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Latitudinal gradients of dispersal and niche processes mediating neutral assembly of marine fish communities

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Abstract

Elucidating the relative importance of niche and neutral processes in structuring ecological communities is a major goal of ecology. We considered multiple components of community structure (beta diversity, species abundance distributions, and niche specialisation) and spatial scales to identify the processes structuring marine fish communities along a tropical to temperate gradient. Beta diversity was explained by local scale environmental and spatial variables, with geographic distance and environmental gradients being stronger drivers of species turnover in tropical and temperate study areas, respectively. Species abundance distributions found a significant component of community structure in all regions to not differ from that expected by chance. Niche specialisation was more prevalent among the endemic, temperate fish species than in tropical fishes. Our results support a strong neutral component of marine fish community assembly, regardless of bioregion. A change in importance from dispersal limitation to niche filtering processes was found from tropical to temperate communities, superimposed over neutrally assembled marine fish communities.

Introduction

Understanding the processes by which communities are assembled and how these processes differ over spatial, environmental, or temporal gradients is one of the fundamental pursuits of community ecology (Hutchinson 1959). The contemporary belief is that niche and neutral processes exist as opposing ends of a continuum that determine community assembly (Chase and Myers 2011; Vellend et al. 2014). Both processes are involved and interact in the assembly of ecological communities, the relative importance of each is the feature often differing among ecosystems. Understanding the balance between these processes has been the motivation of many recent studies (e.g. Chase and Myers 2011; Myers

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et al. 2013; van der Plas et al. 2015; Viana et al. 2016). Niche processes are those such as environmental filtering and inter-specific competition (Stegen et al. 2013), where species without suitable phenotypes or traits are not able to establish or persist in a particular environment (Keddy 1992). Neutral processes are features such as ecological drift (Vellend et al. 2014), or priority effects, where early colonising species influence the success of subsequent colonisers (Fukami 2010).

Inspired by the theory of island biogeography (MacArthur and Wilson 1967), Hubbell's (2001) unified neutral theory of biodiversity and biogeography (UNTB), in which species are deemed ecologically equivalent, is based in the neutral assembly of communities and provides a null hypothesis to test observed patterns against (Hubbell 2006). In the UNTB, differences in species composition among communities are a result of demographic stochasticity, dispersal, and speciation, as opposed to species' ecological competitive abilities, and thus represents dispersal-based (or recruitment limited) structuring of communities (Etienne 2005; Matthews and Whittaker 2014). Hubbell's neutral model is composed of two parameters, θ and m, the former being the 'fundamental biodiversity number' or richness of the species pool, and the latter a measure of dispersal limitation or immigration probability (Hubbell 2001). A further prediction of the UNTB is that species coevolving in species

rich communities structured through dispersal limitation are likely to be functionally equivalent ecological generalists. This can occur as a result of conspecific individuals often being associated with different assemblages of species, and thus no consistent selection for niche differentiation, resulting in generalist species adapted to long term average environmental conditions (Hubbell 2006).

Complementary to Hubbell's (2001) neutral theory, the lottery hypothesis of Sale (1977, 1978) proposed that community assembly of tropical reef fishes was the result of stochastic removal from and colonisation into the community by an individual. As with the UNTB, the lottery hypothesis has similarities to MacArthur and Wilson's (1967) theory of island biogeography. Although the competitive abilities of species may differ, the existence of strong priority effects allows the persistence of an individual in a particular habitat once successfully settled from the larval phase (Ebeling and Hixon 1991). While this hypothesis implies a strong effect of stochastic processes in structuring communities, due to the random nature of vacant habitat becoming available and successful settlement from the larval pool (Hixon 2011; Sale 1978), the effect of dispersal limitation is likely to be enhanced in communities adhering to this assembly rule (Louette and De Meester 2007). Conversely, in temperate marine fish communities, niche filtering (Levin 1993) has been found to structure the communities, through either abiotic (Pérez-Matus and Shima 2010) or biotic effects (Johnson 2006).

Beta (β) diversity, the change in species composition along an environmental or spatial gradient, is the link between local [alpha (α)] and regional [gamma (γ)] diversities (Anderson et al. 2011). β diversity can be partitioned into turnover and nestedness components, the former being changes in species composition, and the latter when species in one sample are a subset of those observed in another (Baselga 2010). When combined with a null model approach, which provides the extent to which observed results deviate from that expected by chance (Chase et al. 2011), and variation partitioning methods (Legendre et al. 2009), β diversity has been advocated as a method to estimate the relative importance of neutral and niche processes in the assembly of communities (Myers et al. 2013; Tucker et al. 2016). A null model approach is necessary to compare patterns of β diversity among regions with varying γ diversity (size of species pools) (Chase and Myers 2011). However, constraining γ and α diversities in null model approaches has the potential to influence the β diversity results obtained from the null model (Ulrich et al. 2017).

Changes in β diversity associated with changes along environmental gradients have been attributed to deterministic processes (often referred to as environmental filtering), caused by differences in the relative fitness of species in different environments (Stegen et al. 2013; Vellend 2010). Changes in β diversity over geographical distances are thought to be the result of limited dispersal or spatially structured environmental variables (Hurtt and Pacala 1995; Myers et al. 2013); the former is Hubbell's (2001) "dispersal-assembly" model. Variability in β diversity, unexplained through variance partitioning, can be attributed to neutral processes such as ecological drift, sampling effects due to different numbers of species with the potential to colonise sites within a region (species pools), and unmeasured environmental variables (Kraft et al. 2011; Myers et al. 2013; Vellend 2010; Vellend et al. 2014). Patterns in β diversity, however, cannot be directly used to infer process and should be used in conjunction with complementary approaches (Myers and LaManna 2016; Tucker et al. 2016).

