

Genetic Structure of Herpetofauna on Halmahera Island, Indonesia: Implications for Aketajawe-Lolobata National Park

MOHAMMAD IQBAL SETIADI,* AMIR HAMIDY,† ZAINAL ABIDIN,‡ DWI SUSANTO,§
 RAFE M. BROWN,** A. TOWNSEND PETERSON,** XINGONG LI,†† AND BEN J. EVANS*‡‡

*Center for Environmental Genomics, Department of Biology, McMaster University, Life Sciences Building Room 328, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada

†Museum Zoologicum Bogoriense, Research Center for Biology, Indonesian Institute of Sciences-LIPI, Gd. Widyasatwaloka Jl. Raya Jakarta Bogor km 46, Cibinong 16911, Indonesia

‡Center for Biodiversity and Conservation Studies, Faculty of Math and Science, University of Indonesia, Gd. E Lt. 2 Kampus UI Depok, Jawa Barat, 16421, Indonesia

§Graduate School of Natural Resource and Environment, Bogor Institute of Agriculture, Bogor, Indonesia

**Department of Ecology and Evolutionary Biology and Natural History Museum & Biodiversity Research Center, University of Kansas, Dyche Hall, 1345 Jayhawk Boulevard, Lawrence, KS 66045-7561, U.S.A.

††Department of Geography, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, KS 66045-7613, U.S.A.

Abstract: *Genetic variation within species—a priority for biodiversity conservation—is influenced by natural selection, demography, and stochastic events such as genetic drift. We evaluated the role of these factors in 14 codistributed species of reptiles and amphibians on the Indonesian island of Halmahera by testing whether their molecular variation was correlated with geographic distance, ecology, riverine barriers, or Halmahera's paleoisland precursors. We found support for isolation by distance effects in four species. Two of these four were also significantly affected either by rivers or by ecology. A fifth species was significantly affected by ecology and a sixth was significantly affected by Halmahera's paleoislands. [Correction added after publication 9 December 2009: the previous sentence was edited for clarity.] These findings—the most comprehensive survey of multispecies genetic variation on Halmahera to date—bode well for the efficacy of the recently established Aketajawe-Lolobata National Park in conserving a substantial component of vertebrate genetic variation on this island. Future success of conservation efforts will depend crucially, of course, on funding for and enforcement of conservation management of this park.*

Keywords: DNA barcodes, ecological niche modeling, Halmahera, herpetofauna, isolation by distance, phylogeography, vicariance

Estructura Genética de la Herpetofauna de la Isla Halmahera, Indonesia: Implicaciones para el Parque Nacional Aketajawe-Lolobata

Resumen: *La variación genética intraespecífica—una prioridad para la biología de la conservación—es influida por la selección natural, la demografía y eventos estocásticos como la deriva génica. Evaluamos el papel de estos factores en 14 especies de anfibios y reptiles codistribuidas en la Isla Halmera, Indonesia probando si la variación molecular se correlaciona con la distancia geográfica, la ecología, las barreras ribereñas o los precursores paleoinsulares de Halmahera. Encontramos soporte para los efectos del aislamiento por distancia en cuatro especies. La estructura genética de dos especies fue afectada por la ecología, una especie fue afectada significativamente por los ríos, y una especie fue afectada por las paleoislas de Halmahera. Estos hallazgos—el muestreo más integral de la variación genética de especies de Halmahera a la fecha—son*

‡‡Address correspondence to B. J. Evans, email evansb@mcmaster.ca
 Paper submitted January 22, 2009; revised manuscript accepted July 15, 2009.

promisorios para la eficacia del recién establecido Parque Nacional Aketajawe-Lolobata en la conservación de un componente sustancial de la variación genética de vertebrados en esta isla. Por supuesto que el éxito futuro de los esfuerzos de conservación dependerá crucialmente del financiamiento para y la puesta en práctica de la gestión de conservación de este parque.

Palabras Clave: aislamiento por distancia, códigos de barra de ADN, filogeografía, Halmahera, herpetofauna, vicarianza

Introduction

Wallacea, a biodiversity hotspot in central Indonesia, lies between Borneo and New Guinea and is characterized by numerous endemic species that face substantial threats from human activity (Myers et al. 2000). Spanning approximately 18,000 km², Halmahera is the second-largest island in Wallacea, after Sulawesi. The unique biota of Halmahera evolved in isolation from other landmasses over millions of years, probably since this island emerged above sea level (Hall 2001). Halmahera's fauna is only moderately diverse, but characterized by exceptional species-level endemism (Allison 1996; Brown 1997; Inger 1999). This situation contrasts sharply, for example, with the neighboring islands in the Sunda Region (Borneo, Sumatra, and Java) and the Sahul region (New Guinea), which were intermittently connected to larger land masses in Asia and Australia, respectively. Within the Moluccan archipelago, several biogeographic regions have been identified, with Halmahera and the nearby islands of Morotai and Bacan generally considered distinct from other major islands such as Buru and Seram (Monk et al. 1997). BirdLife International's "endemic bird areas" identifies similarities between the avian fauna of Halmahera and that of Obi Island to the south, although each also has endemic bird species not found on the other (ICBP 1992).

The Moluccan Archipelago lies in one of the most rapidly deforming tectonic regions on the planet (Puntodewo et al. 1994; Rangin et al. 1999). Halmahera began as two "paleoislands" hundreds of kilometers east of their current locations (Hall 1998, 2001) that were mostly or completely underwater for millions of years before present (Morey et al. 1999). Ancient river valleys suggest that the eastern paleoisland was dry land approximately 30 million years ago but then resubmerged (Hall et al. 1988). Fairly recent emergence (during the last 5 million years or so), followed by rapid uplift of the eastern portion is evinced by ancient reefs at elevations of 1000 m (Nichols & Hall 1991). Collision of the western and eastern paleoislands occurred approximately 1.1 million years ago (Hall & Nichols 1990), creating a thrust line between the present-day western and eastern sections of this island (Hall 2001). Movement and uplift of Halmahera had a large impact on global climate because they altered water flow between the Pacific and Indian oceans, apparently affecting El Niño phenomena, aridification of Africa, and glacial cycles (Morey et al. 1999;

