

The center of the center of marine shore fish biodiversity: the Philippine Islands

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Synopsis

Multiple datasets show global maxima of marine biodiversity in the Indo–Malay–Philippines archipelago (IMPA). Analysis of distribution data for 2983 species reveals a pattern of richness on a finer scale and identifies a peak of marine biodiversity in the central Philippine Islands and a secondary peak between peninsular Malaysia and Sumatra. This pattern is repeated in diverse habitat and higher taxa classes, most rigorously for marine shore fishes, supporting geohistorical hypotheses as the most general unifying explanations. Specific predictions based on area of overlap, area of accumulation, and area of refuge hypotheses suggest that present day eastern Indonesia, or Wallacea, should be the center of marine biodiversity. Processes suggested by these three hypotheses contribute to the diversity in this region and are also a likely explanation for the secondary center of diversity. Our study indicates, however, that there is a higher concentration of species per unit area in the Philippines than anywhere in Indonesia, including Wallacea. The Philippine center of diversity is consistent with hypotheses that this area experienced numerous vicariant and island integration events and these hypotheses warrant further testing. Special attention to marine conservation efforts in the Philippines is justified because of the identification of it as an epicenter of biodiversity and evolution.

Introduction

The Indo-Malay-Philippines Archipelago (IMPA) has long been considered the area of highest marine biodiversity, with decreasing latitudinal and longitudinal gradients in species richness radiating from this center (Bellwood & Wainwright 2002, Mora et al. 2003). There is a wide variety of hypotheses that have been proposed to explain the remarkable diversity found in the IMPA (Rosen 1988). These hypotheses can be classified into four main categories: (1) area of overlap, (2) area of accumulation, (3) area of refuge, and (4) center of origin. There is little agreement as to which of these hypotheses is the most important in shaping diversity in the IMPA

(Bellwood & Wainwright 2002). Reconciling the relative importance of these opposing hypotheses has led some to propose what could be considered a fifth major hypothesis: that a combination of all processes evoked in these hypotheses is responsible for the extreme biodiversity of the IMPA (Palumbi 1996, Wallace 1997, Carpenter 1998, Randall 1998, Wilson & Rosen 1998, Allen & Adrim 2003).

Predictions about concentrations of diversity within the IMPA can be made based on the various hypotheses and the geography and geology of the IMPA. One assumption in these predictions is that large shelf areas of the IMPA were exposed and therefore experienced a series of local marine extinctions during Pleistocene sea-level lows (Springer & Williams 1990, Voris 2000, Figure 1)

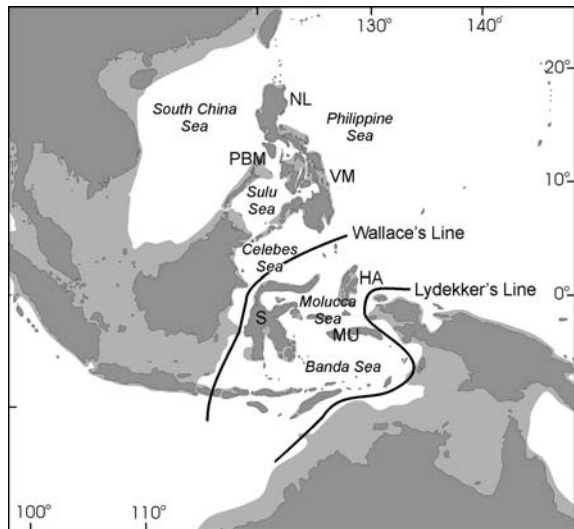


Figure 1. The Indo-Malay-Philippine Archipelago with the area shallower than the 120 m depth contour delineated in light gray. This area estimates the sea bottom that would have been exposed during Pleistocene sea-level lows. Major land masses include the Palawan–Busuanga–Mindoro archipelago (PBM), northern Luzon (NL), Visayas–Mindanao (VM), Halmahera (HA), Moluccas (MU), and Sulawesi (S). Reproduced and modified with permission from Voris (2000), copyright Field Museum of Natural History, Chicago.

and potentially limited diversity in these areas. With these Pleistocene exposed areas excluded, the two major marine habitat areas remaining in the IMPA are the Philippine Islands and the area referred to primarily by terrestrial biologists as Wallacea. Wallacea is a term not frequently used by marine biogeographers (Wallace 1997) and is typically defined as the area between the famed Wallace's (1860) line and Lydekker's line (Simpson 1977, Figure 1). We use it here as a convenient term to refer to the area which encompasses the island groups of Sulawesi, Moluccas, Halmahera, and the Lesser Sunda Islands. The area of overlap, area of accumulation, and area of refuge hypotheses suggest Wallacea as an area of likely peak marine diversity.

Area of overlap hypotheses contend the IMPA is an area where different faunas from different oceans or lithospheric plates aggregate. Overlap between Pacific and Indian Ocean faunas (Woodland 1983, Donaldson 1986) would concentrate diversity in the Wallacean corridor because it is centrally located and has ample habitat to support species. Throughout the later half of the

Cenozoic, elements of Wallacea were positioned across the central dispersal route between the Pacific and Indian oceans. Up until the mid-Miocene, the south equatorial current spanned the Pacific and Indian oceans (Kennett et al. 1985, Figure 2). During the Oligocene and much of the Miocene, elements of Wallacea had mostly formed and were in the path of the Indonesian Seaway that connected the Pacific and Indian oceans (Hall 1998). The Indian Ocean south equatorial current would also have been in contact with elements of Wallacea (Figure 2).