Scale often has a profound effect on the processes being observed in ecological studies (Levin 1992; Trisos et al. 2014). As the spatial scale of the study increases, so does the time frame of operation of the processes responsible for the patterns observed, with broad-scale patterns resulting from speciation and extinction events, and finer-scale patterns the result of more contemporary processes (Jenkins and Ricklefs 2011). Environmental variables can appear more important than spatial variables at coarse scales, as the heterogeneity of the environment being considered will often increase as the spatial extent considered increases (Gilbert and Lechowicz 2004; Jones et al. 2006). This is observed when changes in communities corresponds more to changes in environmental variables, than geographic distance. The effects of dispersal limitation often become more apparent at finer scales due to a decrease in environmental heterogeneity relative to coarser scales, increasing the apparent importance of spatial variables (Arellano et al. 2016).

In a study of the marine fish communities along a temperate–tropical gradient associated with the Western Australian coastline, Ford et al. (2017) found distinct assemblages among the tropical locations sampled, and the temperate assemblages were defined by environmental variables. The broad-scale patterns were thought to be a result of tropical species colonising suitable environments in a region of high environmental heterogeneity, but the temperate species, many of which are endemic, have co-evolved in a region of relative geological stability and habitat homogeneity (Ford et al. 2017).

Recent studies of community assembly have typically been (i) performed on terrestrial plants and (ii) spatially restricted within a particular 'climatic region'. Therefore, this study extends knowledge by (i) being in the marine realm, (ii) having replicate 'locations' within three bioregions across major climate regions—temperate to tropical, and (iii) by using an hierarchical analysis to identify the spatial scale at which geographical distance and/or environmental processes are relevant to the community assembly of marine fishes. This study was performed to reveal the

scale at which assembly processes operate most strongly, and the relative importance of neutral, niche, and dispersal processes in determining the assembly of communities of marine fishes along a latitudinal gradient encompassing three bioregions. We expected that

(i)   based on the UNTB hypothesis of Hubbell (2001) and the lottery hypothesis of Sale (1977, 1978), neutral processes would be a strong component in the assembly of fish communities, and

(ii) considering the results of Ford et al. (2017), we expected that dispersal limitation would display greater dominance in tropical locations, while niche processes would be of greater importance in temperate locations.

Materials and methods

Sampling

Fish abundances

Fish abundances were estimated through multiple recordings made with baited remote underwater video stereo systems (BRUVS) at 11 nearshore locations along the Western Australian continental shelf. Study locations were allocated to one of three bioregions: "North", "Central", or "South", based on Spalding et al. (2007) and Last et al. (2011) (Fig. 1). BRUVS provide a non-extractive and consistent sampling method for demersal and benthopelagic fishes (Murphy and Jenkins 2010). The study region and data used in this study have previously been described (Ford et al. 2017), but the current study only incorporated samples from hard substrate habitats and fishes which had been identified to the species level. The analyses thus incorporated 746 samples comprising 42,637 individuals of 379 species of fishes from 71 families (Table 1).

Environmental variables

Fine-scale environmental variables were recorded for each sample site when BRUVs were deployed (depth), or derived from footage analysis (topography and benthos). Topography was classified as either "high-profile reef" (HPR), "medium-profile reef" (MPR), or "low-profile reef" (LPR). Benthos was determined as either "canopy-forming algae" (CA), "coral" (CO), "foliose algae" (FO), "seagrass" (SG), or "sessile invertebrates" (SI). Further details on topography and benthos classification are described in Ford et al. (2017).

Eighteen coarse-scale environmental variables were estimated from the BioOracle database (Tyberghein et al. 2012): sea surface temperature range (°C), mean sea surface

temperature (°C), maximum sea surface temperature (°C), minimum sea surface temperature (°C), chlorophyll range (mg m^{-3}), mean chlorophyll (mg m^{-3}), maximum chlorophyll (mg m^{-3}), minimum chlorophyll (mg m^{-3}), mean photosynthetically active radiation (Einstein m^{-2} day^{-1}), maximum photosynthetically active radiation (Einstein m^{-2} day^{-1}), dissolved oxygen (ml L^{-1}), mean diffuse attenuation (m^{-1}), calcite (mol m^{-3}), phosphate (μ mol L^{-1}), silicate (μ mol L^{-1}), salinity (PSS), nitrate (μ mol L^{-1}), and pH.

Wave attributes were incorporated to represent typical magnitude of disturbances. We included: wave energy maximum period (max T_E), wave energy mean period (mean T_E), wave max height (max H_S), and wave mean height (mean H_S) created by CSIRO as part of their 'National Marine Bioregionalisation' project and sourced from http://www.marlin.csiro.au/. As an additional source of disturbance, cyclone frequency was included with data sourced from the International Best Track Archive for Climate Stewardship (IBTrACS) (Knapp et al. 2010). Kernel density estimation was used to convert the IBTrACS cyclone point data into grid format in QGIS 2.14.0 (Quantum GIS Development Team 2016). To place all coarse-scale environmental variables on an even spatial resolution, the layers were interpolated to ≈ 1 km^2 resolution grids and values were extracted from these at the location of each sample.

Statistical analyses

We used several complementary methods to assess the relative importance of assembly processes, and the scale at which these processes acted the strongest. Variance partitioning of beta diversity was performed to assess the importance of environmental and spatial variables at regional and local scales. Species abundance distributions (SADs) and species' ecological niche specialisation were then analysed to validate and complement the results of the variance partitioning.