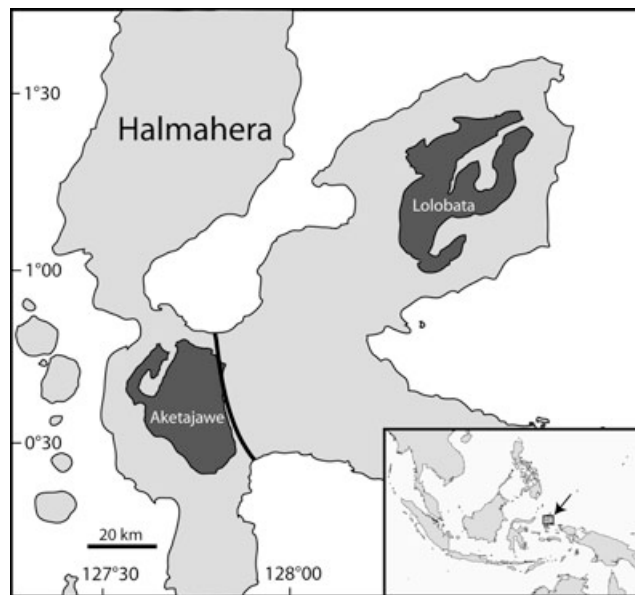


Figure 1. Boundaries of the two sections of Aketajawe-Lolobata National Park, Halmahera Island, Indonesia. The division between the paleoislands defined by Hall (2001) is indicated with a dark vertical line.

Cane & Molnar 2001). Today Halmahera has a sinuous shape, with four peninsulas and a mountainous topography (Figs. 1 & 2). Climate in the Moluccas is strongly affected by seasonal wind patterns, which makes it one of the driest parts of Indonesia, but Halmahera receives more precipitation than most other islands in central Indonesia. Rainy seasons peak in December-January and again in April-May, but rain intensity differs on different parts of the island (Monk et al. 1997).

How does the complex geological history of Halmahera and the unique combination of evolutionary histories that produced its faunal communities affect strategies for conserving biodiversity? The distribution of genetic variation among populations of species can provide useful information for biodiversity conservation and may shed light on the degree to which geographic, ecological, and geological factors affect evolution of a biota. For example, genetic variation in many species in the Philippine Archipelago corresponds closely with paleoislands consisting of multiple modern-day islands that were interconnected during Pleistocene periods of low sea level (Heaney 1986). Geographical isolation in the Philippine

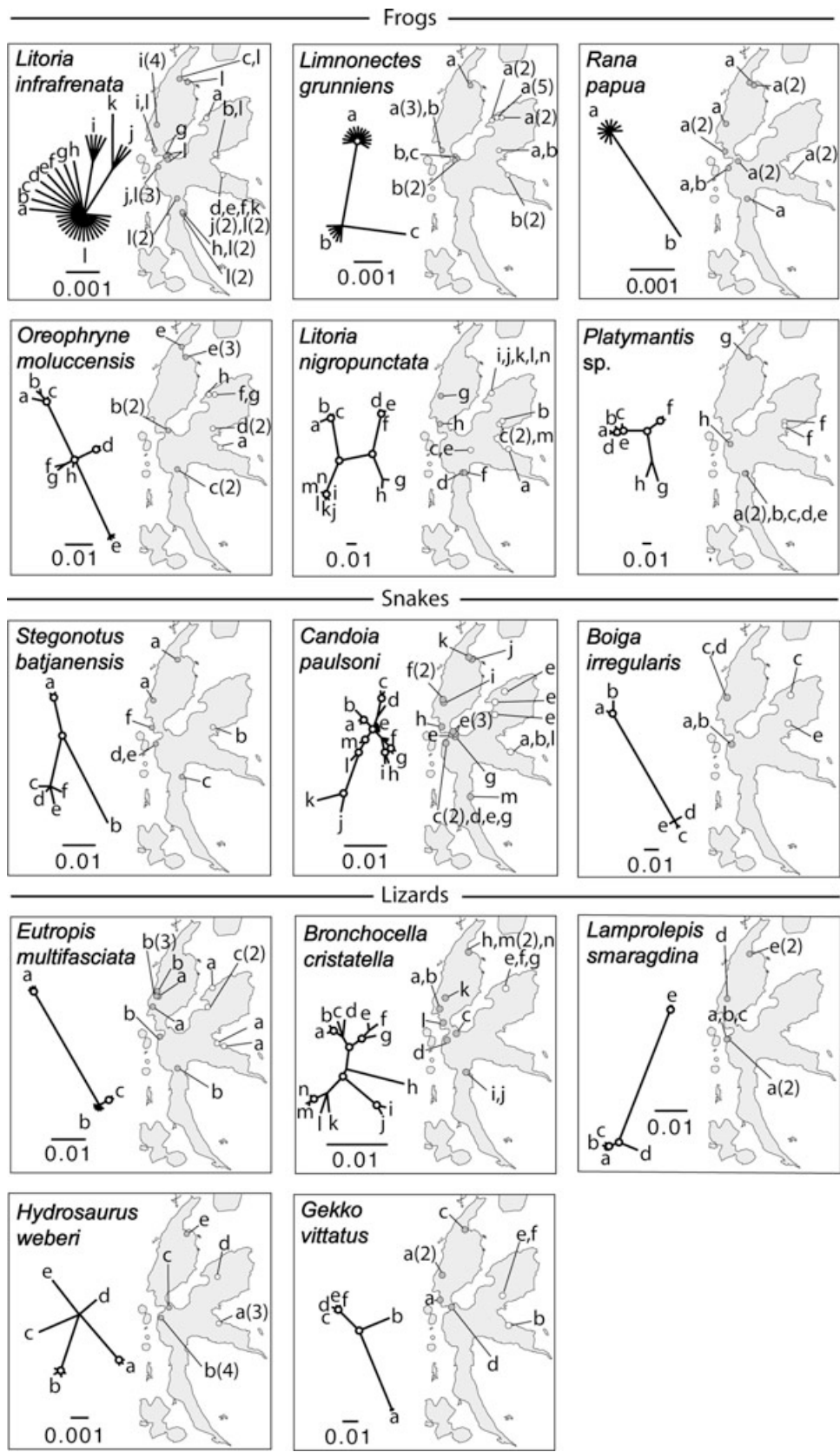


Figure 2. Mitochondrial DNA genealogies and sampling distributions of herpetofauna analyzed in this study. In each panel, a consensus tree from Bayesian phylogenetic analyses illustrates relationships inferred among unique mtDNA haplotypes, which are indicated with a letter. Open nodes have posterior probabilities $\geq 95\%$ and bars next to phylograms indicate the scale of branch lengths in substitutions per site. On the map in each panel, samples on the eastern and western paleoislands are indicated with gray and white circles, respectively. When more than one identical haplotype was found at one locality, the number of identical sequences sampled is in parentheses following the haplotype letter.

