arhuaco* is an 'old' genus possibly emerging prior to the radiation of the closely related *Pronophila*. Why the historical implications were considered challenging was not explained.



**Figure 1.** Lepidoptera disjunctions associated with the Romeral Fault Zone (RFZ), and the Polochic-Motagua fault zone (PMF): (a) *Arhuaco*, (b) *Oressinoma*, (c) *Drucina* (Pyrcz *et al.* 2018, Heads 2016, Heads *et al.* 2023).

Pyrcz *et al.* (2018) noted that the Panamanian land bridge dates back only 3 or 10-15 Ma (depending on the geological model). As a chance dispersal corridor, this route was seen to be effective no earlier than 1.85 Ma when Pleistocene cooling lowered montane habitats and montane South American species (assumed center of origin) to reach the Central American highlands. The historical model assumes: (1) the genus is ecologically constant and upland restricted since its origin, (2) upland habitats in Central America were not occupied until the Pleistocene 'ecological land bridge', and (3) the allopatric distribution originates from a narrow center of origin in the Andes. The Andean center of origin was also seen to be applicable to the origins of the mostly mid- to low altitude species *Pedaliodes lithochalcis* Butler & Druce, 1872, *Eretris suzannae* DeVries, 1890, and *Pronophila timanthes* Salvin, 1871.

The distribution of *Arhuaco ica* in the Andes is geographically confined, whereas upland habitats are more extensive in the region. The species is located on a major tectonic structure – the Romeral fault zone (RFZ) that extends between coastal Ecuador and the Caribbean coast of Colombia (Fig. 1a). This tectonic proximity might be considered coincidental and without historical significance if it were not for the fact that the RFZ is correlated with the distribution of numerous other allopatric distributions. Similarly, the Central American distribution of *A. dryadina* does not mark the limit of high elevation habitats, but it does fall

within the Polochic-Motagua fault zone (PMF) extending across southern Guatemala. Pyrcz *et al.* (2018) did not examine how the distribution of *Arhuaco* compared with other taxa. The distribution pattern is similar to *Oressinoma* (Coenonymphina), the only major difference being a more extensive range along the northern Andes and Roraima mountains of Venezuela (Fig. 1b). A further example is the Central American butterfly genus *Drucina* (Nymphalidae), comprising two species, qith a disjunct distribution between *Drucina leonata* Butler endemic to Costa Rica, and its sister species *D. Championi* Godman & Salvin, 1881 in Guatemala and southern Mexico next to the PMF (Fig. 1c).

The spatial location of these distributions and relationship to major regional tectonic structures is consistent with the origin and differentiation of the butterfly taxa involving geological history in the region. This inference is further illustrated by the distribution of *Ara ambigua* (Bechstein, 1811) that occurs mostly to the west of the RFZ (Heads 2016). This spatial position might be dismissed as incidental if it were not for its sister species, *A. militaris* (Linnaeus, 1766), being mostly to the east of RFZ, and north of the PMF to the Mojave-Sonora Megashear (MSM), a major, but poorly understood, Mesozoic fault system just south of the Mexico-US border (Fig. 2a).



**Figure 2.** Distribution boundaries of taxa with respect to the Romeral Fault Zone (RFZ), and the Polochic-Motagua fault zone (PMF). (a) blue outline, *Ara militaris*, red outline, *Ara ambigua*, (b) Coati sister species *Nasua naricua*, blue outline, and *N. olivacea*, red outline, (c) Distribution range of *Phassus* ghost moths. Figs 2a-b from Heads (2016), 2c from Grehan *et al.* (2022).

Differentiation west and east of the RFZ occurs in two sister species of coati (raccoons: Procyonidae), where the western range of *Nasua narica* (Linnaeus, 1766) extends from the RFZ north to the vicinity of the MSM, while *N. olivacea* Gray ranges east of the RFZ (Fig. 2b). In the Lepidoptera, a similar RFZ-MSM range to that of *N. narica* is seen in the range of the *Phassus* ghost moths (Fig. 2c). To place the tectonic correlations in a global context, the passerine bird *Sapayoa aenigma* (Hartert, 1903) (Sapayoidae) ranges west of the RFZ in Colombia and Panama while its sister group Pittidae is disjunct across the Pacific and Indian oceans (Fig. 3).

