

Are Ecological Factors Correlated with Genetic Variation in the Flying Lizards (Genus *Draco*) of Sulawesi Island

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ABSTRACT

Sulawesi, an island located in one of the biggest biological hotspots in the world, is a unique location to study endemism and species diversity. The island is comprised of four distinct peninsulas, joined at a central landmass that provides a means of geographical isolation due to its mountainous terrain. The species on the four peninsulas, as a result, are extremely varied. One of these species is the genus *Draco*, a species of flying lizard endemic to Southeast Asia. These lizards have evolved membranes that allow them to glide from tree to tree and live in an arboreal habitat. However, while the lizards have garnered interest, very few studies have been conducted on the genetic divergence of the lizard species on the island. This study examines the different ecological factors that may have had an influence in causing the *Draco* species to diverge genetically. By using ArcGIS and MaxEnt to display current/potential distributions of each of the nine *Draco* species, we were able to correlate which factors had the biggest impacts on the species in the context of phylogenetics. By visually correlating climate, soil type, forest type, and paleo-history layers of the island with maps of the lizard distributions, we were able to conclude that forest type and paleo-history had an impact on the divergence of the species. Forest type impacts the most suitable habitats for the lizard species because of their arboreal nature. Additional studies will help focus conservation of the forests on Sulawesi, since forest type appears to have a significant impact on how these lizards are diverging.

KEYWORDS

Species distribution, biogeography, ArcGIS, MaxEnt, phylogenetics

INTRODUCTION

Island systems provide natural mesocosms for the study of ecology and evolution because all islands share a similar trait: geographic isolation (Weigelt et al. 2013). Given an island's limited geographic extent, island systems typically allow species minimal opportunities to expand. However, when island systems first appear they provide countless avenues for ecological opportunity, creating many different niches that each species can fill (Setiadi et al. 2011). Because of the geographic isolation and unique environmental conditions of islands, many species are endemic to their islands and habitats (Parenti and Ebach 2013). As species settle into their ecological niches, differing habitat conditions may cause adaptive radiation, or a rapid evolution of phenotypic diversity within a group of closely related organisms (Setiadi et al. 2011). Phenotypic diversity, although limited on a geographically isolated system, is affected by abiotic factors that are present in all natural systems.

The Indonesian island of Sulawesi has fascinated biogeographers since the time of Alfred Russel Wallace because of its unique paleo-history and resulting biota (Cannon et al. 2007). This island lies at the center of three convergent major tectonic plates along Wallace's Line, an imaginary boundary line that differentiates between the Asian and Australian ecozones, and is composed of at least five paleo-islands that merged beginning about 10 million years ago (Hall 2009, Wilson and Moss 1999). On account of its age and its having never been connected to the SE Asian mainland, Sulawesi is rich in biodiversity (Wilson and Moss 1999). The island has a unique shape, with four peninsulas extending from a large central core. These peninsulas contribute to regional diversity not only because they reflect separate paleo-islands, but also because of peninsula effects which is the tendency for peninsular lineages to remain isolated. As a result of the island's location and shape, Sulawesi is home to a rich assortment of regional endemic species and species assemblages (Cannon et al. 2007).

One of these assemblages is composed of flying lizards of the genus *Draco* (McGuire et al. 2007). These lizards are equipped with patagial membranes that allow them to glide from tree to tree in arboreal habitats (McGuire and Dudley 2005). Although it has been proposed that this gliding behavior is a consequence of arboreality to minimize injuries during a fall, gliding in these lizards is also essential for territoriality and survival (McGuire and Dudley 2011). When the most dominant males establish their ranges, males lacking territories search for unoccupied trees; this

establishment is done strictly by gliding from tree to tree (McGuire and Dudley 2011). Differences in flight mechanics in these lizards may have resulted from differing canopy heights which in turn facilitate varying aerial behaviors (Dudley et al. 2007). The flying lizards of Sulawesi are part of a clade called the *Draco lineatus* group, a monophyletic assemblage of nine species that are present on Sulawesi proper and several of its surrounding islands. Although only three of these species are confined to Sulawesi, each is composed of 12 deeply divergent genetic groupings, each of which could be an incipient species restricted to a biogeographical province of the island. However, the relationship between these differences in habitats across the island and the genetic divergences of *Draco* have yet to be made.

