mantle. Figure 2b illustrates Hf isotope data for >3.5-Gyr-old single zircons[5,6] and deep-seated 3.45-Gyr komatiites[31], plotted as a function of age. Only zircons for which integrated U–Pb and Hf isotope data are available were selected, thus avoiding the possibility that the original isotopic signature has been perturbed by younger geological events.

The most important result emerging from our re-calibration of the $\lambda_{^{176}\mathrm{Lu}}$ value is that most >4-Gyr-old zircons have $\varepsilon_{\mathrm{Hf}} > 0$ (within analytical uncertainty), indicating that these minerals were ultimately derived from a mantle source region with a significant record of depletion. Similarly, younger zircons (<3.8 Gyr) from Greenland, Canada, Australia and South Africa, as well as 3.45-Gyr komatiites from South Africa, were extracted from depleted source regions, in accordance with the extent of fractionation recorded by the >4-Gyr grains. The felsic lithologies from which the zircons crystallized were obviously not directly derived from melting of a mantle source, but involved further differentiation processes and/or re-melting of older perhaps more mafic lithologies, which may have involved a significant time interval. As such, the Hf isotopic composition recorded by these zircons is considered a minimum estimate of the degree of depletion. We thus use the most radiogenic composition recorded by individual grains of the different age groups in Fig. 2b, in order to estimate a ^{176}Lu/^{177}Hf ratio of 0.043 for pre-3.45-Gyr terrestrial depleted mantle. This corresponds to $f_{\mathrm{Lu/Hf}} \approx 0.30$ (where $f_{\mathrm{Lu/Hf}} = [^{176}\mathrm{Lu}/^{177}\mathrm{Hf}]_{\mathrm{mantle}}/[^{176}\mathrm{Lu}/^{177}\mathrm{Hf}]_{\mathrm{CHUR}}$) for the pre-3.45-Gyr mantle compared to $f_{\mathrm{Lu/Hf}} \approx 0.15$ for the modern mantle as sampled by mid-ocean ridge basalts today, indicating a significantly greater depletion of the early Archaean mantle as suggested by a number of studies[3,4,8,16,17].

On the basis of these fractionations, we estimate that Earth's mantle differentiated from a uniform chondritic reservoir ≥4.23 Gyr ago (considering the uncertainty of ±1.7 $\varepsilon_{\mathrm{Hf}}$ of the new CHUR value, and the error of the slope of the regression; Fig. 2b inset). Differentiation of Earth at ~4.3 Gyr ago would have occurred during the life span of the now extinct ^{146}Sm nuclide and, as such, resolvable ^{142}Nd excess should be present in early Archaean lithologies before effective mantle homogenization through convective stirring. This is consistent with recent ^{146}Sm–^{142}Nd analyses of meta-basalts from Isua (Greenland)[9,10], confirming the original discovery of a ^{142}Nd anomaly[8]. The magnitude of the reported ^{142}Nd excess (~15–30 p.p.m.) requires differentiation of Earth's mantle no later than 4.3 Gyr ago[8], in excellent agreement with our results and interpretation. □

Received 4 October 2002; accepted 6 January 2003; doi:10.1038/nature01421.