These examples demonstrate a shared correlated spatial relationship with regional tectonics among animal and plant groups with differing means of dispersal. The PMF and RFZ are important for the geology of the Central American region as they mark the boundaries of displacement of the Caribbean Plate between north and South America in late Mesozoic time (Heads 2016, Heads & Grehan 2021). The impact of this tectonic disruption on the regional biota is evident in the disjunctions and distributional boundaries of many taxa (see Heads 2016 for more examples). These distributions collectively indicate that the origin of the *Arhuaco* butterfly range is no less likely to have occurred during the Caribbean Plate disruption than any other similar allopatric divergence in the region. This tectonic correlation places the origin of *Arhuaco* earlier than the emergence of the Panamanian Isthmus. Any

future scientific argument to the contrary will have to address these facts of biogeographic distribution and correlated tectonics.



Figure 3. Distribution range of the bird genus Sapayoa and its sister group Pittidae. From Heads et al. (2023).

#### Mobility and allopatry of Lepidoptera

An ongoing misconception in biogeography is that observed mobility of organisms is synonymous with chance dispersal being responsible for the origin of allopatric taxa (see Craw 1990 for discussion of red admiral butterflies). Chance dispersal is the theory that allopatry arises through a usually unique dispersal event from one locality (center of origin) to another. This newly colonized locality is supposed to be somehow sufficiently isolated from further immigrants so that the single colonizer (or population of colonizers) can diverge in isolation from the ancestral population. Chance dispersal is different from the observable process of ecological dispersal (which includes migratory behaviour) between habitats (including island habitats) for a metapopulation that is able to persist over an area even if individual habitats may be ephemeral over time. Ecological dispersal can result in range expansion as well as persistence, and some taxa have almost global ranges that are maintained by this process. The distinction between ecological and chance dispersal has been extensively and thoroughly documented for more than a decade now (Heads 2012, Heads & Saldivia 2024).

The biogeographic significance of ecological dispersal for understanding allopatric differentiation and divergence has not yet been addressed in Lepidoptera COCD biogeography. Ecological dispersal responsible for range expansion is usually conflated with chance dispersal responsible for allopatric divergence. The inferred trans-oceanic flights of Painted Lady butterflies, along with other scattered reports, was seen to highlight the importance of aerial highways connecting continents by trade winds as an underestimated mechanism in biogeographic dispersal over time (the possibility of the butterflies hitching a rude on merchant shipping was not considered un this case). Exactly what this role is supposed to be was not stated, but Suchan *et al.* (2024) indicated that this viewpoint was comparable in some unspecified way with panbiogeographic studies by Heads (2012) and Heads *et al.* (2023).

The panbiogeographic perspective on dispersal by Heads (2012) is that "Normal ecological dispersal can involve movement within the distribution area or outside it, and this may lead to range expansion", and "It may take place over long distances—for example, in sea-birds—or over much shorter distances, depending on the organism". Similarly, Heads *et al.* (2023) noted that "normal" or "ecological" dispersal refers to the observed natural movement of individual organisms by their usual means, and also the movement of a biota caused by an

ecological change in a region (e.g. the retreat of a glacier). This understanding is fully consistent with observations of organisms dispersing over long distances, even oceans. It is a process that can result in range expansion. If Suchan *et al.* (2024) are citing panbiogeography for ecological dispersal being responsible for ancestral range establishment, the inferred trans-oceanic dispersal of Painted Lady butterflies is clearly consistent with that understanding.

#### **Missing maps**

Whatever position one may take about centers of origin, chance dispersal, ecological dispersal, and vicariance, in the end what matters are the facts of biogeography. The facts (as much as anything can be a fact) are the localities occupied by taxa and their phylogenetic relationships. This information is accessible to everyone – when presented. Most COCD approaches to Lepidoptera do not map taxa, and even when mapped, the distributions are not objects of direct analysis (Table 1). By subordinating biogeography to a small cluster of artificial geographic areas, localities are lost from direct sight. When biogeography is reduced to a few *a priori* areas, there is no direct information on where the individual taxa are distributed in any of the areas, including potentially significant questions over whether taxa occur throughout the area or how widely distributed, whether there are any patterns of overlap or allopatry, and geographic 'anomalies' where supposedly dispersive taxa have geographically incongruous boundaries (i.e. distributional limits do not match any obvious dispersal barrier).

