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# Species richness of resident and transient coral-dwelling fish responds differentially to regional diversity

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## ABSTRACT

**Aim** To determine whether the diversity of resident and transient coral-dwelling fish responds differentially to gradients in regional species richness.

**Location** Three regions in the Indo-Pacific (Red Sea, western Indian Ocean, Great Barrier Reef) which contain increasingly larger regional diversities of reef fish.

**Methods** I surveyed fish residing within branching coral species. Fish species were a priori categorized as resident or transient based on the degree of affiliation between the fish and live coral. To compare among regions that differ in coral diversity I used a modified species–volume relationship (SVR). Each point in the SVR represents the total number of fish species, resident or transient, found within the cumulative volume of a specific coral species. Empirical SVRs were further compared with random-placement null models.

**Results** For transient species, I found that the observed SVRs did not differ consistently from those expected from random samples drawn from the corresponding regional species pools. In addition, for a given volume of coral, more fish species were found in richer regions, indicating strong regional influences on local diversity. In contrast, resident richness was lower than that expected from random samples of the species pool, and richness in rich regions was reduced comparably more than in poor regions. The SVRs of resident species were similar among regions with different regional diversities.

**Main conclusion** These results suggest that, within coral species, transient fish richness is mostly influenced by stochastic allocation of species from the regional pool. Conversely, richness of resident species within a coral species is limited, making it independent of regional diversity. Since higher regional diversity of resident fish was not accompanied by higher richness per coral species or by decreased niche breadth, higher regional diversity of resident fish species must be rooted in higher coral richness. Consequently, ecological interactions between functional groups (coral and fish) can be powerful drivers of regional biodiversity.

## Keywords

Core species, coral reef fish, Indo-Pacific, local diversity, regional diversity, satellite species, scale.

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## INTRODUCTION

Large-scale processes that shape the size of the regional species pool may influence diversity patterns at small spatial scales (Cornell & Lawton, 1992; Pärtel *et al.*, 1996; Caley & Schluter, 1997; Ricklefs, 2004). Places with similar local conditions which are located in regions with a different biogeographical history,

environmental heterogeneity or total area may exhibit dissimilar local diversity (Harrison & Cornell, 2008). For example, higher regional coral diversity corresponds to an increase in local diversities at spatial scales as small as 10 m (Karlson *et al.*, 2004). Local processes, on the other hand, may limit the membership of species from the regional pool in the local community. Under the species-filtering concept, species are filtered out when scale is

decreased from large to successively smaller scales due to biotic and abiotic constraints (Zobel, 1997; Rajaniemi *et al.*, 2006). The interaction between the strength of local filtering and the size of the regional species pool will ultimately determine local diversity.

Although both the size of the regional pool and local filtering strength will be important in shaping diversity, their relative influence may vary among communities. For example, Huston (1999) suggested that species diversity in habitats with extreme productivity and disturbance rates will be strongly shaped by local filtering processes, while habitats of intermediate productivity or disturbance will be more open to regional influences. Accordingly, habitats facing high abiotic stress may be shaped by stronger species filtering compared with more benign habitats (Chase, 2007). However, a study on wetland plant communities suggests that the contribution of the regional species pool to local diversity may be independent of habitat attributes such as local productivity, heterogeneity and abiotic gradients (Freestone & Harrison, 2006).

While the influence of regional diversity on local diversity patterns has been examined in relation to local conditions, it was seldom examined among groups of species within a community. It is increasingly realized that natural assemblages may be composed of two types of species: resident species, which are usually abundant, occur predictably and are biologically associated with the sampled habitat, and transients, which are rare species that appear unpredictably (Storch & Szilving, 2002; Magurran & Henderson, 2003; Ulrich & Ollik, 2004; Ulrich & Zalewski, 2006). For example, Magurran & Henderson (2003) demonstrated that the species-abundance distribution of estuarine fish can be separated into a group of resident species, which are lognormally distributed, and a group of transients, fitting a log-series distribution. Do these two groups show similar patterns of local species filtering across regions that differ in the size of the species pool?

Resident species, by definition, are adapted to their habitat and show high affinity to it. According to niche models of community assembly, these species may show non-random community assembly, in which some species from the regional species pool consistently fail to appear in certain local communities (e.g. Diamond, 1975). This can result from various processes such as competitive exclusion or unavailability of the favoured niche. I predict that when the number of locally coexisting species is limited, the strength of local filtering processes for resident species will increase with regional diversity. Transient species, on the other hand, may be less closely associated with a particular habitat and their presence more likely to be governed by stochastic events (Magurran & Henderson, 2003; Ulrich & Zalewski, 2006). Consequently, the presence of transient species within a community is less likely to be bounded and I predict that filtering strength will not change with regional diversity.

Commonly, the influence of regional diversity on local diversity is assessed by examining plots of local versus regional diversity, usually within a single habitat type at regions that differ in regional diversity (Cornell & Lawton, 1992). The strength of local processes is indirectly inferred from the degree of nonlinearity in these relationships. However, the use of local–regional plots has been severely criticized as it may be affected by various sampling

artefacts (Rosenzweig & Ziv, 1999; Srivastava, 1999; He *et al.*, 2005; Hillebrand, 2005). By examining how the strength of local species filtering changes with the size of the regional species pool it is possible to overcome many of the sampling artefacts that affect local-to-regional regressions (Rajaniemi *et al.*, 2006).

