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Distribution patterns of tiger beetle species in the Philippines and Southeast Asia

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Abstract
Various animal taxa have been used in the past to elucidate biogeographic patterns in the Philippine archipelago and several hypotheses were proposed. In this study, the tiger beetle fauna was used to verify these hypotheses. The Philippine tiger beetle fauna is one of the highest in the world in richness and endemism. Primary colonization routes were from Borneo via Palawan and via Sulu archipelago. This high richness could not be attributed solely on colonization. Phylogenesis proves to be a dominant force in forming the tiger beetle fauna in the Philippines. This can be attributed to a high speciation rate in the country that may be much higher compared to a temperate setting.

Keywords: bioindicator, Cicindelinae, Gondwanan distribution, phylogenesis, tiger beetle

1. Introduction

The study of island biogeography has greatly evolved since the theory was developed by MacArthur and Wilson [1]. From a simplistic approach of the equilibrium theory, involving only the variables colonization and extinction rates, and affected primarily by island size and distance from mainland, more and more factors have been shown to contribute to the species richness in islands. The biota of the Philippine archipelago has been used as a model to test several hypotheses in island biogeography. Several predictions were made that were challenged by actual observations. For example, the islands were expected to be depauperate of species, probably due to the lack of time for colonization (non-equilibrium theory) or greater extinction rates among islands (equilibrium theory). This was expected by Heaney [2] when he first began to study the mammals of the Philippines. As it turned out, there are at least 206 native terrestrial species of mammals, 117 of which are endemic. This could be the highest rate of endemism in any country per-unit-area even among mainland counterparts [3].

Unlike land-bridge islands, which used to be connected to the mainland and would thus initially have the same assemblage of mainland fauna, oceanic islands are initially devoid of these fauna. Colonization rate by non-volant mammals is very low. It is estimated that a single successful colonization occurs for every 250,000 years [4] and could not have accounted for the high species richness. High species richness in islands was explained by speciation and phylogenesis, apart from colonization [5, 6]. Species richness in islands generally increases with habitat diversity [7, 8]. This habitat diversity would potentially lead to niche partitioning among the colonists and would promote speciation.
Insects share certain characteristics with non-volant mammals that could lead to the same dispersal patterns. Although some insects, including Coleopterans, are capable of flight, their small size would not support enough energy to travel long distances, particularly over-ocean flights [9]. Thus their dispersal is also limited by oceanic barriers.

Among the insect taxa, the tiger beetle subfamily Cicindelinae is a suitable taxon in studying biogeographic patterns. It has been regarded as a good bioindicator for regional biodiversity. A good indicator taxon was defined as having a well-known and stable taxonomy, well understood biology, readily observable individuals, broad geographic range, specialized in narrow habitat types, patterns can be translated to related taxa, and have potential economic importance [10]. Pearson and Cassola [11] were able to test each of those characteristics as it would apply for Cicindelinae. The tiger beetle fauna is represented by over 2300 species from 157 countries and has a world-wide distribution except in the Arctic, Antarctica and very isolated islands such as Hawaii [12].

The tiger beetle group used to comprise the family Cicindelidae before being added to the ground beetle family Carabidae, a family of large predatory beetles. Today, systematists group the tiger beetles under subfamily Cicindelinae, which forms a monophyletic group within family Carabidae. Carabidae is a member of the beetle order Adephaga and class Insecta. Cicindelinae is characterized by large compound eyes, filiform and eleven-segmented antennae, long legs, and long sickle shaped mandibles. The size of tiger beetles ranges from 6 millimeters to 45 millimeters. One reason why tiger beetle taxon is considered as a good bioindicator is that they live in very specific types of habitats. They are mostly found near seashores, rivers and lakes. There are also species adapted to other habitat types such as hill sides, rocky areas near roads, trails and forest openings. Although the occurrence of several species living together is common, there is very little competition among them, particularly because of niche partitioning [13].