Australian and Eurasian continental shelves collided and deflected the southern equatorial currents somewhere between 16 and 8 mya (Kennett et al. 1985) and formed an equatorial barrier between the Pacific and Indian oceans. This transformed the southern equatorial currents into boundary currents and the surface current patterns seen today began to take shape (Figure 3). Throughout the late Miocene and Pliocene the major island groups of Wallacea were in the primary pathway of currents flowing eastward from the Indian Ocean and westward from the Pacific Ocean (Hall 1998). During the Holocene and times of Pleistocene sea-level highs, Indian and Pacific Ocean exchange occurred primarily

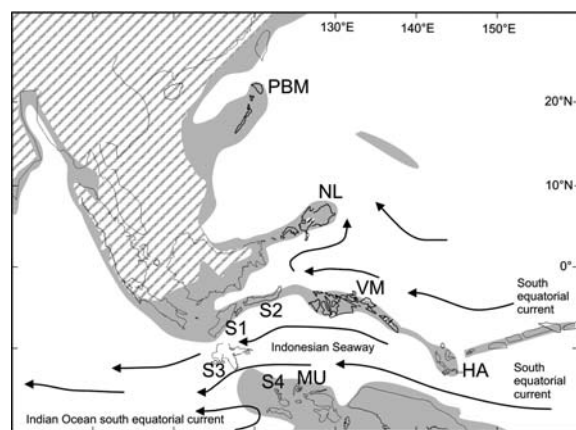


Figure 2. Position of land (diagonal lines), shallow seas (gray), and deep ocean (no color) in Southeast Asia 30 million years ago. Relative position of present-day land masses are drawn with respect to these ancient features, including the Palawan–Busuanga–Mindoro archipelago (PBM), northern Luzon (NL), Visayas–Mindanao (VM), Halmahera (HA), Moluccas (MU), and four components of Sulawesi (S1–S4). Modified from Hall (2002).

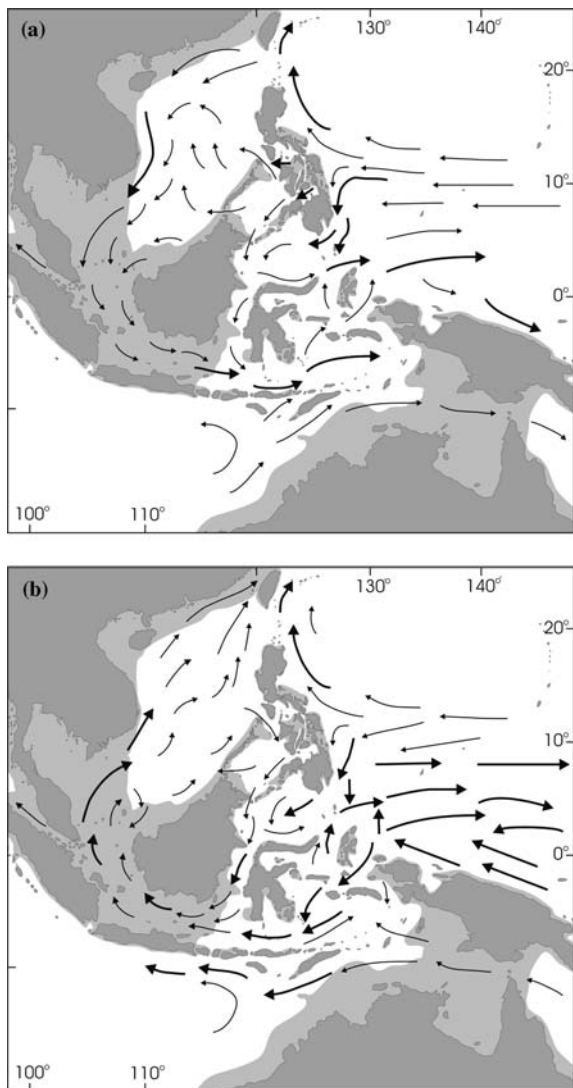


Figure 3. Present-day surface current patterns in the IMPA. (a) Winter, (b) Summer. Light gray indicates areas shallower than the 120 m depth contour that would have been exposed during extreme Pleistocene sea-level lows [current patterns modified from Morgan & Valencia (1983), base map modified from Voris (2000)].

through Wallacea (Flemming 1986, Fine et al. 1994, Figure 3). During Pleistocene sea-level lows, the only pathway between equatorial Pacific and Indian oceans was through Wallacea (Flemming 1986, Figure 3).

The IMPA is also considered an area of overlap with different endemic shore faunas 'rafting' into the area through the movement of

lithospheric plates (Pandolfi 1992, Wilson & Rosen 1998, Santini & Winterbottom 2002). Collision zones between plates would concentrate different faunas. A primary overlap area would be the triple junction zone, located in eastern Wallacea (Figure 4).

The area of accumulation hypothesis (also called the vortex hypothesis) suggests most speciation occurred on remote Pacific islands and prevailing currents concentrated species in the IMPA (Ladd 1960, Jokiel & Martinelli 1992, Connolly et al. 2003). A prediction from this hypothesis is that Wallacea would be a center of diversity within the IMPA based on prevailing currents. The middle to late Cenozoic Pacific equatorial currents primarily flow towards elements of Wallacea (Figures 2 and 3, Kennett et al. 1985, Hall 1998).

Related to the area of accumulation hypothesis is that the IMPA also serves as an area of refuge (Bellwood & Hughes 2001) because it encompasses

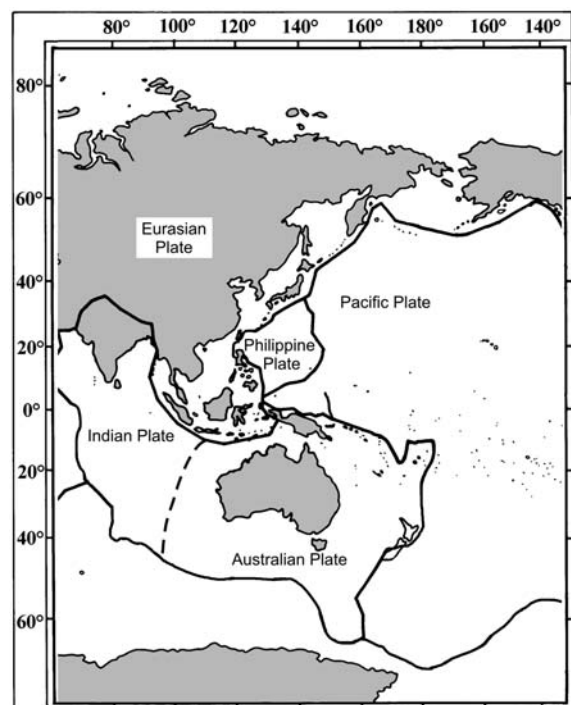


Figure 4. Present-day location of major lithospheric plates of the IMPA as delineated by major subduction zones (black lines). The dashed line indicates the approximate location of the rift zone that separated the Indian and Australian plates in the early Cenozoic.