In Indo-Pacific fishes, as with many other coral reef organisms, large-scale diversity peaks around the Indonesia–Philippine Archipelago (Bellwood *et al.*, 2005). This large-scale gradient is driven by regional reef area availability and by geometrical constraints (Bellwood & Hughes, 2001; Bellwood *et al.*, 2005) and is not accompanied by corresponding gradients in local conditions such as coral cover (Bruno & Selig, 2007), offering an excellent model system for examining how local diversity interrelates with regional diversity. The considerable biological information available for reef fish enables a priori categorization of transients and residents rather than statistical, *post hoc* categorization (e.g. Magurran & Henderson, 2003; Ulrich & Zalewski, 2006). Branching corals provide an important habitat for many species of coral reef fishes (Munday *et al.*, 1997, 2001; Munday, 2002; Jones *et al.*, 2004). In this study, I quantify fish richness and filtering strength within species of branching coral across a gradient in regional diversity and then contrast these patterns between resident and transient species. As analyses were conducted for entire coral species, this study is particularly suited to the examination of evolutionary processes that determine patterns of coral-species habitat selection in fish. I found that resident and transient richness responded differentially to a gradient in regional diversity, thus emphasizing that the importance of regional diversity to local, within-habitat species richness might change within a given assemblage according to the affinity of the species to the habitat.

## METHODS

### Surveys

Surveys were conducted in three geographically distinct provinces: (1) the Gulf of Aqaba, which is a distinct subregion within the Red Sea (27°42′–39°31′ N, 34°11′–34°58′ E); (2) islands off the coasts of Tanzania, in the western Indian Ocean (5°07′–8°06′ S, 39°07′–39°50′ E); and (3) islands on the Great Barrier Reef (GBR; 16°15′–18°40′ S, 145°06′–146°30′ E). These locations represent low, intermediate and high regional diversity of reef organisms, respectively (Bellwood *et al.*, 2005). Sixty randomly placed transects were visually surveyed in each region, spanning an extent of 180–320 km. As analyses were performed on all corals within a region combined (see below), transects describe the way fish were surveyed but were not factored into the analyses. While surveys were conducted both on the reef flat and reef slope, the two habitats were combined for analyses. Surveys were conducted from June to September in the Red Sea, in January and February in Tanzania and from December to February in the Great Barrier Reef. Survey time varied with tidal regime, as it was limited to high tides for surveys on the reef flat.

I surveyed the first 25 coral heads in each transect. As coral density may vary among transects within a region, the actual

distance surveyed differed among transects. Only colonies from the genera *Stylophora*, *Pocillopora*, *Seriatopora* and *Acropora* were included. Branching species belonging to these genera tended to form discrete coral heads, in contrast to other branching forms (e.g. *Montipora digitata*) that often form extensive, possibly monoclonal stands. I sampled colonies that, along their widest dimension, were wider than 20 cm (so as to avoid very small colonies containing few fish) and narrower than 100 cm (to avoid large coral stands that cannot be sampled accurately). Sampled corals were separated by at least 50 cm from other corals to minimize the effect of variation in coral density on fish diversity. Coral volumes were calculated from their length, width and height assuming the corals to be ellipsoid. Corals were generally identified to species level. However, since some closely related species are notoriously difficult to differentiate underwater, some species were combined and analysed together as a single ecomorph (e.g. *Acropora gemmifera* and *Acropora humilis*). I recorded all fishes that were found directly within, above or below each coral. Fishes that showed clear affiliation with the coral and swam around it were also recorded.

Spatial patterns of alpha and beta diversity of coral and fish across these regions have been examined in a separate study (Belmaker *et al.*, 2008), where a more detailed description of the sampling locations can be found. While the above-mentioned paper is concerned with the spatial pattern of resident species diversity, here I focus on contrasting the diversity patterns of two components of the fish assemblage. Moreover, the scale of analysis is shifted towards entire coral species which has implications on the analysis and its ecological interpretation (see 'Discussion' below).

### Resident and transient species

Species were categorized as resident species if they were:

1. Obligate coral-dwelling species, which live most or all of their lives in close proximity to a host coral colony. Typical representatives of this group are the coral-dwelling gobies (e.g. the genera *Gobiodon* and *Paragobiodon*) and some damselfish (e.g. the genus *Dascyllus*).

2. Juveniles that are obligate coral dwelling even if later ontogenetic stages lack clear association with a host coral.

All other fishes were categorized as transients, including adult stages of species that are obligate coral dwellers as juveniles. Therefore, species with marked ontogenetic shifts in their use of corals were categorized as resident or transient based on the specific life stage in which they were observed. Analysing species from group (1) separately did not qualitatively change the results. It should be noted that determining whether a species is a resident or transient will always be scale specific. A species that is transient at the scale of a single coral head may be a resident species at the scale of the entire coral reef.