1. Stevenson, R. K. & Patchett, P. J. Implications for the evolution of continental-crust from Hf-isotope systematics of Archean detrital zircons. *Geochim. Cosmochim. Acta* **54**, 1683–1697 (1990).
2. Vervoort, J. D., Patchett, P. J., Gehrels, G. E. & Nutman, A. P. Constraints on early Earth differentiation from hafnium and neodymium isotopes. *Nature* **379**, 624–627 (1996).
3. Vervoort, J. D. & Blichert-Toft, J. Evolution of the depleted mantle: Hf isotope evidence from juvenile rocks through time. *Geochim. Cosmochim. Acta* **63**, 533–556 (1999).
4. Albarède, F., Blichert-Toft, J., Vervoort, J. D., Gleason, J. G. & Rosing, M. Hf–Nd evidence for a transient dynamic regime in early terrestrial mantle. *Nature* **404**, 488–490 (2000).
5. Amelin, Y., Lee, D.-C., Halliday, A. N. & Pidgeon, R. T. Nature of the Earth's earliest crust from hafnium isotopes in single detrital zircons. *Nature* **399**, 252–255 (1999).
6. Amelin, Y., Lee, D.-C. & Halliday, A. N. Early-middle Archaean crustal evolution deduced from Lu-Hf and U-Pb isotopic studies of single grain zircons. *Geochim. Cosmochim. Acta* **64**, 4205–4225 (2000).
7. Scherer, E., Münker, C. & Mezger, K. Calibrating the Lu-Hf clock. *Science* **293**, 683–686 (2001).
8. Harper, C. L. Jr & Jacobsen, S. B. Evidence from coupled ^{147}Sm–^{143}Nd and ^{146}Sm–^{142}Nd systematics for very early (4.5-Gyr) differentiation of the Earth's mantle. *Nature* **360**, 728–732 (1992).
9. Boyet, M., Albarède, F., Télouk, P. & Rosing, M. ^{142}Nd anomaly confirmed at Isua. *Geochim. Cosmochim. Acta* **66**, Abst. A99 (2002).
10. Caro, G., Bourdon, B., Birck, J.-L. & Moorbath, S. ^{142}Nd/^{144}Nd precise determination in early Archean rocks. *Geochim. Cosmochim. Acta* **66**, Abst. A120 (2002).
11. Yin, Q. *et al.* A short timescale for terrestrial planet formation from Hf–W chronometry of meteorites. *Nature* **418**, 949–952 (2002).
12. Kleine, T., Münker, C., Mezger, K. & Palme, H. Rapid accretion and early core formation on asteroids and the terrestrial planets from Hf–W chronometry. *Nature* **418**, 952–956 (2002).
13. Amelin, Y., Krot, A. N., Hutcheon, I. D. & Ulyanov, A. A. Lead isotopic ages of chondrules and calcium-aluminium-rich inclusions. *Science* **297**, 1678–1683 (2002).
14. Dalmasso, J., Barci-Funel, G. & Ardisson, G. J. Reinvestigation of the decay of the long-lived odd-odd ^{176}Lu nucleus. *Appl. Radiat. Isot.* **43**, 69–76 (1992).
15. Nir-el, Y. & Lavi, N. Measurement of the half-life of ^{176}Lu. *Appl. Radiat. Isot.* **49**, 1653–1655 (1998).
16. Chase, C. G. & Patchett, P. J. Stored mafic/ultramafic crust and early Archean mantle depletion. *Earth Planet. Sci. Lett.* **91**, 66–72 (1988).
17. Bennett, V. C., Nutman, A. P. & McCulloch, M. T. Nd isotopic evidence for transient, highly depleted mantle reservoirs in the early history of the Earth. *Earth Planet. Sci. Lett.* **119**, 299–317 (1993).
18. Patchett, P. J. & Tatsumoto, M. Lu–Hf total-rock isochron for the eucrite meteorites. *Nature* **288**, 571–574 (1980).
19. Tatsumoto, M., Unruh, D. M. & Patchett, P. J. U-Pb and Lu-Hf systematics of Antarctic meteorites. *Proc. 6th Symp. on Antarctic meteorites: Mem. Nat. Inst. Polar Res. (Tokyo) Spec. Iss.* **20**, 237–249 (1981).
20. Blichert-Toft, J. & Albarède, F. The Lu-Hf isotope geochemistry of chondrites and the evolution of the mantle-crust system. *Earth Planet. Sci. Lett.* **148**, 243–258 (1997).
21. Alexander, C. M. O'D., Boss, A. P. & Carlson, R. W. The early evolution of the inner solar system: A meteoritic perspective. *Science* **293**, 64–68 (2001).
22. Lugmair, G. W. & Shukolyukov, A. Early solar system timescales according to ^{53}Mn-^{53}Cr systematics. *Geochim. Cosmochim. Acta* **62**, 2863–2886 (1998).
23. Lugmair, G. W. Sm-Nd ages: a new dating method. *Meteoritics* **9**, 369 (1974).
24. Lugmair, G. W. & Scheinin, N. B. Sm-Nd systematics of the Stannern meteorite. *Meteoritics* **10**, 447–448 (1975).
25. Jacobsen, S. B. & Wasserburg, G. J. Sm-Nd isotopic evolution of chondrites. *Earth Planet. Sci. Lett.* **50**, 139–155 (1980).
26. Göpel, C., Manhès, G. & Allègre, C. U-Pb systematics from equilibrated ordinary chondrites. *Earth Planet. Sci. Lett.* **121**, 153–171 (1994).
27. Blichert-Toft, J., Boyet, M., Télouk, P. & Albarède, F. ^{147}Sm-^{143}Nd and ^{176}Lu-^{176}Hf in eucrites and the differentiation of the HED parent body. *Earth Planet. Sci. Lett.* **204**, 167–181 (2002).
28. Dixon, D., McNair, A. & Curran, S. C. The natural radioactivity of lutetium. *Phil. Mag.* **45**, 683–694 (1954).
29. Barfod, G. H. *A New Lu-Hf Separation Technique for Phosphates and its Application to Apatite Geochronology.* Thesis, Univ. Copenhagen (2002).
30. Bizzarro, M., Simonetti, A., Stevenson, R. K. & David, J. Hf isotope evidence for a hidden mantle reservoir. *Geology* **30**, 771–774 (2002).
31. Blichert-Toft, J. & Arndt, N. T. Hf isotope compositions of komatiites. *Earth Planet. Sci. Lett.* **171**, 439–451 (1999).

