Integrative and Comparative Biology

Integrative and Comparative Biology, volume 62, number 2, pp. 332–344
https://doi.org/10.1093/icb/icac052

Society for Integrative and Comparative Biology

SYMPOSIUM

Ecological Transitions and the Shape of the Decapod Tree of Life

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From the symposium "The deep and shallow history of aquatic life's passages between marine and freshwater habitats" presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 3–February 28, 2022.

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Synopsis Understanding the processes that shaped the distribution of species richness across the Tree of Life is a central macroevolutionary research agenda. Major ecological innovations, including transitions between habitats, may help to explain the striking asymmetries of diversity that are often observed between sister clades. Here, we test the impact of such transitions on speciation rates across decapod crustaceans, modeling diversification dynamics within a phylogenetic framework. Our results show that, while terrestrial lineages have higher speciation rates than either marine or freshwater lineages, there is no difference between mean speciation rates in marine and freshwater lineages across Decapoda. Partitioning our data by infraorder reveals that those clades with habitat heterogeneity have higher speciation rates in freshwater and terrestrial lineages, with freshwater rates up to 1.5 times faster than marine rates, and terrestrial rates approximately four times faster. This averaging out of marine and freshwater speciation rates results from the varying contributions of different clades to average speciation rates. However, with the exception of Caridea, we find no evidence for any causal relationship between habitat and speciation rate. Our results demonstrate that while statistical generalizations about ecological traits and evolutionary rates are valuable, there are many exceptions. Hence, while freshwater and terrestrial lineages typically speciate faster than their marine relatives, there are many atypically slow freshwater lineages and fast marine lineages across Decapoda. Future work on diversification patterns will benefit from the inclusion of fossil data, as well as additional ecological factors.

Introduction

Why do some clades harbor incredible diversity, while their close relatives or even sister clades contain just a handful of species? What factors drive the remarkable asymmetry of species richness across the Tree of Life and across ecoregions? Attempts to quantify and test these drivers now constitute a major research agenda in evolution and ecology. While there has historically been a debate concerning the relative importance of biotic versus abiotic factors in shaping biodiversity on macroevolutionary timescales, a wealth of evidence now demonstrates the significance of both (Benton 2009; Ezard et al. 2011; Condamine et al. 2019). Clade age alone may offer an explanation for the extant species richness of groups in some cases (McPeek and Brown 2007; Bloom et al. 2014; Wiens 2017; Gamisch and Comes 2019), however, it cannot account for the observed discrepancy in species richness between sister clades (Rabosky et al. 2012; Bloom et al. 2014; Scholl and Wiens 2016), which originate at the same time and in the same environments (by definition). Differences in species richness between sister clades must, therefore, result from different rates of net diversification, which itself requires a different type of explanation. Ecological transitions (such as habitat, diet, and mode of life) are one such possibility, offering the potential for lineages to radiate into relatively uncontested eco-space (Schluter 2000; Losos 2010; Poore et al. 2017; Davis et al. 2018). This in turn may lead to increased rates of speciation and, therefore, increased overall net diversifica-

Advance Access publication May 24, 2022

tion. Such ecological transitions are well-documented across the Tree of Life, with examples from invertebrates (Hou et al. 2011; Davis et al. 2018), fishes (Bloom et al. 2013; Rabosky 2020), and even bacteria (Zhang et al. 2019). Many of these transitions are also associated with increases in rates of diversification (Hou et al. 2011; Bloom et al. 2013; Davis et al. 2018; Nakov et al. 2019; Rabosky 2020).

Decapoda are a highly diverse (~17,500 extant species; WoRMS Editorial Board 2021) pancrustacean order that originated around 450 million years ago (Wolfe et al. 2019). They are of great economic importance (Bondad-Reantaso et al. 2012) and are vital constituents of healthy ecosystems in many of the most delicately balanced and endangered biomes, including coral reefs (Kramer et al. 2014; Giraldes et al. 2015; González-Gómez et al. 2018) and mangrove forests (Negromonte et al. 2012; Cannicci et al. 2018; Hajializadeh et al. 2020). Decapod crustaceans occupy a wide variety of aquatic habitats and have even become terrestrial (Watson-Zink 2021). Multiple shifts from marine ancestors have resulted in the ecological heterogeneity observed today (Ashelby et al. 2012; von Rintelen et al. 2012; Anger 2013; Bracken-Grissom et al. 2013; Tsang et al. 2014). In true shrimps (Caridea; circa 3000 species), these transitions are associated with increased speciation rates (Davis et al. 2018) as lineages evolved into vacant ecospace. However, there has been no comparable study across the much more speciose, morphologically and ecologically diverse Decapoda as a whole.

Here, we test the hypothesis that ecological transitions from marine habitats into freshwater and terrestrial ecosystems drove increased diversification across decapod crustaceans. We address this using an extensive phylogeny of decapod species, itself derived using a combination of supertree methods and a molecular backbone. We categorize habitat as either marine, freshwater, or terrestrial and infer ecological transitions using ancestral state reconstruction (ASR). We then model speciation rates through time, partitioned by ecology, in order to determine whether transitions from marine settings resulted in increased speciation. We find that, across all Decapoda, terrestrial speciation rates are significantly higher than in both marine and freshwater lineages, but there is no difference in mean rate between marine and freshwater biomes. However, partitioning by sub-clade reveals that rates are higher in freshwater and terrestrial lineages for those clades that exhibit habitat heterogeneity. This seemingly contradictory result can be explained by the relative contributions of different clades to the overall rates. However, while rates are generally higher in freshwater and terrestrial lineages, we find no evidence for a causal relationship between habitat and speciation rate, with the exception of one clade—Caridea. While some caution should be applied in the absence of accounting for phylogenetic uncertainty, our findings clearly demonstrate a need to seek alternative explanations for the observed relationship between habitat and speciation rate.