Beta diversity

Following Myers et al. (2013), observed beta diversity (β_{obs}) was calculated as the Bray–Curtis pairwise dissimilarity among samples, as dissimilarity-based metrics of β diversity are robust to changes in γ diversity and sampling intensity among regions (Anderson et al. 2011; Legendre and Cáceres 2013). Greater Bray–Curtis dissimilarity represents a greater difference in assemblage composition between samples. β_{obs} was calculated between all sample pairs, Null models were created using 1000 randomisations of the data with the 'permatfull' method in the vegan package (Oksanen et al. 2017) in R V 3.2.0 (R Core Team 2017). To maintain ecological realism of the null model, species relative abundances and sample richness were fixed

Fig. 1 Sample locations along Western Australian coastline. Regions defined according to Last et al. (2011)
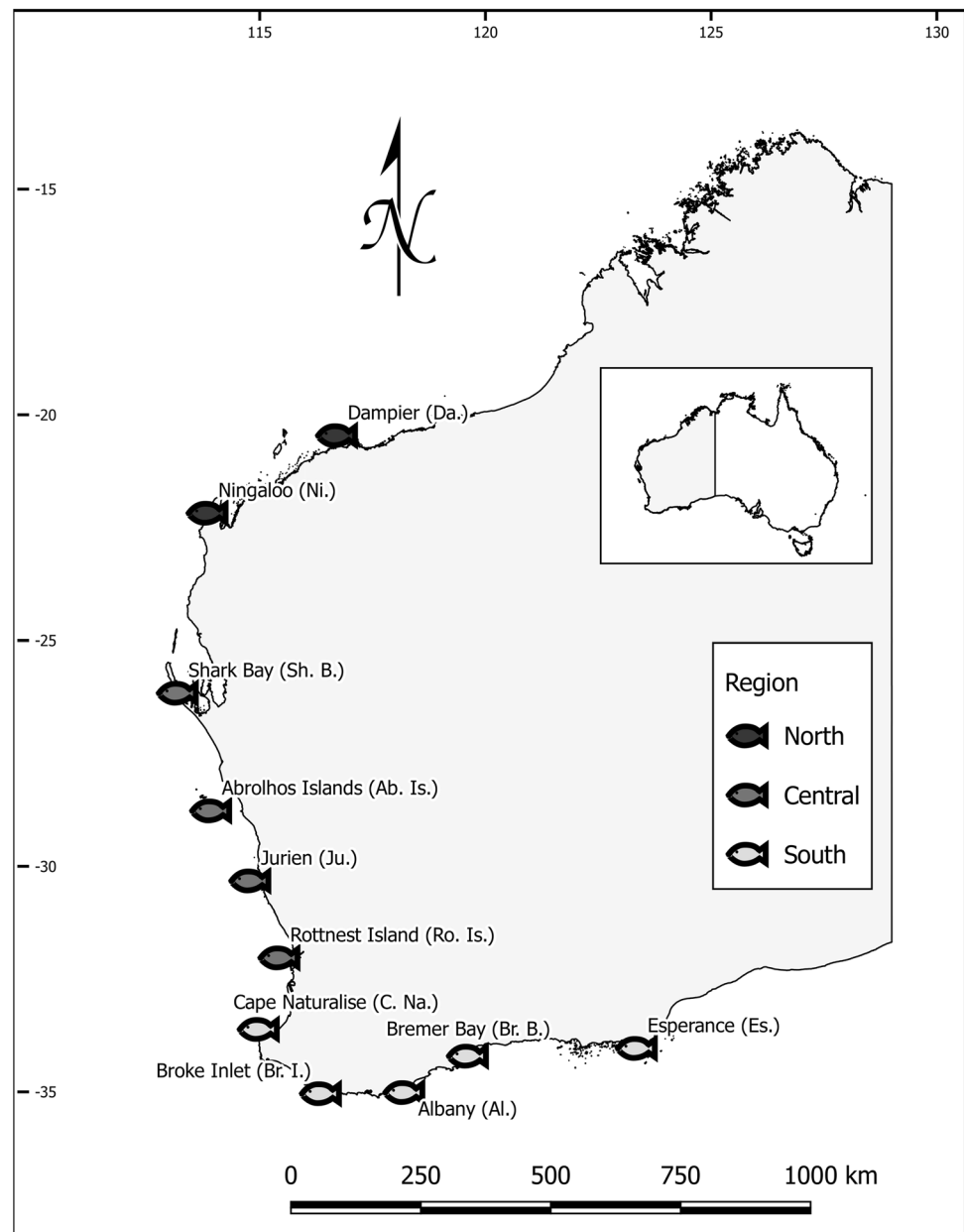
(both margins of the sample x species matrix were fixed), and randomisations were restricted to within study regions. Bray–Curtis dissimilarity matrices were calculated for each of the null models, the mean of the 1000 randomisations of each sample representing the expected beta diversity (β_{exp}) of random communities. Beta diversity deviations (β_{dev}), the standardised deviation of observed beta diversity (β_{obs}) from that expected by chance (β_{exp}), was calculated as

$$\beta_{dev} = \frac{(\beta_{obs}) - \mathrm{mean}(\beta_{exp})}{\mathrm{SD}(\beta_{exp})},$$

with positive β_{dev} indicating greater beta diversity than expected by chance and negative β_{dev} representing lower beta diversity than expected by chance. Comparisons of multivariate homogeneity of group dispersions were used to test for differences in β_{obs} and β_{dev} at coarse (among regions) and fine (among locations) scales. This test is analogous to Levene's test for homogeneity of variances, and compares the average distance of samples to their group centroid among groups and can be applied to any distance/dissimilarity matrix (Anderson et al. 2006). For this test, we used the 'betadisper' function from the vegan package, with distances being calculated to the group centroid, and permutation tests using 9999 permutations to test for global and pairwise differences of dispersion of samples in multivariate space. Homogeneity of dispersion tests were performed first comparing regions, followed by location level comparisons.

