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Local environmental context structures animal-habitat associations across biogeographic regions

Short title: Fish-habitat context

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Abstract

The mechanisms that govern fauna-habitat associations across multiple spatial scales remain largely undefined. Can environmental factors structure fauna-habitat associations over both local and global spatial scales, alongside biogeographical processes and patterns? We compare the extent to which the use of mangroves by fishes is consistent within and between biogeographic locations, and whether any similarities and differences can be attributed to the environmental context of those forests, such as the physical environment, seascape composition, and constraints on access by fishes. We focus on three important proxies of these structuring forces for fish – salinity, distance to reefs, and tidal amplitude. Using directly comparable remote underwater visual census from a range of diverse environmental contexts in the Central and Eastern Indo-Pacific, we examine similarity in the family-level taxonomic composition of fish assemblages in mangrove forests. Local environmental context appears to explain similarities and differences in mangrove association by fishes at both regional and local scales across the Indo-Pacific. There were strong consistencies in taxonomic composition in similar environmental contexts despite geographic separation. Tidal amplitude was a powerful explanatory factor that interacted with both distance to reef and salinity in partitioning variation in fish assemblage structure. Substantial differences in the use of mangroves between regions appear to be independent of historical biogeography, relating instead to local context. Our findings suggest that the effects of local context on habitat suitability can play out over biogeographical scales, and global similarities in fauna-habitat associations may be partially explained by comparable environmental contexts, with important management implications.

Keywords: habitat, spatial scale, nursery, context, setting, coastal ecosystem, seascape, juvenile fish.

Highlights:

- Local environmental context can determine fauna-habitat associations
- Fauna-habitat relationships are consistent in similar environmental settings
- Differences in fauna relate strongly to tidal, seascape and physical factors

Introduction

Contrasting ecosystem functioning and values can arise from geographic variation in fauna-habitat relationships. This variability can result in diverging notions of the importance of different habitats, and the impact of their removal or modification on species survival and community maintenance (Randin and others 2006; Zanini and others 2009). The mechanisms that govern similarities in fauna-habitat relationships across multiple spatial scales remain largely undefined (Bradley and others 2020). Historic phylogeographic mechanisms (i.e. the available species pool) determine large-scale patterns in fauna-habitat relationships across the globe, while environmental and ecological mechanisms (e.g. ecophysiological tolerances, predator-prey dynamics) determine habitat use at smaller spatial scales. However, large-scale patterns must also reflect the outcome of fine-scale interactions. Thus large-scale patterns in habitat use can also be driven by environmental conditions which vary over multiple spatial scales (Wiens and Donoghue 2004), such as temperature and rainfall (Whitehead and others 1992).

Variability in fauna-habitat relationships can often be caused by environmental context-dependence, whereby a suite of interacting environmental factors (physical, ecological, spatial and temporal) provide the context for the use of certain habitats, driving different habitat use under different environmental contexts (Bradley and others 2020). The physical environmental context can interact with abiotic constraints of fauna, leading to changes in habitat use that play out over multiple spatial scales. For instance, in terrestrial ecosystems, the use of vegetative structure can depend on climatic gradients, due to the thermoregulatory requirements of fauna. Amphibian and reptile fauna modify their use of tree habitat, shifting from ground-dwelling to arboreal depending on climatic regimes (Adolph 1990; Scheffers and others 2013). These patterns, observed at local scales within forests, also explain variation in habitat associations over larger biogeographic scales (Scheffers and others 2013). Availability of relevant habitat features in the landscape, and constraints on access, will also modify local habitat use. For instance, in Africa's savanna ecosystems, fauna require access to drinking water, with distance to waterholes a key determinant of habitat use (Redfern and others 2003; Roever and others 2012). These access requirements can interact with variation in the physical environment – for example, under wetter conditions, elephants are no longer constrained by distance to waterholes (Roever and others 2012). Additionally, the use of habitat can be determined by predation risk (Brown 1999), and all of these physical, ecological and landscape factors of local environmental context come together to determine habitat use by African herbivores in the presence of lions (Valeix and others 2009). In some ecosystems, local environmental forces appear to exert such a great influence in determining patterns of fauna-habitat associations (Igulu and others 2014) that some large-scale, global differences in habitat use may be partially explained by differences in local environmental context.

In this study, we ask whether environmental context can be an important driver of habitat use by animals at both local and regional scales. The association between fish fauna and mangrove habitat provides a useful model system for testing this idea. Mangroves occupy a wide range of environmental settings (Worthington and others 2020) – from sandy reef flats to freshwater swamps, and are distributed throughout the tropics and subtropics worldwide (Nagelkerken and others 2008). The fish taxa that use these forests are known to vary considerably, both at finer scales such as between bays and islands in a single region (Kimirei and others 2011), and at regional scales such as between nearby regions (Thollot 1992), and between biogeographic realms (Hemingson and Bellwood 2018). As a result, the ecological role of mangrove forests for fish has long been the subject of international debate (Nagelkerken 2009; Sheaves 2017). This variability complicates our understanding of mangrove-fish relationships, and our ability to employ these relationships, both scientifically (Faunce and Layman 2009) and in conservation and environmental management (Sanchirico and Mumby 2009).

Both environmental context and historic phylogeography will shape the taxa that use mangrove forests, but their relative importance will depend on spatial scale and taxonomic resolution. While phylogeography determines the available species pool across the globe, at the broader family level, phylogeography is less likely to have substantial impact within biogeographic realms with a shared evolutionary history, such as the Indo-Pacific (Cowman and Bellwood 2013). In these situations, it might be possible to tease out the effects of environmental context without the orthogonal influence of phylogeographic history.

The physical environment, landscape-scale habitat requirements, and constraints on access by fauna, all strongly influence the use of coastal habitats by fishes in general, and appear particularly important in determining the use of mangroves. Firstly, salinity can structure fish assemblages throughout the coastal zone due to differing salinity tolerances (Harrison and Whitfield 2006; Whitfield and others 2006). Salinity can determine the fish assemblages found in mangroves at local scales (Ley and others 1999), and appears to be a major determinant of mangrove habitat function globally (Igulu and others 2014). Secondly, the surrounding seascape can have a profound influence on how fish use coastal habitats, with connectivity or distance between mangroves and reefs of particular importance (Nagelkerken and others 2012; Olds and others 2012) due to the ontogenetic use of mangroves by reef fish (Dorenbosch and others 2007; Jones and others 2010; Pittman and others 2007). Finally, the tidal amplitude experienced in a location can profoundly shape how intertidal habitats like mangroves are used by fish (Sheaves 2005). In areas with small tidal amplitudes, fish are able to use mangrove habitat continuously (Dorenbosch and others 2007), whereas in areas of large tidal amplitudes, mangroves are exposed at low tide, and the duration of exposure can vary substantially among locations (Baker and others 2015). To use these intertidal habitats, fish are forced to perform potentially risky intertidal migrations (Dorenbosch and others 2004; Hammerschlag and others 2010; Unsworth and others 2007). The magnitude of inundation can shape the use of intertidal habitat within locations (Castellanos-Galindo and Krumme 2013; Castellanos-Galindo and Krumme 2015; Minello and others 2012; Rozas 1995), and is thought to be a major driver of the use of mangroves by fishes globally (Igulu and others 2014). While each of these three drivers have received considerable attention individually, it has been difficult to study how their interplay shapes fish assemblages. This is because field studies have tended to standardise variation in one or more of these variables through site selection, and because the array of different sampling techniques used in different locations precludes a robust understanding across different environmental contexts.