Since tiger beetles have retained ancient Adephagan characteristics, they constitute a very ancient beetle group that dates back to mid-Cretaceous. The wide distribution of certain tiger beetle groups such as the Megacephalini and Ctenostomini in Africa, South America and Australia, but not so much in the Nearctic and Palearctic regions suggests that this group has a Gondwanian origin and has preceded the splitting of Gondwanaland [14]. This ancient origin is also supported by some genera, such as the *Hipparidium*, that has most of its species in Africa, but with one species that is isolated in Indonesia [15]. Current world distribution of tiger beetles also support Gondwanian origin as tiger beetle species in the Nearctic and Palearctic region account for only a small percentage of the world's species [12]. Current distribution of the tiger beetles in South Asia, including the Southeast, may be explained by the dispersal of species from India to these regions as India was also part of Gondwana.

In this paper, it is hypothesized that the insect diversity in the Philippine archipelago is similar to that of mammals, wherein colonization accounts for only a small fraction of the species assembly and that the rest are products of phylogenesis. The Philippine tiger beetle fauna is used as a bioindicator to test this hypothesis.

2. Materials and Methods

A review of the tiger beetle distribution worldwide and its distribution in the Philippines was conducted based on available data from published literature as of December 2012. Based on reports of occurence in various regions, species richness and endemism was assessed for the Philippine tiger beetle fauna. Conformance to the equilibrium theory constitute the null hypothesis, which maintains the following: (1) the direct relationship between island size with species richness; (2) the inverse relationship between island distance with species richness; (3) the lower species richness in an island compared to its mainland counterpart of the same size; and (4) the dependence of species richness solely to colonization and extinction. Based on current data on the distribution of non-endemic tiger beetle species, hypothetical routes of colonization to the Philippines were also inferred.

3. Results and Discussion

3.1 Tiger beetle distribution

Among the world's major biogeographic regions, the South East Asia has the highest tiger beetle species coverage. About 23% of the world's species are found in this region considering that it constitutes only 2% of the total land area of countries with tiger beetle fauna [12]. Indonesia and the Philippines, in particular rank first and fifth in species richness, respectively (Table 1).

Table 1: Rank of countries in total tiger beetle species count, percentage endamic species and area/species coverage [12].

Rank	Top 10 countries (total number of tiger beetle species)	Top 10 countries (percentage of endemic tiger beetle species)	Top 10 countries (area (km^2)/number of species)
1	Indonesia (237)	Madagascar (98.7%)	Sri Lanka (1156)
2	India (208)	Australia (89.7%)	Laos (2157)
3	Brazil (203)	Philippines (85.4%)	Nepal (2200)
4	Madagascar (176)	Sri Lanka (62.5%)	Philippines (2294)
5	Philippines (130)	Brazil (60.1%)	Vietnam (2854)
6	Congo (128)	Papua New Guinea (58.2%)	Ecuador (3186)
7	Thailand (123)	Indonesia (52.7%)	Madagascar (3335)
8	Mexico (122)	India (51.9%)	Thailand (4161)
9	USA (120)	Mexico (49.2%)	Malaysia (4574)
10	Australia (116)	USA (41.7%)	Papua New Guinea (5718)

Although both Indonesia and the Philippines are archipelagos, they differ in island type. Indonesia is composed of land-bridge islands that form the greater part of the Sunda shelf. It used to be connected to the mainland Asia and is thus expected to have a high species richness. Following the equilibrium theory, however, a land-bridge island upon separation form the mainland would support less species than would be predicted if it is connected to the mainland. This is because the resulting islands would experience a much higher rate of extinction relative to colonization rates. This decline in species richness is referred to as the relaxation fauna [16]. As observed, this is not the case. Indonesia's tiger beetle fauna, having the highest species richness, is certainly not experiencing a relaxation phase. The Philippines on the other hand is mostly formed by oceanic islands. Unlike Indonesia, which is initially occupied by mainland fauna, the Philippines was initially devoid of it. Instead of a relaxation phase, the main factor that would affect its faunal assemblage according to the equilibrium theory is colonization. Colonization rates are expected to be very slow as well, similar to that of the mammals. As such, species richness is not expected to be high.