archipelago generated biogeographic regions spanning multiple present-day islands in this archipelago (Heaney 1986; Brown & Diesmos 2002; Brown & Guttman 2002; Evans et al. 2003a; Roberts 2006). In the absence of other information, this structure argues for a conservation management program that targets, at minimum, each region as opposed to each island (Brown & Diesmos 2009). In contrast, genetic variation in some species on the island of Sulawesi is clustered in pockets or “areas of endemism” within the island, probably a combined consequence of marine incursion and other barriers. Conservation strategies for Sulawesi, therefore, must target multiple regions within this island (Evans et al. 2003a, 2003c, 2008). Vicariance due to paleoislands is also suggested on Cuba (Glor et al. 2004) and Hispaniola (Townsend et al. 2007).

Our goal was to test how ecological and geographic variables affect intraspecific diversification on Halmahera and to assess conservation genetic implications of the position of the recently established Aketajawe-Lolobata National Park, which consists of two disjunct blocks of intact forest (Fig. 1). In particular, whether this park captures adequately the full breadth of genetic diversity in Halmahera’s endemic species is an important issue for biodiversity management. The Aketajawe block is in the center of Halmahera, between the northern and southern peninsulas, in a region that is part of the western paleoisland and also a portion of the zone of accretion between the two paleoislands. The Lolobata block is situated on the northeastern peninsula of Halmahera. Each of these regions was initially proposed as a wildlife sanctuary (Smiet et al. 1981) and identified as an “important bird area” by BirdLife International (BirdLife International 2008). To assess the degree to which genetic variation in this park is representative of variation throughout the entire island, we analyzed mitochondrial DNA sequences of 14 species of frogs, lizards, and snakes, and tested whether molecular variation is correlated with ecological, geographic, and hydrological distances or with Halmahera’s paleoislands. Our sample design did not target the park per se; rather, we attempted to evaluate within-species diversity in these representative species over as much of the island as possible.

Methods

Fieldwork

We collected genetic samples from six frog species, five lizard species, and three snake species on Halmahera in July–August of 2006 and August of 2007 (Fig. 2; Supporting Information). No name was available for one *Platymantis* species, and we refer to it as sp. For each species, at least five distinct localities were sampled, including localities on both of Halmahera’s paleoislands (except *Lamprolepis smaragdina*).

We used ecological niche modeling with the sample locations generated in the field phase of this study to interpolate species’ distributions. Niche models were inferred with Maxent (Phillips et al. 2006) on the basis of occurrence sites from which the genetic samples were drawn and on seven climatic variables (Hijmans et al. 2005): annual mean temperature, mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, and precipitation of the wettest, and driest months. For the purposes of assessing likely distributions of species, we used the least-training presence-thresholding approach (Pearson et al. 2007), in which the lowest nonzero suitability score assigned to any occurrence used in model building is used as the break point between predicted presence and predicted absence. No samples (except one from *Boiga irregularis*) were obtained from within the park boundaries, but niche-modeling results suggested that all the species we examined were likely to occur in both sections of Aketajawe-Lolobata National Park (Supporting Information). Voucher specimens were deposited in the Museum Zoologicum Bogoriense (MZB); tissues were deposited in the MZB Genetics Laboratory and the University of Indonesia Taxonomy Laboratory.

Evolution of Halmahera’s Herpetofauna

We tested the null hypothesis that the geographic distribution of molecular variation in these species could be explained by panmixia (i.e., that stochastic factors alone can account for observed patterns). We evaluated the alternative hypotheses that paleoislands, geographic distance, ecological suitability, or river flow are correlated with genetic variation on the basis of partial Mantel tests with the following distance matrices: paleoisland membership, overland geographic distance, ecological suitability, and riverine distance. Genetic distances were obtained from phylogenetic analysis of 618–660 base pairs of the CO1 gene of mitochondrial DNA (mtDNA). This region has been proposed as a DNA barcode for animals on the basis of variation at the species level (Hebert et al. 2003a, 2003b), although we used it simply as a marker of genetic variation within species. We performed DNA extractions, polymerase chain reaction amplification, and sequencing with Qiagen DNA extraction kits, primers, and other standard techniques (Ivanova et al. 2006). Statistics on molecular variation were calculated with the program DNAsp (version 4.5; Rozas et al. 2003). We performed phylogenetic analyses with MrBayes (version 3.1.2; Huelsenbeck & Ronquist 2001) for 5,000,000 generations, and a model of evolution selected with MrModeltest version 2 on the basis of a hierarchical likelihood ratio test (Nylander 2004). A postrun analysis of tree likelihood scores indicated that a burn-in of 1,000,000 generations was conservative for all the data sets. Patristic genetic distances were

then calculated from consensus topologies with PATRISTIC (version 1.0; Fourment & Gibbs 2006). These sequence data were deposited in GenBank (Supporting Information).

The other distance matrixes were generated as follows. We created a binary “paleoisland” distance matrix by coding pairwise comparisons between samples that were collected in the same paleoisland as 0 and pairwise comparisons between samples that were collected in different paleoislands as 1. Demarcation of paleoislands followed Hall (2001). The overland surface distance matrix was calculated to reflect the minimum on-land distances between sites, which counted topography and therefore included vertical and horizontal distance between sites. We based estimates of riverine distances on accumulated river flow, and they thus represent the minimum accumulated river flow that must be passed between two points, barring travel over marine water. In other words, large riverine distances indicate many rivers or large rivers must be crossed if one is to travel between two points. Finally, we constructed ecological distances with ecological suitability as a friction and, again, barring travel over marine barriers. Ecological suitability was characterized across Halmahera as described above through Maxent modeling (Phillips et al. 2006) and in relation to known occurrences and climate data as above. For analyses of landscape friction, however, we did not use a threshold for the model predictions; instead, we used the full ramp of Maxent suitability values (logistic-suitability output option). Large ecological suitability distances indicate that very different climatic conditions would have to be crossed to travel between two sites. Derivation of such landscape-level ecological profiles is now commonplace (e.g., Peterson et al. 2007). Overland, ecological, and riverine distances between sample points were calculated with ArcGIS (version 9.2; ESRI, Redlands, California) and automated in Python scripts prepared by X.L.