Little is known about how environmental factors interact to determine fauna-habitat associations over multiple spatial scales. Until now, there has been no evaluation of the combined influence of salinity, distance from reef and tidal regime on patterns in coastal fauna-habitat associations across regions using directly comparable data. Therefore, the aim of this study was to understand the role of environmental context in defining habitat associations at multiple spatial scales in the Central and Eastern Indo-Pacific. While there are differences in species distributions across this realm driven by biogeographic forces, at the family level, most taxa are present throughout the realm, due to a shared evolutionary history (Cowman and Bellwood 2013). By examining patterns in family level use of mangrove forests, we aimed to examine broad similarities and differences in mangrove use that could not be attributed solely to biogeography.

Methods

Study sites:

Replicate study sites across five locations (Fig. 1) were selected to approximate the range of contextual variation experienced in mangrove habitats across the Indo-Pacific (Table 1). These locations covered almost the entire spread of tidal amplitudes in the Indo-Pacific, from 0.5 m to 11 m. Within each location, efforts were made to cover the full range of variation present in distance between mangroves and reef, and in salinity. Some locations have larger variation in distance to reef than others due to the underlying geomorphological composition of the seascape. Similarly, some locations had larger variation in salinity than others, due to differences in rainfall. The amphidrome point of the South Pacific lies far from any major landmasses (Luther and Wunsch 1975), meaning that areas with the smallest tidal regimes lack extensive areas of mangroves far from reefs, so the extremes of both variables were partially confounded in this analysis. In addition, salinity is partially correlated with distance to reef, as reef building coral are associated with marine salinities. These imbalances in the dataset (see supplementary material, Fig. S1) are representative of natural variation, and do not violate any underlying assumptions in the exploratory analyses that we employed. All results were interpreted with these imbalances in mind.

Fish Surveys

We studied fish assemblages using remote unbaited video census. Video surveys were conducted throughout the day and tidal cycle, in an attempt to adequately represent natural variability. Cameras were deployed inside mangrove habitat structure, within the first 2 metres of the seaward edge of the mangrove forest, facing mangrove structure at an approximate distance of 1 m. This standardised the part of forest habitat sampled (edge), and the effective sampling distance of each video recording (~1 m). Cameras were placed at a minimum distance of 20 m, but usually much farther (>50 m) from each other to ensure sample independence. Cameras were left undisturbed to record while the vessel maintained a distance of at least 100 m. In-water visibility distance was determined using a patterned image 0.5 m from the lens, and videos below the 0.5 m threshold were discarded. This produced 389 video samples for analysis. A 15 minute section of video was analysed from each deployment, which provides an optimal and consistent comparison of species assemblages between deployments (Piggott and others 2020). Videos were viewed to record the taxa present, and fish identifications were reviewed by relevant experts. Only presence/absence of families was used in the following analyses. Presence data are more robust to variability in visibility, and the fact that differential presence of schooling and solitary species within families could make abundance data non-comparable between locations.

Explanatory variables

Salinity

Salinity surveys were carried out at each location during each sampling trip using either a refractometer or salinometer, measured in psu. These surveys were conducted concurrently with video sampling, but measurements were not taken for each video recording individually. Therefore, salinity values represent the shallow water readings associated with the local area (within 100 m), rather than individual position of each video site. As sampling occurred outside the monsoon season for each location, we are making the assumption, based on previous research carried out in these locations (Aharon 1991; Baker and others 2018; Langer and Lipps 2006; Williams and others 2006; Wolanski and others 1990; Wolanski and Spagnol 2003) that waters were reasonably well mixed and salinity was not fluctuating dramatically during the sampling period, making these values adequately representative.

Distance to reef

Distance to reef was measured using the shortest path through water between the video site, as recorded by GPS position, and the nearest visibly identifiable patch of biogenic reef from satellite imagery. A variety of satellite sources were used to avoid cloud cover and view areas under low wind and low tide conditions to maximise the possibility of reef detection, including Google earth, ARC GIS and DigitalGlobe (http://www.digitalglobe.com accessed August 2018). Ground sample distance (i.e. pixel resolution) ranged between 65 cm and 39 cm. While this method may miss minor patches and deeper reefs, it provides a good indication of the distance from a point to the nearest substantial photic-zone reef.

Tidal amplitude

The maximum tidal amplitude of the location in which the video sample was taken was used as an explanatory variable. Values were derived from tidal gauge data, obtained from Australia’s National Tidal Centre and University of Hawaii’s Sea Level Centre (Caldwell and others 2015).

Multivariate analyses

Family-level assemblage composition (presence/absence) was calculated for each site. While there are differences in the species pool in the different locations sampled, all broadly contain the same families of near-shore fishes (Sheaves 2012). Family-level taxonomic assemblage composition is a meaningful ecological measure, because the family level taxonomy of tropical fishes is broadly related to functional morphology and ecology. Broad trophic ecology (e.g. herbivory vs carnivory) and some broad ecosystem associations (e.g. reef vs estuary) are often persevered at the family level. Therefore, we used family-level taxonomic assemblage to obtain a comparable metric by which to assess differences in the use of mangrove forests by fish throughout the broad geographic area encompassed by our study locations. Not all taxa were included in analysis at the family level; fishes from the families Gobiidae and Blenniidae could not be reliably distinguished in many video samples, therefore the order Gobiiformes was used. Similarly, fishes from the families Atherinidae, Clupeidae and Engraulidae could not be reliably distinguished, and the order Clupeiformes was used. The distinction between Scarinae and other labrid fishes was maintained due to their broadly divergent functional ecologies.