Methods

Phylogenetic supertree

Our goal was to synthesize current knowledge of decapod phylogeny rather than to infer a new phylogeny, and we, therefore, implemented a synthetic approach to tree-building. A recently published phylogenomic tree (Wolfe et al. 2019) was used as a backbone phylogeny, and we then used supertree methods to parsimoniously synthesize published phylogenies for each constituent sub-clade. Following (Wolfe et al. 2019), we split Decapoda into infraorders (Achelata, Anomura, Astacidea, Brachyura, Caridea + Procaridea, Polychelida, Stenopodidea, Gebidea, and Axiidea) plus Dendrobranchiata. The backbone tree did not contain Glypheidea (containing just two extant genera), and we, therefore, omitted this from our analysis. Gebidea and Axiidea were analyzed together as "Thalassinidea" as the source data for Gebidea and Axiidea had almost 100% overlap with each other. We used previously published supertrees for the Achelata (Davis et al. 2015), Anomura (Davis et al. 2016), and Caridea (Davis et al. 2018) sub-clades. Supertrees of all other sub-clades were constructed as detailed below.

Source trees were obtained from the STK database online repository (https://github.com/drkatiedavis/STK_database), which contained Decapoda trees published between 1980 and 2014. These source trees were digitized, along with meta-data, in their published form using TreeView (Page 1996) and the Supertree Toolkit (STK; Davis and Hill 2010; Hill and Davis 2014). The latter is a fully integrated set of scripts designed to process trees and meta-data, and to output matrices for MRP (Baum and Ragan 2004) supertree analysis or sets of trees for analysis using other supertree methods. Meta-data included bibliographic information, the types of characters used (e.g., molecular or morphological) and the methods used for tree inference. No corrections were made for synonyms or any other apparent errors or inconsistencies in the source trees prior to processing.

All source trees were curated and analyzed in a consistent and repeatable manner in assembling the supertree (Davis et al. 2015). Once data collection and entry were complete, we ensured that source trees met three criteria:

(1) Only trees presented by their authors as explicit inferences of evolutionary relationships were included. We also excluded taxonomies, informal phylogenies, and any other trees not derived from an explicit matrix of annotated characters.
(2) Only trees comprising clearly identified species, genera, or higher taxa were included.
(3) Only trees derived from the analysis of a novel, independent dataset were included.

Non-independent studies were defined as those that utilized identical matrices (i.e., the same taxa and characters), or where one matrix was a subset of the other. In the former case, the source trees inferred from "identical" data were weighted in inverse proportion to their number. In the latter case, the tree derived from the least inclusive data set was removed from the analysis. We, thereby avoided pseudo-replication of the source trees and the spurious levels of support for the resampled relationships that might otherwise result from this.

Operational taxonomic units (OTUs) were standardized to reduce the inclusion of higher taxa, and to remove synonyms and vernacular names (which were standardized using the freely available online WoRMS database (WoRMS Editorial Board 2021). Where authors used higher taxa as proxies for particular exemplars, we substituted those higher taxa with the names of the exemplar genera or species. Where no exemplars were specified, higher taxa were removed from source trees by substituting those constituent taxa present in other source trees as a polytomy in the focal tree. This avoided both artificial inflation of the taxon sample and also coding relationships that were not inferred from the focal tree. Definitions for higher taxa were derived from the WoRMS online database (WoRMS Editorial Board 2021).

Taxonomic overlap was checked once the nomenclature had been standardized. Each source tree needed at least two taxa in common with at least one other source tree to be included. Overlap within our dataset was sufficient; therefore, no source trees were removed and we were able to derive a matrix representation without any further edits. The full source data bibliography is available in Supplementary Information 1. Only extant taxa were included in our diversification rate analyses, and all fossil taxa were, therefore, pruned from the source trees.

