



COMMENT

The cost of ignoring cryptic diversity in macroecological studies: Comment on Martínez et al. (2017)

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ABSTRACT: Despite ample evidence indicating that *Excirolana braziliensis* corresponds to a species complex, Martínez et al. (2017; Mar Ecol Prog Ser 583:137–148) considered this isopod as a single species with a wide distribution along the Atlantic and Pacific coasts of the Americas, to evaluate the abundant-centre hypothesis (ACH). Multiple studies, however, have documented the presence of highly divergent lineages within this isopod, some of which may have separated millions of years ago, and with morphological differences reported among some of the lineages. The assumption of a single widespread species has led to misleading inferences regarding the underlying causes of ecological variation in this isopod, as indicated in recent phylogeographic studies. Therefore, it is surprising that a new macroecological study is considering *E. braziliensis* as a single widespread species again. The cost of ignoring its cryptic diversity is that the Martínez et al. (2017) study does not really contribute to our understanding of the ACH.

KEY WORDS: Species complex · Evolutionary lineages · Phylogeography · Cirolanidae · Sandy beaches

The abundant-centre hypothesis (ACH) predicts that the abundance of a species should be highest at the centre of its geographic range and decline towards the edges (Brown 1984). Martínez et al. (2017) set out to test this hypothesis with published records of specimens assigned to the cirolanid isopod species *Excirolana braziliensis*, assuming it constituted a widespread species distributed in tropical and subtropical sandy beaches of the American continent along both the Atlantic and Pacific coasts. They analyzed geographic patterns of abundance for this isopod across its presumed distribution range from both published studies and their own data for 77 sandy beaches in the Atlantic and 62 in the Pacific. They inferred support for the ACH in

the Pacific, but not the Atlantic. We argue, however, that inferences about support or lack thereof for the ACH in their study are not valid, because a key assumption of the test, i.e. that the records examined represent a single species, was violated. The primary basis for our critique is the well-documented cryptic diversity within *E. braziliensis* (see below). A secondary weakness of the Martínez et al. (2017) study is that *E. braziliensis* has been commonly confused in ecological literature with the closely related nominal taxa *E. mayana* and *E. chamensis*, which have overlapping distributions (Brusca et al. 1995). Therefore, some of the records examined by Martínez et al. (2017) may have been incorrectly assigned to *E. braziliensis*.

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Although early studies based on classical morphology suggested that *E. braziliensis* constitutes a single species with a broad amphi-American distribution (Glynn et al. 1975, Brusca et al. 1995), presence of cryptic diversity within this isopod has been documented throughout its range (Hurtado et al. 2016), as well as in localized studies in Panama (Weinberg & Starczak 1988, 1989, Lessios et al. 1994, Sponer & Lessios 2009), Chile (Varela & Haye 2012), and Uruguay (Tourinho et al. 2016). Hurtado et al. (2016) conducted the most comprehensive phylogeographic analyses of *E. braziliensis* to date, spanning a large extension of its geographic range and including data from previous phylogeographic studies. They found up to 13 divergent and geographically restricted lineages, each of which may represent a different species based on genetic divergences (up to 25% Kimura-2-Parameter distances for the mitochondrial COI gene). Among these are 3 lineages from Panama (named C, C', and P), which correspond to different morphs and may warrant separate species status (Weinberg & Starczak 1988, Lessios & Weinberg 1994). Based on molecular clocks, Sponer & Lessios (2009) estimated that the split between C and C' occurred ~6–17 million years ago, and the divergence between them and lineage P occurred ~9–25 million years ago (but see Hurtado et al. 2016). Consistent with a long evolutionary history for *E. braziliensis*, the phylogenetic reconstruction in Hurtado et al. (2016) reveals 3 instances of Atlantic–Pacific divergences, some of which appear to pre-date the closure of the Isthmus of Panama. Accordingly, most (or all) of the 13 *E. braziliensis* lineages observed in Hurtado et al. (2016) may have diverged millions of years ago.

Towards the end of their paper, Martínez et al. (2017) considered that an alternative interpretation of the discontinuous distribution of *E. braziliensis* in the Atlantic is the existence of cryptic species, citing studies from Chile (Varela 2008), Panama (Sponer & Lessios 2009), and Uruguay (Tourinho et al. 2016) which suggest that this isopod corresponds to a complex of species. Although Martínez et al. (2017) highlight the need for phylogeographic studies of *Excirolana* in the Americas, they completely overlook the works of Hurtado et al. (2016) on *E. braziliensis* and Hurtado et al. (2017) on *E. mayana*. The latter represents another putative species complex comprised of highly divergent lineages across its Pacific–Caribbean distribution, with phylogenetic patterns revealing 2 Atlantic–Pacific divergences.

Martínez et al. (2017) state that if *E. braziliensis* actually represents multiple species, their biogeo-

graphical inferences are equally valid at this aggregated level, but that the relationship between trends in abundances and geographic limits, with species turnover and interactions, can only be elucidated once the taxonomy of the genus is fully resolved. However, it is the relationship between abundance and geographic distribution that forms the basis for testing the ACH within a species. It is thus surprising that Martínez et al. (2017) fail to acknowledge that the widely documented cryptic diversity reported for *E. braziliensis* constitutes a major impediment to adequately testing the ACH with their choice of data. To utilize *E. braziliensis* for the purpose of testing the ACH, a separate test would be necessary for each of the divergent lineages that may constitute a different species, which at present would only be possible with the aid of molecular identification (i.e. diagnostic morphological traits for traditional taxonomy have not been identified in this species complex). Furthermore, if done correctly, this system might serve to test the 'between-species' component of the ACH, namely: among closely related, ecologically similar species, spatial distribution is positively correlated with average abundance.

That Martínez et al. (2017) used records of *E. braziliensis* to address a macroecology question is further unwarranted in light of the explicit warning made by Hurtado et al. (2016) regarding the potential flaws of ignoring cryptic diversity in such studies. This was illustrated by the study of Cardoso & Defeo (2004), which examined life-history traits of specimens assigned to *E. braziliensis* from 12 localities along broad latitudinal gradients on both the Atlantic and Pacific coasts and observed a latitudinal effect on several life-history traits. Because Cardoso & Defeo (2004) assumed that such variation occurred within a single species, they concluded that phenotypic plasticity was the underlying cause of the observed patterns. In light of the cryptic diversity and phylogeographic patterns of *E. braziliensis*, however, Hurtado et al. (2016) indicate that convergence rather than phenotypic plasticity is likely responsible for the observed similarities in latitudinal population dynamics.

The phenomenon of cryptic diversity, where a single valid species contains multiple lineages whose divergences may amount to interspecific levels, is pervasive in several marine taxa, including coastal isopods (Hurtado et al. 2017 and references therein). Therefore, as a more general caution, ecological studies should consider the high potential for cryptic diversity in groups where this phenomenon is common, even if genetic data are not available.

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Editorial responsibility: Simonetta Fraschetti, Salento, Italy & Christine Paetzold, Oldendorf/Luhe, Germany

Submitted: April 17, 2018; Accepted: July 19, 2018
Proofs received from author(s): August 1, 2018