3.2 Tiger beetle fauna in the Philippines

In 2000, 130 species of tiger beetles were listed in the

Philippines [12] and 111 (85.4%) are endemic. A decade later, this number went up to 139 species and 120 (86.3%) are endemic [17]. But for the purpose of comparison with other countries, the year 2000 data was used. These numbers make the country the fifth richest in terms of absolute number of tiger beetle species. If endemism is taken into account, the Philippines would rank third behind Madagascar and Australia. If the countries' land areas are taken into account, the Philippines would outrank Madagascar and Australia on a per-unit-area basis, and would just fall behind three much smaller and less specieous countries (Table 1).

There are only 19 species of tiger beetles in the Philippines that are not endemic. A list of these species and the other regions wherein these species are also found is shown in Table 2. Based on these data, most of the non-endemic species are shared with Southeast Asia. This suggests that tiger beetles mostly have colonized the Philippines via Borneo. Given the concentration of tiger beetles both in Palawan and Mindanao [18], over-water colonization from Borneo to Palawan and from Borneo to the Sulu Archipelago, are equally likely. As mentioned previously, given the Gondwanian origin of tiger beetles, the direction of dispersal would originate from regions previously part of Gondwana. As for the Philippines, colonization would come from species whose ancestors came from India or Australia. Indian ancestry is most probable because of ease of propagation of the Sunda Shelf, which is in close proximity to the Philippines. Although this is more common, species of Australian ancestry is also present in the country as evidenced by species in common with the islands of Oceania. There are two species, *Tricondyla aptera* and *Cylindera discreta*, which are in common with Oceania. *C. discreta* is also present in Southeast Asia and it is possible that it entered the Philippines also through Borneo and may have reached the islands of Oceania via Sulawesi. Alternatively, it could have directly colonized the Philippines through Greater Mindanao as would be the case of *Tricondyla aptera* since it is common to Oceania but not to the rest of Southeast Asia. Although these are the only non-endemic species in common with Oceania, it is also likely that some of the endemic species had diverged from an ancestor from Australia. In particular, the genus *Thopeutica*, which has two endemic subgenera, namely, Thopeutica and Philippiniella, is closely associated with Wallacedela, which is widely spread from Sulawesi and Oceania [18]. Other *Thopeutica* species are common in Sulawesi and the islands of Oceania and may have been the source of the Philippine *Thopeutica* species.

Table 2: List of non-endemic tiger beetle species in the Philippines [12, www.carabidae.pro]

		Other Regions Present
Calochroa	*flavomaculata*	Asia*
Calochroa	*sexpunctata*	Asia
Calomera	*angulata*	Asia
Lophyra	*striolata*	Asia
Cylindera	*foveolata*	Asia
Cylindera	*viduata*	Asia
Cylindera	*minuta*	Asia
Tricondyla	*aptera*	Oceania
Cylindera	*discreta*	Southeast Asia and Oceania
Neocollyris	*bonellii*	Southeast Asia including Mainland
Abroscelis	*tenuipes*	Southeast Asia including Mainland
Cylindera	*holosericea*	Southeast Asian Islands
Tricondyla	*beccari*	Southeast Asian Islands
Tricondyla	*doriai*	Southeast Asian Islands
Neocollyris	*emarginata*	Southeast Asian Islands
Neocollyris	*rhodopus*	Southeast Asian Islands
Heptodonta	*analis*	Southeast Asian Islands
Therates	*coracinus*	Southeast Asian Islands
Callytron	*terminatum*	Southeast Asian Islands

*Asian group is inclusive of Southeast Asian countries; could extend as far west to Afghanistan, Kazakhstan, and Pakistan; no species are in common with Mongolia, Russia, former Soviet countries, Japan, and Korea

3.3 Hypothetical routes of colonization

Tiger beetles may have colonized the Philippines oceanic islands through several routes. In any case, it would have involved stochastic colonization over water. Even during the glacial periods, the islands were never connected to the Sunda shelf. With the current information on the Philippine tiger beetles, the different colonization routes from various source regions (Figure 1) to the Philippines were hypothesized.