Table 1 Numbers of BRUVS samples and species from each region and location

Region	Location	Abbreviation	# samples	Total species richness	Average species richness ($\pm$ SE)
North			216	241	18.319 (8.827)
	Dampier	Da.	133	138	17.180 (6.512)
	Ningaloo	Ni.	83	175	20.145 (11.425)
Central			261	230	12.947 (5.995)
	Shark Bay	Sh. B.	66	144	15.545 (8.319)
	Abrolhos Islands	Ab. Is.	23	73	11.391(3.551)
	Jurien	Ju.	80	77	10.012 (3.967)
	Rottnest Island	Ro. Is.	92	92	14.022 (4.721)
South			269	102	11.941 (5.330)
	Cape Naturaliste	C. Na.	84	75	13.536 (4.416)
	Broke Inlet	Br. I.	84	71	9.964 (3.845)
	Albany	Al.	41	78	16.049 (5.585)
	Bremer Bay	Br. B.	20	57	12.100 (4.166)
	Esperance	Es.	40	56	8.450 (6.135)
Full			746	379	14.139 (7.249)

Variation in β_{dev} was partitioned among space, environmental variables, and the combination of space and environment (i.e. spatially structured environmental variables) using partial distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999). To incorporate the hierarchical nature of the data, the hierarchical partitioning of variance approach suggested by Cushman and McGarigal (2002) was adopted. The 'capscale' function in vegan was used to perform partial dbRDA with a Cailliez correction to account for negative eigenvalues (Borcard et al. 2011).

To incorporate the effect of spatial variables on β_{dev}, Moran's eigenvector maps (MEMs—previously called PCNM) (Dray et al. 2006) were created from the geographic co-ordinates of samples. MEMs were produced using the 'PCNM' algorithm in the PCNM package (Legendre et al. 2013), at both the coarse (region) and fine (locations) scales. Prior to analyses, a principal component analysis (PCA) was performed on the coarse-scale environmental variables to account for collinearity, while categorical fine-scale variables were converted to dummy binary variables.

Forward selection of explanatory variables was performed as proposed by Blanchet et al. (2008), using the 'ordiR2step' function of the vegan package. Initially, for each region, dbRDA was performed upon the full set of forward selected explanatory variables. Once significance of the global model was determined through the 'anova.cca' function in the vegan package, subsequent first-tier partial dbRDA analyses were performed on the data with fine-scale variables being partialled out to identify the variance explained by coarse-scale variables. Further partial dbRDA analysis was then performed with the coarse-scale variables being partialled out to ascertain the variance explained by fine-scale variables. For both analyses, the fine-scale variables were nested within locations. The proportion of the variance explained by the global model not explained by the sum of variance explained by coarse- and fine-scale variables was attributed to fine-scale variables being structured at the coarse scale (Borcard et al. 2011).

Second-tier partial dbRDA were then performed to partition the variance into that explained by coarse and fine-scale spatial and environmental variables. The second-tier partial dbRDA were performed again by partialling out the variation due to subsets of the explanatory variables. For example, to identify the variation explained by fine-scale environmental variables, the variability explained by fine-scale spatial, coarse-scale spatial, and coarse-scale environmental variables was partialled out (Cushman and McGarigal 2002). Again, fine-scale spatial and environmental variables were nested within locations and significance was tested using the 'anova.cca' function.

To ensure that the β_{dev} created through the null model with restrained γ and α diversities was not an artefact of these diversities, we compared the β_{dev} variation partition results to those of the turnover component of β diversity (β_{turn}). β_{turn} was calculated using the 'bray.part' function in the betapart package (Baselga et al. 2013) in R. This procedure calculates the Bray–Curtis dissimilarity among samples and then identifies the proportion of dissimilarity created by species replacement (or turnover), with the remaining dissimilarity being attributed to nestedness (Baselga 2010). Homogeneity of multivariate dispersion tests and variation partitioning of β_{turn} were performed as for β_{dev}.

Species abundance distributions

Species abundance distributions (SADs) were investigated to complement the variance partitioning analyses. Jabot and Chave (2011) proposed a non-neutral method which uses the unified neutral theory of Hubbell (2001) as a framework to test for non-neutrality in SADs. This method uses maximum-likelihood estimation of θ and m for each SAD, and then creates neutral SADs with values of species richness, θ, and m matching that of the observed SAD. Shannon's evenness is then calculated for the observed SAD and that of the created neutral SADs, and the evenness of the observed SAD is compared to the distribution of evenness values of the neutral SADs. Deviation from neutrality is reported as δ, with values close to zero being neutral SADs. Positive values of δ indicate positive density dependence (abundant species have lower mortality rates), and negative values indicate negative density dependence (rare species have lower mortality rates) (Jabot and Chave 2011). We used 100,000 simulations for the approximate Bayesian computation in the Parthy software (Jabot and Chave 2011), with uniform prior distributions of $\ln(\theta)$, $\ln(I)$, and δ being [0,25], [0,10], and [−1,1], respectively, where I represents the estimated number of immigrants (Etienne 2005). Prior distributions were selected based on Jabot and Chave (2011), although with broader values of $\ln(\theta)$. The natural log of priors was used, as opposed to $\log_{10}$, as this is the scale of θ and I at which richness and evenness respond (Jabot and Chave 2011). Densities of the distributions of δ were compared among regions using the 'sm.density.compare' function from the sm package (Bowman and Azzalini 2014), with holm adjustment for multiple comparisons. Jabot and Chave (2011) reported δ to not be influenced by number of species in communities of high richness; however, our samples contained fewer species than those of Jabot and Chave (2011). Within each region (log10) sample richness was regressed against values of δ to identify any influence of richness on values of δ.

With the approach of Jabot and Chave (2011), it is possible to estimate SAD departure from that expected under neutrality (δ), but θ and m cannot be estimated with this method (Jabot and Chave 2011). We used the method described by Munoz et al. (2007) to estimate θ and I, where θ is first calculated for a metacommunity (region in our case) through maximum-likelihood estimation, and then I is then calculated for each sample using the sampling formula of Etienne (2007). m can then be calculated as $m = \frac{I}{I+J-1}$. I and m were calculated using the untb package (Hankin 2007).