Supplementary Information accompanies the paper on *Nature*'s website (**http://www.nature.com/nature**).

Acknowledgements We thank F. Albarède and H. C. Larsen for comments on an earlier version of the manuscript, J. Blichert-Toft for access to unpublished data, Y. Amelin for discussion, and T. Waight for help in the Danish Lithosphere Centre MC-ICP-MS laboratory. This project was supported by the Danish Lithosphere Centre (funded by the Danish National Science Foundation). M.B. was supported by an NSERC postdoctoral fellowship.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to M.B. (e-mail: mbi@dlc.ku.dk).

Patterns and processes in reef fish diversity

Camilo Mora*, Paul M. Chittaro*, Peter F. Sale*, Jacob P. Kritzer* & Stuart A. Ludsin*†

* *Department of Biology, University of Windsor, 401 Sunset Avenue, Windsor, Ontario, N9B 3P4 Canada*

A central aim of ecology is to explain the heterogeneous distribution of biodiversity on earth. As expectations of diversity loss grow[1–5], this understanding is also critical for effective management and conservation. Although explanations for biodiversity patterns are still a matter for intense debate[5], they have often been considered to be scale-dependent[6,7]. At large geographical scales, biogeographers have suggested that variation in species richness results from factors such as area, temperature, environmental stability, and geological processes, among many

† Present address: National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan 48105-2945, USA.

others[5,7–14]. From the species pools generated by these large-scale processes, community ecologists have suggested that local-scale assembly of communities is achieved through processes such as competition, predation, recruitment, disturbances and immigration[5–8,15,16]. Here we analyse hypotheses on speciation and dispersal for reef fish from the Indian and Pacific oceans and show how dispersal from a major centre of origination can simultaneously account for both large-scale gradients in species richness and the structure of local communities.

Using a geographical database of species distributions (see Methods), we determined large-scale patterns in species richness for reef fish in the Indian and Pacific oceans. From a centre of high diversity in the Indonesian and Philippine region (IPR), species richness decreases steadily along both latitudinal and longitudinal axes (Fig. 1a, b). Although these patterns are similar in shape to those that one would expect from the mid-domain effect (the pattern expected if species ranges were randomly distributed between geographical boundaries[10]), the overall patterns, and particularly the high number of species in the IPR, result from a nonrandom distribution of species (Fig. 1a, b).

Three major, yet different, hypotheses invoking speciation and dispersal have been suggested to explain these large-scale patterns. The Centre-of-Origin hypothesis suggests that the IPR is a major centre of speciation from which species disperse to marginal locations[9,12,17]. The Centre-of-Overlap hypothesis proposes that the high diversity in the IPR is due to the overlapping of faunas from several biogeographic provinces[9,12,17]. Finally, the Centre-of-Accumulation hypothesis states that speciation occurs in several areas peripheral to the IPR and that species extend their ranges to the IPR by prevailing currents[9,12,17]. A variant to the Centre-of-Accumulation hypothesis holds that after extending into the IPR, many species have suffered range reductions through the loss of populations marginal to the IPR[12]. Whereas the Centre-of-Overlap hypothesis predicts dispersal in all directions within the biogeographic provinces, the Centre-of-Accumulation hypothesis (including its variant) predicts unidirectional dispersal towards the IPR.