### Species–volume relationships

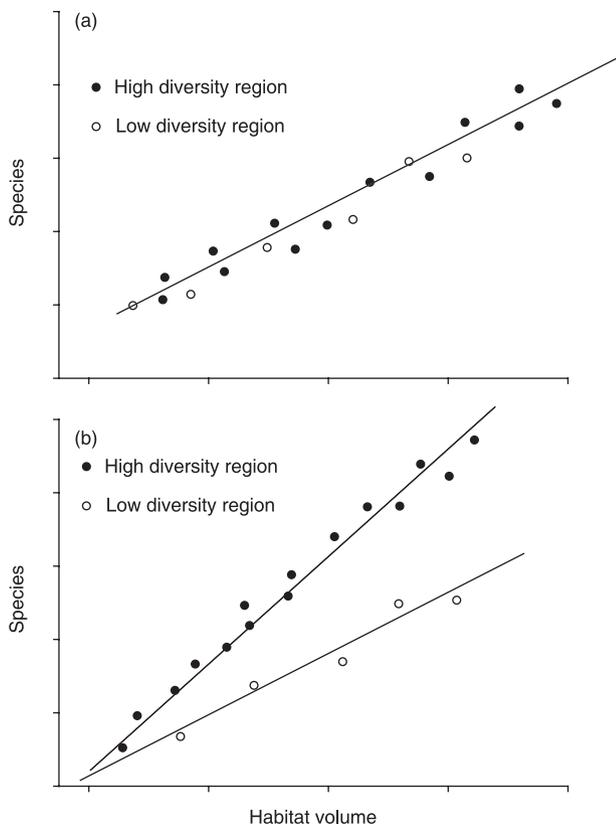
Before comparing richness patterns, it is vital to first control for sampling effort and habitat heterogeneity (Gotelli & Colwell,

2001). Although sampling effort was identical in all regions in terms of the number of coral heads surveyed, coral size might differ, thereby affecting estimates of fish richness. In addition, different coral species can provide slightly different habitats for fish, so that regions of higher coral diversity may contain higher fish diversity. One alternative is to look at the scale of individual coral colonies, while statistically controlling for differences among coral species (e.g. by using restricted randomizations). Another alternative is to focus, as proposed here, on the fish diversity within entire coral species. As richness values are summed over coral species, and not over space, this analysis is not defined at any specific local spatial scale, only by the extent of the area surveyed. As these analyses focus on separate scales, they also examine separate processes. Dispersal limitation and other processes causing spatial autocorrelation may make such a summation across space problematic, as the same coral species from different locations may contain separate fish species. However, no evidence of large-scale spatial autocorrelation in fish assemblage composition was found at these spatial scales (Belmaker *et al.*, 2008).

The relationship between local and regional diversity is typically examined within a single habitat and then compared among regions. Alternatively, it is possible to examine different habitats in the same region. However, the latter is not recommended when habitats are of a fundamentally different nature (Srivastava, 1999). In this study, diversity in a set of very similar habitats (branching coral species) is examined across regions. Since differences among branching coral species, both between and among regions, tend to be subtle and the overall size and form of coral is not known to show regional variation, I believe using this method here is justified.

Comparing directly fish richness per coral species across regions is problematic, as survey effort differed among coral species: common corals were sampled more frequently than rare ones. To control for both the effects of coral sampling effort and coral species diversity on patterns of fish richness I constructed species–volume relationships (SVRs). This is similar to species–area curves that are commonly used to correct for the effect of area on richness so that the effect of other variables can be examined (Connor & McCoy, 1979). Coral volume, as opposed to coral area, was used for the calculation as it is of more relevance to the biology of the organisms studied (see also Black & Prince, 1983). In these SVRs each point is composed of the cumulative volume of a single coral species summed over all individual colonies of that species within the region. Therefore, each point on the SVR represents a different coral species, while the whole plot depicts all coral species in a region. Using this method, regions with more coral species will simply have more points on the graph, but if the number of fish species per coral species is similar among regions, the regression lines should coincide (Fig. 1a). If, on the other hand, regions with higher regional diversity also have higher local richness within a given volume of a coral species the regression line in the more diverse region should lie above that of the less diverse region (Fig. 1b).

To examine whether the SVRs differ among regions I used ordinary least squares (OLS) regressions. The dependent variable



**Figure 1** Schematic representation of two possible scenarios from the species–volume relationship (SVR) analyses, where species richness in each habitat is plotted against the total volume of that specific habitat. Two regions are compared: the filled dots represent habitats within a region with higher regional diversity and habitat richness than the region represented by the empty dots. (a) Although the regions differ in total diversity, both regions share a similar SVR and therefore contain similar species richness per habitat. (b) The region with higher diversity also has higher diversity per given volume of habitat.

was species richness of residents or transients,  $\log_{10}(\text{species richness} + 1)$  transformed, and the independent variables were  $\log_{10}(\text{coral volume})$  and region as a continuous and categorical variable, respectively. As explained above, coral volume was calculated per species by summing up the volumes of all surveyed colonies of that species. Regional influence on local diversity will be indicated by a significant effect of region (either as a main effect or in interaction with coral volume). This is akin to investigating whether fish richness within a coral species differs among regions with different regional diversity (i.e. local-to-regional regressions).

### Random placement null model

Local to regional diversity patterns may be affected by sampling artefacts. For example, local diversity may show similar values across regions simply because of local limits on the number of individuals (Srivastava, 1999). In addition, local and regional

diversities are inherently autocorrelated, making their estimates statistically non-independent. As it is ultimately of interest to gain insight into the strength of local processes, a more direct approach may be warranted. This can be achieved by examining filtering strength across regions, where observed local diversity patterns are compared with those expected from random sampling from the regional pool (Rajaniemi *et al.*, 2006).