Multidimensional scaling ordination

To display variation in fish assemblage composition, and identify the taxa that characterised this variation, non-metric multidimensional scaling (nMDS) ordination was employed. Non-metric ordination was chosen because it uses the internal order of the entire dataset to display similarities and differences between samples without any presupposed stratification. While information about the magnitude of distances is lost, rank-based methods are generally more robust to data which do not have an identifiable distribution, and also avoids the assumption of linear patterns inherent in metric ordinations, for which there is no particular basis in this study. Multivariate data that is dominated by absences can present problems during multivariate analysis due to the undue influence of rare taxa and empty sites (Clarke and others 2006). Therefore, rare taxa are often excluded from multivariate analyses. However, taxa that are rare at the level of the entire dataset can still be important, as they might be common in one location and absent in others. To ensure these potentially important contributions were included, taxonomic assemblage data were treated in two different ways. In the first more conventional treatment, an arbitrary dataset-wide cut-off was used to determine the inclusion of taxa in the analysis (e.g. Davis and others 2014). All taxa present in less than 10% of total sites were excluded, which removed all taxa with low occurrences regardless of location-specific occurrence rates, providing a dataset with minimal influence of rare taxa. In the second, more inclusive treatment, taxa present in at least 10% of sites from any one location were retained in the analyses. This only removed taxa that were rare throughout all locations, and provided a dataset where all non-trivial differences between locations would be maintained. This treatment resulted in substantial outliers in subsequent analysis. These outliers were excluded from the dataset, providing a third and final data treatment.

To examine the variation in taxonomic assemblage composition in all treatments, Jaccard's coefficient similarity matrices were calculated on the binary presence or absence of each taxonomic group in each site. nMDS applied to these similarity matrices was used to display patterns of multivariate variation graphically. This was performed using the 'metaMDS' function in package Vegan (Oksanen and others 2013) in R. The conventional treatment produced a two-dimensional MDS solution with an acceptable (<0.2) level of stress (see supplementary material, Fig. S2). The inclusive treatments resulted in high stress two-dimensional MDS solutions (see supplementary material, Fig. S3 and S4), therefore lower stress three-dimensional solutions were produced, and the first two dimensions (which capture the bulk of variation in the data) were examined. Due to general agreement between the different data treatments, only the results of the inclusive treatment excluding outliers (i.e. the third data treatment described above) is presented in the main text. The results of the other two treatments are provided in the supplementary material (Fig. S5 through to S8).

Multivariate Regression Tree Analysis

To examine whether the broad variation in taxonomic assemblage composition could be statistically explained by environmental context, a multivariate regression tree (MRT) analysis was performed with the 'mvpart' package in R (De'Ath 2007; Ouellette and Legendre 2012). This technique recursively partitions the dataset into homogenous subgroups using explanatory variables (De'Ath 2002), in this case the three descriptors of environmental context: salinity, distance to reef and tidal amplitude, as well as biogeographic province (central vs eastern Indo-Pacific) following Bowen and others (2016). For each partition, the machine learning analysis considers all four explanatory variables, and selects the variable that maximises the reduction in group heterogeneity. In the final tree, the variables that were selected, and how the dataset was partitioned, shows how these variables explain assemblage structure when considered together. The importance of each contextual variable in explaining variability in the tree model was also calculated based on the reduction in mean squared error by each candidate variable at each split, using the 'caret' package in R (Kuhn 2012). Regression tree approaches are robust to the co-variation in explanatory variables as described above (Table 1, supplementary material, Fig. S1). The tree examined was based on the inclusive data treatment excluding outliers, as described above, in order to preserve locational differences and exclude the undue influence of outliers. The analysis was based on the same multivariate taxonomic similarity matrix used in the nMDS analysis above.

Surface fitting

To examine how each environmental contextual variable related to the variation in taxonomic assemblage composition observed, surface fitting of explanatory variables was applied to the nMDS ordinations. This technique uses generalized additive models to fit a smooth surface, with the degree of smoothing determined by generalised cross validation, and was carried out using the ‘ordisurf’ function in package Vegan (Oksanen and others 2013) in R. This technique is appropriate for examining relationships between environmental variables and assemblage composition when relationships are not necessarily linear, as is assumed in vector fitting.

Results

In total, 45 different family-level fish taxa occurred in mangrove habitats throughout our study locations. Most taxa were only present in mangroves in certain locations, with the exception of Carangidae, Gobiiformes and Lutjanidae, which were present in mangroves throughout the Indo-Pacific (see supplementary material, Table S1). Few of these families were commonly encountered, with only 9 families occurring in greater than 10% of total sites.

Variation in mangrove fish assemblages

Overall, there was substantial variation in family-level composition of sites both within and between locations. There was a broad separation of sites into two location-based clusters – sites from French Polynesia and Papua New Guinea vs sites from Australian locations. Sites from French Polynesia and Papua New Guinea were characterised by Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zanclidae, Mullidae, Nemipteridae and Apogonidae. These were separated from the majority of sites from Northern Australian locations, which were characterised by Gobiiformes, Gerreidae and Sparidae. Differences between locations appear to be an important contributor to the overall variation of mangrove fish assemblages across the Indo-Pacific. There was also clear overlap of the locations within each clusters, and some overlap of these two clusters (Fig. 2). This indicates that a substantial portion of the variation in fish assemblages is not explainable in terms of regional difference, and occurs within each location individually. Many sites were more similar to sites in other locations than to the majority of the sites from their own location, demonstrating that mangrove assemblages can be quite similar between locations. The magnitude of variation between locations is similar to the magnitude of variation between sites within locations. North Eastern Australia had the widest spread of sites, covering the entire ordination space. This demonstrates that mangrove assemblages can be highly variable within a location, and implies that this variation can equal the entire span of regional variation. Only the final multivariate data treatment is presented in detail (Fig. 2). This treatment included taxa that were common within locations, but excluded outliers. Both the conventional data treatment (see supplementary material, Fig. S5) and the inclusive treatment prior to removal of outliers (see supplementary material, Fig. S6) captured these same general patterns within and between locations.

Potential contextual drivers of variation in mangrove fish assemblages

All three potential contextual drivers were selected by multivariate regression tree analysis as factors that reduced heterogeneity in the dataset, i.e. explained the structure of the fish assemblage. The resulting tree structure (Fig. 3) indicates the primacy of tidal amplitude in defining mangrove fish assemblages. The major division in the dataset was between small (<2 m, microtidal) and large (>2 m, meso- and macro-tidal) tidal amplitudes. Within sites from small tidal regimes, variability was best explained by the tide again, effectively distinguishing between sites from Polynesia (eastern Indo-Pacific, 0.5 m maximum tidal range) and New Britain (central Indo-Pacific, 0.9 m maximum tidal range). As a location-scale variable, tidal amplitude is confounded with differences in biogeography. However, this analysis indicates that assemblage structure is consistent with the magnitude of tidal amplitude, across biogeographic provinces (central vs eastern Indo-Pacific). Within sites from large tidal amplitudes, the biggest difference between assemblage composition was between sites close to reefs (<560 m) and sites far from reefs (>560 m). Sites in large tidal amplitude locations close to reefs varied most according to tidal amplitude again. Sites from large tidal amplitudes far from reefs diverged most according to salinity, with sites in salinities below 28 (i.e. brackish waters) distinct from those in salinities above 28 (i.e. near-marine and marine waters). Variable importance values (Table 2) indicated that tidal amplitude was the most important factor in explaining variability in the dataset. Salinity and distance to reef were both equally capable of partitioning variation, and biogeographic province less so. These results indicate that tidal amplitude can explain a large amount of variation in assemblage composition between sites, and that the effects of distance to reef and salinity are highly interactive with tidal amplitude.