the most extensive and diverse tropical shallow water marine habitat on earth (Carpenter 1998). The significance of extensive tropical refugia relates to the ecological maxim that larger areas generally support more species than smaller areas and that tropical low latitude habitats have greater available energy to support biomass than cooler latitudes (Gaston 2000). The area of refuge hypothesis would predict that the Indonesian–Malaysian part of the IMPA will have the highest species richness. This area has the greatest extent on earth of tropical shallow water habitat (Carpenter 1998), including the greatest extent of coral reefs (Spalding et al. 2001) and diversity of habitat types (Woodland 1990, Randall 1998).

The center of origin hypothesis predicts that areas of highest diversity would be areas that hosted numerous allopatric speciation events (McManus 1985, Briggs 1999a, Mora et al. 2003). The center of origin hypothesis has also been proposed in terms of numerous competitive or sympatric speciation events (Briggs 1999b) but this mechanism has been dismissed as an important means of speciation in the IMPA (Springer & Williams 1990, Santini & Winterbottom 2002). Both Wallacea and the Philippines are potential areas of concentrated allopatric speciation. Two major vicariant processes occurred within the IMPA during the Cenozoic when most of the shore fish fauna evolved. These were: (1) potential isolation of seas during Pleistocene sea-level lows (McManus 1985) and (2) geological origin through complex tectonic movements (Hall 2002). A number of seas within Wallacea and the Philippines were potentially isolated from one another to varying degrees during Pleistocene fluctuations in sea level. These included the South China, Sulu, Philippine, Celebes, Molucca, and Banda seas (Figure 1). The origins of the Philippine and Wallacean island arcs are particularly complicated because of integration of varied Philippine plate elements (Hall 2002).

The purpose of this paper is to examine results of a geographical information system analysis of marine species found in the western central Pacific Ocean with respect to hypotheses proposed to explain the biodiversity found in the IMPA. We also comment on the importance of these findings with respect to conservation.

Methods and results

The geographical information system database and analyses

We used a geographical information system (GIS) overlay of 2983 generalized distributions of marine species (Carpenter & Niem 1998–2001) to examine the pattern of diversity in the IMPA. Species included seaweeds (62), corals (27), bivalves (189), gastropods (249), cephalopods (87), stomatopods (13), shrimps (110), lobsters (47), crabs (73), holothurians (18), sharks (150), batoid fishes (116), chimaeras (6), bony fishes (1775), estuarine crocodile (1), sea turtles (6), sea snakes (21), and marine mammals (33) produced by 84 specialists in their respective taxonomic groups (Carpenter & Niem 1998–2001 and authors cited therein). Taxa were from continental shelf and epipelagic environments. A subset of this database contains the 2047 shore fish species that included Elasmobranchii (sharks and batoid fishes), Holocephali (chimaeras), Sarcopterygii (Sulawesi coelacanth), and representatives from 24 orders of Teleostei.

The mix of species in this study includes mostly common fisheries species whose distributions are well known throughout the IMPA. It largely excludes species such as smaller gobioid or blennioid fishes for which distributions are mainly derived from sampling in highly restricted areas. Indonesia has a rich history of research on fishes beginning in the early 19th century, including very diverse collections made by the Dutch natural historian, Pieter Bleeker (Weber & deBeaufort 1913). Extensive collections around Indonesia continued through the present including notable surveys of trawled (Gloerfelt-Tarp & Kailola 1984) and coral reef fishes (Allen & Adrim 2003). There were limited studies of Philippine fishes in the 19th century (Herre 1953) but extensive collections began in the early 20th century (Smith & Williams 1999). Because of the extensive collections in both Indonesia and the Philippines, distribution records for common fisheries species would be thoroughly covered in both countries. And, since the distribution records are based primarily on museum collections and not fisheries statistics (taxonomists consider these mostly unreliable unless tied to a museum specimen), uneven fisheries pressure also would not influence these distributions. We do not,

therefore, suspect sampling bias in our dataset within the IMPA.

One potential source of bias in the current dataset is taxonomic bias in that fishes and vertebrates are covered in greater proportion to overall diversity than invertebrates. Far more species of invertebrates make up the diversity of the IMPA than the fishes but these are not as important proportionally in fisheries. This is particularly the case when it comes to corals that make up a conspicuous part of the macrofaunal invertebrate fauna of the IMPA. Taxonomic bias has been criticized in other biogeographic studies (Baird et al. 2002, Roberts et al. 2002). We examine all the maps in combined analyses and also examine a partition including only the shore fishes since this later group was covered more rigorously.

All 2983 generalized maps were digitized in PC ArcInfo and analyzed using ArcView (Environmental Systems Research Institute, Inc.) with a cell size set at 10 km × 10 km. Species were chosen based on their likelihood to enter fisheries in the western central Pacific FAO fishing area 71 and the South Pacific Commission Area (Carpenter 1998). This region corresponds to most of the tropical and subtropical western Pacific from about 98°E to 122°W longitude excluding the Hawaiian Islands and Johnston Island.