To quantify filtering strength it is first necessary to estimate the expected richness under a scenario of no species filtering. A simulation model was constructed to estimate numerically the expected fish species richness on coral species under such random placement. The simulation was performed following the procedure described by Gotelli & Graves (1996) and Belmaker *et al.* (2007). Regional diversity of fish is defined here as the total species richness found in the full collection of samples. Since conspecifics within a coral may be part of a social group and thus not truly independent, only species presences within corals were randomized. In each simulation the observed fish species presences within all coral heads belonging to a coral species were reshuffled among coral species, such that the probability of inhabiting each coral species was proportional to the total volume, across all coral heads, of that coral species. Therefore, if  $V_j$  is the volume of coral species  $j$  and  $n$  is the total number of coral species examined, the probability of the presence of a certain fish at a coral species is given by

$$V_j \left( \sum_{j=1}^n V_j \right)^{-1}.$$

Since the observed number of fish species presences was used as the basis for the randomization, there was no need to assume any specific underlying species abundance distribution. This procedure was repeated 1000 times, and empirical data were then compared with the range of values produced from the simulation. This simulated a scenario of random colonization from an external pool in which fish species arrive completely independent of one another (i.e. no interspecific interactions) into a uniform habitat (i.e. no fish–habitat interactions). The general fit of the simulation model to the data was evaluated by regressing observed diversity values against diversity values predicted by the model. A slope equal to 1 and an intercept equal to 0 indicate an unbiased fit.

To evaluate whether filtering strength varied among regions, I first controlled for the expected richness by using the mean values predicted by the random sampling null model as a covariate in the OLS regressions. The dependent variable was fish richness (resident or transient) within a coral species and the independent variables were the predicted diversity values from the simulation model and region as a continuous and categorical variable, respectively. Different filtering strengths across regions will appear as a significant effect of region (either as a main effect or in interaction with predicted diversity).

### Coral-use across regions

Higher fish richness in more diverse regions can result from several separate processes at the community level: (1) higher

coral (habitat) richness, (2) more fish species per coral species, or (3) fewer coral species used by each fish species. SVRs directly examine the number of fish species per coral species, while controlling for coral richness, but they do not address the niche breadth of the fish in each region. More fish species can coexist in a given region if fish species decrease their niche breadth, i.e. use fewer species of coral. To examine this, I first used the number of coral species used by a fish species as a simple measure of niche breadth (Krebs, 1999). Only fish species with 10 or more occurrences were included to reduce biases resulting from rare species necessarily occupying few coral species. In addition, as the number of coral species used may be affected both by coral availability and by fish abundance, I used the simulation model described in the previous section to compare the observed number of corals used by each fish species with the expected number of coral species that a fish species would use if it had no habitat preference. This was used as a habitat selectivity index. I used the log of the ratio between observed number of coral species used and expected values as the per-species effect size [ $\log(\text{observed/expected})$ ].

## RESULTS

### General patterns

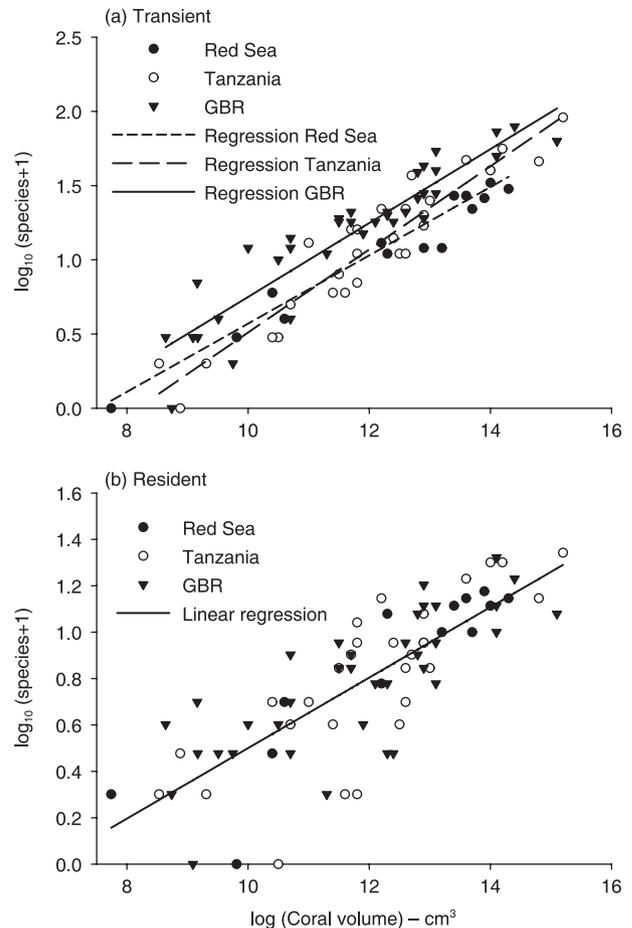
Overall, 4500 coral colonies were surveyed. The total number of fish and coral species differed greatly among the regions. Resident and transient fish richness was highest in the GBR (35 and 155 species for resident and transients, respectively), followed by Tanzania (27 and 129) and then the Red Sea (20 and 63). These patterns were paralleled by coral diversity which decreased from 36 species (ecomorphs) in the GBR, through 28 in Tanzania, to 14 in the Red Sea. Coral colony volume was smaller in the Red Sea than in Tanzania and the GBR [ $P < 0.05$ , Tukey honestly significant difference (HSD) *post hoc* following an ANOVA], which were themselves not significantly different from one other.

### Species–volume relationships

Both resident and transient fish species produced a positive SVR, i.e. fish species richness increased significantly with coral volume (Table 1, Fig. 2). For transient species, region significantly affected the number of fish species within a coral-species volume (Table 1). Contrast tests found that the GBR has higher richness per given volume of coral than both the Red Sea and Tanzania ( $P < 0.001$ ), which are not significantly different from each other ( $P = 0.14$ ). For resident species, no significant effect of region on the number of species per given volume of coral was found (Table 1).