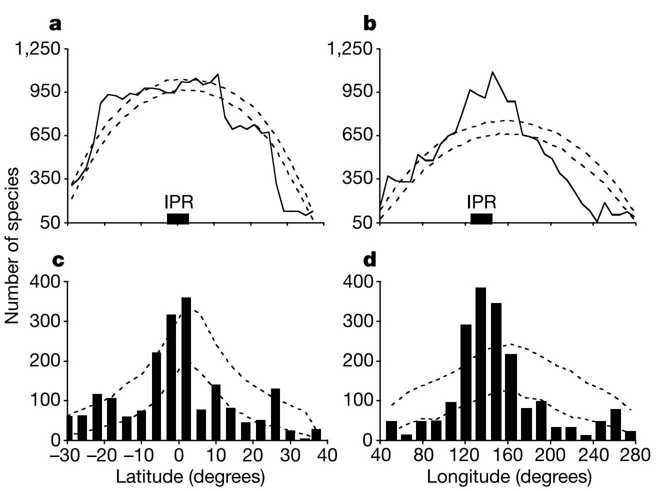

Figure 1 Geographical patterns in reef fish biodiversity in the Indian and Pacific oceans. IPR, Indonesian and Philippine region. Latitudinal (**a**) and longitudinal (**b**) clines (solid lines) were defined as the number of species whose geographical ranges included a point in latitude or longitude, respectively. Distributions of mid-latitudinal (**c**) and mid-longitudinal (**d**) ranges (filled bars) are also shown. The effects of geographic constraints on such patterns (the mid-domain effect[10]) were tested by running a null model in which the ranges (for **a** and **b**) and mid-ranges (for **c** and **d**) were randomly allocated between boundaries. These boundaries were the 'hard' limits imposed by the coasts of Africa and America in longitude and the 'soft' limits implied by the 37° N and 32° S latitude where tropical organisms show striking reductions in species richness[20]. Dotted lines correspond to the maximum and minimum values after running the model 1,000 times.

The Centre-of-Overlap and the Centre-of-Accumulation hypotheses state that only the tails of species' ranges extend into the IPR. Consequently, most species should have their range midpoints marginal to the IPR, resulting in bimodal or multi-modal distributions. However, plots of species mid-ranges (both longitudinal and latitudinal) show nonrandom unimodal distributions with peaks coinciding with the geographical position of the IPR (Fig. 1c, d). These distributions rule out these two hypotheses and provide support for the Centre-of-Origin hypothesis. They also support, to some extent, the variant of the Centre-of-Accumulation hypothesis because range reductions through loss of peripheral populations would shift mid-ranges towards the IPR, and, if extensive, this could result in a unimodal distribution of mid-ranges in the vicinity of the IPR.

The Centre-of-Origin and the Centre-of-Accumulation (including its variant) hypotheses predict different places of species origination. Whereas the Centre-of-Origin hypothesis predicts speciation within the IPR, the Centre-of-Accumulation hypothesis predicts speciation in locations marginal to the IPR. To discern between these predictions, we analysed the geographic pattern in reef fish endemism. We assume that centres of endemism contain a preponderance of recently derived species that are yet to expand their ranges (neo-endemics) and thus provide insights into areas where species are most likely to originate. It is reasonable to expect that palaeo-endemic species, if present, will represent only a small proportion of endemics. Palaeo-endemic extinction rates should be high because of their small ranges and longer exposure to factors causing extinction. The IPR stands out as the major centre of endemism in the Indian and Pacific oceans (Fig. 2), as has been previously reported for fish as well as for other taxa[4]. This result supports the IPR as a major centre of speciation and confirms the expectation of the Centre-of-Origin hypothesis. In addition, Springer[11] has argued that large-scale extinctions have not occurred marginal to the IPR, casting doubt on the variant of the Centre-of-Accumulation hypothesis.

(We note that Hughes *et al.*[18] have recently reported low levels of endemism for the IPR. We believe their result, which is in contrast to our results and previous studies, is partially a consequence of the manner in which they sub-sampled their database. Specifically, they excluded sites less than 400 km apart, which means that many proximal sites within the IPR might be excluded and perceived endemism within the region would be artificially reduced.)

