

REGIONAL VARIATION IN THE HIERARCHICAL PARTITIONING OF DIVERSITY IN CORAL-DWELLING FISHES

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Abstract. The size of the regional species pool may influence local patterns of diversity. However, it is unclear whether certain spatial scales are less sensitive to regional influences than others. Additive partitioning was used to separate coral-dwelling fish diversity to its alpha and beta components, at multiple scales, in several regions across the Indo-Pacific. We then examined how the relative contribution of these components changes with increased regional diversity. By employing specific random-placement null models, we overcome methodological problems with local–regional regressions. We show that, although alpha and beta diversities within each region are consistently different from random-placement null models, the increase in beta diversities among regions was similar to that predicted once heterogeneity in coral habitat was accounted for. In contrast, alpha diversity within single coral heads was limited and increased less than predicted by the null models. This was correlated with increased intraspecific aggregation in more diverse regions and is consistent with ecological limitations on the number of coexisting species at the local scale. These results suggest that, apart from very small spatial scales, variation in the partitioning of fish diversity along regional species richness gradients is driven overwhelmingly by the corresponding gradients in coral assemblage structure.

Key words: additive partitioning; coral reefs; fish; gamma diversity; scale; similarity; species diversity.

INTRODUCTION

Natural communities are conspicuously hierarchical and are shaped by processes operating over several spatial scales. Based on the view that local interactions limit coexistence, ecologists historically have emphasized competition and predation as regulators of community structure (e.g., Diamond 1975). However, it is increasingly being realized that processes operating at regional scales, which shape the available species pool, can also influence local patterns of diversity (Partel et al. 1996, Caley and Schluter 1997, Karlson et al. 2004). Reconciling the effects of local biotic interactions and regional processes is one of the most challenging tasks facing contemporary ecology (Ricklefs 2004).

Initial insight into the relationship between local and regional processes was achieved by examining plots of local (α) vs. regional (γ) diversity (Cornell and Lawton 1992). A linear relationship was considered an indication of the overriding importance of regional processes while a curvilinear relationship was interpreted as the outcome of strong local interactions. It was hypothesized that these interactions limit the number of coexisting species,

thereby reducing the influence of regional processes. However, the interpretation of local–regional relationships can be ambiguous, because a linear relationship may appear in competitively structured communities (Rosenzweig and Ziv 1999, Hillebrand 2005), and a curvilinear relationship may appear in the absence of interspecific interactions (Srivastava 1999, He et al. 2005).

Loreau (2000) suggested focusing on patterns of local (α) and turnover (β) diversity, because the relationship between them will ultimately determine regional (γ) diversity (note that the terms “species diversity” and “richness” are used here interchangeably). The relationship between α and β diversity depends on many processes that may vary across different spatial scales. For example, at small spatial scales, local interactions may determine α diversity, while at larger spatial scales, dispersal limitation may be the prime determinant of β diversity.

Several studies have examined how α and β diversities change with spatial scale (Lennon et al. 2001, Arita and Rodriguez 2002, Crist et al. 2003, Cornell et al. 2007). Others have examined how β diversity changes with γ diversity, usually along latitudinal gradients (e.g., Blackburn and Gaston 1996, Koleff et al. 2003). Few studies have examined how the response of α and β diversities to γ diversity differs according to the scales at which α and β diversity are defined. For example, Koleff and Gaston (2002) found no relationship between β and γ diversities

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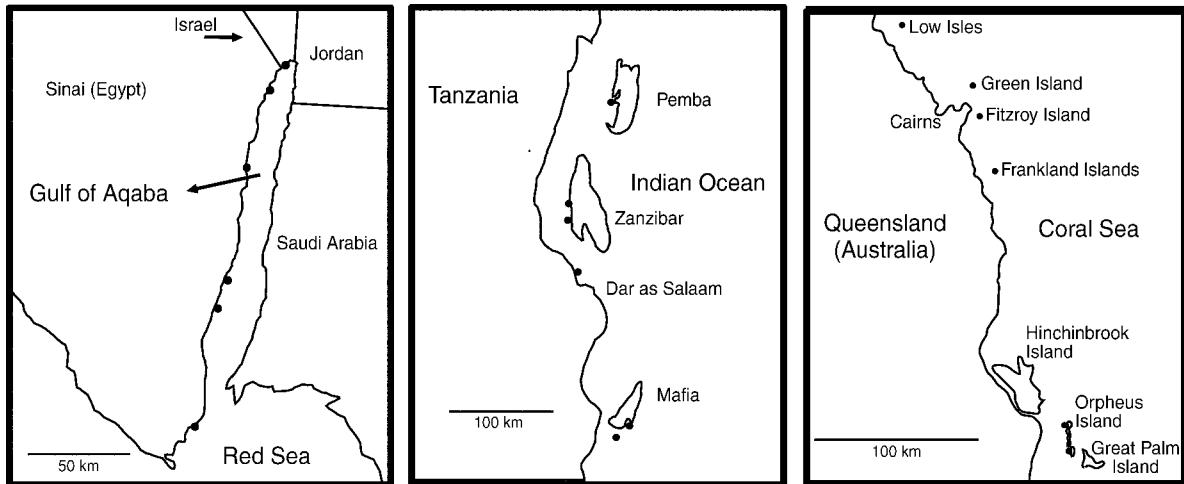


FIG. 1. Location of the sampling sites in the three biogeographical provinces sampled (from left to right): (A) Gulf of Aqaba, Red Sea; (B) Tanzania, western Indian Ocean; and (C) wet-tropics region of the Great Barrier Reef (GBR), Australia.

for birds in Scotland over the spatial scales examined (landscape to regional scales). However, it is still unclear how β diversity changes with γ diversity across a wide range of scales, particularly the small spatial scales at which species interactions are likely to have the greatest influence (Huston 1999, Loreau 2000). Identifying the spatial scales at which β diversity is correlated most, or least, with changes in γ diversity may indicate changes in the relative influence of the underlying processes among regions. If β diversity increases more strongly with γ diversity at a particular scale, relative to other scales, then it indicates that the processes responsible for heterogeneity at that scale make a disproportionate contribution to the overall γ diversity gradient.