Niche specialisation

Species were placed on a continuum of niche specialisation to generalisation using the method proposed by (Fridley et al. 2007), termed θ (to avoid confusion with the SAD θ, we will refer to the generalist–specialist θ as θ_{gs}). Species niche specialisation is scored as the average value of beta diversity values of sites a species is observed in. Generalist species possess higher values of θ_{gs} as they are consistently associated or observed with different species. Specialist species score low values of θ_{gs} as they are found in communities which do not differ greatly among samples (Fridley et al. 2007). We used the multiple-site Simpson index as a measure of beta diversity. This measure is robust to changes in γ diversity (Zeleny 2008), species being found only in samples with low richness (skewed richness distributions) (Manthey and Fridley 2009), and changes in sample richness (Baselga et al. 2007). As the degree of a species' ecological specialisation can change across environments (Fajmonová et al. 2013), analyses were performed on each region separately, using only species observed in at least ten samples. For each species, eight samples were randomly selected from the samples in which the species was observed, and the Simpson index calculated from these. This procedure was repeated 100 times to provide a measure of θ_{gs} unbiased by number of samples. Analyses were performed using the R code provided in Appendix 1 of Manthey and Fridley (2009). Differences in species' m and θ_{gs} values were compared among regions with Kruskal–Wallis tests with subsequent pairwise tests performed using Dunn tests with Holm correction using the FSA package (Ogle 2017).

Results

Beta diversity

β_{obs} differed among regions (Fig. 2a; homogeneity of multivariate dispersion test on average distance to medians, $F = 43.514$, $p < 0.001$) and locations (Fig. 2a; $F = 21.207$, $p < 0.001$). Pair wise comparisons revealed the North region to typically possess significantly higher β_{obs} than the Central or South regions (Fig. 2a). This pattern is also reflected at the location level, with the greatest β_{obs} typically observed in the northern locations and the lowest β_{obs} typically in central locations (Fig. 2a). Differences in β_{dev} among locations were not great, although significant ($F = 9.152$, $p < 0.001$), and significant differences were found among regions (Fig. 2b; $F = 19.383$, $p < 0.001$). β_{dev} values were mostly positive at all locations, indicating some degree of non-random structure in the communities. Large, positive β_{dev} outlier values at Dampier and Ningaloo are due to
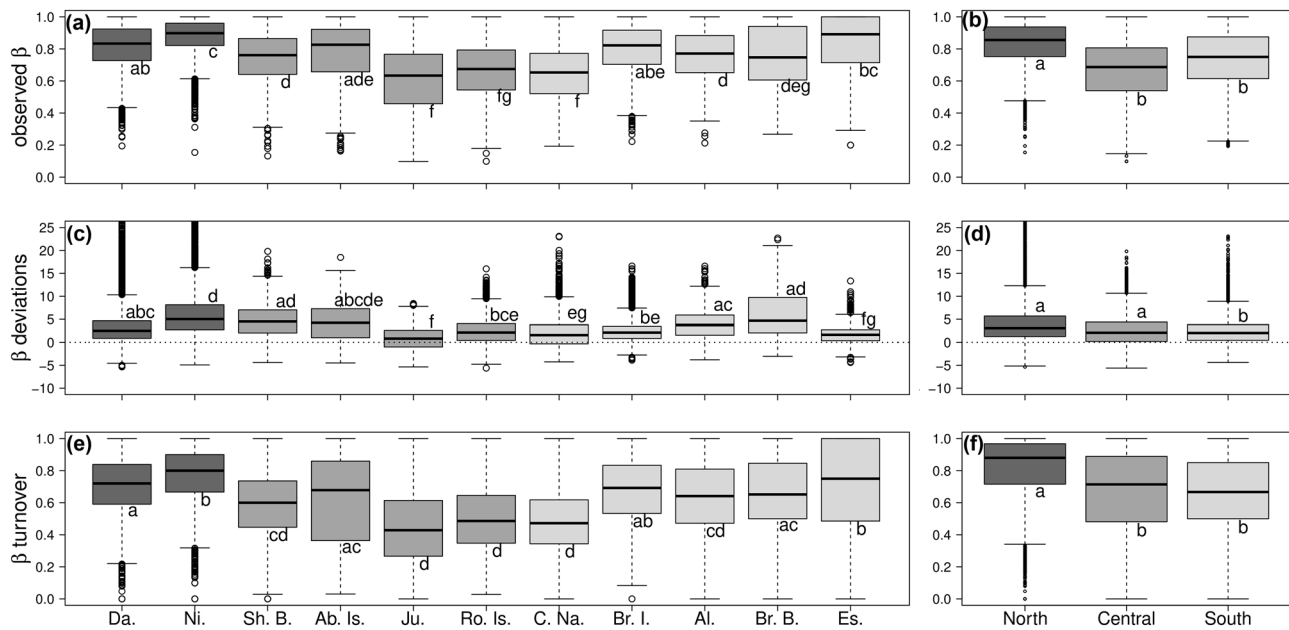
Fig. 2 Sample pairwise dissimilarities of (**a**, **b**) Observed β diversity, (**c**, **d**) β deviations, and (**e**, **f**) β turnover. Plots to the left (**a**, **c**, **e**) are values within locations, plots to the right (**b**, **d**, **f**) are values within regions. Lowercase letters represent significance of comparisons among locations, with identical letters indicating no difference.