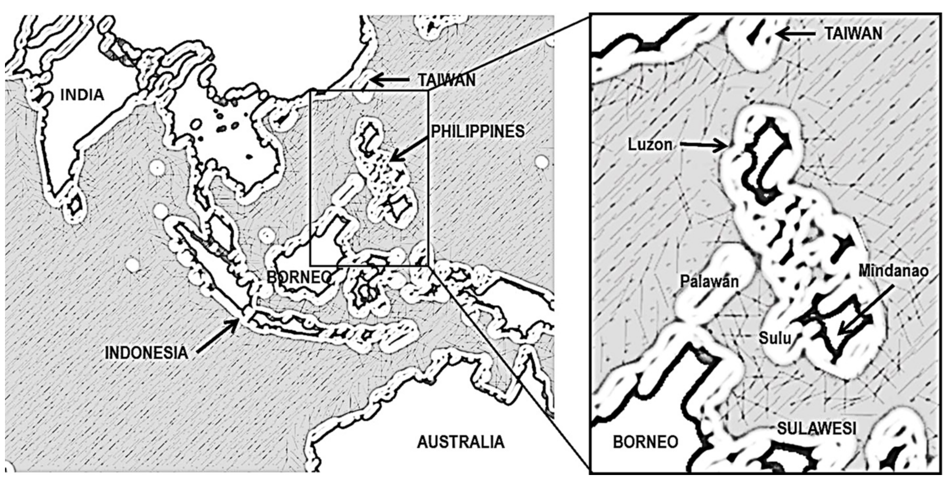

Fig 1: Map of Southeast Asia

3.3.1 Palawan ark hypothesis

In contrast to the other islands of the archipelago, Palawan used to be part of mainland Asia and migrated southeast with the formation of the South China Sea basin [19]. As it drifted from the mainland, it could have carried with it species that are mainland in origin, and would have served as a raft to ferry these species [20]. Tiger beetles, however, would not have been included in the raft. The separation of Palawan from the mainland occurred 30 million years ago. The spread of tiger beetles throughout Asia, however, did not occur until about 20 million years ago when the Indian subcontinent started to smash to the mainland, carrying with it the Gondwanian species. Thus, this hypothesis is not applicable to the tiger beetle fauna.

3.3.2 Stochastic routes of colonization

Jones and Kennedy [21] proposed four possible routes by which the Philippine flora and fauna have colonized the islands. The first route is colonization from the North, by which species from Eastern China and Taiwan migrated to Northern Luzon via the Luzon Strait. The second route is colonization from Northeast Borneo to Palawan. The third route is colonization from Southeast Borneo to the Sulu archipelago. The fourth route is colonization from Sulawesi to Southern Mindanao. Of these four routes, the second and the third are the most plausible cases for tiger beetle colonization. As discussed above, most of the non-endemic species are shared in common with Southeast Asia (Table 2). Furthermore, the regions with the highest concentration of tiger beetles are Palawan and Mindanao [17, 18, 22]. The first route on the other hand is the least probable and is not supported by any tiger beetle data available. Since the Sunda shelf used to be interconnected, it is more parsimonious for tiger beetles from East Asia to colonize the Philippines via land travel to Borneo. The fourth route, although most likely not the most prominent route, could be true to some tiger beetle taxa. *Tricondyla aptera*, in particular is shared only with the islands of Oceania. Also, as discussed above, the genus *Thopeutica* is associated with *Wallacedela*, a genus found only in Sulawesi while being widespread in both Mindanao and Sulawesi [18].