In many coral reef organisms, γ diversity peaks globally in the Indonesia-Philippine Archipelago, and declines approximately monotonically with increasing distance from this peak (Bellwood et al. 2005). In this study, we determined how α and β diversity of corals and fishes changes along this global γ diversity gradient. To do this, we employed a hierarchical sampling design in several regions, which allowed us to use additive partitioning to separate total diversity into the distinct contribution of each of several spatial scales. Next, we quantified how diversity at each spatial scale changes with γ diversity, by comparing observed patterns with those predicted by several different null models that omit or incorporate local aggregation effects and affinity of fishes for particular host coral species. This use of multiple null models allows us to identify better the underlying mechanisms creating diversity patterns in this study system.

METHODS

Data collection

Our study focused on fish diversity within branching-coral heads. Such use of natural sampling units has

several important advantages over line or belt sampling because it enables easy characterization of fish habitat units, reduces sampling bias, and, most importantly, ensures that the sampling scale is small enough to allow examination of local ecological interactions (Huston 1999, Loreau 2000).

Surveys were conducted in three geographically distinct provinces: (1) the Gulf of Aqaba, which is a distinct subregion within the Red Sea; (2) islands off the coasts of Tanzania, in the Western Indian Ocean; and (3) islands on the Great Barrier Reef (GBR). These locations represent low, intermediate, and high regional diversity of reef organisms, respectively (Bellwood et al. 2005). Sampling locations are shown in Fig. 1. Surveys were conducted on reefs in the Gulf of Aqaba along the east coast of the Sinai Peninsula. Reefs in this region are well developed coastal fringing reefs. Since the Gulf of Aqaba is a closed sea, wave action is typically limited. In Tanzania, surveys were conducted on reefs situated around offshore islands. In the GBR, surveys were confined to inner-mid shelf reefs of the wet-tropics coast. Both in Tanzania and the GBR, surveys were performed on the calm leeward east side of the islands.

An identical hierarchical sampling design was employed in all regions. This consisted of six sampling sites, separated from each other by at least 15 km. All sites were located in relatively calm waters exposed to little wave action and showed clear zonation with a distinct reef flat and slope. Differences among sites in terms of reef structure and other possible gradients were minimized as much as possible. At each site, 10 transects were established, five on the reef flat and five transects on the adjacent reef slope. Reef flats were approximately 2–10 m inshore of breaking waves, whereas reef slopes were seaward at depths of 3–8 m. Transects were placed haphazardly to encompass the spatial heterogeneity in reef types present in a site and were separated from

each other by a minimum of 300 m (usually ~500 m). Transect sampling was conducted by swimming along a straight line parallel to the depth contour and sampling coral heads that fell within 0.5 m of the sampler from either side. Sampling was performed by a single surveyor (J. Belmaker) to reduce observer bias.

We surveyed the first 25 coral heads in each transect. As coral density may vary, the actual distance surveyed differed among transects. Only colonies from the genera *Stylophora*, *Pocillopora*, *Seriatopora*, and *Acropora* were included. By focusing on these relatively common genera, we ensured that the data set was not dominated by a large number of rare species, which would have substantially compromised statistical power in the “constrained” null models described later. In addition, 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. We only sampled colonies that, along their widest dimension, were wider than 20 cm (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 so that fish movement among coral during sampling was minimized. Corals were generally identified to species level. However, since some closely related species are notoriously difficult to differentiate underwater, some species were combined and analyzed together as a single ecomorph (e.g., *Acropora gemmifera* and *A. humilis*). We 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.

Fish species were separated into three groups based on the degree of affiliation between the fish species and live coral. The first group is 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*). The second group is coral-dwelling only as juveniles, with later ontogenetic stages lacking clear association with a host coral colony. The third group consists of transient species and species that may use branching coral occasionally, but are not obligate coral dwellers. Our sampling design is tailored to species in the first two groups, for which coral heads are natural habitat units within which local interactions occur. Therefore, we included only fish species from these coral-dwelling groups (only the coral-dwelling life stage for the second group) in our null model analyses and restricted the use of transient species to the description of the general diversity patterns.

Data analyses

Diversity components and responses to γ diversity.—Traditionally, the relationship between alpha and beta diversity has been characterized as multiplicative (i.e., γ

$= \beta \times \alpha$). The major disadvantage with this relationship is that alpha and beta components of diversity are expressed using different units, thereby making comparisons problematic (Lande 1996). Additive partitioning of diversity (i.e., $\gamma = \beta + \alpha$) does not have the same disadvantage and the contribution of α and β diversity to total diversity can be directly compared (Lande 1996, Veech et al. 2002). Using additive partitioning, the total number of species can be partitioned into the average number of species within a given sample (α) and the among-sample diversity or the average number of species absent from a randomly selected sample, calculated as total diversity minus average local diversity ($\gamma - \bar{\alpha} = \beta$). Thus, for instance, when local richness is small, on average, compared to regional richness, this implies high variation in species composition among sites (i.e., high β diversity; see Lande [1996] and Veech et al. [2002] for further discussion). Because, in a nested sampling design, samples at one scale are themselves composed of samples at a smaller scale, this partitioning of diversity can occur at each scale in the sampling hierarchy. Consequently, total sampled diversity can be partitioned into the diversity contributed by each spatial scale, making possible the hierarchical analysis of diversity across multiple spatial scales (Veech et al. 2002, Crist et al. 2003, Cornell et al. 2007).

We used additive partitioning to separate total diversity (γ) within each habitat and region into its α and β components. Total (γ) diversity is defined here as the total species richness found in the full collection of samples (Crist et al. 2003, Crist and Veech 2006). Alpha diversity (α) is defined here as the average fish richness within individual corals, β_1 is the average fish richness among corals within transects, β_2 is the average fish richness among transects within sites, and β_3 is the average fish richness among sites within regions. We define γ diversity as the total species richness found in the full collection of samples for a region (Crist et al. 2003, Crist and Veech 2006), and thus we can express regional sampled diversity additively, in terms of its α and β components as $\gamma = \beta_3 + \beta_2 + \beta_1 + \alpha$. Using the number of observed species as a measure of regional diversity is likely to underestimate the true regional richness, but this is not expected to alter the shape of the local to regional regressions (Srivastava 1999). Separate null models were constructed for the reef flat and slope within each biogeographical province because they represent distinct zones, characterized by dissimilar environmental conditions (Huston 1985, Karlson et al. 2004).