Partial correlation between genetic distance and each of the four distance matrices was estimated with the program PASSaGE (version 2.0, release 7.29; Rosenberg 2008). To test for a correlation between two matrixes (**X** and **Y**) while holding the effects of other matrixes constant (e.g., **A**, **B**, and **C**), multiple regressions are performed between the elements of **X** and **Y** on **A**, **B**, and **C**, and the residuals of each multiple regression were then used in a standard Mantel test. To assess significance, Smouse et al. (1986) suggest permutation of rows and columns of the residual matrixes, but Legendre (2000) shows that this procedure produces inaccurate estimates of type I error. For this reason, PASSaGE2 permutes one of the original matrixes (**Y**) before recalculating residuals from a multiple regression on **A**, **B**, and **C** and then recalculates the Mantel correlation from these residuals and those from the original multiple regression of matrix **X** on **A**, **B**, and **C**. The permutation is then re-

peated to generate a null distribution of partial Mantel statistics.

Because we have a one-sided alternative hypothesis (that the partial correlation between genetic distance and the other distances are positive in each comparison), we used a right-tailed distribution generated from 1000 permutations to evaluate the probability of type I error (i.e., rejecting the null hypothesis when it is true). Given the multiple comparisons involved, we applied a sequential Bonferroni correction to assess species-level significance, where $\alpha = 0.05$ (Rice 1989). Alternative permutation approaches may be more appropriate under specific conditions, such as a ring species (Raufaste & Rousset 2001; Rousset 2002). Nevertheless, simulations indicated that the permutation procedure we used had a correct level of type I error; this approach is also recommended when data are skewed or there are outliers (P. Legendre, personal communication; Legendre 2000).

Results

Frogs

A significant effect of paleoislands was recovered in only one of the 14 species examined, the frog *Litoria infrafrenata* (Table 1). This species shows high genetic diversity despite low divergence between unique alleles, and private alleles were present on each paleoisland (Table 2, Fig. 2). *L. infrafrenata* was also the only species in which Tajima's *D* departs significantly from neutral expectations (Table 2). A negative Tajima's *D* derives from high levels of segregating sites (*S*) relative to the average pairwise nucleotide diversity (π) and could be a genetic signature of a recent selective sweep of mtDNA or population expansion. Analysis of other unlinked loci would help discriminate between these alternatives. In addition to *L. infrafrenata*, molecular variation was also low in two other frogs (*Limnonectes grunniens* and *Rana papua*; Table 2, Fig. 2), but none of their partial correlations were significant (Table 1). Low molecular variation could result from small effective population size, low mutation rate, or nonequilibrium processes such as founder effects or recent population bottleneck.

Another frog, *Oreophryne moluccensis*, showed a significant partial correlation between genetic distance and ecological distance, which suggests isolation of populations by factors related to environmental variation (Table 1, Fig. 2). Isolation by distance effects were indicated by significant correlations between genetic distance and geographic distance in *Litoria nigropunctata* and in *Platymantis* sp. (Table 1).

Lizards and Snakes

The aquatic lizard *Hydrosaurus weberi* showed low levels of molecular variation on Halmahera (Table 1);

Table 1. Partial correlation and probability of type I error of partial Mantel test of the correlation between genetic distances and four abiotic variables: on-land surface distance (surface), river flow accumulation (flow), ecological suitability (ecology), and within versus between paleoislands (paleoisland).

Species	Comparison	Correlation	p (right tailed) ^a
Frogs			
<i>Limnonectes grunniens</i>	surface	-0.02624	0.593
	flow	-0.07095	0.762
	ecology	0.09480	0.242
	paleoisland	0.07023	0.178
<i>Litoria infrafronata</i>	surface	-0.21161	0.970
	flow	0.19946	0.053
	ecology	0.18505	0.076
<i>Litoria nigropunctata</i>	paleoisland	0.21712	0.009*
	surface	0.48357	0.001*
	flow	0.03880	0.341
<i>Oreophryne moluccensis</i>	ecology	-0.24742	0.994
	paleoisland	0.25209	0.019
	surface	-0.05446	0.662
<i>Platymantis</i> sp.	flow	-0.07355	0.819
	ecology	0.28975	0.001*
	paleoisland	-0.23573	0.982
<i>Rana papua</i>	surface	0.57099	0.002*
	flow	-0.18785	0.860
	ecology	-0.45830	0.999
	paleoisland	-0.29733	0.977
<i>Boiga irregularis</i> ^b	surface	0.12472	0.383
	flow	0.10619	0.139
	ecology	-0.18641	0.856
	paleoisland	0.11013	0.285
Snakes			
<i>Candoia paulsoni</i>	surface	-0.44772	0.955
	flow	0.37177	0.105
	ecology	0.45670	0.064
	paleoisland	0.16872	0.367
<i>Stegonotus batjanensis</i>	surface	0.56594	0.008*
	flow	-0.22315	0.948
	ecology	-0.15304	0.812
	paleoisland	-0.53029	0.997
Lizards			
<i>Bronchocella cristatella</i>	surface	0.35076	0.163
	flow	0.43026	0.171
	ecology	-0.17956	0.632
	paleoisland	0.73671	0.013
<i>Eutropis multifasciata</i>	surface	0.01356	0.432
	flow	-0.08965	0.774
	ecology	0.21754	0.026
	paleoisland	-0.28598	0.993
<i>Gekko vittatus</i>	surface	0.23269	0.043
	flow	0.04049	0.233
	ecology	-0.24220	0.959
	paleoisland	0.16534	0.129
<i>Hydrosaurus amboinensis</i>	surface	0.20148	0.137
	flow	0.41576	0.121
	ecology	-0.20525	0.895
	paleoisland	0.03889	0.406
<i>Lamprolepis smaragdina</i>	surface	0.64462	0.002*
	flow	0.55709	0.012*
	ecology	-0.76883	1.000
	paleoisland	-0.65567	1.000

continued

Table 1. (continued).

Species	Comparison	Correlation	p (right tailed) ^a
Lizards			
<i>Lamprolepis smaragdina</i>	surface	0.90910	0.003*
	flow	-0.78397	0.999
	ecology	0.99943	0.001*
	paleoisland	N/A	N/A

^aFor each of the 14 species, significance after Bonferroni correction for four tests is indicated (*).