### Random placement models

For transient species, the simulation model was unbiased in explaining observed diversity as the regression slope did not significantly differ from 1 (0.86–1.05, 95% CI) and the intercept did not differ from 0 (–1.81 to 2.76, 95% CI; Fig 3a). Therefore,



**Figure 2** The number of fish species within the cumulative volume of each coral species for (a) transient and (b) resident fish species. Results are plotted separately for each of the three regions. Coral volume ( $\text{cm}^3$ ) was  $\log_{10}$ -transformed and species richness was  $\log_{10}(x+1)$ -transformed. The species–volume relationships significantly differ among regions for transient species but not for residents. GBR, Great Barrier Reef.

the observed number of fish species generally closely follows the central trend of the random placement model (Fig. 4). Nevertheless, more than 5% of the coral species had richness values that lay beyond the 95% CIs of the random placement null model (7, 29 and 25% for the Red Sea, Tanzania and the GBR, respectively). Consequently, the level of variation around the central trend exceeds the level expected by random placement alone.

For resident species, the random placement null model was biased in predicting species richness as the slope was significantly lower than 1 (0.51–0.71, 95% CI; Fig. 3b; while the intercept did not differ from 0 (–0.51 to 1.97, 95% CI). Consequently, the observed number of fish species was below that predicted by the random placement model (Fig. 4). The percentage of coral species that had fish richness values outside the 95% CIs of the random placement null model was higher for resident species than for transients and greatly exceeded the 5% threshold expected by chance (43, 36 and 42% for the Red Sea, Tanzania and the GBR, respectively).

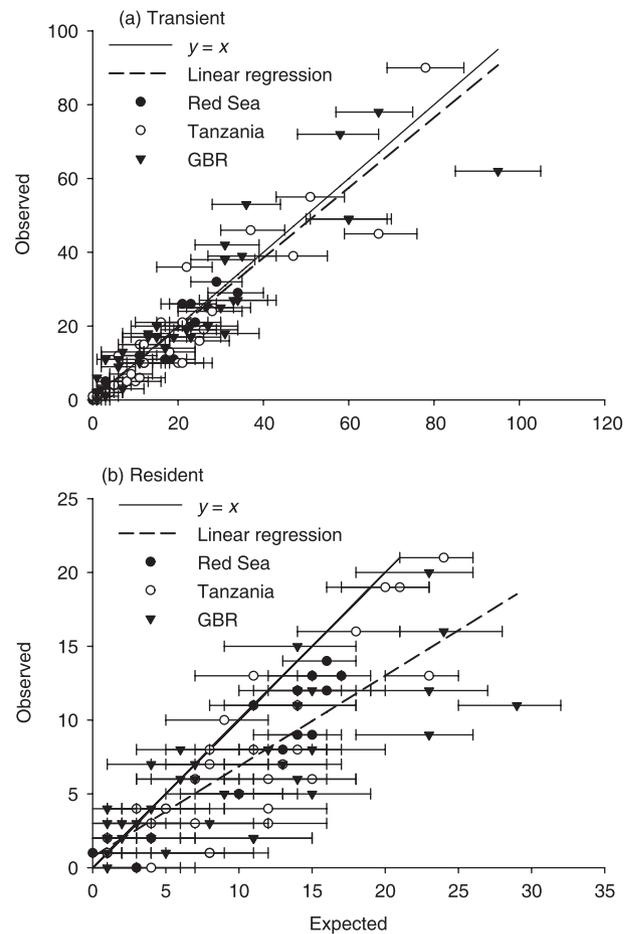
**Table 1** Ordinary least squares (OLS) regressions relating resident or transient fish richness to region and coral volume [species–volume relationship (SVR) analysis] or to region and mean predicted values from the random placement model (random placement analysis). The latter served to quantify filtering strength by accounting for the process of stochastic allocation of species from the pool. For the SVR analysis, species richness was  $\log_{10}(x + 1)$ -transformed and coral volume was  $\log_{10}$ -transformed. Partial regression coefficients of the independent variables are shown below the summary statistics for the full model.

| Species group | Analysis                        |                   | <i>P</i>      |
|---------------|---------------------------------|-------------------|---------------|
| Resident      | SVR                             | $R^2 = 0.65$      | $P < 0.001$   |
|               | <i>Independent variable</i>     |                   |               |
|               | Coral volume (cm <sup>3</sup> ) | $F$ ratio = 123.8 | $P < 0.001$   |
|               | Region                          | $F$ ratio = 0.0   | $P = 0.96$    |
|               | Interaction                     | $F$ ratio = 0.9   | $P = 0.41$    |
| Resident      | Random placement                | $R^2 = 0.70$      | $P < 0.001$   |
|               | <i>Independent variable</i>     |                   |               |
|               | Predicted random placement      | $F$ ratio = 129.2 | $P < 0.001$   |
|               | Region                          | $F$ ratio = 0.7   | $P = 0.50$    |
|               | Interaction                     | $F$ ratio = 4.9   | $P \leq 0.01$ |
| Transients    | SVR                             | $R^2 = 0.89$      | $P < 0.001$   |
|               | <i>Independent variable</i>     |                   |               |
|               | Coral volume (cm <sup>3</sup> ) | $F$ ratio = 507.0 | $P < 0.001$   |
|               | Region                          | $F$ ratio = 17.3  | $P < 0.001$   |
|               | Interaction                     | $F$ ratio = 1.7   | $P = 0.18$    |
| Transients    | Random placement                | $R^2 = 0.86$      | $P < 0.001$   |
|               | <i>Independent variable</i>     |                   |               |
|               | Predicted random placement      | $F$ ratio = 169.7 | $P < 0.001$   |
|               | Region                          | $F$ ratio = 0.4   | $P = 0.68$    |
|               | Interaction                     | $F$ ratio = 1.0   | $P = 0.38$    |

Filtering strength was compared among regions by using the richness values predicted by the random placement model as a covariate in a regression analysis. For transient species, I found no effect of region on species richness and no significant interaction (Table 1). This suggests that the strength of transient species filtering is independent of the size of the regional species pool. In contrast, for resident species I found a significant interaction between region and the simulation model prediction (Table 1). Specifically, the slope in the GBR was lower than the slope for the Red Sea and Tanzania ( $P < 0.01$ ), indicating that filtering strength is higher in the GBR.