With the exception of Stenopodidea and Polychelida (each of which contributed just a single source tree: Saito and Takeda 2003; Ahyong 2009), we used Matrix Representation with Parsimony (MRP; Baum and Ragan 2004) to produce phylogenetic supertrees for each of the six subclades for which a supertree was not already available (see Supplementary Information 2 for a breakdown of taxa by clade). Source trees were encoded as a series of group inclusion characters using standard Baum and Ragan coding (Baum and Ragan 2004), and the process was automated within the Supertree Toolkit software (Hill and Davis 2014). All taxa subtended by a given node in a source tree were scored as "1," taxa not subtended from that node were scored as "0," and taxa not present in that source tree were scored as "?." Trees were rooted with a hypothetical, "all zero" outgroup. The resulting MRP matrices were analyzed using standard parsimony algorithms in TNT (Goloboff et al. 2000). See Supplementary Information 3 for all the newly generated MRP matrices. We used the 'xmult = 10' option, and ran 1000 replicates for the analysis, each using a different random starting point for the heuristic search. This improved exploratory coverage of the tree space, potentially avoiding local minima in the solutions. For Astacidea, Brachyura and "Thalassinidea" we computed a Maximum Agreement Subtree (MAST) of the MPTs using PAUP* (Swofford 2001) to remove conflicting leaves. One limitation of the MRP method is the potential generation of spurious clades and relationships that are not present in any of the source trees ("novel clades"; Bininda-Emonds and Bryant 1998; Davis and Page 2014; Davis et al. 2016). The misplaced taxa that result in these novel clades are known as "rogue taxa" and are usually a result of either poorly constrained or poorly represented taxa contained in the source trees. While there is a synthetic metatree methodology that addresses this issue (Lloyd et al 2016), we were unable to employ it in this study as it requires reanalysis of all source data and is, therefore, not tractable for data sets of this size. This rogue taxon problem is not limited to supertree methods. Moreover, identifying and removing rogue taxa *a priori* is problematic, because rogues can constrain the positions of other taxa in the phylogeny. Removing rogues simply creates new rogue taxa. Nonetheless, it is important that spurious clades are removed from the phylogeny before undertaking any further analysis (Trautwein et al. 2011). A small number were identified, and subsequently removed, from the Brachyura and "Thalassinidea" trees. A list of rogue taxa is given as Supplementary Information 4. The resulting and pre-existing supertrees for each clade were then combined into a single larger tree using the (Wolfe et al. 2019) phylogeny as a backbone tree.

Supertrees derived from parsimony analyses do not contain branch lengths that can be used to infer dates of relative splits or rates of diversification. Rather, branch lengths in MRP supertrees reflect a parsimonious resolution of all the inferences of clade membership across the set of source trees; inferences that are potentially (and often) mutually incompatible. In order

to time-scale, we therefore, calibrated nodes using fossil first occurrence data obtained from the palaeobiology database (paleobiodb.org). Fossils selected for calibration were those that conclusively showed the characteristics of the family concerned. These were assigned to clades using the decapod genus list classification (De Grave et al. 2009). Within Brachyura, there were few fossil calibrations relative to the number of leaves in the clade, and we, therefore, obtained 23 additional calibration points from published molecular phylogenetic analyses using the approach of Davis et al. (2018) (as implemented successfully hitherto for Caridea). The R package '"paleotree" (Bapst 2012) was used to scale the tree and extrapolate dates to the remaining nodes. To extend node calibration to the whole tree, we used the "equal" method, with minimum branch lengths set to 0.1 Myr. We performed the time-scaling on the full decapod tree, rather than on sub-clades, to allow calibrated nodes to inform node dates throughout the supertree. Finally, we also used molecular dates from the backbone phylogeny to help constrain the ages of the major splits in the tree (Wolfe et al. 2019). Our final, time-calibrated phylogeny contained 3039 taxa, see Supplementary Informations 5 and 6 for node calibration dates and sources.

Ancestral State Reconstruction

We used ASR to infer when, and how often, major transitions between marine, freshwater, and terrestrial habitats occurred. We collected trait data for all 3039 taxa in our supertree. Taxa are defined as freshwater if they live permanently in freshwater or require freshwater to complete their life cycle. Only the infra-orders Anomura and Brachyura contain terrestrial species but, even so, there is a wide variety of terrestrial adaptation amongst Decapoda. We, therefore, define taxa as terrestrial if they live predominantly on land, including those species that need to return to the sea in order to release larvae (e.g., *Birgus latro*) and those that are independent from the sea (e.g., *Metopaulias depressus* and other arboreal crabs). Semi-terrestrial crabs, such as those in the genus *Potamon*, were classified as freshwater. Crayfish were classified as freshwater although so-called "primary burrowers" might perhaps be better considered as terrestrial (Welch and Eversole 2006; Reynolds et al. 2013; Richman et al. 2015). We then applied stochastic character mapping to our time-calibrated supertree, implemented using 'make.simmap' in PhyTools (Revell 2012). The variables for habitat (marine/freshwater/terrestrial) were both discrete and three-state, and were optimized using equal-rates models. See Supplementary Information 2 for species traits lists.

Diversification dynamics

Diversification rates were modeled from the phylogeny using BAMM (Rabosky 2014). BAMM implements an MCMC approach to calculate diversification rates. A total of four chains were executed, each running a total of 50 million generations, with a minimum clade size of five taxa used to aid convergence. A total of 10,000 of the resulting trees were stored, with 10% discarded as "burn-in," leaving 9001 trees for subsequent analysis. The analysis also accounted for incomplete coverage of taxa in the tree by specifying a sampling bias factor derived from taxonomy. Again, the WoRMS online database provided the taxonomic basis for this (WoRMS Editorial Board 2021). For full details of our sampling regime and BAMM implementation, see Supplementary Informations 7 and 8 for details of the sampling bias factors.

State dependency

The relationship between speciation rate and habitat was tested formally using STRAPP (STructured Rate Permutations on Phylogenies; Rabosky and Huang 2016) implemented with BAMMtools (Rabosky et al. 2014). While the analyses comparing speciation rates between different habitats tests for significant differences in mean values, STRAPP tests for causality (i.e., does a change in habitat result in a change in speciation rate). This is done by assessing the significance of any association between tip rates and traits by comparing it to a null distribution. This null is generated by randomly permuting the speciation rates across the phylogeny whilst still maintaining the position of rate shifts in the tree. We ran 1000 replicates and assessed significance using a Kruskal–Wallis test for speciation rates in each habitat partition; marine, freshwater, and terrestrial. This test was repeated across all Decapoda and also within each sub-clade.