Our analysis also demonstrates that other minor centres of endemism exist, which might contribute to regional species pools. Most of these minor centres are, however, geographically isolated or in places where current direction is predominately from tropical to temperate latitudes[4] (Fig. 2). Thus, species generated in these outlying centres of origin probably would not contribute significantly to species pools in other communities. By contrast, the IPR occurs in a highly interconnected area that may facilitate species migration or dispersal to marginal locations. That the IPR harbours

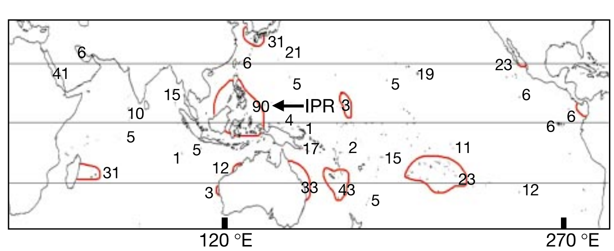

Figure 2 Geographical pattern of reef fish endemism in the Indian and Pacific oceans. Endemic species were defined as those species restricted to a single location in the database. Numbers in the graph indicate the number of endemic species at each location. To simplify the figure, we combined endemic species of nearby locations into a single number. These locations are enclosed with a red line.

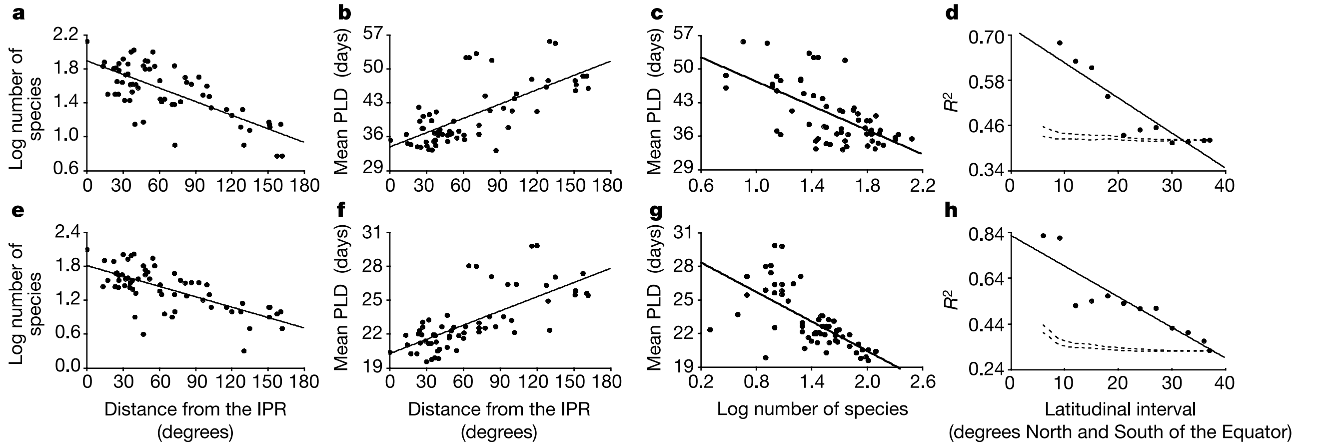

Figure 3 Pairwise comparisons of species richness, pelagic larval duration and distance from the Indonesian and Philippine region. Data is shown for Labridae (**a**: $r = -0.73$, $P < 0.001$; **b**: $r = 0.70$, $n = 62$, $P < 0.001$; **c**: $r = -0.64$, $n = 62$, $P < 0.001$) and Pomacentridae (**e**: $r = -0.69$, $P < 0.001$; **f**: $r = 0.72$, $P < 0.001$; **g**: $r = -0.67$, $P < 0.001$). The sample size in all correlations, except **b** and **c**, was 63 locations between 29° N and 29° S. Panels **d** and **h** show the coefficients of determination for regression analyses between species richness (dependent variable) and mean pelagic larval duration (PLD) (independent variable) for 12 latitudinal intervals (**d**: Labridae: $r = -0.92$, $P < 0.001$; and **h**: Pomacentridae: $r = -0.90$, $P < 0.001$). We tested the extent to which the latitudinal pattern in the coefficient of determination was a statistical artefact by simulating the regressions for each latitudinal interval, using the same number of locations, but randomly selecting these from all latitudes. Dotted lines are 95% limits of confidence for coefficients of determination of 1,000 regression analyses for each of the 12 latitudinal intervals.

among the highest number of islands per unit of geographical area makes it a place where allopatric speciation might be frequent, especially when considering patterns of recent geological sea level change. Whatever the ultimate causal factor, the IPR seems to be a centre of species origination and a source of species for reef fish communities in the Indian and Pacific oceans.