### Coral-use across regions

For transient species, the number of coral species used by each fish species differed among regions ( $F_{2,51} = 11.5$ ,  $P < 0.0001$ , Welch ANOVA allowing for unequal SD) and was higher in richer regions (Fig. 5a). However, coral selectivity, which controls for the different availability of coral and abundance, did not differ among the regions ( $F_{2,86} = 1.6$ ,  $P = 0.21$ , ANOVA; Fig. 5b). Moreover, in all regions but Tanzania the 95% CI included 0 indicating, on average, no selectivity in coral use (Red Sea,  $-0.20$  to  $0.02$ ; Tanzania,  $-0.20$  to  $-0.06$ ; GBR,  $-0.11$  to  $0.02$ ).

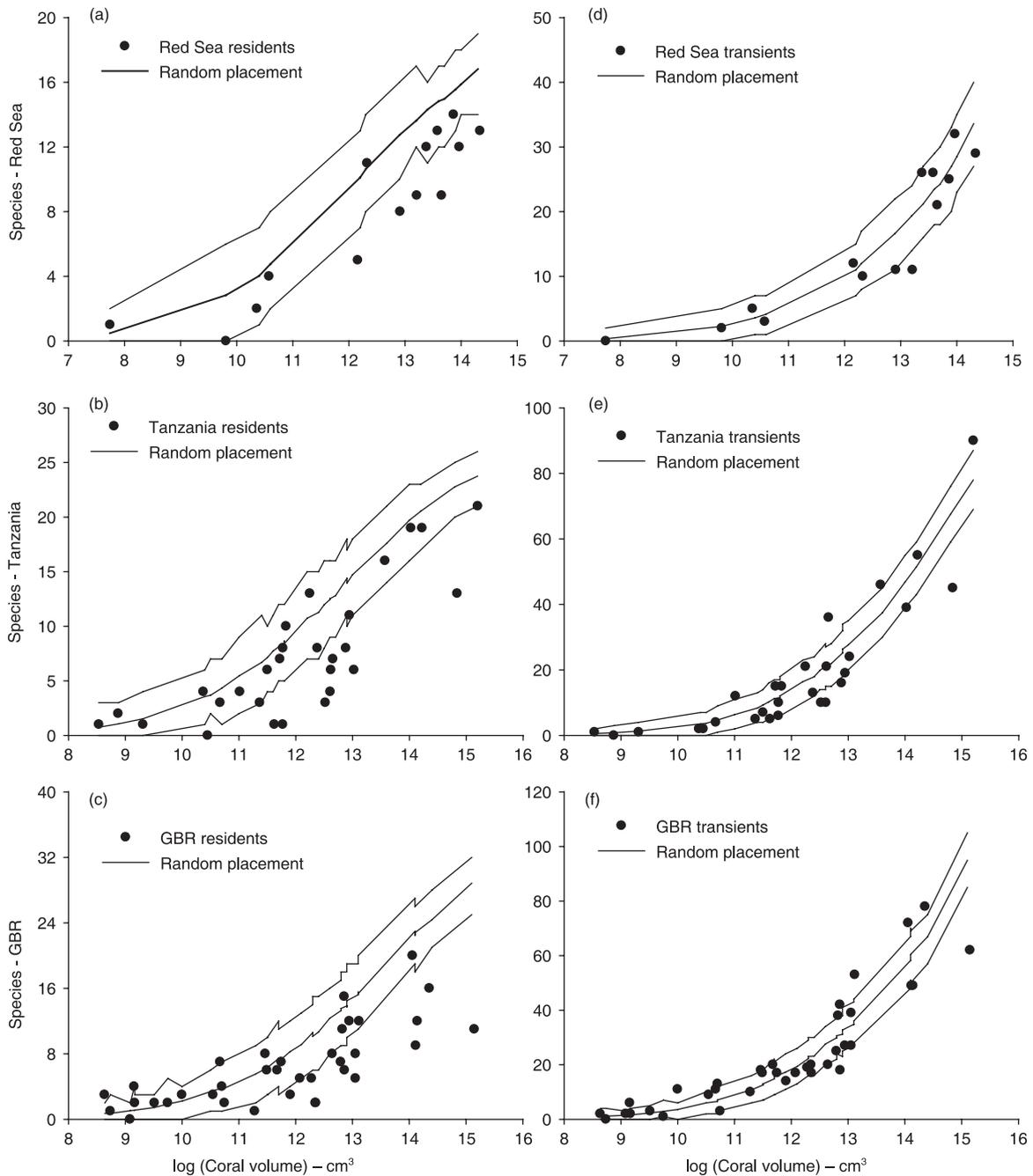


**Figure 3** Observed number of fish species within a coral species versus mean (of 1000 iterations) number of species predicted by the random placement null model for (a) transients and (b) residents. Error bars represent the 2.5th and 97.5th percentiles of the simulation model. The observed number of fish species is generally predicted well by the simulation model for transient species, but richness is overpredicted for resident species. GBR, Great Barrier Reef.