The distribution of each species was categorized according to concordance with a major lithospheric plate (Figure 4). If the major portion of a species distribution was found on one lithospheric plate but it extended marginally onto another plate it was considered endemic only to the plate that it covered most completely. These plates were the Eurasian plate (including the Philippine and Moluccan marginal arc systems), the Pacific plate, the Indian plate, and the Australian plate. The Indian and Australian plates are currently considered a single plate. However, these plates were separated during the early Cenozoic (Hall 2002, Figure 4) and the shore faunas on these plates were widely separated and presumably evolved separately. In addition, the Indian portion of the Indo-Australian plate was not directly encompassed in this study. The Philippine Sea plate is also a major lithospheric plate but is mostly open sea with few identifiable endemics (Myers 1989) when its marginal arc island systems are considered part of Eurasian or Australian

shore faunas. Distributions covering more than incidentally one lithospheric plate were categorized as: Indian–Eurasian, Eurasian–Australian, Western Pacific (distributions that encompassed inclusively the Eurasian, Pacific, Philippine, and Australian plates), Indo-westmost (species found inclusively on the Indian, Australian, and Eurasian plates but not extending onto the Pacific plate), and Indo-West Pacific (widespread on all Indian and Pacific ocean plates). Habitat type was categorized as to either primary coral reef, primary soft bottom, rocky, estuarine, generalized demersal, generalized neritic, and epipelagic habitat types if this was indicated in the habitat section of each species account (Carpenter & Niem 1998–2001).

Results from preliminary GIS analyses

Analysis of the 2983 combined ranges reveals the central Philippines as the area of highest diversity and endemism (Figure 5a, b). A secondary area of high diversity is located between the tip of Malaysia and Sumatra and extends along northeastern Sumatra and northern Java (Figure 5a). Both diversity centers are repeated in subsets of data based on distribution, habitat, all invertebrate taxa, and shore fishes (Figure 5c–f, Table 1).

Families and genera with predominantly small-bodied species, which tend to have a higher proportion of restricted-range endemics than taxa with large-bodied species, were not included in our study. Nevertheless, 120 restricted-range endemics were included because they enter area fisheries. The greatest concentration of these restricted-range endemics is in the Philippines (Figure 5b) which has 38. Indonesia/Malaysia has 19 such endemics, Australia 18, New Guinea/Bismark/Louisade 18, Coral Sea/New Caledonia/Vanuatu 17, and seven other localities had either one or two endemics.

Analysis of distribution and habitat types in the primary and secondary center of diversity

To examine the components of biodiversity we analyzed the frequencies of general distribution and habitat types in the primary and secondary centers of diversity. We used the assemblage of species in the single 10 km × 10 km pixel with the most species (1736 or about 58% of all species in

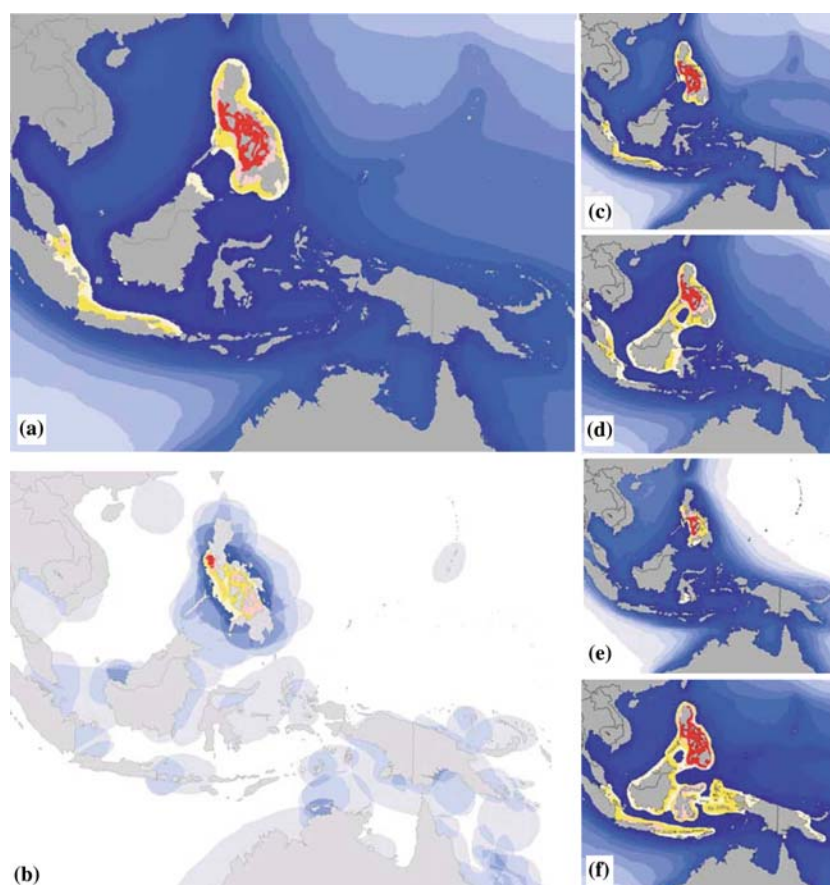


Figure 5. (a) Pattern of species richness in the IMPA from an overlay of the 2983 ranges of species. Each change in color or shade represents an increase or decrease in 43 species (40 classes total or a 2.5% change per class). The top 10% of species richness is in shades of red and yellow and the remaining decreasing increments of species richness are indicated by lighter shades of blue. The greatest diversity is red (1693 to 1736 species), followed by pink (1650 to 1692 species), yellow (1606 to 1649 species), and light yellow (1563 to 1605 species). (b) Overlap of restricted-range endemic species in the IMPA from the 120 of these endemics covered in this study. Each darker shade of blue indicates an increase in one restricted-range endemic overlapping in the area; red indicates the highest area of overlap with 19–20 endemics; pink indicates overlap of 17–18 endemics; yellow indicates an overlap of 15–16 endemics; light yellow indicates an overlap of 13–14 endemics. (c–f) Each change in color or shade represents an increase or decrease in 2.5% of the maximum number of species found in any one spot; the top 10% of species richness is in shades of red and yellow and remaining decreasing increments of species richness are indicated by lighter shades of blue. The greatest diversity is red (highest 2.5%), followed by pink (highest 2.5–5%), yellow (highest 5–7.5%), and light yellow (highest 7.5–10%). (c) All fish species (maximum overlap, 1010 species). (d) All invertebrate species (maximum overlap, 623 species). (e) Eurasian–Australian plate distributions (maximum overlap, 179 species). (f) Indo–West Pacific distributions (maximum overlap, 750 species).