Despite the limited taxonomic studies on Sulawesi, *Draco* have been extensively sampled and researched by Dr. Jimmy A. McGuire since 1999. Using his data, I will correlate genetic variation within the genus with several abiotic factors present on the island. Primarily my study will focus on climate, forest type and vegetation layers, the soil and geology, as well as plate tectonics. It would be very exciting if any of these features correlate strongly with lineage divergence within *Draco*. This study has the potential to identify key abiotic factors underpinning regional speciation on the island of Sulawesi.

METHODS

Study site and species

Because of Sulawesi's unique geological history, the island presents an interesting site to study speciation. The island's four peninsulas (Minahasa, Eastern, Southern, and Southeastern Peninsulas) stem from its tectonic origins, a collision between the Asian plate and the Australian plate (Fig. 1). Because of its tectonic origin, the island's interior landscape is shaped by mountainous terrain. As a result of the mountainous regions that make up the central portion of the island, the four peninsulas are geographically isolated from each other both by land and sea.

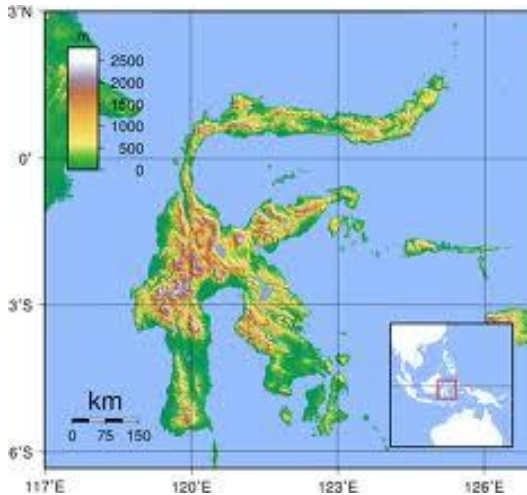


Figure 1: Sulawesi's geology. As shown by the topography, Central Sulawesi exhibits extreme mountainous regions, which is the primary reason why the four peninsulas are geographically isolated. Although the environmental conditions are similar across the entire island, this isolation provides an avenue for the *Draco* species to diverge.

Most of the species found on this island, through geographic isolation, are endemic and have evolved into the major extant clades. I studied the nine species of lizards of the genus *Draco* that are present on the island (Table 1). For the purposes of examining a broader distribution of the species, I only examined *D. beccarri*, *D. rhytisma*, *D. spilonotus*, and *D. walkeri*. The other five species were too confined or not widely distributed enough to try to determine the environmental factors that may have led to their divergence from a mother species. Most of these species also had very little data, less data than the species that were found on the main island of Sulawesi. Additionally, there were a few points that suggest that regions of Sulawesi are becoming a hybrid zone. Species marked “hybrid” in the Excel sheets were also taken out of the study, due to a sheer lack of data, but the presence of these point data provide further direction for predicting *Draco* distributions.

Table 1. A summary of *Draco* distributions across Sulawesi. “Geographically confined” here means located exclusively off the mainland of Sulawesi. For a broader understanding of the species distribution in response to

environmental factors, I focused on just the species that were located on the main island.

Species name	Distribution	Geographically confined?
<i>D. beccarri</i>	Eastern Peninsula, Southeastern Peninsula	No
<i>D. biaro</i>	Desa Lalinsaheng	Yes
<i>D. caerhulians</i>	Tahuna	Yes
<i>D. iskandari</i>	Desa Haasi	Yes
<i>D. lineatus</i>	Maluku	Yes
<i>D. rhytisma</i>	Eastern Peninsula	No
<i>D. spilonotus</i>	Minahasa Peninsula, Central Sulawesi, Southern Peninsula	No
<i>D. supriatnai</i>	Togian Islands	Yes
<i>D. walkeri</i>	Minahasa Peninsula, Central Sulawesi, Southern Peninsula	No

Data sources and processing

I correlated species divergence with four abiotic factors using GIS: climate, forest type, soil type, and paleo-history. I used climate GIS layers, consisting of precipitation and mean temperature, which I downloaded from WorldClim (Sobek-Swant et al. 2012). The rest of the datasets were obtained from free web databases and other GIS layers were obtained from other researchers (Table 2).

Table 2. Datasets and their sources. All of the datasets (except climate) were obtained from researchers who had previously done research on Sulawesi's environmental factors.