^bFor comparisons with small sample sizes, permutation tests could exaggerate significance if the number of permutations exceeds the number of possible combinations of data in the matrix.

this variation was correlated with both geographic and river distances (Table 2). This finding supports isolation by distance and is consistent with these riparian specialists dispersing along (as opposed to across) river valleys, although inferred evolutionary relationships among mtDNA haplotypes in this species were not strongly supported (Fig. 2), which can affect the accuracy of the genetic distances used in the partial correlations. The only other lizard species with significant departure from panmixia was *Lamprolepis smaragdina*, in which genetic distance was significantly correlated with geographic and ecological distances; no tests for effects of paleoislands were possible for this species because samples were not obtained from the eastern paleoisland. Of the three snakes in this study, only *Candoia paulsoni* showed significant departure from panmixia as a consequence of isolation by distance (Table 1).

Correlations among Environmental Variables

Impacts of geographic distance, ecological suitability, riverine distance, and paleoislands were recovered in seven of the 14 species examined. In the other seven species, no marked departure from panmixia was observed. Of interest for conservation, then, is the question of whether the habitat distances (geographic, ecological suitability, riverine, paleoisland) themselves are correlated with one another. For instance, does variation in ecological suitability tend to be correlated with geographic distance? Does each paleoisland have a unique ecology? To explore these questions, for each species we evaluated partial correlations between each habitat distance holding the other distances constant. Results were highly consistent across taxa (Supporting Information): ecological distance was often significantly correlated with geographic distance, but other partial correlations were generally not significant. This result supports the intuition that ecological variation on Halmahera was affected by variation in climate, topography, and geology in different sectors of the island, but that this variation was not tightly linked to the palaeoislands. Significant

Table 2. Molecular variation in mitochondrial CO1 sequences of 14 species of herpetofauna on Halmahera.*

Organism	No. of samples	No. of sites	No. of silent sites	S(s)	S(τ)	π (JC silent)	θ (silent)	D
Frogs								
<i>Limnonectes grunniens</i>	22	640	168	2	0	0.00344	0.00327	0.11197
<i>Litoria infrafronata</i>	34	657	163	10	1	0.00562	0.01453	-1.96717†
<i>Litoria nigropunctata</i>	16	633	165	89	1	0.22854	0.16217	0.88658
<i>Oreophryne moluccensis</i>	14	618	160	29	2	0.08270	0.05685	1.65192
<i>Platymantis</i> sp.	10	642	169	85	2	0.19776	NR	-0.14969
<i>Rana papua</i>	13	629	155	1	0	0.00100	0.00208	-1.14915
Snakes								
<i>Boiga irregularis</i>	6	660	164	26	1	0.08417	0.06939	0.94804
<i>Candoia paulsoni</i>	23	657	163	25	0	0.02495	0.04148	-1.53221
<i>Stegonotus batjanensis</i>	7	652	170	19	2	0.04828	NR	0.00000
Lizards								
<i>Bronchocella cristatella</i>	15	629	165	35	6	0.05633	0.06539	-0.76801
<i>Eutropis multifasciata</i>	12	649	169	25	1	0.07119	0.04712	1.97023
<i>Gekko vittatus</i>	8	652	165	68	0	0.21053	NR	0.94110
<i>Hydrosaurus weberi</i>	10	657	172	3	1	0.00701	0.00617	-0.03786
<i>Lamprolepis smaragdina</i>	10	642	167	38	1	0.10479	0.08763	0.55654

*Indicated are number (No.) of samples; total number of sites; number of silent sites; number of polymorphic (S[s]) silent and replacement sites (S(τ)); nucleotide diversity based on silent sites and with Jukes-Cantor correction (π [JC-silent]); estimate of the population parameter θ based on silent sites (θ [silent]); and Tajima's (1989) D statistic (†, significant departure from zero). Some θ (silent) are not reported (NR) because some codons differ with multiple changes.

correlations between geographic distance and paleoislands occurred in *L. infrafronata* and *C. paulsoni* (Supporting Information), which indicated that comparisons for these species between paleoislands tended to be geographically farther apart than comparisons within paleoislands given the geometry of the sampling locations. In *L. infrafronata*, there was a significant correlation between ecological and riverine distances (Supporting Information), suggesting that ecological variation among collection sites for this species tended to be greater across rather than along rivers.

Discussion

Genetic Diversity of Halmahera Herpetofauna

In many species multilocus testing of demographic hypotheses is impeded by the number of known PCR primers that can successfully amplify DNA for sequencing and by the time, effort, and cost required to develop new primers that target additional regions. Because PCR primers have already been designed that amplify regions of the mitochondrial genome that are variable within and between reptile and amphibian species (e.g., Smith et al. 2008), this source of information offers a tractable first step toward exploring within-species diversity across multiple species, such as the present analyses. Of course, interpretation of these data comes with the caveat that conclusions are derived from only one marker per species and therefore reflect patterns of genome-wide variation only incompletely.

With this caveat in mind, support for a strong role of paleoislands in influencing multitaxon intraspecific divergence was not recovered in most species. In the one species for which we found statistical support for an effect of paleoislands, *Litoria infrafronata*, molecular divergence was low and the most common haplotype (haplotype 1 in Fig. 2) occurred on all four peninsulas of Halmahera. In this species, haplotypes found on only one paleoisland (the "private alleles") were genetically similar to (i.e., recently diverged from) this widespread haplotype. Under the assumption of a rough molecular clock, this association suggests that impacts of paleoislands on genetic diversity of *L. infrafronata* is an odd result, in light of the relatively old nature of the paleoislands. Overall, then, scant evidence for a substantial or long-term genetic impact of Halmahera's paleoislands was recovered in these 14 species, which could be a result of any of at least five possibilities: their ancestors dispersed to Halmahera after accretion of the paleoislands; recent dispersal in each species homogenized ancient population structure; at least one of the paleoislands was underwater when they collided; at least one of the paleoislands resubmerged after accretion; or dispersal between previously separated paleoislands was not substantially impeded by marine barriers. A scenario similar to the first possibility may explain patterns of diversification of macaques (*Macaca*) on nearby Sulawesi. Population structure of these primates does not correspond with the suture zones of Sulawesi's paleoislands (Evans et al. 2003b), even though some features of Sulawesi's paleoislands match population structure or geographic

distributions of species in other groups (Evans et al. 2003a; McGuire et al. 2007).