the study), which is located in the Verde Island Passage (VIP) between Mindoro and Luzon. The cell with the greatest number of species in the secondary center of diversity near Pulau Bintan (PB) in Indonesia off the southern tip of peninsular Malaysia has 1670, or about 56% of all species in the study. Both the VIP and PB cells corresponded very closely with the primary and secondary peaks in shore fishes and were also used in a separate

analysis of shore fish distributions. Expected frequencies were calculated from the combined database or all shore fishes separately. For distribution types this included all species that could potentially be found on the Eurasian plate (i.e. excluding Pacific and Australian plate endemics). For habitat types this encompassed the entire dataset. Expected frequencies of distribution categories and habitat types from the VIP and PB

Table 1. Areas with highest diversity according to different categories of distribution type, habitat type, and major taxonomic groups.

| Distribution/ Habitat/Taxa | Highest diversity | Secondary diversity |
|---------------------------------|------------------------|---------------------------|
| All maps | Central Philippines | NE Sumatra–N Java |
| Australian plate | SE Queensland | none |
| Eurasian plate | W Taiwan | SW Luzon |
| Indo-West Pacific | Central Philippines | Sulawesi, N Java |
| Indian-Eurasian plate | Straits of Malacca | none |
| Western Pacific | Central Philippines | none |
| Indo-westmost Pacific | NE Sumatra–N Java | Central Philippines |
| Eurasian + Australian plates | Central Philippines | none |
| Coral Reefs | Central Philippines | Sulawesi, N Sunda Ids. |
| All soft bottoms | NE Sumatra | Central Philippines |
| Estuarine | NE Sumatra | S Kalimantan |
| All invertebrates | Central Philippines | NE Sumatra, N Sabah |
| All fish | Central Philippines | N Java |

Highest diversity was defined as cells with the upper 5% of the maximum diversity (the red and pink areas of Figure 5a). Secondary diversity was defined as those cells with 5–10% of maximum diversity.

centers of diversity differed significantly ($X^2 = p < 0.001$; Table 2) from frequencies expected for all distributions and for shore fishes separately. The VIP and PB centers had significantly greater frequencies ($p < 0.001$) of widespread Indo-Pacific distributions, widespread Indo-westmost Pacific distributions, and coral reef species than overall and shore fish expected frequencies. Both centers had significantly fewer ($p < 0.001$) Eurasian plate endemics and generalized demersal species compared to expected frequencies. The VIP center had significantly fewer ($p < 0.001$) Indian–Eurasian plate distributions than expected frequencies.

Statistical comparison of observed versus predicted primary centers of diversity

According to predictions from area of overlap, area of accumulation, and area of refuge hypoth-

eses, Wallacea should have the highest species richness. To test if the observed center of diversity had a significantly higher species richness than that observed in the predicted area, a random subsample of 50 cells were chosen from continental shelf areas within each of the Philippine area and the Sulawesi–Moluccan area of Indonesia. After a test of normality, a *t*-test was performed (more sophisticated Monte Carlo simulation methods were considered but the strength of the *t*-test and readily apparent distribution of species concentrations make it obvious that such a test is unnecessary). The Philippine center of diversity was found to have significantly higher species richness ($p < 0.001$) than Wallacea for all distributions combined and also when shore fish distributions are treated separately. A similar comparison with the Pulau Bintan area of secondary diversity also indicates that the central Philippines has a significantly higher species richness ($p < 0.001$).

Discussion

A Philippine center of marine diversity is both supported and refuted by previous studies. The Philippines is shown with highest diversity at different taxonomic levels in some biogeographical studies (e.g., Springer 1982, Woodland 1983). Randall (1998), however, used expected rates of discovery of new species to predict that the greatest diversity of shore fishes would eventually be recorded from Indonesia, which has far greater shelf area and over twice the reef area of the Philippines (Spalding et al. 2001). Allen & Adrim (2003) indicate that Indonesia has the highest coral reef fish diversity. Because of its greater area, Indonesia may eventually be shown to have a greater overall marine biodiversity than the Philippines. However, there is a higher concentration of species per unit area in the Philippines than anywhere in Indonesia, including Wallacea, according to our study.

Identification of the center of marine biodiversity provides tests of the various hypotheses that have been proposed to explain the remarkable diversity found in the IMPA. The central Philippine center of diversity falsifies predictions from at least three of four major categories of these

Table 2. Observed and expected frequencies of distribution and habitat types in the Philippine Verde Island Passage (VIP) area of highest diversity and secondary area of high diversity near Pulau Bintan (PB) in Indonesia for all distributions combined and separately for shorefishes.