Dataset	Source(s)	URL, citation
Climate (mean temperature, precipitation)	WorldClim – free worldwide climate database	Worldclim.org
Forest type	World Wildlife Fund Ecoregion, Charles Cannon of Texas Tech University	http://worldwildlife.org/biomes
Soil type	Robert Hall of Royal Holloway University of London	n/a
Paleo-history	Jimmy McGuire of the Museum of Vertebrate Zoology, UC Berkeley	n/a

To map the distributions of each species, I used collection records for the genus *Draco* collected from Sulawesi available in the University of California, Berkeley Museum of Vertebrate Zoology. Dr. Jimmy McGuire and colleagues compiled the presence-only point data on multiple trips to Sulawesi, noting the coordinates at where each species were observed. I sorted through 1070 data points to and corrected missing data fields, insufficient coordinates, or biases. From the 1070 data points, I took out the points for the five species exclusively found on islands off the mainland, as well as the hybrid species. To make mapping easier, I compiled each of the species data points into spreadsheets by species. In this way I could create maps according to the species type and analyze them individually with the ecological variables.

I first georeferenced each of the species in ArcGIS (ESRI 2011). In this way I could start creating maps of each of the species' distributions. Using the shapefiles from the different environmental datasets, I created maps of each of the different abiotic layers on the island. Once all these data layers were compiled, I used the point data of all the collection records to extract the points' values from all the different GIS layers.

Each of the species was correlated against each variable in MaxEnt, a modeling program that uses presence-only data to determine where predicted distributions of species based on the

information it is given (Philips et al. 2006). I input a distribution of a species (the point data) with an ecological variable, and MaxEnt's created a series of graphs that showed significance of the model and correlations with the environmental variables. Additionally, the program produced a map showing the species' niche. MaxEnt provided a preliminary indication as to whether the environmental variable was significant enough to a cause for species divergence.

Using the fundamental niches provided by MaxEnt's outputs, I compared them to the point data maps from ArcGIS to determine whether the species' realized niche was smaller, similar to, or bigger than the predicted values. To identify relationships between abiotic factors and species occurrences, I looked for visual patterns by layering the maps without the use of statistical methods. I looked for patterns in environmental factors along the regions where each species was observed, and if a significant pattern was observed, it was used to create more substantial evidence for a cause for divergence.

RESULTS

Merely from visual correlations, the *Draco* species were found to be divergent based on forest type while soil type and climate had no impact on the divergence. In addition, the paleo-history of island provided more context for the phylogenetic distribution of the species, but it was determined that more research could be done in that direction for more concrete claims.

Draco beccarri were found on the Eastern and Southeastern Peninsulas. *Draco rhytisma* was found on the Eastern Peninsula. *Draco spilonotus* was found on the Minahasa and Southern Peninsulas, as well as Central Sulawesi. *Draco walkeri* was found on the Southern Peninsula and Central Sulawesi. Through map correlations, *D. spilonotus* and *D. walkeri* had overlapping distributions, although the evidence of a hybrid species proves that *D. walkeri* and *D. beccarri* also have overlapping distributions.

Climate and soil type were found to have little to no impact on the species. All values of climate (including temperature and precipitation) are constant throughout the entire island. Soil type was also constant and no visual patterns could be drawn according to the *Draco* distributions. Forest type, however, was a better indicator behind the distributions. There were five types of forest involved: lowland forest, hill forest, upland forest, montane forest, and tropalpine forest. Lowland forest is found at the lowest points on the island, from 0 – 400 meters in elevation. Hill

and upland forests encompass elevations from 401 – 1500 meters. These three forest types were found exclusively on the peninsulas. However, montane and tropalpine forests, which have elevations of 1501 meters and higher, were found only in Central Sulawesi, in accordance with Central Sulawesi's mountainous regions.

DISCUSSION

Influences on the *Draco*'s distributions

The distributions of many of the species were limited by environmental factors found only in specific regions of the island. With the influence of forest type, *Draco* were able to adapt to its environment through morphological changes, shifting in wingspan/membrane size depending on if the trees they occupied were taller or shorter.

Some species were found to have overlapping ranges, but as a result of occupying different niches, these species are able to coexist. When two species with similar niches attempt to occupy the same niche, one of the species has to either adapt to a different niche or move to a different niche. This appears to be the case with *D. walkeri* and *D. spilonotus*, which have similar morphologies, diets, and distributions. Other times, like with *D. walkeri* and *D. beccarri*, a mere presence can influence a hybrid species.