Results

Supertree

Our final phylogeny is fully bifurcating and contains 3039 extant taxa. We used a synthetic approach to tree-building using a backbone phylogeny that constrained the position and monophyly of all sub-clades. Gebidea and Axiidea were the only clades to be analyzed non-independently as many papers considered these holistically as "Thalassinidea." These were accordingly recovered as reciprocally monophyletic and could, therefore, be placed in the phylogeny as in Wolfe et al. (2019). Our resulting phylogeny is, therefore, by definition, congruent with recently published molecular phylogenies (Wolfe et al. 2019) for the divergences be-

tween sub-clades. At the family level, our phylogeny is also remarkably congruent with the relationships recovered by Wolfe et al., (2019), the only differences being within the Anomura and Brachyura. In the supertree, the basal anomuran clade is Hippidae (reflecting previous molecular analyses: Tsang et al. 2011; Bracken-Grissom et al. 2013), whereas Eumunididae is basal in Wolfe et al. (2019). Within Brachyura, both our superee and Wolfe et al. (2019) recover the podotremes as the earliest diverging clade, as well as a monophyletic Thoracotremata. However, in contrast to Wolfe et al. (2019), the supertree recovers a paraphyletic Heterotremata, a result that reflects paraphyly of Heterotremata in the source data (Jamieson 1994; von Sternberg and Cumberlidge 2001; Ahyong et al. 2007; Brösing et al. 2007; Ji et al. 2014; Bai et al. 2018). This synthetic approach to combining additional phylogenetic information to an accepted backbone tree does not provide any new insight into decapod phylogenetics (this was not—by definition—the objective) but does enable large-scale comparative analyses.

Ancestral State Reconstruction

Our ASR analysis (Fig. 1) was carried out in *PhyTools* (Revell 2012) and shows a marine ancestor for Decapoda with multiple independent transitions into freshwater environments in four infra-orders as well as independent transitions onto land in two infra-orders. There are no transitions from freshwater to terrestrial. Although there are a number of semi-terrestrial brachyurans found within freshwater clades (e.g., within Potamidae; Ng and Yeo 2001), we find no evidence for fully terrestrial taxa originating from a freshwater ancestor.

The freshwater transitions are the most numerous and occur within Anomura, Astacidea, Brachyura, and Caridea. Anomura and Astacidea each contain a single large freshwater clade; the genus *Aegla* and the clades Astacoidea and Parastacoidea, respectively. Caridea contains two transitions that result in large, speciose clades. These are Atyidae and a clade largely consisting of the genus *Macrobrachium* (Palaemonidae). Within the latter there are a small number of reversals back to marine habitats. The genus *Palaemon* contains approximately equal numbers of marine and freshwater taxa but the analysis shows that it most likely had a marine ancestor with a number of independent transitions to freshwater within the genus. There are a further seven freshwater transitions within Caridea consisting of either isolated lineages or lineages leading to small clades of three or fewer taxa. Brachyura is shown to have three independent freshwater transitions with no reversals. The superfamilies Pseudothelphusoidea, Gecarcinucoidea, and Potamoidea represent a single invasion into freshwater biomes. The two remaining transitions are the superfamily Trichodactyloidea, and the genus *Eriocheir* (Grapsoidea).

The terrestrial transitions are found within Anomura and Brachyura. Anomura has a single transition to a terrestrial mode of life in the clade *Birgus* + *Coenobita* (Coenobitidae), while the other three transitions are found within Brachyura. A total of two of the brachyuran transitions are within Sesarmidae, including a single reversal to the marine habitat, while the other two terrestrial transitions occur in *Cardisoma* (Gecarcinidae) and *Geograpsus* (Grapsidae).

Diversification dynamics

Using BAMM (Rabosky et al. 2014; Rabosky 2014), we tested for significant associations between habitat and diversification rates. Recent studies suggest that diversification rate inference from extant-only phylogenies has limitations (Louca and Pennell 2020), however, simulations have also shown that BAMM is remarkably accurate when modeling speciation rates on trees of extant taxa, despite some shortcomings when modeling extinction rates (Rabosky 2010). Hence, we only report speciation rates here. For each partition, differences in the speciation rates were analyzed by one-way analysis of variance (ANOVA). We then used a *post-hoc* Tukey test to assess significance. All results were significant with a P-value of < 0.01. All the analyses were based on 9001 simulations (one for each tree) of speciation rate for clades containing at least five taxa. Hence, the marine Procarididea (two taxa) and the terrestrial anomurans (three taxa in the genera *Coenobita* and *Birgus*) were excluded from analysis.

Overall, we found no statistically significant difference between speciation rates in marine versus freshwater taxa. However, terrestrial speciation rates were twice as high as those in either marine or freshwater taxa. Mean rates of speciation in marine taxa are 0.02497, in freshwater taxa they are 0.02510 and in terrestrial taxa they are 0.05292. As the speciation rates are not normally distributed, we report the 25% and 75% quantiles, rather than standard deviation, as a measure of the spread in the data. See Table 1 for full speciation rate statistics for all Decapoda and for each constituent clade.