For corals, one fewer hierarchical level is present, and therefore alpha diversity (α) is defined as the average coral richness within transects, β_1 is the average coral richness among transects within sites, and β_2 is the average coral richness among sites within regions. Therefore, for coral the total diversity of a region can be partitioned as $\gamma = \beta_2 + \beta_1 + \alpha$.

To examine how the relationships among different diversity components changes with increased γ diversity, we regressed the log of each local diversity component (α , β_1 , β_2 , and β_3) against the log of regional diversity (γ , Hillebrand and Blenckner 2002).

Null models

For relationships between the logarithm of γ diversity and the logarithm of a particular diversity component, a slope equal to 1 indicates that the relative contribution of that specific spatial scale to total diversity remains constant across different regional diversities. However, such regressions are prone to bias and misinterpretation, because the slope may be affected by sampling artifacts. One particular concern in such analyses is the inherent autocorrelation between estimates of the local and regional species pool, which can artificially enhance linearity in the relationship between regional diversity and its components (Hillebrand and Blenckner 2002); on a log scale, this would tend to bias estimated slopes toward 1. A second possible artifact, pseudosaturation at small scales (i.e., saturating local-regional richness relationships that emerge because of a limit on the number of individuals at small spatial scales [Caley and Schluter 1997, Srivastava 1999]), would tend to bias local-regional slopes downward. To overcome these problems, we applied random-placement null models in a two-step procedure, to obtain null distributions of regression slopes, which we then compared with the corresponding empirical slopes. The first step was to construct (separate) null models for diversity components within each region, for which local communities were random samples of the regional species pool. Next, we conducted regressions of each of our null model α and β diversity components against γ diversity (all diversity variables log-transformed), exactly as in our analysis of the empirical data, to determine whether the importance of a given diversity component varied among regions. By repeating this procedure 1000 times, we obtained a frequency distribution of regression slopes, which provided the null distribution against which the observed slopes were tested. Significant departure from such a null distribution, therefore, indicated that increases in local diversity components with γ diversity could not be explained solely by random sampling of fish from the species pool.

For fishes, we constructed four different null models, each of which represented a different null hypothesis about how local fish assemblages sample diversity from the regional pool. By examining the magnitude and direction of departure from each of these different null model predictions, we were able to better identify the processes most likely to be responsible for the empirical relationships between γ diversity and its α and β components.

Unconstrained, individual-based (UIB) model.—The simplest null model randomized individual fishes among all corals within a region (individual-based randomiza-

tion [Crist et al. 2003]). This model assumes that within a region fish colonize corals independent of location and the presence or absence of other fish. This approach preserves the original regional species-abundance distribution and local differences in sample size (e.g., if a larger coral has more individuals, it retains that high local population size in the randomization). Deviations from this model indicate non-random spatial distribution of individuals, e.g., from interspecific interactions, or from intraspecific aggregation.

Unconstrained, presence-based (UPB) model.—Since conspecifics within a coral may be part of a social group and thus not truly independent, a second type of randomization was constructed in which only species presences within coral were randomized. This presence-based randomization constrains γ diversity (total diversity within a region) and α diversity (local diversity within a coral) to their observed values, but allows variation in local species composition and thus variation in the different β diversity components. Because this approach constrains α diversity to its observed value, it cannot be used to examine patterns at the smallest spatial scale (diversity within coral heads).

Constrained, individual-based (CIB) and presence-based (CPB) models.—In the unconstrained randomizations described previously, fish (individuals or presences) are randomized among all corals across all sites and transects. However, coral-dwelling fish may have a strong preference for certain coral species (e.g., Munday et al. 2001). Therefore, constrained randomizations were also performed in which fish could only be randomized to a coral from the same species in which they were found, thereby maintaining observed fish-coral associations. For example, if a damselfish *Dascyllus marginatus* was found within a *Stylophora pistillata* coral it could only be randomized to another *S. pistillata* coral. This randomization preserves the component of β diversity that is due to associations with particular host coral species, and thus allows testing of the null hypothesis that nonrandomness in the diversity components of fishes is due solely to fish assemblage responses to changes in the diversity patterns of their host corals.

To analyze coral diversity patterns, we used only unconstrained individual-based randomizations, as we had no unambiguous way to constrain coral randomization (analogous to the constrained models for fishes), and because individuals within transects are likely to be relatively independent of conspecifics, compared with, e.g., schools or family groups of fishes within a host coral colony.

All of the above randomizations were performed across an entire region (i.e., local assemblages were produced by random-sampling from the regional pool of species abundances or occurrences). Alternatively, randomization can be restricted according to spatial sampling design, with assemblages at one scale produced by random-sampling from the next-higher scale (e.g., assemblages within coral heads produced by random-

TABLE 1. Summary statistics of the coral and fish regional (γ) diversity patterns.

Province	Habitat	Coral diameter (cm)	γ diversity		
			Coral	Coral-dwelling fish	All fish [†]
Red Sea	flat	18.5 \pm 4.3	12	9	40
	slope	21.5 \pm 5.2	12	20	70
Tanzania	flat	23.2 \pm 8.0	23	24	109
	slope	23.3 \pm 7.9	25	24	127
GBR	flat	22.9 \pm 8.3	30	25	142
	slope	23.8 \pm 9.0	33	33	153

Notes: Coral diameter (mean \pm SD) was calculated as the geometric mean of length, width, and height. "GBR" is the Great Barrier Reef.

[†] All fish species observed in and near the coral heads.

sampling only from coral heads on the same transect: see Crist et al. [2003] for an extensive discussion of differences between whole-region and spatially-restricted randomizations). We use whole-region randomizations in this study because it allows comparing the response of several diversity components simultaneously to increased γ diversity, i.e., diversity at the regional level. Examining each scale independently, through spatially-restricted randomization, does not assess a single gradient in γ diversity but rather several gradients corresponding to the various scales (e.g., when α diversity is defined as diversity within coral heads, γ diversity is transect-level diversity; α diversity is defined as diversity within transects, γ diversity is site-level diversity; and so on). As regional and local diversity components are calculated from adjacent scales this will tend to increase the autocorrelation between estimates of the local and regional species pool, artificially enhance linearity in the relationship and make it difficult to detect saturating or other nonlinear relationships. In addition, spatially restricted randomization could not be used in conjunction with our constrained randomization, because it is difficult to simultaneously constrain randomizations by spatial structure and by habitat since there are few coral from a particular species within a lower level unit resulting in few options for randomization and extremely low power of analyses.