Paleo-history also had somewhat an impact on the species' distributions. While not enough evidence could be drawn for a surefire claim, the existence of fault lines on Sulawesi suggest that some of these species were affected by them. From a phylogenetic standpoint, by observing *D. spilonotus*, it was found that while it is the only species that occupies the Minahasa Peninsula, all the species located on islands to the north of Minahasa Peninsula are located further down the phylogenetic tree than *D. spilonotus*. This suggests that *D. caerhulians*, *D. biaro*, and *D. iskandari* are descendants of *D. spilonotus*. This species either found its way to the northern islands where it diversified into the species we see today, or tectonic movements geographically isolated the species.

Implications of a hybrid zone

The *Draco* datasets implied the existence of a hybrid zone between the regions in which *D. beccarri* and *D. walkeri* were found. A hybrid zone is region in which two species unimpeded by reproductive isolation interbreed to create a new “hybrid” species. Only a couple points were recorded so there is not enough information for this region to be declared a *beccarri/walkeri* hybrid zone, but we may be watching a new *Draco* lineage appear. In a couple hundred years this species may have reproduced enough to become its own distinct species, bound by its own environmental conditions as well as isolation from its mother species. The implications of a hybrid zone actively forming on Sulawesi now suggest that new species are still appearing because of the environmental factors examined in this study.

Limitations and future direction

When gathering the necessary datasets, many of the datasets were not available in high resolution for the region of Southeast Asia. Specifically, climate data were hard to find in high resolution, even though they were found on a public domain for people to download and access for all regions of the world. The *Draco* point datasets also provided limitations because of undersampling in certain regions (very few *Draco* were recorded in the Southeastern Peninsula), and oversampling in more *Draco*-prominent regions (Central Sulawesi and the Southern Peninsula). The other five species, which were only found on remote islands away from the mainland, did not have enough point data to be used in the study.

Further studies can be conducted to include all nine of the *Draco* species, as well as any hybrid species that may be present on the island. The entirety of the *Draco* species’ distributions outside of Sulawesi can also be examined. Environmental influences can be observed for all the species’ distributions in Southeast Asia. With other species distributions, there can be further examination of environmental factors for all species and how environmental factors will have affected the general biota of the island.

Broader implications

Sulawesi is known to be a hotspot for biodiversity, and the *Draco* species is known to only exist in Southeast Asia, but very little research has been done on the species. The island is currently undergoing urbanization and in places where forests no longer exist, and as a result the *Draco* species is unable to adapt to new environments or even stay in their current habitats. With forest type as a determining factor in the evolution of these lizard species, conservation efforts must be increased so the species can continue to evolve based on the environmental conditions they are given. Without it, the species as a whole has nowhere to go.

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REFERENCES

- Aarts, G., J. Fieberg, S. Brasseur, and J. Matthiopoulos. 2013. Quantifying the effect of habitat availability on species distribution. *Journal of Animal Ecology* 82: 1135-1145.
- Araujo, M. B., and R. G. Pearson. 2005. Equilibrium of species' distributions with climate. *Ecography* 28:693-695.

- Brame, H. R., and A. L. Stigall. 2014. Controls on niche stability in geologic time: congruent responses to biotic and abiotic environmental changes among Cambrian (Late Ordovician) marine invertebrates. *Paleobiology* 40: 70-90.
- Cannon, C. H., M. Summers, J. R. Harting, and P. J. A. Kessler. 2007. Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. *Biotropica* 39:747-759.
- Culmsee, H., C. Leuschner, G. Moser, and R. Pitopang. 2010. Forest aboveground biomass along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain forests. *Journal of Biogeography* 37:960-974.
- Dudley, R., G. Byrnes, S. P. Yanoviak, B. Borrell, R. M. Brown, and J. A. McGuire. 2007. Gliding and the functional origins of flight: biomechanical novelty or necessity? *The Annual Review of Ecology, Evolution, and Systematics* 38:179-201.
- ESRI 2011. ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.
- Feldman, R. E., and B. J. McGill. 2013. How important is nectar in shaping spatial variation in the abundance of temperate breeding hummingbirds? *Journal of Biogeography* 41: 489-500.
- Gonzalez, C., A. Paz, and C. Ferro. 2014. Predicted altitudinal shifts and reduced spatial distribution of *Leishmania infantum* vector species under climate change scenarios in Colombia. *Acta Tropica* 129: 83-90.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009.
- Hall, R. 2009. Southeast Asia's Changing Palaeogeography. *Blumea* 54:148-161.
- Ko, C. Y., O. J. Schmitz, M. Barbet-Massin, and W. Jetz. 2014. Dietary guild composition and disaggregation of avian assemblages under climate change. *Global Change Biology* 20: 790-802.
- Lee, M. L., N. S. Sodhi, and D. M. Prawiradilaga. 2007. The importance of protected areas for the forest and endemic avifauna of Sulawesi (Indonesia). *Ecological Applications* 17:1727-1741.
- Lima, P. A., L. S. Andrade, C. E. R. D. Alencar, R. T. Pereira, G. M. Teixeira, and A. Fransozo. 2014. Two species of swimming crabs of the genus *Achelous* (Crustacea, Brachyura): environmental requirements determining the niche. *Hydrobiologia* 727: 197-207.

