



REPLY COMMENT

Genetics, taxonomy and species complex in sandy beach macrofauna: Reply to Mattos et al. (2018)

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ABSTRACT: Mattos et al. (2018; Mar Ecol Prog Ser 601:269–271) commented on our evaluation of the abundant-centre hypothesis (ACH) for the distribution of the isopod *Excirolana braziliensis* (Martínez et al. 2017; Mar Ecol Prog Ser 583:137–148). They stated that our treatment of *E. braziliensis* as a single species (i.e. ignoring cryptic diversity) invalidates the connection between reported distribution patterns and the ACH. However, from the introduction of the ACH, the set of mechanisms determining distribution patterns has been considered equally important for a single species and for a set of species with similar functional traits, as is the case for the *E. braziliensis* complex.

KEY WORDS: Morphologically related species · Cryptic diversity · *Excirolana*

Mattos et al. (2018) commented on our article about the distribution of the isopod *Excirolana braziliensis* on sandy beaches of the Atlantic and Pacific Oceans, and the evaluation of the abundant-centre hypothesis (ACH) for this species (Martínez et al. 2017). They call attention to recent genetic results that identified 13 divergent and geographically restricted lineages along Atlantic and Pacific beaches (Hurtado et al. 2016), where *E. braziliensis* was formerly considered as a single species (Glynn et al. 1975, Brusca et al. 1995). In this context, Mattos et al. (2018) stated that ignoring this cryptic diversity results in our study not contributing to the general understanding of the ACH. However, unless there is a population rescue effect (Holt & Keitt 2000), the mechanisms that we considered as determinants of the ACH are valid for the distribution trend of ecologically closely related species: sister species (Péron & Altwegg 2015) and species assemblages (Enquist et al. 1995, Ren et al. 2013, Dallas et al. 2017) throughout their geographic range. This is particularly important for the species that comprise the complex grouped as

E. braziliensis, which occupy the supralittoral and upper-littoral zones on sandy beaches and have similar biology, life-history traits, and relationships with environmental variables (e.g. Cardoso & Defeo 2003, 2004, Martínez & Defeo 2006). As mentioned by Mattos et al. (2018), morphological revisions concluded that *E. braziliensis* constitutes a single species (Glynn et al. 1975, Brusca et al. 1995) and, therefore, most of the results and interpretations in our article (Martínez et al. 2017) are valid. This is also true if the analysis reflects the geographic trend in a group of very closely morphologically related species, as detailed in Brown (1984), where the theoretical basis of the ACH was developed.

Unfortunately, we were not aware of the results that identified 13 divergent and geographically restricted lineages along Atlantic and Pacific beaches (Hurtado et al. 2016) that had formerly been considered as a single species, i.e. *E. braziliensis*. However, we explicitly discussed the potential existence of cryptic species in our paper. We are aware that the direct development mode in these ovoviviparous

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species tends to isolate populations with low gene flow and connectivity, thus increasing the probability of genetic differentiation between scattered populations over their extensive range (McLachlan & Defeo 2018). In this context, Sponer & Lessios (2009), Varela & Haye (2012), Tourinho et al. (2016) and Hurtado et al. (2016, 2017) have also provided critical insight into the genetic diversity and evolutionary history of *E. braziliensis* and other congeneric species, which could set the basis for a deeper understanding of macroecological distribution patterns in sandy beach macrofauna.

The identification of the existence of cryptic species by Hurtado et al. (2016, 2017) represents a significant advance in our understanding of evolutionary processes and macroecological patterns in *E. braziliensis*, which has been one of the main model species in sandy beach macrofauna. However, morphologically cryptic species could likely respond similarly to environmental conditions when living in sympatry at similar latitudes (Struck et al. 2017). These responses are mostly driven by selection pressures towards very similar morphological forms regardless of the reproductive isolation between them. Therefore, in this context also, our approach is valid to test the ACH. A separate test for the ACH taking into account divergent lineages, as suggested by Mattos et al. (2018), would represent a valuable evaluation of the sensitivity of macroecological distribution patterns to the existence of cryptic species. However, we think that phylogeographic studies and taxonomic revision of the genus *Excirrolana* need to be completed (see also Hurtado et al. 2016). Even though cryptic species could represent a substantial fraction of biodiversity (including those inhabiting sandy beaches), Struck et al. (2017) recently highlighted that an effort should be made to clearly differentiate taxonomical errors from true cryptic biodiversity. This topic is under debate (Heethoff 2018). In the specific case of *E. braziliensis*, taxonomic uncertainties still remain. We think that a useful approach to fill these gaps should be to follow an integrative taxonomy framework, combining information from different approaches and disciplines (e.g. geometric morphometrics methods, DNA barcodes, nuclear gene sequences, full mitochondrial genome data) to provide a comprehensive description of species (Zúñiga-Reinoso & Benítez 2015, Beermann et al. 2018, Eme et al. 2018, Struck et al. 2018). These different approaches, combined with morphological, ecological, and geographical information, will facilitate a rigorous identification of entities within species complexes and therefore a deeper understanding of macroscale patterns in sandy beach populations.

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