In contrast, for residents the number of coral species used by fish species did not differ among regions ( $F_{2,33} = 2.3$ ,  $P = 0.11$ , Welch ANOVA allowing for unequal SD; Fig. 5a). Coral selectivity did not differ among the regions ( $F_{2,50} = 1.4$ ,  $P = 0.24$ , ANOVA; Fig. 5b); however, in all regions the 95% CI was lower than 0 indicating selectivity in the use of coral species (Red Sea,  $-0.75$  to  $-0.08$ ; Tanzania,  $-0.72$  to  $-0.14$ ; GBR,  $-1.00$  to  $-0.45$ ).

### DISCUSSION

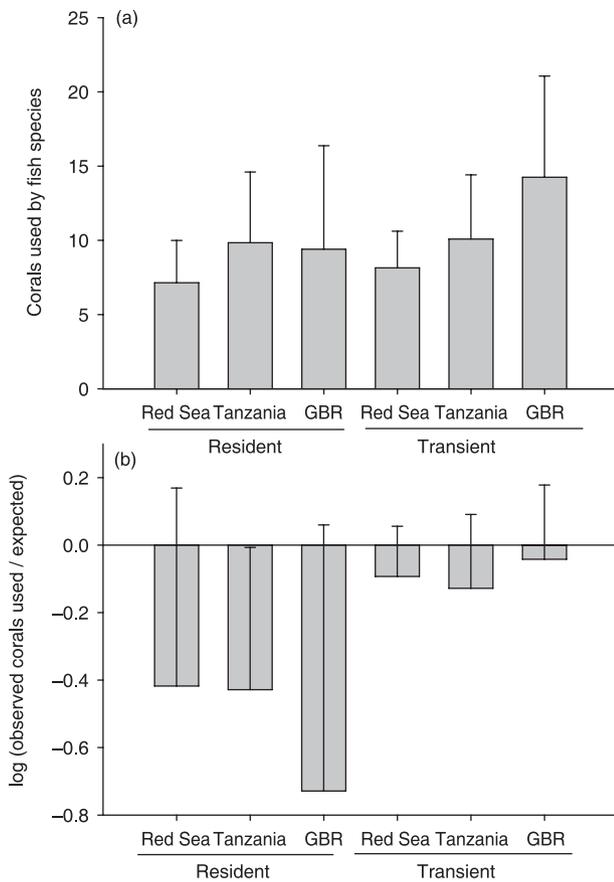
Both resident and transient coral-dwelling fish species exhibited strong gradients in regional diversity. However, the way this regional gradient interrelates with fish richness at the scale of a coral species and with the corresponding gradient in coral richness differed among these groups. Transient richness within coral species differed among regions and was generally consistent with the random placement null model, suggesting low levels of



**Figure 4** The number of fish species within the cumulative volume of each coral species for (a)–(c) resident and (d)–(f) transient fishes. Results are plotted separately for each of the three regions. Lines represent the mean (and the 2.5th/97.5th percentiles) of 1000 iterations of the random placement null model. The observed number of fish species generally lay below the random placement model for residents, but closely follows the random placement model for transients. GBR, Great Barrier Reef.

species filtering and a generally stochastic community assembly. Resident species richness, on the other hand, was similar in different regions. Strong species filtering was present in all regions, but its magnitude was largest in the highly diverse GBR. This is in line with niche-related community assembly processes for resident species limiting local diversity. These results suggest that the balance between the strength of local filtering processes and regional influences in determining local diversity may differ between groups within a given assemblage.

For transients, species richness within coral species closely followed the random placement null models (Figs 3a and 4d–f), and the fit with the model did not differ consistently across regions (Table 1). Consequently, the magnitude of fish species filtering into coral species seems to be minimal and independent of regional diversity. A direct corollary of the good fit with the random placement model is that the actual number of fish species within a coral species is higher in richer regions (Fig. 2a). Therefore, processes which may influence regional species diversity,



**Figure 5** (a) The average (+SD) number of coral species used by fish species with 10 or more occurrences. (b) The log ratio between the observed number of coral species used (as in a) and that predicted by the random placement model (+SD). The results are the mean of 1000 iterations of the null model. Values lower than 0 indicate a preference toward certain coral species. GBR, Great Barrier Reef.

such as climate, habitat area and proximity to domain boundaries (e.g. Bellwood *et al.*, 2005; Storch *et al.*, 2006; Kreft & Jetz, 2007) will directly contribute to transient fish richness within a given volume of a coral species.

As a whole, coral reef fish assemblages are dynamic and not believed to be structured by strong interactions with the habitat (Sale & Douglas, 1984; Sale *et al.*, 1994; Chittaro & Sale, 2003). In agreement with this view, the good match between observed richness and random placement central trends suggests that transient species do not have a strong preference for specific coral species. This is directly supported by the low specificity in coral use found for transient species (Fig. 5b). Nevertheless, the richness values were more 'noisy' than expected from random placement alone. This may reflect some association between transient fish and certain coral species, brought about, for example, by variation among coral species in morphological attributes such as coral branch spacing (Vytopil & Willis, 2001). However, the match between the observed and null central trends suggests that these coral attributes do not affect transient richness consistently across regions or with increased coral volume.