Support for a genetic impact of geographic distance was recovered in five of 14 species examined, indicating that their genetic variation was not distributed evenly across the island as a consequence of low dispersal distances relative to species' ranges. Significant correlations between genetic and ecological distance in *O. moluccensis* and *L. smaragdina* could point to population structure being based on environmental variation across Halmahera. This would be interesting from the standpoint of understanding natural selection and speciation on Halmahera, although clearly further sampling and multilocus data are needed to tease apart the possibility from type I error.

Conservation Genetic Consequences of Aketajawe-Lolobata National Park

Halmahera is part of a biodiversity hotspot (Myers et al. 2000), its rainforests belong to a distinct ecoregion (Wikramanayake et al. 2001), and its biota is a conservation priority under other criteria as well (Jepson & Whitaker 2002). In 2004 Aketajawe-Lolobata National Park was established on Halmahera (Keputusan Menteri Kehutanan No. SK.397/MenHut-II/2004), the first and only national park in Maluku Utara province. This park consists of two separate regions of intact forest (Fig. 1). Our failure to reject the null hypothesis of panmixia in half of the herpetofauna species studied suggests that, for such species, reserve design need not incorporate the dual nature of Halmahera's paleoisland history. We also observed in some species a significant correlation between geographic distance or ecological suitability. Overall then, the geographic distribution of molecular variation in these herpetofauna suggests that peninsulas of Halmahera are not areas of genetic endemism beyond the effects of isolation by distance, at least in the species we studied. These results together suggest that multiple, geographically dispersed conservation areas—such as the two forest blocks of Aketajawe-Lolobata—are highly useful for preservation of extant molecular variation and future adaptive potential. This utility is achieved more because these forest blocks are geographically separated than because they happen to be situated on different paleoislands.

A reasonable concern relating to these conclusions is that we included almost no samples from within the boundaries of the park. The ecological-niche model projections derived from our sampling design, however, suggests that all 14 species are likely to occur in both blocks of this park (Supporting Information). Results of previous studies indicate ample predictive ability for niche-modeling tools when presented with the challenge of predicting unknown populations of poorly characterized species (Raxworthy et al. 2003; Engler et al. 2004; Bourg

et al. 2005; Almeida et al. 2009; Siqueira et al. 2009). To our knowledge, there are no records of microendemism on Halmahera. This suggests our sampling strategy—which targeted as many parts of the island as possible during our fieldwork—provides a reasonable basis with which to evaluate the utility of the Aketajawe-Lolobata National Park for conservation of Halmahera-wide genetic diversity.

Of course, some species have patchy distributions on Halmahera or occur in ecosystems not present in the park (e.g., coastal ecosystems); these species may require additional species-specific or ecosystem-specific protection efforts. Additionally, we did not extensively sample all parts of Halmahera for each focal species and thus may not have completely characterized the full breadth of their genetic diversity. Although logistical obstacles to sampling large numbers of taxa uniformly across a landscape typically prevent this kind of ideal sampling, future studies of genetic variation across Halmahera would be well served to improve on the geographic sampling included here. We also did not address the question of whether there is substantial variation in between-species diversity over different portions of Halmahera and, if so, whether the Aketajawe-Lolobata National Park coincides with areas of high between-species diversity. Although this is probably the case for birds (Smiet et al. 1981; BirdLife International 2008), further comparative studies are needed to address this question for other taxa.

Original proposals for protected areas were larger than the present Aketajawe-Lolobata National Park, but were modified in response to habitat loss (Poulsen et al. 1999). Significant ongoing threats to this region and other remaining forests on Halmahera include mining and logging interests, establishment of transmigration sites, and other changes associated with agriculture (Poulsen et al. 1999). A corridor between the two blocks of the national park would contribute to demographic exchange between populations in each, thereby reducing deleterious impacts of small population size (Lynch & Gabriel 1990). The forests between the two blocks are, however, not part of the national park, and two mining concessions are located in this area (M. Zimsky, personal communication). Connection of habitat has implications for metapopulation processes that permit recolonization of areas that experience local population extinction (McCallum & Dobson 2002) and for synchronization of natural fluctuations in population size (e.g., Earn et al. 2000) and transmission of wildlife diseases, such as chytrid fungus (Kriger & Hero 2007). Another concern is that population extinction rates tend to be higher near edges of protected areas (Bradshires et al. 2001), which supports the point that although larger protected areas are better, their shape is also important.

Additional questions relevant to conservation planning on this island include whether the park will protect a sufficient proportion of each of Halmahera's diverse

ecosystems, will pressures exerted by human populations allow for sustainable protection of species in this park, and do the genetic benefits of a corridor between these blocks outweigh possible demographic risks. The long-term success of this park, which at the moment has little infrastructure or demarcation on the ground, will therefore depend critically on human activities inside and outside of its boundaries, including funding and enforcement of conservation management of this park.

Acknowledgments

We thank J. Dushoff, A. Jiménez-Valverde, P. Legendre, and M. Rosenberg for statistical advice, M. Zimsky for providing information about Aketajawe-Lolobata National Park, N. Ivanova and R. Hanner for technical assistance, and two anonymous reviewers for constructive comments on this manuscript. We also thank the residents of Kampung Pisang, Sofifi, Subaim, Weda, and Lelilef for their hospitality. The Aketajawe-Lolobata National Park office and the Ambon Natural Resource and Conservation Office (BKSDA Ambon) provided permits and field assistance, and the Indonesian Department of Treasury and regional offices of Jakarta, Ternate, Tobelo, Ambon, and Masohi provided logistical assistance. This research was supported by the Declining Amphibian Populations Task Force, National Science Foundation (NSF) (0640967), Canadian Foundation for Innovation (10715), National Science and Engineering Research Council (RGPIN-283102-07), and McMaster University. R.M.B. was supported by NSF (DEB 0640737) during the preparation of this manuscript.