All randomizations were performed by maintaining fixed marginal sums for the species' incidence and fish occurrences within coral. Such randomizations are relatively robust to both type I and type II errors (Gotelli 2000). One thousand iterations were used. Random presence-absence matrixes were created using a "fill" algorithm, where presences are added in a random manner to a blank matrix until a matrix with the observed marginal sums is obtained. We matched randomizations across regions, and regressed the logarithm of each diversity component against log (γ diversity) for each set of randomizations (e.g., we took the first randomization for each region, conducted a log-log regression of each diversity component against γ diversity, and then repeated this procedure for each of our 1000 randomizations). We then used the estimated slopes from these analyses as the null distribution of

regression slopes for comparison with the observed data. Departure from null expectation was considered significant if the magnitude of the observed slope was $<2.5\%$ or $>97.5\%$ of the randomized values. In addition, we examined whether observed diversity component are consistently different across regions from those predicted by each of the null models. For this, the observed proportional contribution of each α or β diversity component was compared with the mean value obtained from the null models using paired t tests on angular transformed data.

Intraspecific aggregation and large-scale autocorrelation

Nonrandom patterns of diversity can arise due to spatial autocorrelation due, for instance, to dispersal-limitation. Therefore, Mantel tests were used to examine whether geographical distance between sites contributes to variation in β diversity between sites (β_3 , Appendix A). To further examine mechanisms responsible for observed diversity patterns, we also tested whether coral and coral-dwelling fish intraspecific aggregation at small spatial scales (α), as measured by the standardized Morisita index (Veech 2005), changes as a function of γ diversity (Appendix A).

RESULTS

General diversity patterns

The total number of fish species, or γ diversity, differed greatly among the habitats and provinces sampled (Table 1, Fig. 2A, B). In general, species richness, both for obligate coral-dwelling fishes and for all fish species observed in and near the coral heads (coral-dwelling and transient species combined), was highest in the GBR, followed by Tanzania and then the Red Sea. In addition, regional diversity on the reef slope was greater than the reef flat, apart from the coral-dwelling species in Tanzania which had similar total species richness in the two habitats (Table 1).

Coral-dwelling fish richness constituted a modest and relatively consistent proportion of the total number of fish species surveyed, ranging from 17% in Tanzania to 25% in the Red Sea. (Of course, because our protocol specifically targets coral-dwelling fishes, this group will be a smaller proportion the total regional fish diversity.)

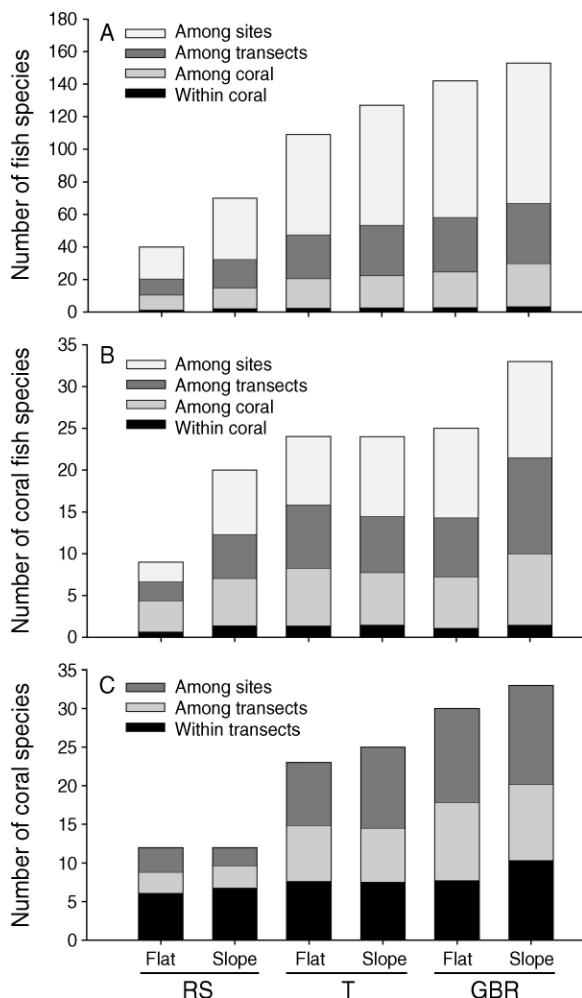


FIG. 2. Hierarchical partitioning of species richness. (A) All fish species observed in and near the coral heads; (B) obligate coral-dwelling species; and (C) corals. For fishes, four spatial scales were examined: within corals (α), among corals within a transect (β_1), among transects within a site (β_2), and among sites within a region (β_3). For corals, three spatial scales were considered: within transects (α), among transects within a site (β_1), and among sites within a region (β_2). Results are shown for each of the two habitats (flat and slope) within each of the three biogeographical provinces (Red Sea [RS], Tanzania [T], and the Great Barrier Reef [GBR]).

Due to incomplete sampling, the true regional diversity of coral-dwelling fishes is likely to be somewhat higher than reported. Nevertheless, additional visual surveys suggest that only few such species within each region were not sampled.

Coral diversity reflected fish diversity trends, with the highest diversity recorded on the GBR slope and the lowest diversity on the Red Sea flat and slope (Fig. 2C). Differences in coral colony size were small: except for the Red Sea reef flat, mean colony size differed by <2 cm among habitats and regions (Table 1). Nevertheless, colonies were significantly smaller on the reef flat than the reef slope overall ($P < 0.05$, Tukey hsd post-hoc test

following a two-way province \times habitat ANOVA), and they were also smaller in the Red Sea than both Tanzania and the GBR ($P < 0.05$, Tukey hsd post-hoc test), which were themselves not significantly different from one other. These variations should not alter the deviation of fish diversity patterns from null model predictions, because all null models used implicitly take into account differences in fish population size and species diversity that might arise due to coral size differences. In other words, null model predictions, like the observed data, will implicitly include the effects on diversity partitioning that are due to differences in local abundance or diversity due to differences in host colony size.