| Distribution & Habitat type | All taxa | | | Fish | | |
|-------------------------------|----------|--------|----------|--------|--------|----------|
| | VIP | PB | Expected | VIP | PB | Expected |
| Circumtropical + Circumglobal | 7.09 | 6.59 | 7.92 | 7.33 | 6.42 | 8.58 |
| Eurasian plate | 6.39* | 6.41* | 12.81* | 5.75* | 5.80* | 13.79* |
| Indo–West Pacific | 42.91* | 41.68* | 32.92* | 40.63* | 38.41* | 29.11* |
| Indian–Eurasian plate | 3.80* | 8.68 | 7.13* | 3.07* | 9.94 | 7.22* |
| Western Pacific | 9.45 | 6.11 | 8.86 | 10.60 | 6.21* | 9.35* |
| Indo-westmost Pacific | 20.45 | 22.46* | 18.93* | 21.41 | 23.91* | 19.35* |
| Eurasian + Australian plates | 9.91 | 8.08 | 11.44 | 11.20 | 9.32 | 12.60 |
| All Soft bottoms | 35.37 | 37.72 | 36.74 | 25.97* | 30.33 | 30.92* |
| Coral Reef | 28.57* | 25.45* | 21.99* | 37.07* | 32.09* | 25.16* |
| Mostly rocky | 14.63 | 13.35 | 12.34 | 7.73 | 6.63 | 8.11 |
| Estuarine/fresh water | 3.17 | 3.59 | 4.46 | 2.58 | 2.59 | 4.49 |
| Demersal hard & soft bottoms | 2.13* | 2.28* | 5.80* | 3.27* | 3.21* | 7.43* |
| Neritic demersal and pelagic | 6.97 | 7.60 | 7.81 | 9.71 | 10.46 | 9.53 |
| Epipelagic & deep pelagic | 9.16 | 10.00 | 10.86 | 13.68 | 14.70 | 14.36 |

An asterisk (*) indicates a significant ($p < 0.001$) difference in observed versus expected frequencies. All numbers are percentages based on: 1736 total taxa at VIP, 1670 total taxa at PB, 2552 total taxa expected distributions possible on the Eurasian plate, 2983 total taxa possible for expected habitat types, 1009 shorefishes at VIP, 966 shorefishes at PB, 1690 shorefishes expected distributions possible on Eurasian plate, and 2047 total shorefishes for expected habitat types.

hypotheses. Different interpretations of the area of overlap hypotheses indicate that Wallacea is the likely center of overlap. The central Philippines are removed northwesterly from the potential central zone of overlap between Pacific and Indian Ocean biotas. The Philippines are also removed from the triple juncture zone of Pacific, Australian, and Eurasian plates and further removed from the broad collision zone between Indian–Australian and Eurasian plates (Figure 4). The distribution of species found only on the Eurasian and Australian plates shows a Philippine center of diversity (Figure 5e, Table 1). Assuming that species with this distribution type originated on one of the plates and subsequently dispersed to the other plate, the expected zone of overlap would be the boundary zone. The Philippine center of diversity for this distribution type does not support the idea that species originating on these plates should overlap at their boundary, unless there is uneven extinction occurring in the IMPA. There is evidence that extinction within the IMPA influenced distributions, presumably because of land loss (Voris 2000, Figure 1), cooling (Flemming 1986), or presumed increased turbidity during Pleistocene gla-

cial maxima (Springer & Williams 1990). However, both the Philippines and Wallacea are in the warmest region of the oceans, the western Pacific warm pool, which would have undergone approximately 3°C decrease during the last glacial maximum (Lea et al. 2000). Both areas also have ample deep water as refuge from lowered sea level (Figure 1). Although Pleistocene glacial events undoubtedly excluded shallow water species from large areas and presented barriers to dispersal (Flemming 1986), there is no apparent reason to predict that extinction would have occurred more frequently in either the Philippines or Wallacea. Therefore, the Philippine center of diversity of Eurasian–Australian endemics suggests predominate origin on the Eurasian plate. This is consistent with routes of gene exchange away from the Philippines toward Australian and western Pacific areas observed in populations of the giant clam (Benzie & Williams 1997).

The direction of prevailing equatorial currents implicates Wallacea as the primary area of accumulation of species that originated on the Pacific plate. A center of diversity in the Philippines does not coincide with predictions from this

hypothesis. Both northern and southern equatorial currents enter Wallacea directly (Figure 3). The northern equatorial current does directly enter the Philippines but much of this is deflected as a boundary current and the majority of Pacific islands are in the South Pacific. To explain a Philippine center of diversity through accumulation requires invocation of secondary dispersal and special habitats in the Philippines that allowed species to thrive there preferentially over habitats across the Wallacean southern equatorial current corridor. We have no evidence of such special habitats in the Philippines.

The central Philippines center of diversity also appears to falsify predictions from the area of refuge hypothesis. The available shallow water habitat and insolation of the Philippines are substantially less than those of the Indo-Malay part of the IMPA.

The hypothesis that the IMPA is a center of origin is not falsified by the central Philippine epicenter of diversity. However, it is not readily apparent why geological events that promoted allopatric speciation may have been more prevalent in the Philippines than in Wallacea. Both regions host a number of sea basins that may have been isolated during Pleistocene sea level lows (McManus 1985, Figure 1). The geological origin of both the Philippines and Wallacea involved highly varied and concentrated island integration events (Rotondo et al. 1981, Hall 2002). Molecular phylogeographic studies of extant marine species show that population structuring within the IMPA occurs over distances as short as 300 km (Barber et al. 2000, Perrin & Borsa 2001). Allopatric speciation at the scale of Pleistocene isolated seas and Miocene and Pliocene elements of the Philippines and Wallacea is therefore plausible.

The Philippine epicenter of diversity suggests that the geological events that lead to allopatric speciation within the IMPA were more prevalent in the Philippines than in Wallacea. The sea basins around the Philippines do appear to have more potential for isolation than those around Wallacea. During Pleistocene ice ages, the South China, Sulu, Celebes, and Philippine seas were potentially isolated from one another through land barriers (Figure 1) and perhaps cooler surface sea temperatures or restriction of currents. It is also possible that smaller seas within the central

Philippines became isolated. The potential for isolation is not as readily apparent across the Celebes, Philippine, Molucca, and Banda seas (Figure 1).