Boxes represent first to third quartiles, and solid line in box represents median. Abbreviations are explained in Table 1 and Fig. 1. The y axis has been reduced on plot (**b**) for ease of interpretation, β deviation outliers at Dampier and Ningaloo extend to 73.88 and 43.42, respectively

large, anomalous abundances of a species in a single sample, i.e. > 1200 individuals of the doubleline fusilier (*Pterocaesio digramma*) were recorded in one sample from Dampier. β_{turn} demonstrated similar patterns to that of β_{obs} and to a lesser extent β_{dev}, indicating that species turnover is the dominant feature creating differences among samples (Fig. S1). β_{turn} differed between regions (Fig. 2c, $F = 36.988$, $p < 0.001$), and locations ($F = 14.093$, $p < 0.001$). A common pattern observed with β_{obs}, β_{dev}, and β_{turn}, with respect to among location patterns is that of greater β diversity in the North region locations, followed by a slight decrease at Shark Bay and Abrolhos Islands, a further decrease at Jurien, Rottnest Island, and Cape Naturaliste, then an increase in β diversity for the remaining South region locations (Broke Inlet, Albany, Bremer Bay, and Esperance) (Fig. 2). In addition, at the regional scale, the North region displays significantly greater β_{obs}, β_{dev}, and β_{turn}, than the Central and South regions, with the Central region having significantly greater β_{dev} than the South region. This implies greater β diversity among the northern locations, than among the southern locations, regardless of the within location β diversity (Fig. 2).

Variance partitioning

Coarse-scale environmental attributes were characterised by PCA axes with the first two axes explaining 59.27 and 13.56% of variability, respectively, in the North region,

with 99.04% explained by the first ten axes. The first two Central region PCA axes explained 56.75 and 19.04%, variability in coarse-scale environmental features, with 99.8% variability explained by the first ten axes. For the South region, the first two PCA axes explained 35.96 and 28.80% variability in coarse-scale environmental variables, respectively, with the first ten axes explaining 99.70% of variability in the coarse-scale environmental attributes (Fig. S2). The β_{dev} variability explained by the spatial and environmental variables was 16, 21, and 22% for the North, Central, and South regions, respectively (Fig. 3). The large unexplained variability represents stochastic processes (i.e. ecological drift) and/or unmeasured environmental variables. At all regions, fine-scale variables explained more variability in β_{dev} than coarse-scale variables. At the fine-scale in the North region, spatial variables were more significant and explained more variability in β_{dev} than environmental variables, while at the coarse-scale spatial variables explained less variability than the (non-significant) environmental variables (Fig. 3). The Central region displayed the greatest overlap between fine and coarse-scale variables and between spatial and environmental variables, this is likely due to the Central region being in a temperate-tropical overlap zone, creating stronger spatial structuring of environmental variables. At the fine-scale in the Central region, the β_{dev} variability explained by spatial variables was greater than that explained by environmental
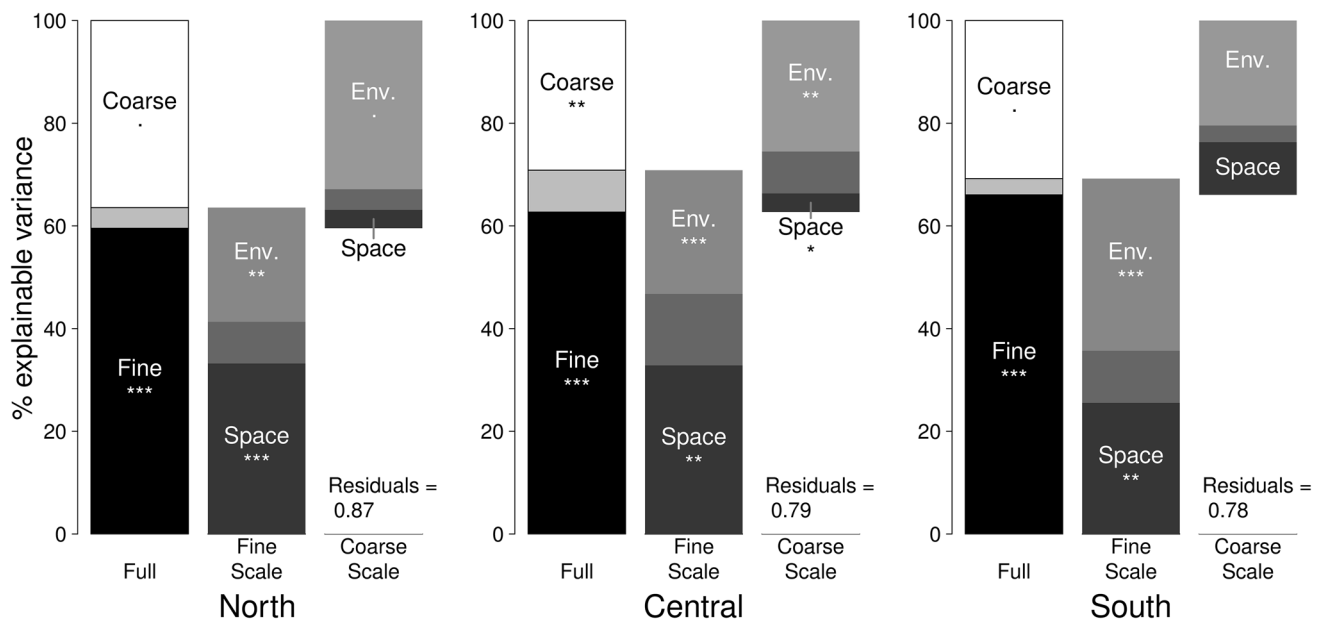
Fig. 3 Hierarchical partitioning of explainable variance of β diversity deviations attributed to space and environment at the coarse and fine scales for each region. Non-labelled components represent variation explained by a combination of either fine and coarse or spatial and environmental variables. $^{\cdot}p<0.1$, $*p<0.05$, $**p<0.01$, $***p<0.001$

variables, although the environmental variables displayed greater significance. At the coarse-scale, environmental variables explained more variability than spatial variables (Fig. 3). In the South region at the fine-scale, environmental variables explained more β_{dev} variability than spatial variables, and displayed greater significance. At the coarse scale in the South region, greater variability was explained by environmental variables, although neither environmental nor spatial variables were found to be significant (Fig. 3). Hierarchical variation partitioning of β_{turn} provided similar results to that of β_{dev} (Fig. S1).