Diversity components within regions

Coral-dwelling fishes.—Coral-dwelling fish diversity showed consistent deviations from null model predictions of richness; that is, deviations of a particular diversity component from a null model prediction tended to be similar for all regions analyzed. While the magnitude of difference between observed values and model predictions differed slightly according to the null model used, the general trends were consistent among null models: relative to null model predictions, among-site diversity (β_3) was greater than expected ($P < 0.01$, paired t test on angular-transformed data), among-transect diversity (β_2) was not significantly different from expected ($P > 0.05$), and both among-coral (β_1) and local diversity (α) were smaller than expected ($P < 0.01$; note that local diversity analysis was only possible for the individual-based randomization; Fig. 3A). See Appendix B for separate significance tests for each region.

Corals.—For corals, using only unconstrained individual-based randomizations, we found consistent deviations from expected richness among regions similar to patterns exhibited by fishes. Among-site diversity (β_2) was greater than expected ($P < 0.001$, paired t test on angular-transformed data), among-transect diversity (β_1) was not significantly different from expected ($P > 0.05$), and within-transect diversity (α) was smaller than expected ($P < 0.001$; Fig. 3B). See Appendix B for separate significance tests for each region.

Comparison of null models.—When using the constrained models, at all spatial scales and in all regions examined, expected diversity components were always closer to observed values compared to the unconstrained models (both when using presence-based and when using individual-based randomization, see appendix B). Similarly, expected diversities obtained from presence-based models, regardless of spatial scales and regions, were always closer to observed values compared to the corresponding individual-based models (Appendix B).

Diversity components: responses to among-region variation in γ diversity

Both for corals and for coral-dwelling fishes, diversity of all spatial scales increased with regional richness (i.e.,

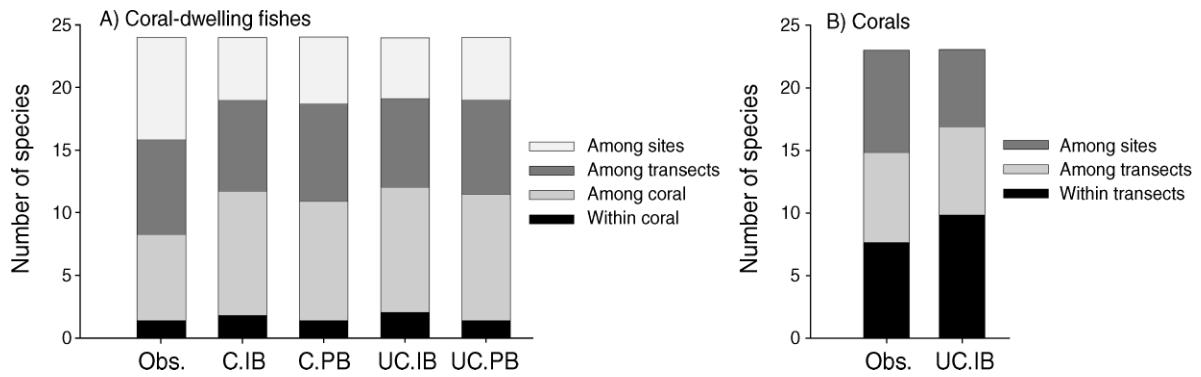


FIG. 3. Observed diversity partitioning patterns (Obs.) compared with those predicted from the null models for (A) coral-dwelling fishes and (B) corals. Four separate null models were used: constrained individual-based (C.IB), constrained presence-based (C.PB), unconstrained individual-based (UC.IB), and unconstrained presence-based (UC.PB) models. Only unconstrained individual-based (UC.IB) randomizations were used for corals. Results are illustrated using the reef flat in Tanzania only.

regression slope $\neq 0$) and the log-log regression slope at all scales differed significantly from 1 (Table 2). This means that the relationship among α and β diversity components changes with γ diversity. For coral-dwelling fishes, the slopes of the regressions for β_3 (among-sites) and β_2 (among-transects-within-sites) diversity were larger than 1, indicating that the relative contribution of these spatial scales to total diversity increases with regional diversity. Conversely, the slopes of the regressions for β_1 (among-coral-within-transect) and α (within coral) were smaller than 1, indicating that the relative contribution of these spatial scales to total diversity decreases with regional diversity (i.e., these diversity components saturate as regional diversity increases). For corals, the slopes of the regressions for β_2 and β_1 (among-sites and among-transects) were larger than 1 while for α (within transects) the slope was smaller than 1.

However, when we compared these observed slopes to the corresponding expected slopes generated by our null models, we found that all null models also produced slopes that were different from 1. For corals, we found that observed slopes did not differ significantly from null

model predictions at larger spatial scales (among sites, β_2 , and among transects β_1). However, the observed slope was significantly lower than predicted at the smallest spatial scale, within transects (α), indicating that within-transect diversity of corals saturates more than predicted by random sampling from the regional pool of colonies (Table 3).

For coral-dwelling fishes, we found strong departures from null models in the unconstrained randomizations, but most of these disappeared once the effects of variation in coral community structure were taken into account via the constrained randomizations. Specifically, when using the unconstrained randomizations (both presence-based and individual-based), the observed slopes were significantly different from expected at all spatial scales, apart from β_3 when using presence-based randomization for which the result was marginally nonsignificant ($P = 0.11$; Table 3). Observed values were lower than predicted at small spatial scales (β_2 , β_1 , and α), and higher than predicted at large spatial scales (β_3). However, when using the constrained randomizations (i.e., accounting for fish species' affinities for particular host coral species), increases in β_3 and β_2 diversity did

TABLE 2. Observed (Obs.) slopes of the regression of log α and β diversity components against log γ diversity.

Scale	Taxa	Obs. slope	95% CI†	R ²	P
α	fish	0.62	0.31–0.94	0.80	<0.05
	coral	0.33	0.04–0.63	0.71	<0.05
β_1	fish	1.20	1.03–1.37	0.98	<0.001
	coral	1.31	1.09–1.53	0.99	<0.001
β_2	fish	1.20	1.03–1.37	0.98	<0.001
	coral	1.61	1.23–2.01	0.97	<0.001
β_3	fish	1.30	1.04–1.55	0.96	<0.001

Notes: Diversity metrics are local diversity (α), turnover diversity (β), and the total species richness found in a region (λ). In scales, α is defined at a scale of individual corals for fish and at a scale of transects for coral, β_1 is defined among individual corals (within a transect) for fish and among transects (within a site) for coral, β_2 is defined among transects (within a site) for fish and among sites (within a region) for coral, and β_3 is defined among sites (within a region).