Supporting Information

Sample location information (Appendix S1), ecological niche projections (Appendix S2), and partial correlations between environmental variables (Appendix S3) are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Allison, A. 1996. Zoogeography of amphibians and reptiles of New Guinea and the Pacific region. Pages 407–436 in A. Keast and S. E. Miller, editors. The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: patterns and processes. SPB Academic Publishing, Amsterdam, The Netherlands.
- Almeida, C. E., E. Folly-Ramos, A. T. Peterson, V. Lima-Neiva, M. Gumiel, R. Duarte, M. Locks, M. Beltrão, and J. Costa. 2009. Could the bug *Triatoma sberlocki* be vectoring Chagas disease in small mining communities in Bahia, Brazil? Medical and Veterinary Entomology. in press.
- BirdLife International. 2008. BirdLife's online world bird database: the site for bird conservation. Version 2.1. BirdLife International, Cambridge, United Kingdom.
- Bourg, N. A., W. J. McShea, and D. E. Gill. 2005. Putting a CART before the search: successful habitat prediction for a rare forest herb. *Ecology* **86**:2793–2804.
- Bradshires, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London B* **268**:2473–2478.
- Brown, R. M., and A. Diesmos. 2002. Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. *Silliman Journal* **42**:133–162.
- Brown, R. M., and A. C. Diesmos. 2009. Philippine biodiversity. Pages 723–732 in R. G. Gillespie, and D. Clague, editors. *Encyclopedia of islands*. University of California Press, Berkeley.
- Brown, R. M., and S. I. Guttman. 2002. Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: reconsideration of Huxley's modification of Wallace's line at the Oriental-Australian faunal zone interface. *Biological Journal of the Linnean Society* **76**:393–461.
- Brown, W. C. 1997. Biogeography of amphibians in the islands of the southwest Pacific. *Proceedings of the California Academy of Sciences* **50**:21–38.
- Cane, M. A., and P. Molnar. 2001. Closing of the Indonesian seaway as a precursor to east African aridification around 3–4 million years ago. *Nature* **411**:157–162.
- Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. *Science* **290**:1360–1364.
- Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* **41**:263–274.
- Evans, B. J., R. M. Brown, J. A. McGuire, J. Supriatna, N. Andayani, A. Diesmos, D. T. Iskandar, D. J. Melnick, and D. C. Cannatella. 2003a. Phylogenetics of fanged frogs (Anura; Ranidae; *Limnonectes*): testing biogeographical hypotheses at the Asian-Australian faunal zone interface. *Systematic Biology* **52**:794–819.
- Evans, B. J., J. A. McGuire, R. M. Brown, N. Andayani, and J. Supriatna. 2008. A coalescent framework for comparing alternative models of population structure with genetic data: evolution of Celebes toads. *Biology Letters* **4**:430–433.
- Evans, B. J., J. Supriatna, N. Andayani, and D. J. Melnick. 2003b. Diversification of Sulawesi macaque monkeys: decoupled evolution of mitochondrial and autosomal DNA. *Evolution* **57**:1931–1946.
- Evans, B. J., J. Supriatna, N. Andayani, M. I. Setiadi, D. C. Cannatella, and D. J. Melnick. 2003c. Monkeys and toads define areas of endemism on Sulawesi. *Evolution* **57**:1436–1443.
- Fourment, M., and M. J. Gibbs. 2006. PATRISTIC: a program for calculating patristic distances and graphically comparing the components of genetic change. *BMC Evolutionary Biology* **6**:1.
- Glor, R. E., M. E. Gifford, A. Larson, J. B. Losos, L. R. Schettino, A. R. C. Lara, and T. R. Jackman. 2004. Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles. *Proceedings of the Royal Society of London Series B* **271**:2257–2265.
- Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pages 99–131 in R. Hall, and D. J. Holloway, editors. *Biogeography and geological evolution of southeast Asia*. Backhuys Publishers, Leiden, The Netherlands.
- Hall, R. 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. Pages 35–56 in I. Metcalfe, J. Smith, M. Morwood, and I. Davidson, editors. *Faunal and floral migrations and evolution in SE Asia-Australia*. Swets and Zeitlinger Publishers, Lisse, The Netherlands.
- Hall, R., M. G. Audley, F. T. Banner, S. Hidayat, and S. L. Tobing. 1988. Late Palaeogene-Quaternary geology of Halmahera, eastern