- Maharaj, S. S., and M. New. 2013. Modelling individual and collective species responses to climate change within Small Island States. *Biological Conservation* 167: 283-291.
- McGuire, J. A., and A. C. Alcala. 2000. A taxonomic revision of the flying lizards (Iguania: Agamidae: Draco) of the Philippine Islands, with a description of new species. *Herpetological Monographs* 14:81-138.
- McGuire, J. A., R. M. Brown, Mumpuni, A. Riyanto, and N. Andayani. 2007. The flying lizards of the Draco Lineatus group (Squamata: Iguania: Agamidae): a taxonomic revision with descriptions of two new species. *Herpetological Monographs* 21:179-212.
- McGuire, J. A., and R. Dudley. 2005. The cost of living large: comparative gliding performance in flying lizards (Agamidae: Draco). *The American Naturalist* 166:93-106.
- McGuire, J. A., and R. Dudley. 2011. The biology of gliding in flying lizards (Genus Draco) and their fossil and extant analogs. *Integrative and Comparative Biology* 51:983-990.
- McGuire, J. A., and K. B. Heang. 2001. Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: Draco) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean Society* 72:203-229.
- Parenti, L. R., and M. C. Ebach. 2013. Evidence and hypothesis in biogeography. *Journal of Biogeography* 40:813-820.
- Phillips S., R. Anderson, and R. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Porretta, D., V. Mastrantonio, S. Amendolia, S. Gaiarsa, S. Epis, C. Genchi, C. Bandi, D. Otranto, and S. Urbanelli. 2013. Effects of global changes on the climatic niche of the tick *Ixodes ricinus* inferred by species distribution modelling. *Parasites and Vectors* 6: 271.
- Sequeira, A. M. M., C. Mellin, D. A. Fordham, M. G. Meekan, and C. J. A. Bradshaw. 2014. Predicting current and future global distributions of whale sharks. *Global Change Biology* 20 778-789.
- Setiadi, M. I., J. A. McGuire, R. M. Brown, M. Zubairi, D. T. Iskandar, N. Andayani, J. Supriatna, and B. J. Evans. 2011. Adaptive radiation and ecological opportunity in Sulawesi and Philippine fanged frog (*Limnonectes*) communities. *The American Naturalist* 178:221-240.
- Sheppard, C.S. 2013. How does selection of climate variables affect predictions of species distributions? A case study of three new weeds in New Zealand. *Weed Research* 53: 259-268.

- Silva, D. P., V. H. Gonzalez, G. A. R. Melo, M. Lucia, L. J. Alvarez, and P. De Marco Jr. 2014. Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America. *Ecological Modelling* 273: 200-209.
- Sobek-Swant S., D. A. Kluza, K. Cuddington, and D. B. Lyons. 2012. Potential distribution of emerald ash borer: What can we learn from ecological niche models using Maxent and GARP? *Forest Ecology and Management* 281:23-31.
- Weaver, J. E., T. M. Conway, and M. J. Fortin. 2012. An invasive species' relationship with environmental variable changes across multiple spatial scales. *Landscape Ecology* 27: 1351-1362.
- Weigelt, P., W. Jetz, and H. Kreft. 2013. Bioclimatic and physical characterization of the world's islands. *PNAS* 110:15307-15312.
- Wiens J. J. and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics* 36:519-539.
- Wilson, M. E. J., and S. J. Moss. 1999. Cenozoic palaeogeographic evolution of Sulawesi and Borneo. *Palaeogeography, Palaeoclimatology, Palaeoecology* 145:303-307.