Surface fitting was used to model the gradient of change for each of the three explanatory context variables across the ordination space (Fig. 4, 5 and 6). Salinity, distance to reef and tidal amplitude were all significantly correlated with the ordination ($p<0.001$), meaning that the distribution of sites in the ordination was in some way concordant with changes in values of each of these variables. The variation explained by each variable differed markedly. Patterns were consistent across all three different data treatments for the exclusion of rare taxa (see supplementary material, Fig. S7 and S8).

Tidal amplitude explained 61% of the variation in the ordination (Fig. 4). The gradient in tidal amplitude is generally linearly correlated with dimension 1, mirroring the broad differences in locations captured across the ordination space (Fig. 4a). The strong gradient apparent on the surface plot between micro-tidal (Polynesia and New Britain) and macro-tidal regimes (Northern Australia), indicates that tidal amplitude explains differences in this part of the space, but the lack of a gradient over Northern Australian sites indicates that other factors are important in this part of the space. This is consistent with the multivariate tree (Fig. 3).

Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zanclidae, Mullidae, Nemipteridae and Apogonidae appear to be associated with small tidal amplitudes and Gobiiformes, Gerreidae and Sparidae appear to be associated with large tidal amplitudes (Fig. 4b).

Distance to reef explained 47% of the variation in the ordination (Fig. 5). The surface appears to explain variation both within and between locations, with the gradient running diagonally across the space, varying substantially over both dimensions 1 and 2 (Fig. 5a). Gobiformes, Sparidae, Gerreidae, Tetraodontidae, Ambassidae, Toxotidae, Carangidae, Terapontidae and Scatophagidae appear to be associated with large distances from reefs, and Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zanclidae, appear to be associated with small distances from reefs (Fig. 5b).

Salinity explained 14% of the variation in the ordination space (Fig. 6). Variation across much of the space is likely driven by tidal range and distance to reef, as indicated by the multivariate regression tree (Fig. 3), where salinity was the most important discriminator only within sites far from reef in large tidal amplitude locations. Salinity appears to predominantly describe variation that occurs within locations rather than between them (Fig. 6a), with the gradient mainly occurring along dimension 2. Sparidae, Gerreidae, Tetraodontidae, Ambassidae, Toxotidae, Carangidae, Terapontidae and Scatophagidae appear to be associated with brackish salinities, and Gobiformes, Lethrinidae, Scarinae, Labridae, Acanthuridae, Chaetodontidae, Pomacentridae, Ostraciidae, Zanclidae, Mullidae and Nemipteridae associated with higher salinities (Fig. 6b).

Despite natural imbalances in the dataset, each variable appears to explain a somewhat different component of variation in the ordination space. Gradients occurred along different axes, reflecting the separation between different sets of species. However, both distance to reef and tidal range explained variation occurring along dimension 1, indicating correctly that they co-varied across our study locations (see supplementary material, Fig. S1). As a result, these three variables explain more than 100% of the variation in the ordination space, i.e. variation is not strictly partitioned between them. Due to the natural structure of variability in our study systems, sites from micro-tidal Polynesia were all close to reef (<500 m), whereas the majority of sites from macro-tidal North Central and North West Australia were far from reefs (>500 m). Thus, differences between locations (and thus tidal regimes) cannot be clearly distinguished from differences in distance to reef in the overall analysis. However, by examining the sites that are close to reefs (<500 m) across all locations (Fig. 7), the potential effects of locational differences in tidal range can be observed independently of the effects of distance from reef. In the ordination, the arrangement of points is consistent with the directional gradient of tidal range across the space.

Discussion

Environmental context explained variation in the habitat associations of fishes at both regional and local scales across the locations sampled in the central and eastern Indo-Pacific. Faunal composition at the family level was clearly not location specific, and locations showed considerable overlap in assemblage composition. Instead, the response of fish fauna was largely consistent with environmental variation. Locations with broadly similar tidal amplitudes showed considerable overlap in fish assemblage composition. While the natural structuring of environmental contexts in the Indo-Pacific meant that tidal range covaried with proportion of sites close to reef in the dataset, the fish assemblage of sites close to reefs at each location were different, and these differences largely aligned with tidal magnitude. While this is not conclusive evidence that tidal mechanisms are responsible for these interregional patterns, tidal amplitude has been identified as a potential global determinant of the use of mangroves by fish (Faunce and Layman 2009; Igulu and others 2014), and results from our study supports this hypothesis. The variation seen within locations with broadly similar tidal regimes was explained by both salinity gradients and seascape structure. This is consistent with the findings of other mangrove studies from across the Indo-Pacific, which together show that geographically distant mangrove forests in similar environments can share similarities in fish taxa. In coastal marine environments close to reefs, mangroves tend to be characterised by reef associated taxa, including families that occur in mangroves as juveniles, such as Nemipteridae, Scarinae and Labridae, and those that more typically occur as adults such as Chaetodontidae (Barnes and others 2012; Unsworth and others 2009, Nagelkerken and Van der Velde 2004). In brackish environments far from reefs, mangroves tend to be characterised by coastal and estuarine taxa such as Ambassidae and Toxotidae (Blaber and others 1989, Sheaves and others 2016). This is not the only important axis of variation in these two factors. In large tidal amplitude locations, in mangroves far from reefs, there was an important difference in fish fauna based on salinity alone. This is consistent with the idea that salinity plays a key role in structuring fish fauna in coastal and estuarine environments (Blaber 2008; Bradley and others 2019; Ley et al 1999; Weinstein and others 1980). These results are consistent with the idea that variation in habitat use is driven by specific environmental conditions, and demonstrate that in the Central and Eastern Indo-Pacific, abiotic environmental context can largely explain differences in the use of coastal habitats by fauna.