The notion that reef fishes originate in the IPR and disperse to marginal communities leads to two testable predictions about patterns in reef fish biodiversity: (1) both the longitudinal and latitudinal gradients of species richness, as one moves away from the IPR, are due to variation in dispersal abilities; and (2) this process will supply the species structuring communities marginal to the IPR. To test the first prediction, we correlated data on species richness for all locations analysed with the mean pelagic larval duration (PLD) of the species inhabiting those locations. This analysis was restricted to labrids and pomacentrids, the only families for which extensive information on PLD exists (see Methods). We found that species richness in both families was negatively correlated with distance from the IPR (Fig. 3a, e), and that mean PLD for these families increased with increasing distance from the IPR[19] (Fig. 3b, f). Consequently, species richness was negatively correlated with mean PLD at local sites (Fig. 3c, g). These results indicate that species richness declines as one moves away from the IPR, probably owing to limitations in dispersal. Using multiple regression analysis, we found that 57% and 60% of the geographical variation in species richness of Labridae and Pomacentridae, respectively, was explained by PLD and distance from the IPR.

Interestingly, we also found that communities at high latitudes were usually outliers in the relationship between PLD and species richness. The geographical variation in species richness that is explained by PLD increases when the latitudinal scope of the analysis is reduced (Fig. 3d, h). We presume that shallow-water habitats, which are poorly interconnected in longitude owing to deep-water gaps between islands and coasts, but continuous in latitude owing to the margins of the continents, make PLD more critical for expansion in longitude than for expansion in latitude. Additionally, sharp barriers (for example, current and temperature shifts) may limit species expansion at high latitudes regardless of PLD[20]. This suggests that PLD gains additional importance for species distribution and richness where geographical isolation is predominant, and that, owing to the shape of the Indian and Pacific oceans, the extent to which different processes regulate local communities may vary geographically. Assembly of local communities at lower latitudes is probably determined by the distance to, and the abilities of species to disperse across, open water from the IPR, whereas extreme abiotic factors may cause local extinctions at higher latitudes regardless of dispersal capabilities.

If the IPR is a centre of origin and a source of species to reef fish communities in the Indian and Pacific oceans and if local processes affect local diversity only minimally, then reef fish communities throughout this region should have a large number of species in common with the IPR. Indeed, we found that about 86% of the species comprising reef fish assemblages in the Indian and Pacific oceans were species present in the IPR, a result that differs from expectations based on random assembly (Fig. 4). Moreover, local speciation seems to have a minor role in structuring marginal communities given that only around 2% of the species in any community were endemics (Fig. 4). These results suggest that speciation in and dispersal from the IPR play a major role in assembling communities in the Indian and Pacific oceans. That is, dispersal governs which species from the IPR are capable of reaching communities at marginal locations. The fact that the total number of species present in any location is almost equal to the number of

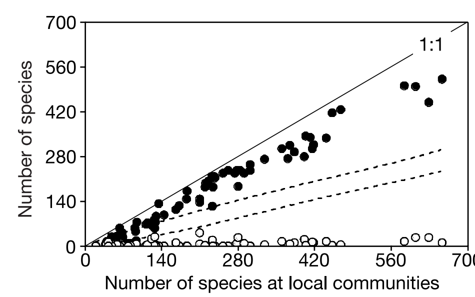

Figure 4 Contribution of IPR and endemic species to local reef fish assemblages in the Indian and Pacific oceans. Filled circles, IPR species; open circles, endemic species. We assessed the extent to which the number of IPR species at local communities is due to chance by determining the number of IPR species in communities (of the same size as observed) randomly generated from the total species pool (species selected with equal probability and without replacement). The upper and lower limits of the number of IPR species in 1,000 iterations for each community are shown as broken lines.

species that it shares with the IPR suggests that no location contributes as much to the overall alpha diversity of the Indian and Pacific oceans as does the IPR.