Considering patterns within clades, however, we find significant differences in speciation rates between all three habitat states. The infraorders Anomura, Astacidea, Brachyura, and Caridea all show transitions to freshwater habitats, while Anomura and Brachyura also show transitions to freshwater and terrestrial habitats. In Anomura, the mean speciation rate for ma-

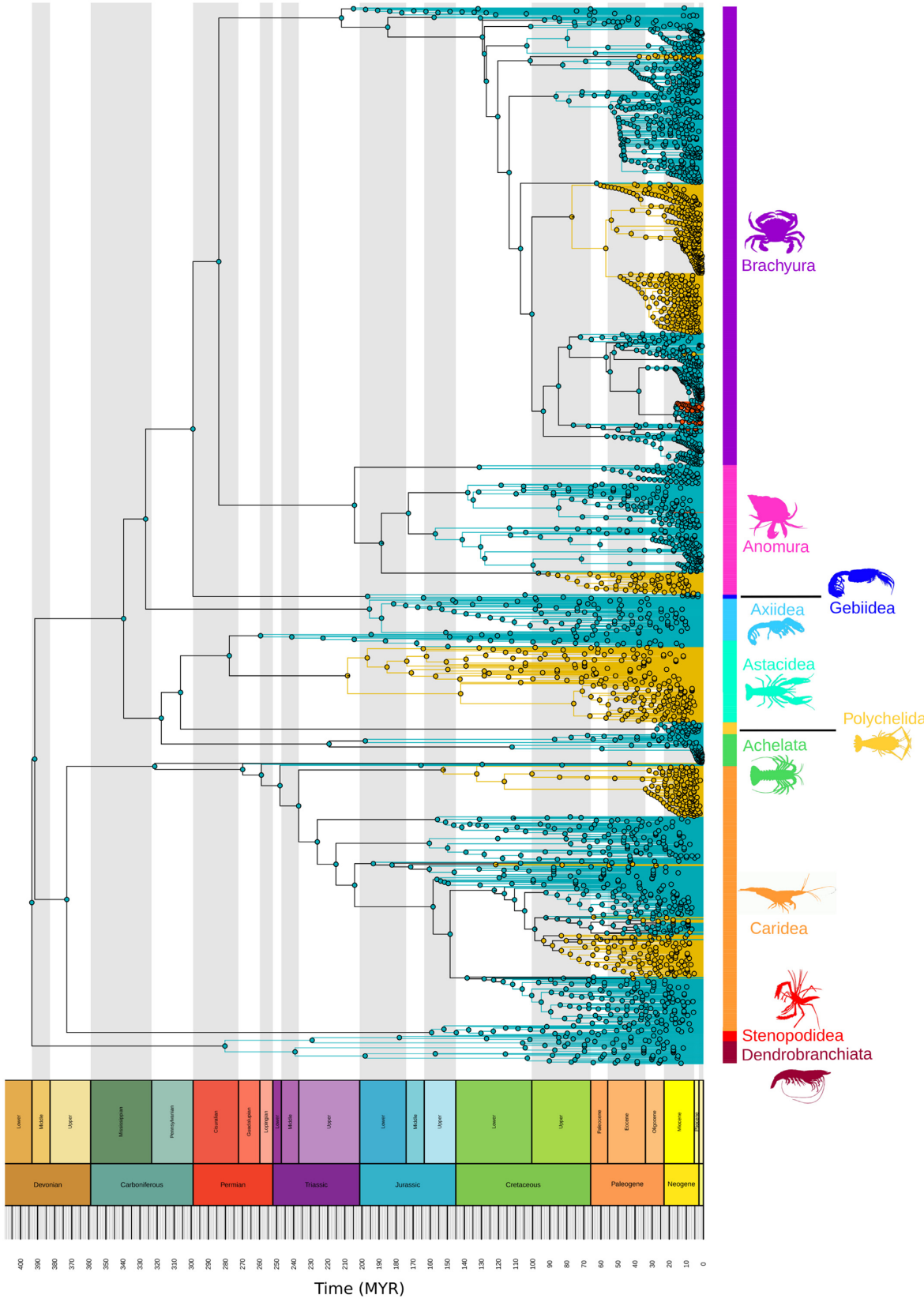

Fig. 1. Phylogenetic tree of Decapoda showing the results of the ASR. Branch colors are as follows: blue = marine, yellow = freshwater, and orange = terrestrial. Reconstructed states were plotted using the R package "phytools" (Revell 2012) and the geological time scale was added using the R package "strap" (Bell and Lloyd 2015). Procarididea consists of two taxa as sister to Caridea and are omitted for clarity. Silhouettes are from Phylopic (phylopic.org). Colors used to denote clades are as in Wolfe et al. (2019)

Table 1 Summary statistics for each sub-clade

	Clade	Mean lambda	25% quantile	75% quantile
Marine	*Astacidea*	*0.0189*	*0.01644*	*0.0208*
	Stenopodidea	*0.02042*	*0.01769*	*0.0222*
	Caridea	0.02195	0.01468	0.02759
	Dendrobranchiata	0.02431	0.01462	0.03349
	Axiidea	0.02665	0.01949	0.03191
	Achelata	0.02857	0.01757	0.02759
	Brachyura	0.02894	0.01468	0.02906
	Gebiidea	0.03684	0.01621	0.05130
	Anomura	**0.04408**	**0.02862**	0.04631
	Polychelida	**0.09467**	**0.08285**	**0.10477**
Freshwater	Astacidea	0.02334	0.01777	**0.02795**
	Caridea	0.03475	0.01981	0.04205
	Anomura	**0.06428**	**0.05587**	**0.07373**
	Brachyura	**0.08427**	**0.06125**	**0.09429**
Terrestrial	**Brachyura**	**0.11584**	**0.05963**	**0.15903**