In contrast to transient species, similar richness of resident fish in regions with dissimilar regional diversity (Table 1 and Fig. 2b) suggests an upper limit to the number of resident fish coexisting within a coral species, and is therefore consistent with saturation in local richness (Cornell & Lawton, 1992). These results support a previous study, on one coral species (*Pocillopora damicornis*), that found similar local epifaunal species richness along a gradient of regional diversity (Black & Prince, 1983). By focusing on species filtering and using a null model approach I controlled for sampling artefacts associated with local to regional regressions, most importantly pseudosaturation due to physical limits on the number of individuals that may occupy a coral species (Caley & Schluter, 1997; Srivastava, 1999). The strength of species filtering into coral species was stronger in the regionally diverse GBR than in the Red Sea and Tanzania (Table 1), verifying that richness within a coral species may be limited and relatively independent of regional diversity.

The consistent overestimation of observed richness by the null models within each region suggests that resident species do not inhabit coral species in direct proportion to their volume but instead select certain coral species. This is supported by the similar number of coral species used across regions and the greater than expected overall specificity in coral use (Fig. 5). This analysis also suggests that specificity in coral use is higher in the GBR, although differences among regions were not significant, possibly due to the high variation among species. Similar use of coral habitat across regions that differ in total coral richness and in regional fish diversity may be indicative of evolutionarily constrained patterns of habitat selection, placing a limit on the number of coexisting fish species within a coral species. Some coral-dwelling fish species may compete intensively for living space within a coral but exhibit trade-offs in their use of different coral species (Munday *et al.*, 1997; Munday, 2001; Caley & Munday, 2003). These trade-offs might drive selection towards habitat specialization in a few coral species, thereby maintaining a narrow niche breadth. In addition, speciation driven by host shifts is a potentially important contributor to regional species richness of coral-dwelling fish (Munday *et al.*, 2004). If resident fish speciate when they start utilizing a novel coral species, the resulting pattern will be of high selectivity in habitat use and niche breadth that does not necessarily differ among regions.

In a separate study, similar data were analysed at the level of single coral colonies (Belmaker *et al.*, 2008). It was found that within coral heads, resident richness increased with increased regional diversity, but this increase was lower than predicted by null models. In this study, I find that at the scale of coral species, fish species filtering increased with regional diversity. Therefore, local processes limit the increase in resident fish richness across regions both at the scale of single coral heads and within entire coral species. Nonetheless, the time-scales of the processes operating at these two scales are likely to be different. Focusing on single coral heads allows examination of local interactions among members of a local community (Huston, 1999; Loreau, 2000). Here, by focusing attention on the scale of coral species, emphasis is shifted towards evolutionary processes that determine patterns of coral-habitat selection by fish. Analysis at

the scale of a single coral colony and an entire coral species thus complement each other as they examine different processes. The limit on the number of ecologically coexisting species within a coral head indirectly suggests a role for interspecific interactions at ecological time-scales in limiting local diversity (Belmaker *et al.*, 2008). However, a similar pattern at the scale of an entire coral species is indicative of constraints shaping fish habitat preference patterns over evolutionary time-scales.

Although resident species filtering strength in Tanzania fell between the values of the Red Sea and those of the GBR, as expected, it was not significantly different from that of the Red Sea. For Tanzania, taxonomic identification is lagging behind that of the Red Sea and the GBR, especially of residents which are typically cryptic and hard to identify. It is therefore likely that some residents in Tanzania were not identified correctly at the species level, thereby reducing the power of analyses.

The relationship between regional diversity and local diversity can be viewed from another perspective, essentially turning the question on its head: What enables the maintenance of higher regional fish diversity? A larger number of species can be accommodated by increased habitat diversity, higher overlap among species in habitat use or by decreased niche breadth (Begon *et al.*, 1996). In the context of this study, this translates to higher coral richness, more fish species per coral species or fewer coral species used by each fish species, respectively.

For resident fish species, richness for a given volume of coral did not increase with regional diversity (Fig. 2b). In addition, similar to transients, residents did not use fewer coral species in richer regions and therefore did not decrease their niche breadth (Fig. 5a). Consequently, regional differences in resident fish diversity must be attributed to increased habitat diversity. Indeed, the number of branching coral species increased among regions from 14 in the Red Sea, through 28 in Tanzania, to 36 in the GBR. Therefore, even if fish richness within a coral species (i.e. alpha diversity) is limited, turnover in fish assemblages among coral species (i.e. beta diversity) will enable higher fish diversity with higher coral diversity. In fact, filtering strength can be regarded as a measure of alpha versus beta diversity, in which higher filtering corresponds to higher beta diversity compared with alpha diversity (Rajaniemi *et al.*, 2006). As species filtering was larger in diverse regions (i.e. the GBR), beta diversity among coral species must also be higher. Therefore, higher regional diversity of resident species seems to be contingent on higher coral richness. Similarly, regional gradients in herbivorous insect diversity have been found to be a direct function of plant diversity (Novotny *et al.*, 2006). Together, these studies suggest that ecological interactions between functional groups can be powerful drivers of regional biodiversity patterns.

Coral reefs world-wide are being degraded rapidly (Wilkinson, 2002). It is becoming clear that decline in coral cover can significantly reduce fish diversity and change its composition (Jones *et al.*, 2004; Munday, 2004; Bellwood *et al.*, 2006; Graham *et al.*, 2006; Wilson *et al.* 2008). However, the effects of decline in coral diversity on reef fish are not well understood. This study implies that a decline in coral diversity will negatively affect the diversity of resident coral-dwelling fish, even when coral cover is unaltered.

From a conservation perspective, preserving the diversity of the underlying coral habitat may be imperative for maintaining high richness of resident fish species. Nevertheless, when the distinction between transient and resident species is ignored we may fail to identify changes in resident fish communities as they are masked by the higher richness of transient species.

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## BIOSKETCH

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