† All slopes are significantly different from 1.

TABLE 3. Slopes of the regression of log α and β diversity components against log γ diversity compared to expected slopes generated from the various null models.

Diversity component	Coral-dwelling fish						Coral	
	Obs. slope	Constrained		Unconstrained		Unconstrained		
		Expected (IB)	Expected (PB)	Expected (IB)	Expected (PB)	Obs. slope	Expected (IB)	
α	0.62	0.73–0.77†	NA	0.71–0.76†	NA	0.33	0.40–0.47†	
β_1 (all points)	0.61	0.73–0.81†	0.63–0.70†	0.75–0.83†	0.61–0.69†	1.31	1.26–1.54	
β_1 (excluding Red Sea flat)	0.81	0.34–0.54†	0.44–0.65†	NA	NA	NA	NA	
β_2	1.20	1.14–1.48	1.14–1.47	1.24–1.66†	1.27–1.65†	1.61	1.60–2.00	
β_3	1.30	0.99–1.31	1.09–1.42	0.88–1.22†	1.01–1.33	NA	NA	

Notes: For coral-dwelling fish, results from both presence-based (PB) and individual-based (IB) randomizations are shown. “NA” indicates not applicable.

† The observed slope differs significantly from the null model prediction.

not differ significantly from null model predictions (Table 3). These findings held for both presence-based and individual-based randomizations. Although β_1 increased less than expected from the constrained null models (both presence and individual-based), visual inspection of the data suggests that this result is due solely to a single anomalously high value in the Red Sea flat. Indeed, after excluding this point, we actually found β_1 to increase more than predicted by the constrained null model (Table 3). Also, α diversity increased with γ diversity less than expected from the constrained individual-based null model.

In all regressions, the residuals' magnitude and direction did not differ consistently between the flat and slope, supporting the use of a single regression line for both habitat types.

Intraspecific aggregation and Mantel tests

For coral-dwelling fishes, we found strong evidence for regional variation in intraspecific aggregation: Morisita's standardized aggregation index was positively correlated with γ diversity (Spearman's $r = 0.93$, $P < 0.01$, Fig. 4A) and negatively correlated with α diversity (Spearman's $r = -0.94$, $P < 0.01$, Fig. 4B). Similar, but weaker, patterns were evident for corals: Morisita's index was negatively correlated with α diversity (Spearman's $r = -0.94$, $P < 0.01$) and positively, but not significantly, correlated with γ diversity (Spearman's $r = 0.58$, $P = 0.23$; Fig. 4C, D). Conversely, there was little evidence for spatial autocorrelation at large scales: geographical distances between sites were significantly correlated with variation in fish assemblage compositions only for the reef flat in the Red Sea (Appendix C). Furthermore, we found no significant correlations between geographical distances and distance in fish assemblage compositions after partialing out the distance in coral assemblages (Appendix C).

DISCUSSION

This study shows that, for both coral-dwelling fishes and corals, local diversity (within transects and [for fishes] within coral heads) increases less than expected with increasing regional diversity. For corals there

appears to be no compensatory greater-than-expected increase in β diversity at any of the particular scales measured in this study. For coral-dwelling fishes, however, β diversity increases more than expected with regional diversity at the largest (among-site) scale; in other words, among-site β diversity makes a progressively greater contribution to total diversity as regional richness increases. The fact that this latter result vanishes once fishes' species-specific association with host corals is taken into account, via the “constrained” null models, suggests that a major cause of this increasing importance of among-site β diversity is greater variation in coral species composition among sites in more species-rich regions.

In contrast, within regions, fish diversity components showed consistent deviations from random-placement null models that appear not to be driven by variation in the assemblage structure of the corals that they inhabit. Among-site fish diversity (β_3) was higher than expected, while diversity at the smaller spatial scales (within and among coral) was lower than expected. These patterns remained even when species-specific associations with host corals are taken into account with the “constrained” null models. In other words, β_3 diversity is higher than predicted within each region (even after accounting for host coral associations), even though it's relative importance does not change significantly as γ diversity increases.

Diversity components: responses to among-region variation in γ diversity

We tested for changes in the importance of α and β diversity components to γ diversity by regressing the log of each local diversity component against the log of regional diversity (see Hillebrand and Blenckner 2002), for both empirical data and for several different null models that represent different hypotheses about how local assemblages sample from the regional species pool. Slopes less than 1 indicate saturation of a diversity component with increasing γ diversity, and slopes greater than 1 indicate that a diversity component makes an increasingly large contribution as γ diversity increases. Our null models show that random sampling