The substantial differences in family-level mangrove fish assemblage composition observed at the locations sampled in the Central and Eastern Indo-Pacific appear to be broadly independent of historical biogeography. The major biogeographic division in our dataset was between the biogeographic provinces of the East Pacific (represented by Polynesia) and Central Indo-Pacific (all other locations), as defined by Bowen and others (2016). Assemblages in mangrove forests did not diverge according to biogeographical province in either analysis, but instead converged according to similarities in tidal amplitude, distance to reef, and salinity. While the use of family-level taxonomic composition intentionally avoids much of the differences between locations caused by species distributions across the Indo-Pacific (Sheaves 2012), some of the families that distinguished our North Central Australian and North Western Australian sites are entirely absent from French Polynesia – namely Sparidae and Gerreidae (Siu and others 2017) – so their absence from mangroves there can be directly attributed to their absence from the species pool at these locations due to biogeographic history. However, these families are common in New Britain (Froese and Pauly 2018), and their absence from mangroves there serves to distinguish mangrove sites in this location from those with larger tidal ranges. Importantly, none of the families that distinguished small tidal regime locations (Polynesia and New Britain) were unique to these regions – they are all common reef taxa found across biogeographic provinces in all locations sampled (Froese and Pauly 2018), yet they were absent from mangroves in all larger tidal regimes (northern Australian locations). This demonstrates that there are strong commonalities in mangrove assemblages found in low tidal amplitudes close to reefs, in high tidal amplitudes close to reefs, and high tidal amplitudes far from reefs, that are independent of historical biogeography.

The mechanisms by which salinity, seascape structure and tidal range might interactively determine the use of coastal habitats by fish are not well understood. It is possible that the direct ecological costs and benefits of inhabiting mangroves shape fish assemblages in regions where mangrove roots are routinely exposed during the tidal cycle. Regular migration between mangroves and suitable low tide habitat are likely to involve increased risk of predation (Gilliam and Fraser 2001), and incur a substantial energetic cost (Alexander 2002, Bernatchez and Dodson 1987). The duration, frequency and depth of inundation of intertidal habitats all vary with tidal amplitude (Baker and others 2015; Minello and others 2012), which will directly affect the specific values of mangrove habitat for fish (Ellis and Bell 2004). Fish that use mangroves must respond to these dynamics with strategies for coping with temporal variation in habitat suitability, including inter-habitat migrations (Reis-Filho and others 2016; Krumme 2009, Sheaves 2005). In tidally-influenced areas, mangroves should be predominantly inhabited by taxa that have developed adaptations to these challenges (Castellanos-Galindo and Krumme 2015). Under these conditions, the surrounding seascape, particularly the kind of habitat that is available at low tide, will strongly influence the set of fish that are able to use mangrove habitat (Pittman and others 2007). Some of the variability observed in the present study could relate to qualities of the surrounding seascape that were not examined, such as distance to subtidal habitats other than reef, e.g. seagrass (Gilby and others 2016), or level of predation risk across different habitats across the intertidal zone (Grol and others 2011; Kimirei and others 2013; Kimirei and others 2015). As the results of the present study suggest, tidal amplitude and seascape structure are likely to interact to determine the use of intertidal habitat by fish. Overall, regional differences in mangrove fish communities across the Indo-Pacific are likely due to the pervasive, ecosystem-wide effects of differences in climate, geomorphology and tidal regime.

While there is certainly taxonomic variation in fauna-habitat associations among regions due to biogeographic history, a large proportion may be predictable based on environmental context. The presence or absence of entire family level taxa can illustrate only broad differences in the use of mangroves, and is likely to conceal important species-level differences among locations. That such large differences in habitat use are apparent, and are partly explainable by environmental context, highlights the primacy of these drivers for coastal ecosystem function. There were consistencies in mangrove use in similar environmental contexts despite geographic separation, suggesting that divergent, context-specific notions of habitat function are valid and necessary. Habitat associations underpin our understanding of the requirements of fauna, and inform the way we manage natural ecosystems. Due to the complex interplay of factors found in this study, it is important to consider the breadth of factors that define environmental context together, in order to understand habitat function. If the context-dependence of a habitat is properly understood, notions of its function for animals may be properly informed, enhancing our ability to make robust environmental decisions.

Data Accessibility Statement – We have deposited our data at the Tropical Data Hub, James Cook University.

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Table 1. Study location details, including environmental parameters and associated meta-data. Biogeographic region follows the biogeographic provinces in Bowen and others (2016). Climate data from www.climate-data.org, accessed October 2018. Tidal pattern data from data.shom.fr, accessed October 2018.

Location	Biogeo graphic region	Max. tidal range	Tidal pattern	Sampling period	Yearly average rainfall, Climate	Salinity: range sampled	Distance to reef: range sampled	Coordinates
Polynesia	East Indo-Pacific	0.5 m	Semi-diurnal with diurnal inequality	October 2017	1800 mm, Tropical monsoon climate	32-34	30 m - 360 m	17° S 149° W
New Britain	Central Indo-Pacific	0.9 m	Mixed	Sept. – Nov. 2015 & 2016	3700 mm, Tropical monsoon climate	0-35	30 m - 14 km	4° S 151° E
North eastern Aust.	Central Indo-Pacific	3.9 m	Semi-diurnal with diurnal inequality	June – Dec. 2014 & 2015	2237 mm, Tropical monsoon climate	0-35	30 m - 25 km	18° S 146° E
North central Aust.	Central Indo-Pacific	7.8 m	Semi-diurnal with diurnal inequality	September 2015	1694 mm, Tropical savanna climate	29-35	1 km - 27 km	12° S 130° E
North western Aust.	Central Indo-Pacific	10.8 m	Semi-diurnal	June 2017	562 mm, Tropical semi-arid climate	34-35	230 m - 8 km	16° S 123° E

Table 2. Variable importance for the three contextual variables used in multivariate regression tree analysis.