3.4 High speciation rate in the Philippines

Since colonization alone could not explain the diversity of Philippine tiger beetle species, speciation rates in the archipelago was examined. Speciation rate of tiger beetles has been estimated by using the North American tiger beetle fauna [23]. Diversification rate was determined by constructing species-level phylogenies derived from mitochondrial DNA sequences. By assigning ages to ancestral groups that were estimated from sequence data and calibrated with geological and bio geographical information, the average per-lineage diversification rate was calculated to be at least 0.22 ± 0.08 species per one million years. If this rate was applied to explain the species richness in the country, and considering that the Philippines currently has 120 endemic species described (111 in year 2000) [12, 17], the process would have taken over 500 million years to reach this point. That would date back to the early Paleozoic era, preceding the mid-Cretaceous period 100 million years ago when the tiger beetles were estimated to have first emerged [15]. Furthermore, the oceanic Philippines only started to take form around 30 million years ago [19]. This would translate to 4 species per one million years, almost 20 times as fast as the estimated rate in North America. Setting errors aside, these numbers still imply a much faster evolutionary rate in the Philippine archipelago compared to the mainland. In this section, different factors affecting evolutionary rate will be discussed.

3.4.1 Population Structure

Evolutionary rate is usually higher in subdivided populations compared to those that are interconnected and homogenous [24]. In the equilibrium theory, it is predicted that islands would support less species than a mainland population of the same size. This is due to the slow rate of island colonization as compared to migrations in the mainland. This does not take into account that in a group of islands, several isolated subpopulations would have different selective pressures acting on each. This would increase the rate of speciation as populations would conform to the phenotype with the highest adaptive value. This is especially true if the adaptive phenotype differs among the islands and among different habitat types within an island. Random colonization of previously uninhabited islands would also respond more to the effects of genetic drift [25, 26]. As different individuals of potentially different genotypes colonize different islands, they would eventually propagate to form distinct populations. This is in contrast to the mainland scenario where admixture of population gene pool is common. Gene flow between populations leads to homogeneity and would further slow the process of evolution. For these reasons, diversification in archipelagos such as the Philippines is expected to occur at a higher rate than was estimated in North America.

3.4.2 Habitat Diversity

As mentioned previously, habitat diversity is directly proportional to species diversity. Insects particularly, have been shown to have a high correlation with plants in terms of species richness and homogeneity [27]. The Philippines, having 9,250 species of vascular plants, a third of which are endemic, would thus be expected to support a large number of insect species. Although tiger beetles are mostly predatory, they also rely on other folivorous and detritivorous insects.

3.4.3 Latitudinal Gradient

There is a general trend among the world biota wherein species richness in the tropics is higher compared to temperate areas. One explanation is that the total energy production in the tropics is greater than that in temperate regions and would thus support more species [28]. Climate would also play a role in species richness as fewer species can physiologically tolerate conditions at higher latitudes than at low latitudes [29]. Climate stability in the tropics would promote specialization on resources that are perennially available. Temperate conditions on the other hand may experience a higher extinction rate due to fluctuations in environmental conditions. Species in tropical regions have been shown to have a higher evolutionary rate due to higher temperature, higher mutation rate, and faster generation time [30].

3.5 Direction for Future Research

The Philippines has been flagged internationally due to its huge biodiversity and the depletion of natural environment. It was assumed that since most species, including many tiger beetles, were associated with forest environment, few could adapt to secondary forest or to non-forested habitat and would have led to mass extinction. Based on the current data, however, the species richness of tiger beetles in the Philippines shows that the country's biodiversity is in good shape. Although concerns over depletion of natural resources are valid, what is overlooked is the ability of species to adapt, which has been the story of how species diversity in this country came to be. Just as speciation occurred by differential adaptation of populations in different islands and habitat types, species have also thrived amidst a century of deforestation and habitat destruction. This is stated not to advocate such practices but to focus our attention not only on the species number only but on the extant populations. In order to assess if the species of tiger beetles are endangered or not, genetic variation among different populations must be assessed. It is unfortunate that although the tiger beetle fauna in the Southeast Asia is richest among the world's biogeographic regions, very little studies in this region have been generated apart from taxonomic studies. Genetic diversity studies would help detect if there is sufficient polymorphism that would sustain the existing tiger beetle species in the country, despite their distribution and population size. Phylogenetic analyses would help understand the relationship of different species and to verify the patterns observed and explanations proposed in this study.

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