The loss of biogeographic information created by *a priori* areas as units of analysis is illustrated by the "fine-scale" study of *Papilio* subgenus *Achillides* by Condamine *et al.* (2013b). Species ranges were mapped, but the biogeographic analysis focused on eleven 'biogeographical identities' created from unspecified paleogeographic 'arguments' with tectonic reconstructions, biodiversity hotspot information, and present day distribution. No explanation was provided to justify these areas being biogeographic 'identities' or natural (empirical) biogeographic units. Subordination of distribution to these area units obscured the allopatric and partial overlapping of sister taxa consistent with vicariance differentiation and range expansion by ecological dispersal (Grehan 2019), and made it impossible to recognize tectonic correlations (e.g. *Achillides* clade 3b, Fig. 4). This information was made available to the authors, but subsequently excluded from a global study of *Papilio* biogeography by Condamine *et al.* (2023).



**Figure 4.** Example of tectonic correlation for four species (color shading) of clade 3b (Condamine *et al.* 2013b) *Achillides* butterflies. Black lines – faults or plate boundaries. See Grehan (2019) for details.

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 Table 1. Absence of empirical geography in recent center of origin-chance dispersal Lepidoptera biogeography. Method categories: DIVA – dispersal-vicariance analysis, DEC – dispersal-extinction-Cladogenesis,

 S-DIVA - Statistical Dispersal-Vicariance Analysis, BGB – BioGeoBEARS, DIVALIKE - Likelihood equivalent of Dispersal-Vicariance approach, LAGRANGE – DEC program, Mesquite – clustering program.

 Tectonics, as correlation with tectonic structures. Geography: where taxa are mapped. Area units – areas designated in ancestral areas analysis. List is illustrative, not exhaustive.