Predictor	Rank	Reduction in MSE	Proportional reduction in MSE relative to best predictor
Tidal amplitude	1	0.56	1
Salinity	2	0.37	0.66
Distance to reef	3	0.35	0.63
Biogeographic region	4	0.21	0.36

Figures

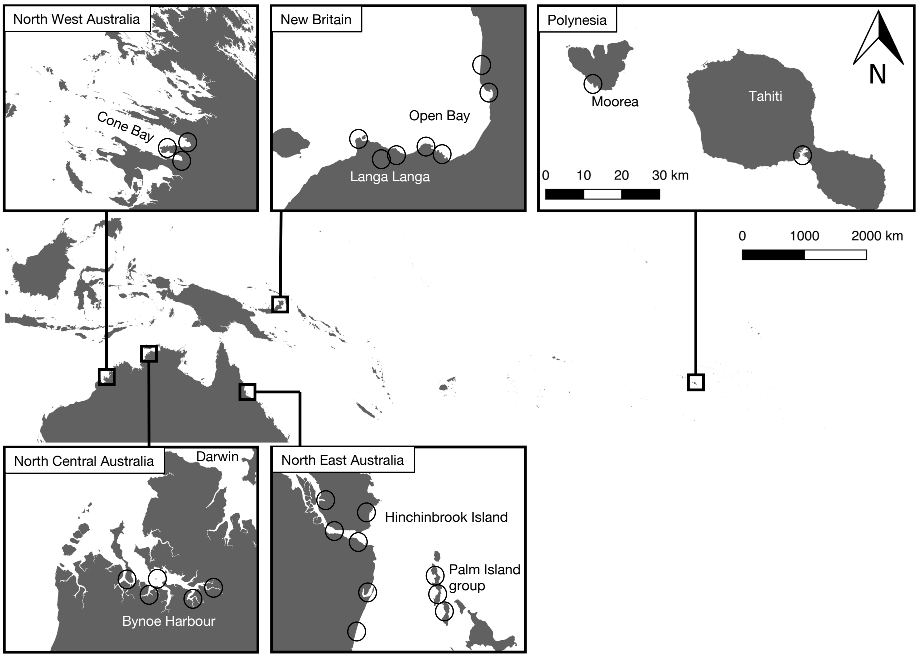

Figure 1. Distribution of sampling effort. Central map shows the Central and Eastern Indo-Pacific, and the location of our study locations. Each study region map is identically scaled (scale bar located in French Polynesia map). Black circles show video sampling sites.

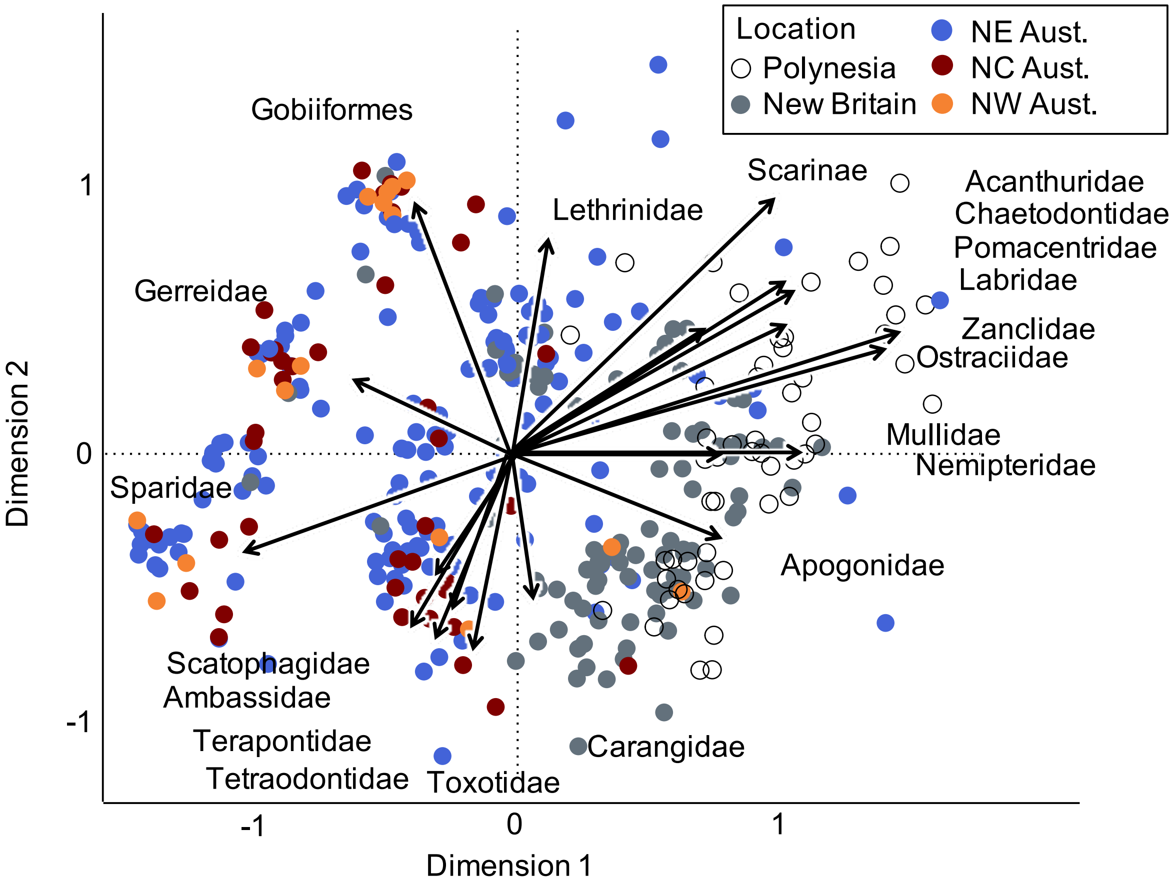

Figure 2. nMDS ordination displaying the first two dimensions of a 3D solution (stress: 0.152) capturing the differences between sites (individual data points) based on an inclusive data treatment (excluding outliers) of family level taxonomic assemblage composition (n = 349). Dimensional values are scaled such that a distance of one unit represents a halving of assemblage similarity between sites. Taxonomic vectors represent the direction of positive correlation with the ordination space. Vector terminal position represents a taxa's centre of occurrence in the ordination space, calculated using the weighted average of site abundances. Only taxa that are far (>0.5 dimensional units) from the centre of the ordination space (i.e. taxa that differ strongly across the ordination space) are shown. Points have been jittered (at a scale of 0.1 on each dimensional axis) to reveal quantities of points occurring at identical positions in the ordination.