Species abundance distributions and ecological specialisation

Species richness had no effect on values of δ in any of the regions (Fig. S3). The density distributions of species abundance distributions (SADs) δ values differed among regions ($P<0.001$), with all pairwise comparisons being significant (North–Central, $P<0.001$; North–South, $P=0.004$; Central–South, $P=0.011$, Fig. 4a). In all regions, more than half of the samples did not differ from the neutral expectation (North$=53.5\%$, Central$=52.8\%$, South$=60.2\%$) (Table S1).
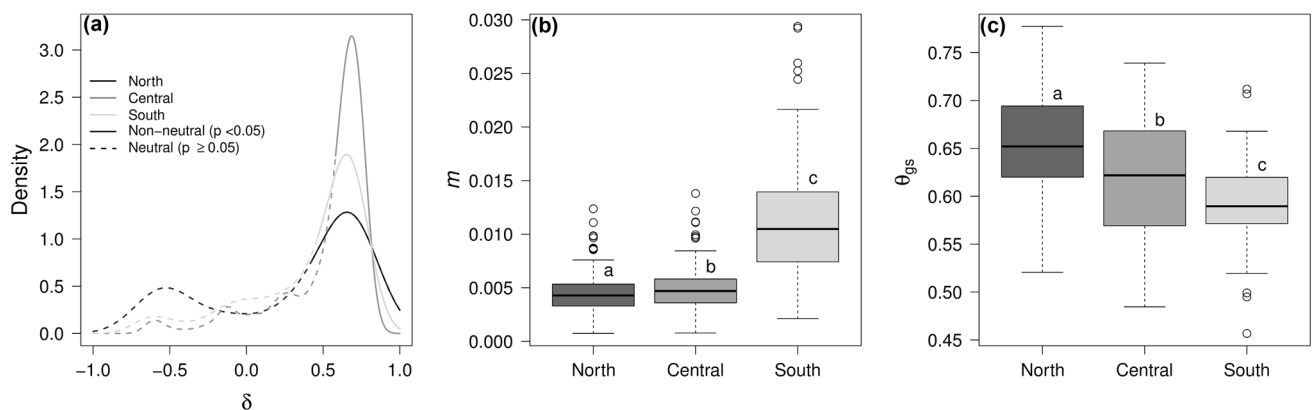
Fig. 4 **a** Density distributions of species abundance distributions (SADs) within each region. Solid portion of lines represent non-neutral SADs, and dashed portion of lines represent neutral SADs. **b** Values of m, with lower values of m indicating lower migration rates and thus stronger dispersal limitation, and **c** extent of species specialisation within each region; higher values of θ_{gs} indicate greater ecological generalisation

Values of m differed among regions (Kruskal–Wallis $\chi^2 = 334.27$, $df = 2$, p value < 0.001), being smallest in the North and greatest in the South regions (Fig. 4b), implying lower migration rates and thus stronger dispersal limitation in the North region. The values of θ_{gs} also differed among regions (Kruskal–Wallis $\chi^2 = 58.172$, $df = 2$, p value < 0.001), with species' specialisation lowest in the North and greatest in the South region, with specialisation of Central species being intermediate (Fig. 4c).

Discussion

The results of several analytical methods—hierarchical variance partitioning of β diversity, species abundance distributions (SADs) deviation from neutrality, estimation of degree of immigration from the regional species pool, and extent of species ecological specialisation—displayed congruence in the processes structuring Western Australian marine fish communities. As predicted, we detected (i) a large influence of neutral processes regardless of bioregion and (ii) changes in the relative importance of dispersal limitation and niche filtering along a latitudinal gradient mediating the neutral assembly of marine fish communities. Additional results included (iii) scale dependent importance of variables in structuring marine fish communities, and (iv) species' ecological specialisation increased from fish associated with tropical regions to fish found in temperate regions. Therefore, the results of this study indicate a combination of niche and neutral processes operating in the assembly of Western Australian marine fish communities.

The processes involved in the assembly of Western Australian marine fish communities appears to operate most at the local scale, where species interactions with their biotic and abiotic environments occur. Neutral processes are a prominent process in the assembly of the marine fish of all communities studied. The relatively small β deviation values in this study indicate that changes in community composition do not differ greatly from that expected by chance. This is further supported by most SADs not deviating from that expected by a neutral model, and the large degree of unexplainable variability in the variation partitioning analyses. Unexplained variability may be due to unmeasured variables, but in concert with small β deviation values, and the SADs neutrality, the prevalence of ecological drift in structuring the fish communities is strongly suggested (Vellend 2010; Vellend et al. 2014). The nature of larval dispersal and settlement in the marine realm supports the existence of strong stochastic forces in the assembly of many marine fish communities (Cowen and Sponaugle 2009; Siegel et al. 2008). This effect is likely to be compounded by the existence of priority effects (Geange et al. 2017) and the random creation of available habitat through disturbances such as storms

(Sousa 1984) or predation (Stier et al. 2014). While some of the unexplained variability in the variation partitioning analyses is likely to be due to unmeasured variables (i.e. large-scale ocean current movement or habitat features at a finer resolution than used here), the coarse-scale environment would be well represented by the variables included in the variation partitioning, with any additional environmental variables likely to be correlated with those incorporated. Furthermore, while the resolution of the fine-scale environmental variables may be too coarse to detect features such as species-specific associations between fish and benthos, temperate algal assemblages have been shown to differ along substrate topography and depth gradients (Kendrick et al. 2004), and coral communities often demonstrate turnover along depth gradients (Harborne et al. 2006). Both substrate topography and depth were included as environmental variables, therefore, while not directly measured, these species-specific associations were not completely unaccounted for.