The distribution of biodiversity on Earth can be described in terms of a few well documented, and intriguing, small- to large-scale patterns. Our findings recognize a major link between the evolutionary processes regulating these patterns. That is, the processes of speciation, extinction and dispersal that yield large-scale patterns of species richness also seem to determine which species are present within local assemblages. Given the importance of the IPR to the overall structure of reef fish assemblages in the Indian and Pacific oceans, it should certainly be a target for strategic management and protection. □

Methods

Analyses were based on the presence or absence of 1,970 reef fish species in 70 locations in the Indian and Pacific oceans. These species belong to the families Labridae, Pomacentridae, Serranidae, Blenniidae, Apogonidae, Chaetodontidae, Acanthuridae, Scaridae, Holocentridae, Lutjanidae, Pomacanthidae, Scorpaenidae and Lethrinidae. These families are among the most diverse, best-known taxonomically, and represent >70% of the total species expected in any community. Owing to the high covariation in species richness among families[8], these families are a good indicator for the remaining diversity of species. The database includes all data from the 63 locations used in ref. 8. Data for the following locations were added: the Philippines, Madagascar, Easter Island, Cook Islands (all from www.fishbase.org), Cocos Keeling[21]; Gorgona Reef[22]; and Korea (http://ricos.cnu.ac.kr/~kocofish/list/elistintro.htm). Data for the following locations were updated: Galapagos[23]; Gulf of California[24]; and Malpelo (C.M., personal observations). All species records were corrected for synonymy and other taxonomic problems using The Catalog of Fishes (http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html). More than 300 species were duplicated in the original database as a result of synonymy, misspelled names or misallocation of species to families.

Pelagic larval durations were obtained for 95 labrid species and 116 pomacentrids. These species represent 28% of all labrid species and 42% of the pomacentrids. Data were obtained from references 19, 25–27.

Received 8 October; accepted 27 December 2002; doi:10.1038/nature01393.

1. Walther, G. R. *et al.* Ecological responses to recent climate change. *Nature* **416,** 389–395 (2002).
2. Chapin, F. S. I. *et al.* Consequences of changing diversity. *Nature* **405,** 234–242 (2000).
3. Roberts, C. M. & Hawkins, J. P. Extinction in the sea. *Trends Ecol. Evol.* **14,** 241–246 (1999).
4. Roberts, C. M. *et al.* Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295,** 1280–1284 (2002).
5. Gaston, K. J. Global patterns in biodiversity. *Nature* **405,** 220–227 (2000).
6. Keddy, P. & Weiher, E. in *Ecological Assembly Rules* (eds Weiher, E. & Keddy, P) 1–20 (Cambridge Univ. Press, Cambridge, UK, 1999).
7. Cornell, H. V. & Karlson, R. H. Coral species richness: Ecological vs. biogeographical influences. *Coral Reefs* **19,** 37–49 (2000).
8. Bellwood, D. & Hughes, T. Regional-assembly rules and biodiversity of coral reefs. *Science* **292,** 1532–1535 (2001).
9. Veron, J. E. N. *Corals in Space and Time: The Biogeography and Evolution of the Scleractinia* (UNSW Press, Sydney, 1995).
10. Colwell, R. K. & Lees, D. C. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* **15,** 70–76 (2000).
11. Springer, V. G. Pacific plate biogeography, with special reference to shorefishes. *Smithson. Contrib. Zool.* **177,** 1–182 (1982).
12. Bellwood, D. R. & Wainwright, P. C. in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P. F.) 5–32 (Academic, San Diego, California, 2002).
13. Harmelin-Vivien, M. L. in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P. F.) 265–274 (Academic, San Diego, California, 2002).
14. Rosenzweig, M. L. *Species Diversity in Space in Time* (Cambridge Univ. Press, Cambridge, UK, 1995).
15. Caley, M. J. & Schluter, D. The relationship between local and regional diversity. *Ecology* **78,** 70–80 (1997).
16. Karlson, R. H. & Cornell, H. V. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecol. Monogr.* **68,** 259–274 (1998).
17. Planes, S. in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P. F.) 201–220 (Academic, San Diego, California, 2002).
18. Hughes, T. P., Bellwood, D. R. & Connolly, S. R. Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecol. Lett.* **5,** 775–784 (2002).
19. Bonhomme, F. & Planes, S. Some evolutionary arguments about what maintains the pelagic interval in reef fishes. *Environ. Biol. Fish.* **59,** 365–383 (2000).
20. Gaylord, B. & Gaines, S. D. Temperature or transport: species range boundaries mediated solely by flow. *Am. Nat.* **115,** 769–789 (2000).
21. Allen, G. R. & Smith-Vaniz, W. F. Fishes of the Cocos (Keeling) Islands. *Atoll Res. Bull.* **412,** 1–21 (1994).
22. Zapata, F. & Moralez, Y. A. Spatial and temporal pattern of fish diversity in a coral reef at Gorgona Island, Colombia. *Proc. 8th Int. Coral Reef Symp.* **1,** 1029–1034 (1998).
23. Grove, J. S. & Lavenberg, R. J. *The Fishes of the Galapagos Islands* (Stanford Univ. Press, Stanford, 1997).
24. Thomson, D. A., Findley, L. T. & Kerstich, A. N. *Reef Fishes of the Sea of Cortez* (Univ. Texas Press, Austin, 1999).
25. Victor, B. C. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Mar. Biol.* **90,** 317–326 (1986).
26. Victor, B. C. & Wellington, G. M. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* **205,** 241–248 (2000).
27. Victor, B. C. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Mar. Biol.* **101,** 557–567 (1989).