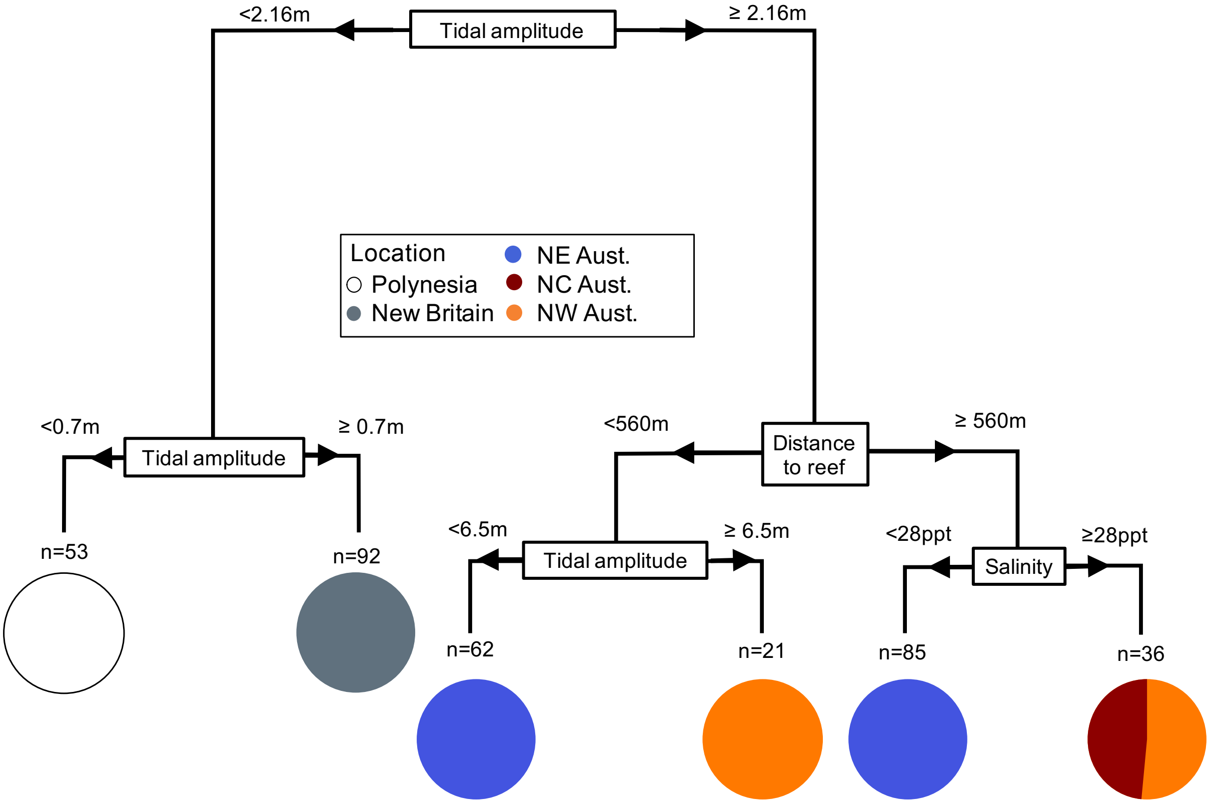

Figure 3. Multivariate regression tree describing the major divisions in fish assemblage composition of mangrove habitat based on environmental context, throughout the Indo-Pacific (n = 349 sites). Each division is labelled by the contextual factor that is best able to split the data into homogenous groups, and the values that best distinguish them. The difference between group community structure is proportional to vertical distance in the dendrogram. Circles at each final node show the regional composition of samples in each node – only the far right node contains a mix of samples from different regions.

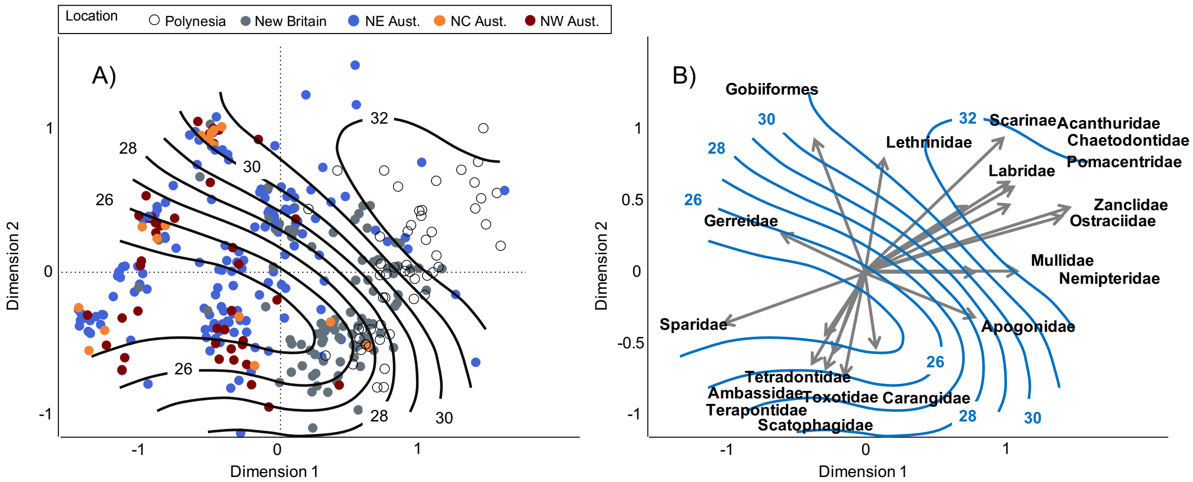

Figure 4. Surface fitting of tidal amplitude as an explanatory variable, depicting how modelled gradients in tidal amplitude relate to fish families and locations. Panel A shows surface with site points for reference, Panel B shows surface with species vectors for

reference. Lines describe the topography of the gradient, and units are log (cm). Deviance explained: 60.9%, indicating to what extent changes in assemblage composition across the space mirror changes in the values of tidal amplitude.

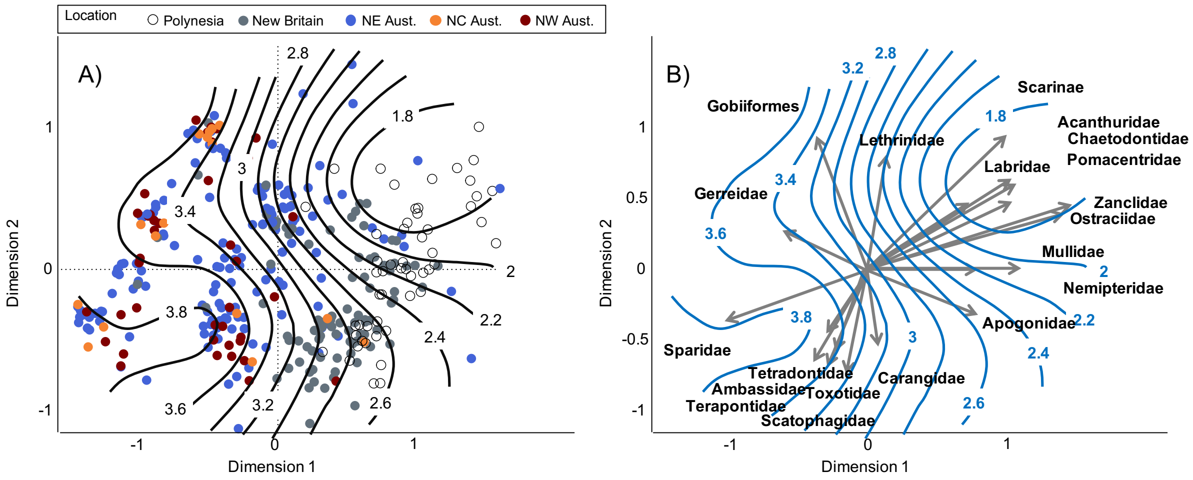

Figure 5. Surface fitting of distance to reef as an explanatory variable, depicting how modelled gradients in distance to reef relate to fish families and locations. Panel A shows surface with site points for reference, Panel B shows surface with species vectors for reference. Lines describe the topography of the gradient, and units are in log (metres). Deviance explained: 46.7%, indicating to what extent changes in assemblage composition across the space mirror changes in the values of tidal amplitude.