Mean speciation rate (lambda) is reported along with the 25% and 75% quantiles. Italic font indicates clade rates that are lower than the average rates for all Decapoda, bold font indicates clade rates that are higher than the average rates for all Decapoda. Rates are considered to be low or high if the mean speciation rate for Decapoda falls outwith the quantiles. For reference mean speciation rates across Decapoda are as follows - marine: 0.02497 (25% quantile: 0.01482042, 75% quantile: 0.02784870), freshwater: 0.02510 (25% quantile: 0.014734764, 75% quantile: 0.024335542), terrestrial: 0.05292 (25% quantile: 0.02022809, 75% quantile:0.02022809).

rine taxa is 0.04408 while that in freshwater is 0.06428; nearly 1.5 times as fast. In Astacidea the mean marine speciation rate is 0.0189, compared with 0.02334 in freshwater taxa (1.2 times as fast). In Caridea, the mean speciation rate in marine taxa is 0.02195, compared with 0.03475 in freshwater (1.5 times higher; a result that is consistent with previous work; Davis et al. 2018). In Brachyura, the mean marine speciation rate is 0.02894, compared with 0.08427 in freshwater and 0.11584 in terrestrial lineages. Therefore, freshwater speciation rates in Brachyura are nearly three and four times higher in freshwater and terrestrial taxa respectively compared with marine taxa. Mean speciation rates in terrestrial taxa are also 1.3 times higher than in freshwater taxa. Mean speciation rates for marine-only clades are as follows: Achelata, 0.02857; Axiidea, 0.02665; Dendrobranchiata, 0.02431; Gebiidea, 0.03684; Stenopodidea, 0.02042; and Polychelida, 0.09467. Figure 2 shows the relative rates for speciation across all Decapoda and within each subclade. Note that all speciation rates reported are measured in units of species per million years.

State dependency

Using our formal test of the effects of habitat transitions on speciation rate (implemented in STRAPP; Rabosky and Huang 2016), we found no significant effect within Decapoda as a whole (marine-freshwater, $P = 0.65$; freshwater-terrestrial, $P = 0.196$; and marine-terrestrial, $P = 0.213$). Within sub-clades, the only significant effects were within Caridea, where marine to freshwater transitions were associated with elevated speciation rates ($P = 0.05$). Other large clades, including Anomura (marine-freshwater, $P = 0.607$; freshwater-terrestrial, $P = 0.753$; and marine-terrestrial, $P = 0.678$), Astacidea (marine-freshwater, $P = 0.778$), and Brachyura (marine-freshwater, $P = 0.703$; freshwater-terrestrial, $P = 0.485$; and marine-terrestrial, $P = 0.419$) had no effects even approaching significance.

Discussion

Terrestrial biomes are more diverse than marine biomes

The species-area effect (MacArthur and Wilson 1967; Rosenzweig 1995) predicts a relationship between the area of an "island" and the number of species found within it. The oceans occupy around 70% of the Earth's surface (Wiens 2015) and—all other things being equal—might, therefore, be expected to contain the majority of species diversity. However, estimates suggest that between 80 and 95% of macroscopic species are terrestrial (May et al. 1990; Vermeij and Grosberg 2010; Grosberg et al. 2012). The continental land masses are geologically much younger than marine habitats (Vermeij and Grosberg 2010; Nakov et al. 2019) and this discrepancy cannot, therefore, be explained by the clade-age effect (Rabosky et al. 2012; Wiens 2017;