Another aspect of the geological history that could have contributed to a concentration of species in the Philippines is the integration of islands that created the archipelago. Springer (1982) drew attention to Indonesia as a potential area of highest diversity because of proximity to frequent tectonic events associated with plate margins (Figure 2). Allen & Adrim (2003) point to the varied geological origins of Indonesia as a probable cause for the high diversity of coral reef fishes found there. The amalgamation of the diverse elements of Sulawesi is perhaps the most complicated of all major islands in the IMPA (Hall 2002, Figures 1 and 2). However, Hall's (2002) reconstructions of southeast Asia and southwest Pacific during Cenozoic show the Philippines as also having a highly complicated geological history. The Philippines are integrated from at least three major island systems that were widely separated during much of the Cenozoic (Hall 2002, Figure 2). Most of present-day Mindanao and eastern Visayas was a shallow sea in the early Cenozoic at a position equivalent to that currently occupied by Papua New Guinea. Northern Luzon, western Visayas, and other elements of Southeast Asian islands originated at this time near present-day eastern Borneo. Also in the early Cenozoic, the Palawan–Calamianes–Mindoro archipelago was associated with continental Eurasian lithospheric plate and were an established island arc continuous with the present-day island of Taiwan. Each of these three major elements were displaced over 1000 km to reach their current locations, with the Palawan–Calamianes–Mindoro archipelago moving mostly southeast, the northern Luzon–western Visayas mass moving mostly north and the Mindanao–eastern Visayas arc moving mostly west and north. During this time, the northern Luzon–western Visayas and Mindanao–eastern Visayas arcs were associated mostly with the Philippine lithospheric plate but later coalesced on what is currently recognized as the Eurasian lithospheric plate, with the primary subduction zone shifting to the eastern side of the Philippines. The amalgamation process created barriers when the larger islands took shape and potentially

separated populations and provided conditions for allopatric speciation. For example, present-day Negros collided with the southern tip of Luzon around 22 million years ago (Hall 2002) and separated previously contiguous eastern and western basins. In addition to potentially generating vicariant events, the accretion of the archipelago would also have concentrated diversity, assuming that the different elements of the Philippines developed their own endemic biotas. This island integration bioconcentration is consistent with the conclusions of Santini & Winterbottom (2002) who consider the derived fauna of the IMPA a consequence of different faunas rafting into the region through association with geologically diverse terranes. Hall's (2002) reconstructions of Wallacea also show complex geological origins with elements from Eurasian, Australian, and Philippine plates integrating. However, strong prevailing southern equatorial currents (Figure 2, Kennett et al. 1985, Hall 1998) and associated eddies may have prevented barriers and hence endemic biotas from forming, within the basins of proto-Wallacea during the Miocene and Pliocene.

The Philippines center of diversity has a significant overabundance of both widespread Indo-Pacific species (Figure 5f, Table 2) and species found on coral reefs indicating that it could be a source of widespread diversity. These two categories are expected to co-occur because coral reef species tend to be more widespread in their distributions than other shore species (41% of widespread Indo-Pacific species are coral reef species, although species in this primary habitat type comprise 22% of all distribution categories). This preponderance of widespread species is consistent with arguments by Springer & Williams (1990) that extinction may have played an important role in shaping Indo-Pacific diversity. Local extinction events would have a higher probability of eliminating limited-range endemics while widespread species would have had a better chance to survive. A Philippine center of origin is also consistent with recent evidence that the IMPA was a center of origin based on apparent dispersal to marginal areas distant from an IMPA center of endemism (Mora et al. 2003).

The potential for Miocene, Pliocene, and Pleistocene vicariance provides a credible explanation

for the primary center of diversity observed in the Philippines, but fails to explain the secondary concentration of diversity near Pulau Bintan of Indonesia (Figure 5a). This area would have experienced total extinction of local marine populations several times during the Pleistocene (Figure 1). Area of refuge, area of overlap, and area of accumulation hypotheses offer best explanations for this secondary area of diversity. This secondary center is in the middle of the largest and longest standing Cenozoic equatorial shelf area of the world, the Sunda Shelf, with ample shallow water habitats as refugia. Unlike the Philippine center, Pulau Bintan does not have a significantly lower frequency of Indian–Eurasian plate endemics (Table 2) and, therefore, potentially serves as an area of overlap between Indian and Pacific Ocean faunas. Similar to the Philippine center of diversity, the Pulau Bintan center has an overabundance of widespread Indo-West Pacific species (Table 2). As a potential refuge, this area of Indonesia could have accumulated widespread species that originated anywhere in the Indo-Pacific.

However, if the Philippine center of diversity is a result of concentrated vicariance, proximity to this center may have allowed the sunda shelf to flourish through accumulation. This area of accumulation hypothesis is different from the vortex hypothesis proposed by Jokiel & Martinelli (1992) in that the primary source for species origin is not the remote Pacific Islands, but the Philippine center of origin. And, the primary current dispersal vehicle is not the southern equatorial current but the surface circulation generated by monsoons. Holocene and Pleistocene current patterns within the IMPA are governed primarily by monsoons, although fluctuations in relative strength of paleomonsoons have varied (Huang et al. 1997). Monsoons would have also been a major factor for currents in the region during earlier Cenozoic, although the IMPA would also have been strongly influenced by the southern equatorial current prior to its deflection in the Miocene. The Pulau Bintan region is at a primary crossroads of monsoon currents and could have received surface dispersal from the Philippines during both seasonal monsoons (Figure 3). This area is bathed by southeasterly directed circulation from the South China Sea in winter (Figure 3a), and northwesterly directed circulations around Borneo from Wallacea and the

Celebes Sea in the summer (Figure 3b, Huang et al. 1997).