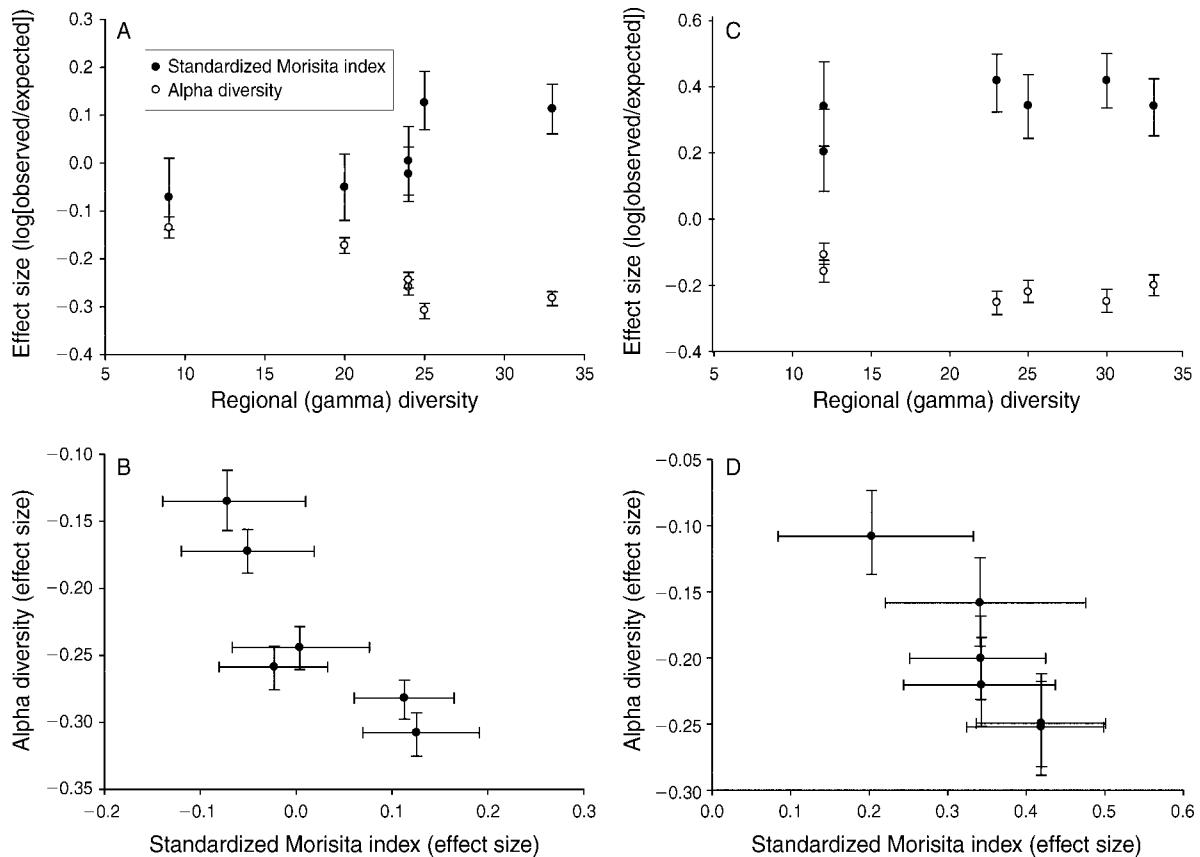


FIG. 4. (A, C) The effect size for α diversity and the standardized Morisita index plotted against γ diversity for (A) coral-dwelling fishes and (C) corals. Effect sizes were calculated as the deviations of observed values from those expected (log[observed/expected]) from a constrained (fish) or unconstrained (coral) individual-based randomization at the local scale (α). (B, D) Effect size for α diversity against the effect size for the standardized Morisita index for (B) coral-dwelling fishes and (D) corals. Error bars denote 95% CI.

from the species pool tends to produce apparent saturation (expected slopes < 1) for small-scale diversity components, as previous workers have proposed, and, for at least some null models, produces a converse pattern of apparent increases in the contribution of large-scale β diversity components (expected slopes > 1) at large scales. This highlights the importance of adopting a null model approach to testing for significant increases or decreases in the importance of diversity components along regional richness gradients, rather than simply testing empirical slopes for significant departure from 1.

For corals, we found that observed slopes of log β diversity vs. log γ diversity increased as expected from the null model predictions, from which they did not differ significantly, both among transects (β_1) and among sites (β_2). In contrast, for coral-dwelling fishes we found that observed slopes, using the unconstrained null model, are in general significantly different from null model predictions (for both individual and presence-based randomizations; Table 3). However, once we accounted for variation in coral assemblage structure,

by using constrained randomizations, increases in β_3 and β_2 diversity became consistent with null model predictions (since the slope of β_1 diversity among regions was strongly influenced by a single outlier, we cannot conclusively determine how diversity at this scale is influenced by γ diversity).

These results suggest that, for coral-dwelling fishes, spatial variation in coral assemblages is a major driver of the increasing importance of among-site β diversity along a gradient of γ diversity. Several studies have found β and γ diversity to be uncorrelated (Koleff and Gaston 2002, Koleff et al. 2003, Hunter 2005). However, most such studies have examined patterns of diversity over landscape to regional scales, with data obtained chiefly from species distribution maps. Our study extended down to very small spatial scales (i.e., diversity among coral heads at the scale of meters), where the fingerprints of local ecological interactions are most likely to be found (Huston 1999, Loreau 2000). We found that β diversity at large spatial scales, i.e., among-sites, becomes increasingly important as γ diversity increases while β diversity at among-transects and

among-corals scales become less important. Indeed, by using multiple null models, we have been able to identify heterogeneity in the assemblage composition of corals as the principal mechanism underlying this relationship: when we remove it, by constraining fish to retain their affinities for particular host coral species, the apparent changes in the importance of β diversity with increasing γ diversity disappears.

Because coral-dwelling fish diversity closely follows coral diversity, one might well have expected to find significant deviations from the unconstrained null models for corals as well as fishes. Indeed, the fact that we found coral α diversity to be significantly less important in richer regions suggests that β diversity, at some scale, must be making a greater contribution to make up the difference. One possibility is that this greater β diversity is apparent at a scale that is not measured in this study. An alternative is that the greater β diversity is spread across many scales, so that it is not statistically detectable in our null model analysis for any particular scale. However, we view this latter possibility as unlikely, because the estimated slopes of our log β vs. log γ regressions were toward the low end (i.e., smaller-than-expected slopes) of their corresponding null distributions (Table 3). A third possibility is that some subgroup of corals does show increased among-site β diversity with increased γ diversity (even though corals as a whole do not), and that coral-dwelling fish respond particularly strongly to this subgroup.

In contrast to β diversity, α diversity increased among regions less than expected from the null models, regardless of the null model used, both for coral-dwelling fishes (within corals) and for corals (within transects). Studies that have examined the influence of a similar γ diversity gradient on local diversity of corals have found most spatial scales, apart from the smallest scale of 1-m quadrats, to be sensitive to regional enrichment (Karlson and Cornell 2002, Karlson et al. 2004). In our study, by comparing observed patterns to specific null models, we were able to demonstrate that although regional diversity does influence local diversity it does so less than expected. A major proximate cause for lower than expected α diversity is intraspecific aggregation (He and Legendre 2002, Veech 2005). Indeed, we found that the way in which observed fish diversity deviates from null model predictions is strongly related to the degree of intraspecific aggregation, and that aggregation increases with γ diversity (Fig. 4A, B). A similar, though not significant, trend of increased aggregation at the smallest spatial scale with increased regional diversity was found for corals (Fig. 4C). This extends findings from a recent study on aggregation patterns of corals along a regional diversity gradient (Karlson et al. 2007). Biologically, this means that, on average and on small scales, species' dispersion patterns are patchier in richer regions. Such a pattern is consistent with ecological factors, such as competitive exclusion, limiting diversity at small scales. For fishes,

ecological limitation on the number of coexisting fish species at the scale of a single coral fits well with the life history of some coral-dwelling fish species, which may compete intensively for living space within a coral but exhibit trade offs in their use of different corals (Munday et al. 2001). Whether species interactions can reduce local diversity within transects for corals is more controversial (Cornell and Karlson 2000); if not, then other mechanisms (e.g., aggregated settlement or fine-tuned environmental adaptations) would be required to explain this pattern.