Fine-scale variables explained greater variation in β diversity than coarse-scale variables in all regions, implying that the non-stochastic component of west Australian marine fish community assembly is strongly due to niche processes (species interactions with their abiotic and biotic environments) and dispersal limitation at a local scale. The importance of spatial variables in the variance partitioning decreased from the tropical region to the temperate region, with the importance of environmental variables demonstrating an opposing pattern. Similarly, species immigration from the regional species pool (m) increased from the tropics to the temperate zone. This implies a decrease in the importance of dispersal/recruitment limitation and an increase in the effect of niche processes in the assembly of fish communities along the latitudinal gradient (Myers et al. 2013). DiBattista et al. (2017) recently reported isolation by distance (IBD) among populations of stripey snapper (*Lutjanus carponotatus*) throughout Northwestern Australia, implying restricted dispersal of larvae within the region. Chust et al. (2016) compared the distance decay between community level (β diversity) and genetic levels (F_{ST} and IBD) of diversity of marine macroinvertebrate and planktonic species, finding patterns observed at the genetic level were reflected at the community level. This finding, in conjunction with the results of DiBattista et al. (2017), supports the existence of dispersal/recruitment limitation in structuring tropical Western Australian marine fishes.

Dispersal/recruitment limitation was estimated by the importance of spatial variables in the variation partitioning analysis and the calculation of m. Both measures identified dispersal limitation to be strongest in the North region and weakest in the South. Dispersal limitation appears to have greater influence in the assembly of fish communities in the tropical region, while species interactions with their environment and other fish species to be responsible for the

assembly of fish communities in the temperate region. Studies have found the extent of dispersal of tropical marine species to often be less than that of their temperate counterparts (Bradbury et al. 2008; Brown 2014), although the variables often attributed to this feature are confounded with latitude (i.e. temperature and habitat fragmentation) (Leis et al. 2013). Regardless of the driving variable, decreased larval dispersal or successful recruitment by tropical species is consistent with the increased importance of spatial variables and lower values of m in the tropical region in this study. The increased importance of environmental variables in the temperate region implies stronger deterministic processes in the assembly of temperate marine fish assemblages. The analyses used in this study do not allow for the elucidation of the nature of deterministic processes involved as this result may also be due to abiotic (environmental filtering) or biotic (competition/facilitation) processes (HilleRisLambers et al. 2012; Kraft et al. 2015). Greater ecological specialisation of the temperate fishes is also congruent with stronger niche processes acting in the South region. Relative to the tropical species, the temperate species are typically observed with the same suite of species, implying the importance of habitat filtering and/or species interactions in the assembly of these fish communities. Conversely, the greater ecological generalisation of the tropical species supports the neutral theory of Hubbell (2001). In this scenario, conspecifics in species rich communities are observed with suites of different species. Over evolutionary timescales there is no consistent selective force acting upon a species, resulting in generalist species adapted to the average environmental conditions of the regions in which they are found (Hubbell 2006).

A feature of note arises from Fig. 2. The classification of locations into (bio) regions in this study is based on the bioregionalisation of Last et al. (2011), and the allocation of the Cape Naturaliste location within the South region may be due to taxonomic similarities more so than aspects of ecosystem functioning. The values of β_{obs}, β_{dev}, and β_{turn} for this location (Fig. 2) are more consistent with of the Central region than the South region, suggesting processes operating within this location are more similar to that of the Central than the South region. This is also in contrast to the pattern observed by Ford et al. (2017), where the Cape Naturaliste location was included with the South locations based on species abundances. A related aspect of this feature is the similarity of these locations with respect to β diversity patterns and the orientation of the coastline where they are located. Reduced values of β_{obs}, β_{turn}, and, to a lesser extent, β_{dev} are found within locations associated with the west facing coastline. Further investigations will be required to elucidate the drivers of this pattern.

To our knowledge, this study is the first to apply the suite of analytical methods used here to identify the processes assembling marine fish communities over a latitudinal gradient. This study found support for the UNTB and lottery hypotheses of Hubbell (2001) and Sale (1977, 1978) in structuring temperate and tropical west Australian marine fish communities. However, fine-scale variables (local spatial structure and reef topography and/or benthos) are more important in the assembly of communities than coarse-scale variables (i.e. gradients in sea surface temperature and primary productivity), regardless of bioregion, with dispersal limitation and niche processes structuring tropical and temperate communities, respectively. A recent study by Janzen et al. (2017) also found a dominance of neutrality in structuring cichlid communities at Lake Tanganyika, in Zambia, with secondary importance of niche processes.

When β diversity is primarily a result of species turnover, as opposed to nestedness, broader geographical scale conservation measures are more likely to be effective than focussing primarily on locations possessing greater species richness (Si et al. 2015). In addition, when dispersal limitation is a primary force at play in structuring communities, conservation and/or management activities should consider the degree of connectivity among the communities/populations of interest (DiBattista et al. 2017).

To our knowledge, this is the first study which has compared the relative importance of processes involved in the assembly of Western Australian marine fish communities among bioregions. Neutrality was found to be a major component of community structure in both tropical and temperate environments. Dispersal limitation and environmental filtering were important processes in the tropical and temperate communities, respectively, and acted strongest at the local, not regional scale. Not only do these results expand our understanding of the functioning of marine ecosystems, but also provide information which can be used in management of the marine realm for fisheries and marine protected areas.

Compliance with ethical standards

procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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