Acknowledgements We thank R. H. Karlson, J. Lovett-Doust, F. Zapata, J. Ciborowski and D. Hogan for discussion and comments. The staff at the Leddy Library (University of Windsor) assisted in obtaining copies of the manuscripts required to build the database. Funding was provided by NSERC (to P.F.S.) and OGS (to C.M. and P.M.C.).

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to C.M. (e-mail: moracamilo@hotmail.com).

Mechanism of genetic exchange in American trypanosomes

Michael W. Gaunt*, Matthew Yeo*, Iain A. Frame*†, J. Russell Stothard†‡, Hernan J. Carrasco§, Martin C. Taylor*, Susana Solis Mena*, Paul Veazey*, Graham A. J. Miles*, Nidia Acosta||, Antonieta Rojas de Arias|| & Michael A. Miles*

* *Department of Infectious and Tropical Diseases, London School of Hygiene and Tropical Medicine, Keppel Street, London WC1E 7HT, UK*
‡ *Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
§ *Facultad de Medicina, Universidad Central de Venezuela, Caracas, Venezuela*
|| *Departamento de Medicina Tropical, Instituto de Investigaciones en Ciencias de la Salud, Universidad Nacional de Asuncion, Asuncion, Paraguay*

The kinetoplastid Protozoa are responsible for devastating diseases[1]. In the Americas, *Trypanosoma cruzi* is the agent of Chagas' disease—a widespread disease transmissible from animals to humans (zoonosis)—which is transmitted by exposure to infected faeces of blood-sucking triatomine bugs[2]. The presence of genetic exchange in *T. cruzi* and in *Leishmania* is much debated[3,4]. Here, by producing hybrid clones, we show that *T. cruzi* has an extant capacity for genetic exchange. The mechanism is unusual and distinct from that proposed for the African trypanosome, *Trypanosoma brucei*[5]. Two biological clones[6] of *T. cruzi* were transfected to carry different drug-resistance markers[7,8], and were passaged together through the entire life cycle. Six double-drug-resistant progeny clones, recovered from the mammalian stage of the life cycle, show fusion of parental genotypes, loss of alleles, homologous recombination, and uniparental inheritance of kinetoplast maxicircle DNA. There are strong genetic parallels between these experimental hybrids and the genotypes among natural isolates of *T. cruzi*. In this instance, aneuploidy through nuclear hybridization results in recombination across far greater genetic distances than mendelian genetic exchange. This mechanism also parallels genome duplication[9,10].

The species *T. cruzi* is divided into two divisions (I and II) on the basis of isoenzyme phenotypes, DNA profiles, ribosomal and mini-exon DNA sequence polymorphisms, and microsatellite analysis[11–13]. In addition, *T. cruzi* II, which predominates where Chagas' disease is more severe[14], can be divided into up to five sublineages (IIa–e)[11,15]. Population genetics has emphasized clonal propagation and the lack of genetic exchange in *T. cruzi* when natural isolates, from dispersed geographical localities, have been tested for random mendelian genetic exchange[4,8,16]. Nevertheless, recent phylogenetic evidence suggests that *T. cruzi* IId and IIe may have an ancient hybrid origin[3,16]. Surprisingly, meticulous quantification studies demonstrated that

† Present address: The Wellcome Trust, 183 Euston Road, London NW1 2BE, UK (I.A.F.); Department of Infectious Disease Epidemiology, Imperial College, London W2 1PG, UK (J.R.S.).