Diversity components within regions

By comparing observed diversity patterns with null models we were able to formally assess how diversity patterns differ from those produced by random samples from the species pool. Additive partitioning patterns were significantly different from null model predictions for most spatial scales, and were consistent across the regions. Both for coral and coral-dwelling fishes, diversity among sites was higher than expected, while diversity at the smaller spatial scales (β_1 and α for fish, α for coral) was lower than expected. For fish, presence-based and individual-based randomization gave comparable results, although the correspondence between data and null model was slightly better when using presence-based randomization (Fig. 3A). This comparability between individual and presence-based analyses indicates that the deviations from null models cannot be attributed to the lack of independence among individuals within coral.

Deviations from null model predictions within regions can be driven by small-scale aggregation in the distribution of corals and fishes, or by spatial heterogeneity and dispersal limitation acting at larger scales. For coral-dwelling fishes, neither spatial variation in coral assemblage structure, nor dispersal limitation, appear to explain our within-region results: in contrast to the between region analyses, among-site β diversity was higher than null model predictions regardless of whether constrained or unconstrained randomizations were used (e.g., Fig. 3A), nor was there any evidence for large-scale spatial autocorrelation in fish assemblage composition. Potentially, intraspecific aggregation depresses diversity at small scales, and thus causes β diversity at larger scales to be higher than predicted (because the diversity components must sum to a fixed regional diversity). In addition, for fishes, part of the β diversity among-sites can be attributed to environmental heterogeneity that, because of the concordance between the results of unconstrained and constrained null models, is unrelated to variation in coral assemblage structure.

Like our within-region analyses, studies in other systems have also found evidence for positive deviations from null models at large spatial scales (i.e., more large-scale, among-site, β diversity than expected) and negative deviation at small spatial scales (i.e., less local diversity than expected; e.g., canopy beetles [Crist et al.

2003] and plants [Freestone and Inouye 2006]). Like our study, these studies used randomizations across the entire region (i.e., local communities were assembled via random sampling from the regional pool of species abundances or species occurrences). Our results appear upon first consideration to conflict with those of Cornell et al. (2007), who report scale-invariance of β diversity for Indo-Pacific corals: observed β diversity exceeds null model predictions in a similar way at all spatial scales. However, it is important to note that Cornell et al. (2007) used spatially restricted randomizations that are conducted at each hierarchical level separately (e.g., randomized transects were generated by resampling from the corresponding site, rather than randomizing all transects in a given region by resampling from the region, as in our study). Their approach is particularly well suited to testing the hypothesis of scale-invariance, because null model predictions will not be affected simultaneously by spatial nonrandomness at multiple hierarchical levels. However, as noted previously (see *Methods*), it is less well suited to studies such as ours, which test for changes in the contribution of particular diversity components with changes in regional diversity.

To determine whether our data exhibited a different spatial scaling of β diversity than that of Cornell et al. (2007), we reanalyzed our data using a spatially restricted randomization. We found deviations from the null models at the scales of sites (within regions) and transects (within sites) to be similar (expected similarities were 13–14% higher than observed for coral-dwelling fishes and 20–26% higher for corals), and thus scale invariant (Appendix D). This supports their previous analysis for corals, and shows that a similar scale-invariance applies to coral-dwelling fishes. Dispersal limitation, acting over large spatial scales, is expected to produce large β diversity. Therefore, scale invariance in this system suggests that coral-dwelling fishes, like corals, can disperse among sites (15 km apart) as easily as they can among transects (300–500 m apart).

Implications

The use of null models to study γ diversity influences on α and β diversity components enabled us to begin to identify the mechanisms that underlie regional enrichment. Although reef-fish diversity increases with γ diversity at all spatial scales, the contribution of among-site β diversity is proportionately greater in richer regions. This phenomenon seems almost entirely due to corresponding regional gradients in coral diversity: once fish–coral associations were accounted for, increases in fish β diversity became consistent with null model predictions. In other words, among-site variation in the assemblage composition of corals is responsible for amplifying β diversity components of coral-dwelling fishes in species-rich regions. Most investigations of regional patterns in biodiversity focus on abiotic mechanisms, such as habitat availability, energy input, or proximity to domain boundaries, as

potential explanations for those patterns (e.g., Bellwood et al. 2005). In contrast, we have found that patterns in the hierarchical partitioning of fish β diversity along a γ diversity gradient are driven almost entirely by corresponding variation in the assemblage structure of corals. This indicates that ecological interactions between functional groups can also be powerful drivers of regional patterns in biodiversity. Although other processes (such as habitat selection, dispersal, environmental fluctuation, and disturbance) will undoubtedly influence β diversity within each region, their relative importance seems to be independent of γ diversity. This underscores the similarity in the relative influence of processes at relatively large scales in determining diversity across the Indo-Pacific biodiversity gradient. In contrast, α diversity, at the scale of a single coral head, is increasingly limited with increased γ diversity. This effect is correlated with increasingly aggregated dispersion pattern in richer regions, which suggests that ecological interactions may limit diversity at that scale. In addition, we believe the new analytical approach presented here offers a potential solution to long-standing statistical problems associated with interpreting local-regional relationships and is therefore broadly applicable for analyzing regional influences on diversity patterns.

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APPENDIX A

The role of intraspecific aggregation and geographical distance in producing observed diversity patterns (*Ecological Archives* E089-161-A1).

APPENDIX B

Diversity partitioning within each region (*Ecological Archives* E089-161-A2).

APPENDIX C

Mantel tests (*Ecological Archives* E089-161-A3).

APPENDIX D

Comparison with the method of Cornell et al. (2007) (*Ecological Archives* E089-161-A4).