	Taxon	Method	phylogeny	Tectonics	geography	Area units	calibration
2007 Braby & Pierce	Delias (Pieridae)	DIVA	yes	no	no	2	fossil
2007 Kodandaramaiah & Wahlberg	Junonia Nymphalidae	DIVA	yes	no	no	4	fossil
2009 Aduse-Poku et al.	Charaxers Nymphalidae	DIVA	yes	no	no	5	fossil
2009 Kawahara et al.	Sphingindae	Mesquite	yes	no	no	2	none
2010 Müller & Beheregaray	Cethosia Nymphalidae	DIVA	yes	No	no	14	fossil
2012 Condamine et al.	NW Triodini Papilionidae	DEC	yes	no	no	6	fossil
2012 Kergoat et al.	Spodoptera Noctuidae	DEC	yes	no	no	8	fossil
2013a Condamine et al.	Papilio Papilionidae	DIVA, DEC	yes	no	General dispersal maps	11	fossil
2013b Condamine et al.	Achillides Papilionidae	DEC	yes	no	species mapped	11	fossil
2014 Matos-Maraví et al.	Calisto Nymphalidae	BGB	yes	no	no	7	fossil
2015 Aduse-Poku et al.	Mycalesina Nymphalidae	DEC, S-DIVA	yes	no	no	5	fossil
2015 Condamine et al.	OW Triodini Papilionidae	DEC	yes	no	Genera ranges	9	fossil
2015 Espeland et al.	Riodinidae	BGB	yes	no	no	8	fossil
2015 Kaliszewska et al.	Miletinae Lycaenidae	DIVA, LAGRANGE	yes	no	no	3	fossil
2016 Fagua et al.	Tortricidae	BGB	yes	no	no	9	fossil
2016 Rota <i>et al.</i>	Choreutidae	BGB	yes	no	no	6	fossil
2016 Toussaint & Balke	Polyura Nymphalidae	BGB	yes	no	no	15	fossil
2016 Zenker et al.	Neotropical Arctiinae Erebidae	Mesquite	yes	no	no	7	none
2018 Kodandaramaiah et al.	Conenonymphina Nymphalidae	BGB	yes	no	no	9	fossil
2018 Sahoo et al.	Hypolimnas Nymphalidae	iTOL	yes	no	no	6	fossil
2019 Fagua et al.	Choristoneura Tortricidae	BGB	yes	no	no	9	fossil
2019 Huang et al.	Parnara Hesperiidae	BGB	yes	no	no	8	fossil
2019 Rubinoff & Doorenweerd	Holarctic giants Saturniidae	BGB	yes	no	genera ranges	3 & 5	fossil
2019 Toussaint et al.	Baorini Hesperiidae	BGB	yes	no	no	7	fossil
2020 Braby <i>et al</i> .	Candalidini Lycaenidae	BGB	yes	no	no	2 (5 habitat)	fossil
2020 Tousaint et al.	Adoliadini Nymphalidae	BGB	yes	no	no	7	fossil
2021 Aduse-Poku et al.	Bicylcus Nymphalidae	BGB	yes	no	no	9	fossil
2021 Murillo-Ramos et al.	Boarmiini Geometridae	BGB	yes	no	no	6	fossil
2021a Toussaint et al.	Coeliadinae Hesperiidae	BGB	yes	no	no	9	fossil
2021b Toussaint et al.	Heteropterinae Hesperiidae	BGB	yes	no	no	6	fossil
2022 Boyle <i>et al.</i>	Portiinae Lycaenidae	BGB	yes	no	no	9	fossil
2022 Fric et al.	Symbrenthia Nymphalidae	BGB	yes	no	species locality maps	12	fossil
2022 Li <i>et al</i> .	Xylophanes (Sphinigidae)	BGB	yes	no	no	6	paleogeography
2022 Tseng <i>et al.</i>	Limenitidinae Nymphalidae	BGB	yes	no	no	4	fossil
2023 Condamine et al.	Pseudocoladenia	DEC	yes	no	no	11	fossil
2023 Hou <i>et al</i> .	Pseudocoladenia Hesperiidae	s-DIVA	yes	no	no	7	fossil
2023 Hu <i>et al</i> .	Graptholitini Tortricidae	BGB	yes	no	no	8	fossil
2023 Kawahara et al.	Papilionoidea	DEC, DIVALIKE	yes	no	no	14	fossil
2023 St Laurent et al.	Cerurinae Notodontidae	BGB	yes	no	no	7	fossil
2023 Toussaint et al.	Trapezitinae Hesperiidae	BGB	ves	no	no	6	fossil

Chance dispersal and vicariance are not observable events, but they are qualitatively different in how each is connected to empirical evidence. Chance dispersal explanations are based on assumptions built into ancestral areas models or derived from underestimation of phylogenetic age when calibrated by fossil or island age. Vicariance explanations are derived from recognizing patterns of sister group allopatry, and spatial relationships to Earth tectonics. There are currently two major competing research programs in Lepidoptera biogeography: (a) panbiogeography that analyzes distributional and phylogenetic patterns of relationship with respect to Earth's tectonic structures, and (b) COCD biogeography that estimates centers of origin and vicariance or chance dispersal from ancestral areas analysis. COCD methods remain, by far, the most popular approach in Lepidopteran biogeography. The brief reference to a panbiogeographic approach by Suchan et al. (2024) represent a significant step forward in COCD Lepidoptera biogeography that acknowledges the existence of an alternative to COCD methods, but COCD studies have yet to address the significance of tectonic correlations identified in panbiogeographic studies of Lepidoptera (e.g. Heads 2012, 2014, 2017, 2019; Grehan 2017, 2019, 2024; Grehan & Mielke 2018, Grehan et al. 2022; Heads et al. 2023).

Ancestral areas approaches analyze the relationships of *a priori* areas according to the presence or absence of taxa in those areas. In this sense, the actual distributions of taxa are recognized, but they are not the direct objects of analysis. In losing sight of the real world geography of taxa, one is essentially losing the biogeography. COCD biogeography of Lepidoptera becomes, ironically, about what is not seen, what is not known – effectively an inversion of knowledge into 'maps of ignorance' of what is left out (cf. García-Barros 2023). When *a priori* areas have a greater reality than the actual distribution of taxa, Lepidoptera biogeographers are left not knowing what they don't know.

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