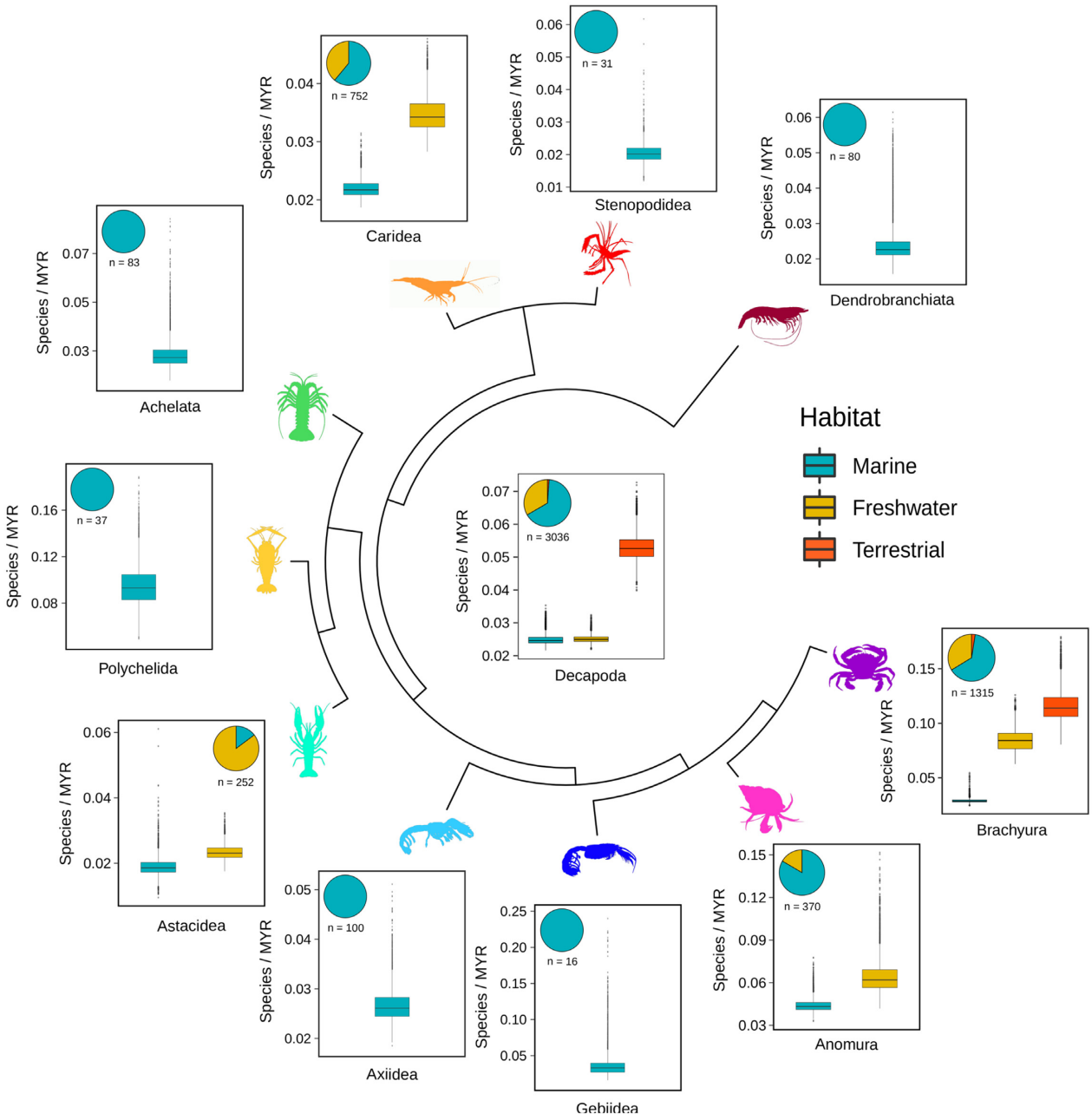

Fig. 2. Schematic phylogeny of Decapoda showing speciation rates for all Decapoda (centre) and for each sub-clade. All plots show speciation rate measured in species per million years as computed in BAMM (Mitchell et al. 2019) and plotted in BAMMtools (Rabosky et al. 2014). Box plots are colored according to broad habitat type; blue = marine, yellow = freshwater, and orange = terrestrial. Rates could not be calculated for Procarididea due to the small number of taxa, therefore, Procarididea is omitted for clarity. Pie charts represent the proportions of marine, freshwater, and terrestrial taxa for each clade with the same color coding as the speciation rate plots; blue = marine, yellow = freshwater, and orange = terrestrial. Silhouettes are from Phylopic (phylopic.org), colors used to denote clades are as in Wolfe et al. (2019)

Gamisch and Comes 2019). What other factors might therefore determine the strikingly higher species richness of terrestrial biomes? One possibility is that key innovations, such as those associated with ecological transitions, might facilitate adaptation and radiation into new ecospace (Schluter 2000; Losos 2010). Transitions from marine to freshwater and terrestrial habitats have occurred across the Tree of Life and have often resulted in higher rates of speciation. There are prominent examples in amphipods (Hou et al. 2011), caridean shrimps (Davis et al. 2018), diatoms (Nakov et al. 2019), and fishes (Bloom et al. 2013; Rabosky 2020).

Multiple freshwater and terrestrial decapod clades have increased speciation rates

Across decapods, we observe multiple independent shifts from marine into freshwater habitats (within Anomura, Astacidea, Brachyura, and Caridea), and four shifts from marine to terrestrial habitats (one in Anomura and three within Brachyura). Some of these result in large radiations. While our initial analysis found that speciation rates are not consistently higher in non-marine environments across all Decapoda, they are consistently higher in these environments for clades that retain habitat heterogeneity. Therefore, while we do not show that speciation rates are always higher in non-marine decapod lineages, our results are consistent with the general rule that non-marine speciation rates are higher than marine speciation rates within clades. We note that major subclades make strongly differential contributions to overall speciation rates. Partitioning by infra-order revealed that mean marine rates are skewed upwards by two clades; Anomura and Polychelida. Marine anomurans have rates that are 43% higher than the mean for all marine lineages, while Polychelida (which are exclusively marine) have rates that are elevated by 74%. Freshwater anomurans also have elevated rates (61% higher) compared to the mean freshwater rates in Decapoda. We also found that Brachyura have elevated rates in both freshwater and terrestrial lineages as compared to the mean decapod rates, with freshwater rates increased by 70% and marine rates by 54%. We caution, however, that all other terrestrial species are anomurans, which we could not analyze separately given their low numbers (three taxa) in our tree. However, since we found no evidence for a causal association between habitat and speciation rates in any of these clades, an explanation for the observed rate heterogeneity is still required. One potential confounding factor in Polychelida is the absence of extinct taxa in our analyses. Decapoda originated in the Ordovician (Wolfe et al. 2019) and have a rich and taxonomically diverse fossil record. Polychelida have just 38 extant representatives, forming a relatively young radiation from approximately 32 million years ago. However, an additional 55 species are known from the fossil record (De Grave et al. 2009; Audo et al. 2014). No other decapod clade contains such a large proportion of fossils. The exclusion of these extinct polychelidans in combination with the relatively young origin of extant Polychelida might have caused the anomalously high rates that we recovered. We were unable to consider the role of extinction on decapod diversity here as trees exclusively comprising extant taxa do not produce reliable extinction rates (Rabosky 2010). Other confounding factors include the paucity of the fossil record for some decapod infra-orders, such as the ghost shrimps (Axiidea), which are soft-bodied and, therefore, likely to be underrepresented in the fossil record. Moreover, these fossils are difficult to confidently assign to higher level taxa (Hyžný and Klompmaker 2015). It is likely that new fossil discoveries will lead to better calibrations for the phylogeny and this could help to clarify the diversification dynamics across the group.