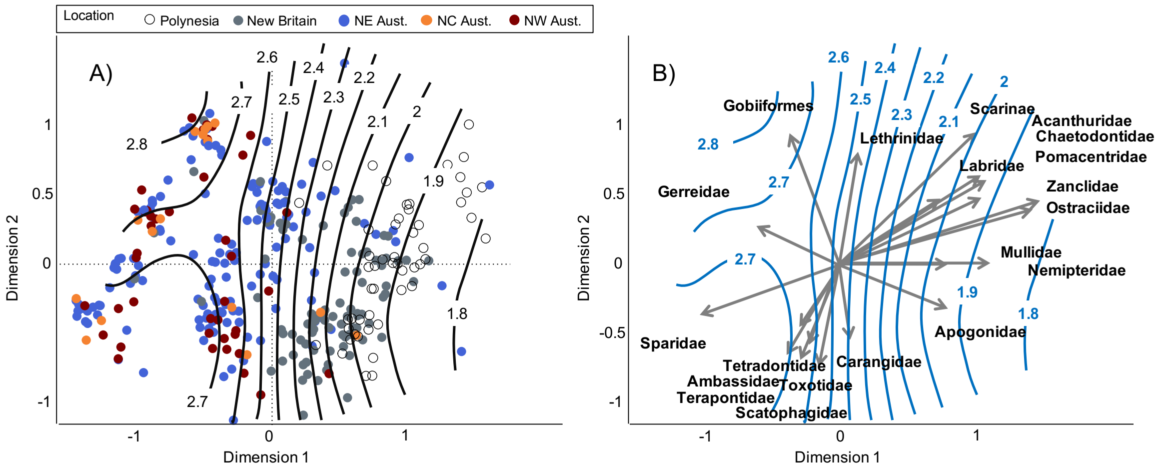

Figure 6. Surface fitting of salinity as an explanatory variable, depicting how modelled gradients in salinity relate to fish families and locations. Panel A shows surface with site points for reference, Panel B shows surface with species vectors for reference. Lines describe the topography of the gradient, and units are in psu. Deviance explained: 14.5%, indicating to what extent changes in assemblage composition across the space mirror changes in the values of tidal amplitude.

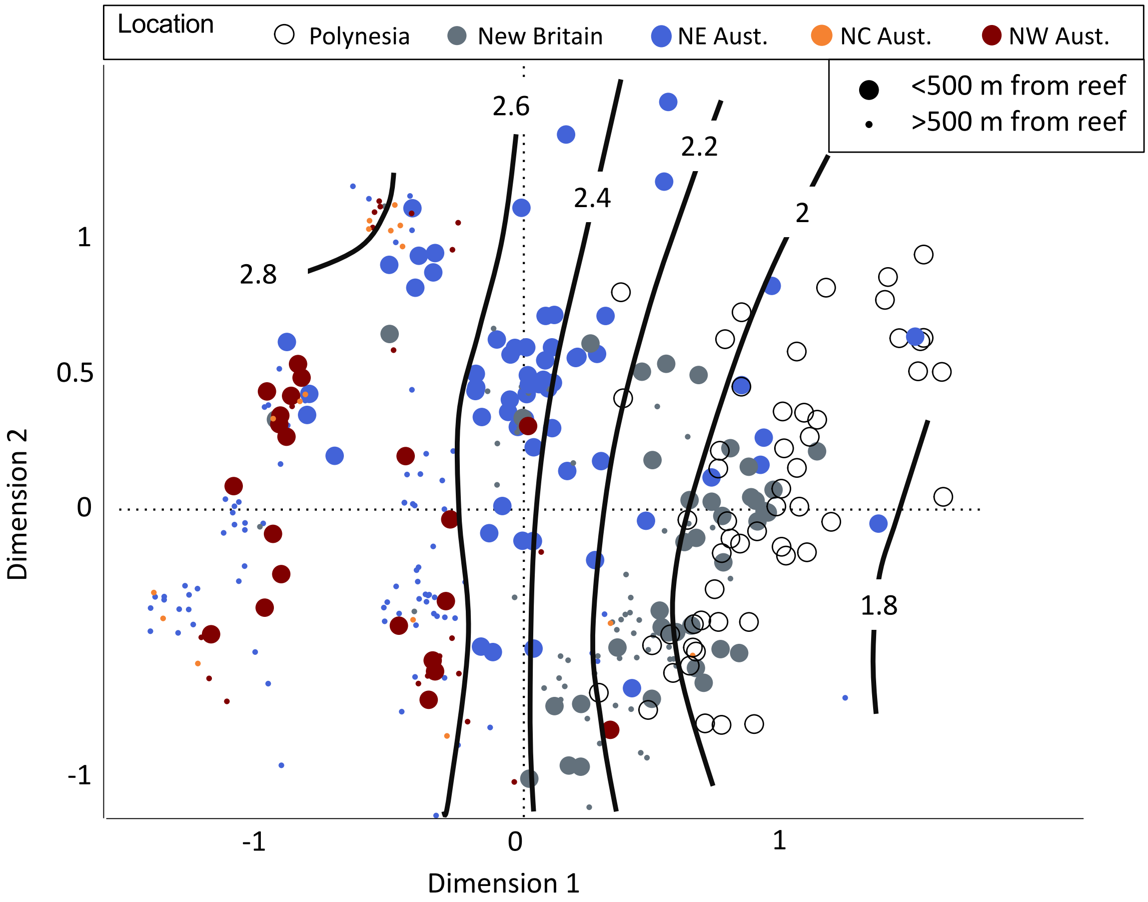

Figure 7. nMDS ordination showing the relationship between family-level taxonomic assemblage and tidal amplitude. The ordination is a revisualisation of the ordination displayed in Figures 2-6, where sites close to reefs (<500 m) are visible and sites far from reefs (>500 m) have been reduced in size. Surface fitting of tidal amplitude as an explanatory variable is displayed as in Figure 4, with reduced contours for visual clarity. Lines describe the topography of the gradient, and units are log-transformed (cm).