The Philippine and northern Sumatra areas are not the only diversity centers identified in our study. Another pattern that emerges from our analysis is the apparent marginal centers of diversity on the Australian and Eurasian plates (Table 1). Australian plate endemic diversity reaches a peak in southeastern Queensland, just south of the Great Barrier Reef. This peak in diversity is presumably the zone of overlap between tropical and temperate faunas. Likewise, an apparent zone of tropical–temperate overlap appears in Eurasian plate endemic diversity that reaches a peak at the island of Taiwan. Because the Philippine center of origin is substantially north of Wallacea, there is also the suspicion that it may be a zone of tropical–temperate overlap. However, the Philippine center of diversity has significantly fewer Eurasian plate endemics (Table 2) where most of the northern temperate biota in this study resides and, therefore, would not be substantially enhanced by temperate biota. The identification of the Australian and Eurasian plate endemic diversity peaks is likely a consequence of inclusion of many non-coral reef species. Only 22% of the species in our study were considered primary coral reef species and much of the temperate fauna that contribute to these marginal diversity peaks are obviously not primary coral reef species. A recent study utilizing a large database of both corals and coral reef fishes by Connolly et al. (2003) shows a peak in diversity outside the tropical latitudes of the IMPA. This observation may be a result of a temperate and tropical overlap of biotas since many reef species restricted to subtropical and temperate waters in the western Pacific are also found at extreme latitudinal limits of corals.

A test of the Philippine center of origin would be a comparative molecular phylogeographic study (Arbogast & Kenagy 2001, Zink 2002) of marine populations across the basins proximal to the Philippines and the major geological elements of the archipelago. The most parsimonious explanation for diverse taxonomic groups showing the same distribution pattern of phylogenetically related taxa is that they have a shared biogeographic history (Wiley 1988, Avise 2000). Historical vicariance biogeography relies on well supported

phylogenetic hypotheses and accurate distribution information to infer relationships between geographical areas. Santini & Winterbottom (2002) amassed a dataset of available phylogenetic and distribution organisms for coral reef organisms of the Indo-Pacific and implied that the diversity of the IMPA is a result of amalgamation of varied geological elements. However, they concluded that there is a need to develop new methods in order to further test hypotheses relating to the complex IMPA region. Phylogeography holds promise in elucidating both the timing and detail of biogeographic history through examination of populations and closely related species and has already contributed to our knowledge of IMPA biogeography (Perrin & Borsa, 2001, Barber et al. 2000). Comparative phylogeography incorporates individual phylogeographic studies of widely separated taxa in the same geographic area to help reveal common geohistorical isolating events that shape population structure and drive speciation (Arbogast & Kenagy 2001, Zink 2002). Comparative phylogeography as a form of vicariance biogeography may be crucial to supporting or falsifying the notion that a Philippine primary center of allopatric origins constitutes the elusive unifying hypothesis to explain IMPA biodiversity.

An additional test of the Philippine center of origin would be expanding the present database to include all shore fishes of the western Pacific. This would require extensive taxonomic work and careful review of distribution records, many of which are available in museum databases but would require identification verification by taxonomic specialists before they can become reliably used. Unfortunately, support for taxonomists has dwindled perilously in recent years despite their importance to biodiversity studies (Cotterill 1995, Carpenter & Paxton 1999, Blaber 2002). Our study is similar to all previous studies on IMPA biogeography in that it relies on the work of taxonomists to examine specimens and distribution records in order to determine the limits of the species distributions. Analytical studies that utilized location lists (Bellwood & Hughes 2001, Mora et al. 2003), range data (Hughes et al. 2002, Connolly et al. 2003), and general distribution information (Roberts et al. 2002, Santini & Winterbottom 2002) ultimately are derived from the same taxonomic work that forms the basis for the

present study (Carpenter & Niem 1998–2002). Continued expansion of these databases and more precise judgments on conservation strategies will rely on continued rigorous taxonomic work.

Recent analytical studies examining the biogeography or biodiversity of the IMPA have focused on coral reef biota. These have included distributional analyses of corals (Wallace 1997), a select group of coral reef fishes (Mora et al. 2003), a select group of corals and fishes (Bellwood & Hughes 2001, Hughes et al. 2002, Connolly et al. 2003), and a broad range of select coral reef groups (Roberts et al. 2002, Santini & Winterbottom 2002). An assumption of all these studies and our study is that the subset of taxa chosen is representative of overall biodiversity patterns and that omission of any other taxa will be compensated by the use of an extensive database. Our study adds the dimension of marine biota beyond the coral reef. Soft bottom, rocky intertidal, rocky reef, and estuarine habitats also harbor an extremely high biodiversity and are under extreme anthropogenic stress within the IMPA (Carpenter & Paxton 1999).

In terms of the different hypotheses of IMPA diversity outlined here, recent analytical studies have concluded nearly the full range: area accumulation (Connolly et al. 2003), area of refuge (Bellwood & Hughes 2001), center of origin (Mora et al. 2003), and a combination of some or all of the hypotheses (Wallace 1997, Santini & Winterbottom 2002). The overall conclusion from our study is that the diversity found in the IMPA is likely a combination of many processes, as evidenced by the secondary center of diversity we observed. However the higher number of species per unit area in the Philippines than elsewhere in the IMPA indicates that concentrated allopatric speciation and island integration across the Philippine archipelago appears to have played an important role in shaping the diversity of the IMPA. These hypotheses warrant further testing through refined vicariance biogeography methods and molecular phylogeographic approaches.

The identification of the Philippines as the major center of marine biodiversity is troubling because of the heightened level of threat to marine environments there (Bryant et al. 1998). Roberts et al. (2002) list the Philippines as being the most highly threatened center of endemism. The concentration

of limited-range endemics in the Philippines poses a danger of mass extinctions on a marine scale similar to endangered Brazilian rainforests. The concentration of species indicates that there are a variety of unique biotic communities in the area. These unique communities would also be under threat due to habitat degradation. Knowledge of the underlying processes that govern uneven distribution of biodiversity is crucial to understanding ecology, and for effective conservation (Gaston 2000, Mora et al. 2003). Understanding factors that control patterns of endemism and richness should also help prioritize sites for conservation even when data are sparse, as they often are in marine environments. Solely as an example of peak diversity and endemism, there is ample justification to prioritize the Philippines for conservation. As a probable epicenter of allopatric speciation and island integration bioconcentration, it is imperative to conserve the habitats and diversity that can help us understand the processes of evolution that govern biodiversity in the marine realm. Clearly, marine conservation efforts in the Philippines warrant special attention.

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