Freshwater transitions are a causal driver of higher diversity in Caridea but not in other clades

We also tested whether there is a causal relationship between habitat and speciation rates. However, with the exception of Caridea, we found no evidence for a repeated effect of habitat on speciation. As highlighted by Rabosky (2020), this makes it impossible to determine whether the higher freshwater and terrestrial rates recovered here result from habitat transitions *per se* (i.e., interactions with the environment) or from other properties of the clade. How then can we explain the higher rates of speciation in freshwater and terrestrial lineages without any evidence of causality? Given that our interest here is in explaining macroevolutionary patterns of biodiversity, we can still consider the mechanisms by which the exploitation of a new habitat might promote speciation, even though we cannot say with any certainty that the observed habitat transitions are causally associated with observed faster speciation rates. One such mechanism is the greater habitat fragmentation seen in non-marine environments (Hugueny et al. 2011; Wiens 2015) contrasting with the sparse geographic barriers and larger species ranges seen in the oceans (Palumbi 1992, 1994). Adaptive radiation theory also predicts that clades entering new habitats will undergo rapid diversification as they exploit new ecospace (Schluter 2000; Losos 2010; Herrera 2017). Note, however, that we do not formally test for macroevolutionary signatures of adaptive radiation here (Herrera 2017; Law et al. 2018; Moen et al. 2021). As well as independent transitions into new habitats, our analyses found a number of reversals from freshwater to marine environments. However, we found no evidence for transitions from terrestrial to aquatic environments. In contrast with the situation in vertebrates (Vermeij and Motani 2018), there is no evidence for transitions from terrestrial to marine environments in decapods (Vermeij and Dudley 2000). Endothermy and high metabolic rates in mammals (Vermeij and Dudley 2000) may be instrumental in their transitions back into marine biomes. Further work using new methods (Mitchell et al. 2019) to include extinct taxa would help

to elucidate the relative roles of speciation and extinction in shaping the decapod Tree of Life. Accounting for uncertainty in the tree (both in terms of topology and inferred divergence dates) would also enable more rigorous tests.

There are other possible drivers of differential diversity across Decapoda

While we cannot draw strong conclusions about the role of habitat transitions in shaping rates of speciation across Decapoda, we can nonetheless consider other mechanisms that could potentially underlie the patterns recovered in this study. One possible driver of differential diversity across decapods is the marine latitudinal gradient, with higher tropical speciation rates already established in corals (Kiessling et al. 2010), molluscs (Jablonski et al. 2006), and plankton (Allen and Gillooly 2006). However, the opposite pattern is found in fishes, with the fastest rates being in the species-poor regions outside the tropics (Rabosky et al. 2018). Other variables can also drive differential speciation rates. For example, rates are lower in caridean shrimp that live in symbiosis with other organisms (Davis et al. 2018), while species richness in plant-feeding crustaceans is 21 times greater than in their sister clades (Poore et al. 2017). We, therefore, conclude that while transitions from marine to non-marine environments have influenced decapod diversity, the diversity and distribution of species that we see today results from a complex interplay of environmental and biotic factors through time rather than from the action of a single driver. Furthermore, while there are common patterns to be found within Decapoda, these patterns are unlikely to be driven by a common explanatory variable. Future work aimed at further disentangling these drivers should consider the interplay of other environmental and ecological variables, along with biotic interactions and full evolutionary history. This will allow a fuller picture of the drivers of clade diversity change through time, with important implications for our understanding of the dynamics of the ongoing biodiversity crisis. Such understanding is vital, since patterns of diversity that were shaped over tens or hundreds of millions of years are now being rapidly reconfigured by anthropogenic activity.

Authors' contributions

K.E.D. designed the study, collected and processed phylogenetic data, carried out the analyses, and wrote the manuscript. C.D. and S.M. collected and processed phylogenetic data. A.R.D.P. and S.D.G. collected trait data. S.D.G. and M.A.W. helped write the manuscript. K.E.D. and A.R.D.P. made the figures. All authors approved the final manuscript.

Acknowledgments

We would like to thank Eric Schultz and Lisa Park Boush for the opportunity to take part in the Society for Integrative & Comparative Biology symposium: "HaloDaSH: The deep and shallow history of aquatic life's passages between marine and freshwater habitats." This is Paleobiology Database publication no: 430.

Funding

K.E.D. was supported by the BBSRC grant [BB/K006754/1] awarded to K.E.D. and M.A.W. and the Leverhulme Trust grant [RPG-2016–201] awarded to K.E.D. C.D. was also supported by the BBSRC grant [RPG-2016–201]. M.A.W. was supported by the JTF grant [61408]. S.M. was supported by a University of Bath PhD studentship and ARDP by a University of York, Department of Biology, undergraduate bursary awarded to K.E.D.

Supplementary data

Supplementary data available at *ICB* online.

Data availability statement

All the data underlying this research can be found in the supplementary files.

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