- Indonesia: initiation of a volcanic island arc. *Journal of the Geological Society, London* **145**:577–590.
- Hall, R., and G. J. Nichols. 1990. Terrane amalgamations in the Philippine Sea margin. *Tectonophysics* **181**:207–222.
- Heaney, L. R. 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction, and speciation. *Biological Journal of the Linnean Society* **28**:127–165.
- Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003*a*. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London Series B* **270**:313–321.
- Hebert, P. D. N., S. Ratnasingham, and J. R. deWaard. 2003*b*. Barcoding animal life: cytochrome c oxidase subunit I divergences among closely related species. *Proceedings of the Royal Society of London Series B* **270**(suppl.):S96–S99.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**:1965–1978.
- Huelsenbeck, J. P., and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**:754–755.
- ICBP (International Council for Bird Protection) 1992. Putting biodiversity on the map: priority areas for global conservation. ICBP, Cambridge, United Kingdom.
- Inger, R. F. 1999. Distribution of amphibians in southern Asia and adjacent islands. Pages 445–482 in W. E. Duellman, editor. *Patterns of distribution of amphibians: a global perspective*. Johns Hopkins Press, Baltimore, Maryland.
- Ivanova, N. V., J. R. DeWaard, and P. D. N. Hebert. 2006. An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes* **6**:998–1002.
- Jepson, P., and R. J. Whittaker. 2002. Ecoregions in context: a critique with special reference to Indonesia. *Conservation Biology* **16**:42–57.
- Kruger, K. M., and J.-M. Hero. 2007. The chytrid fungus *Batrachochytrium dendrobatidis* is non-randomly distributed across amphibian breeding habitats. *Diversity and Distributions* **13**:781–788.
- Legendre, P. 2000. Comparison of permutation methods for the partial correlation and partial Mantel tests. *Journal of Statistical Computation and Simulation* **67**:37–73.
- Lynch, M., and W. Gabriel. 1990. Mutational load and the survival of small populations. *Evolution* **44**:1725–1737.
- McCallum, H., and A. P. Dobson. 2002. Disease, habitat fragmentation and conservation. *Proceedings of the Royal Society of London B* **269**:2041–2049.
- 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.
- Monk, K. A., Y. de Fretes, and Reksodiharjo-Liley 1997. The ecology of Nusatenggara and Maluku. *Periplus, Hong Kong*.
- Morey, S. L., J. F. Shriver, and J. J. O'Brien. 1999. The effects of Halmahera on the Indonesian throughflow. *Journal of Geophysical Research* **104**:23281–23296.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853–858.
- Nichols, G. J., and R. Hall. 1991. Basin formation and Neogene sedimentation in a backarc setting, Halmahera, eastern Indonesia. *Marine and Petroleum Geology* **8**:50–61.
- Nylander, J. A. A. 2004. MrModeltest. Version 2. Evolutionary Biology Centre, Uppsala University, Uppsala.
- Pearson, R. G., C. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**:102–117.
- Peterson, A. T., M. Papes, and M. Eaton. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* **30**:550–560.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259.
- Poulsen, M. K., F. R. Lambert, and Y. Cahyadin 1999. Evaluation of the proposed Lalobata and Ake Tajawe National Park in the context of biodiversity conservation priorities on Halmahera. *BirdLife International, Indonesia Programme, Bogor*.
- Puntodewo, S. S. O., et al. 1994. GPS measurements of crustal deformation with the Pacific-Australia plate boundary in Irian Jaya, Indonesia. *Tectonophysics* **237**:141–153.
- Rangin, C., X. L. Pichon, S. Mazzotti, M. Pubellier, N. Chamot-Rooke, M. Aurelio, A. Walpersdorf, and R. Quebral. 1999. Plate convergence measured by GPS across the Sundaland/Philippine Sea plate deformed boundary: the Philippines and eastern Indonesia. *Geophysical Journal International* **139**:296–316.
- Raufaste, N., and F. Rousset. 2001. Are partial Mantel tests adequate? *Evolution* **55**:1703–1705.
- Raxworthy, C. J., E. Martínez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta, and A. T. Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* **426**:837–841.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- Roberts, T. E. 2006. Multiple levels of allopatric divergence in the endemic Philippine fruit bat *Haploonycteris fischeri* (Pteropodidae). *Biological Journal of the Linnean Society* **88**:329–349.
- Rosenberg, M. S. 2008. PASSaGE: pattern analysis, spatial statistics and geographical exegesis. Arizona State University, Tempe, Arizona.
- Rousset, F. 2002. Partial Mantel tests: reply to Castellano and Balletto. *Evolution* **56**:1874–1875.
- Rozas, J., J. C. Sanchez-DelBarrio, X. Messegyer, and R. Rozas. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19**:2496–2497.
- Siqueira, M. F. D., G. Durigan, P. D. Marco Jr., and A. T. Peterson. 2009. Something from nothing: using landscape similarity and ecological niche modeling to find rare plant species. *Journal for Nature Conservation* **17**:25–32.
- Smiet, A. C., D. H. Susilo, and I. S. Sangadji. 1981. Feasibility study and proposals for conservation areas in Maluku Utara. Pages 5–7 in UNDP/FAO National Parks and Development Project FO/INS/78/061 Field report 22. United Nations Development Programme, New York.
- Smith, M. A., A. Nikolai, and P. D. N. Hebert. 2008. CO1 DNA barcoding amphibians: take the chance, meet the challenge. *Molecular Ecology Resources* **8**:235–246.
- Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple regression and correlation extension of the Mantel test of matrix correspondence. *Systematic Zoology* **35**:627–632.
- Townsend, A. K., C. C. Rimmer, S. C. Latta, and I. J. Lovette. 2007. Ancient differentiation in the single-island avian radiation of endemic Hispaniolan chat-tanagers (Aves: *Calyptophilus*). *Molecular Ecology* **16**:3634–3642.
- Wikramanayake, E., C. Dinerstein, D. Loucks, J. Olson, J. Morrison, M. Lamoreux, M. McKnight, and P. Hedao 2001. *Terrestrial ecoregions of the Indo-Pacific: a conservation assessment*. Island Press, Washington, D.C.

Supplementary Material

- S1. Sample locality information
- S2. Ecological niche projections
- S3. Partial correlations between environmental variables.

Supplementary Material S1. Locality information for samples in this study. All samples are from Halmahera island, which is in Maluku Utara province. Some subdistricts were not recorded (NR).

Species and field tag	Village	Subdistrict	District	Latitude	Longitude	Accession
<i>Limnonectes grunniens</i>						
BJE01048	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952266
BJE01051	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952267
BJE01090	Desa Tabacampaka	Kecamatan Sahu	Kabupaten Halmahera Barat	0.9388	127.5170	FJ952268
BJE01091	Desa Tabacampaka	Kecamatan Sahu	Kabupaten Halmahera Barat	0.9388	127.5170	FJ952269
BJE01141	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952270
BJE01188	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952271
BJE01189	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952272
BJE01199	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952273
BJE01200	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952274
BJE01215	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952275
BJE01242	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952276
BJE01243	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952277
BJE01244	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952278
BJE01245	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952279
BJE01267	Subaim-Buli Route	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952280
BJE01268	Subaim-Buli Route (Km10)	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952281
BJE01276	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952282
BJE01277	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952283
BJE01426	Desa Pintatu	Kecamatan Wasile Selatan	Kabupaten Halmahera Timur	0.8344	127.7170	FJ952284
BJE01427	Desa Pintatu	Kecamatan Wasile Selatan	Kabupaten Halmahera Barat	0.8344	127.7170	FJ952285
BJE01458	Desa Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952286
BJE01459	Desa Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952287
<i>Litoria nigropunctata</i>						
BJE01073	Desa Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	1.2889	127.5330	FJ952288
BJE01074	Desa Tabacampaka	Kecamatan Sahu	Kabupaten Halmahera Barat	0.9388	127.5170	FJ952289
BJE01185	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952290
BJE01186	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952291
BJE01187	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952292
BJE01193	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952293
BJE01241	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952294
BJE01270	Subaim-Buli Route	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952302
BJE01271	Subaim-Buli Route	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952295
BJE01272	Subaim-Buli Route	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952303
BJE01304	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952296
BJE01604	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952297
BJE01649	Sungai Ma, Lelilef	Kecamatan Weda	Kabupaten Halmahera Tengah	0.6072	127.9045	FJ952298
BJE01651	Sungai Ma, Lelilef	Kecamatan Weda	Kabupaten Halmahera Tengah	0.6072	127.9045	FJ952299
BJE01669	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3230	127.8258	FJ952300
BJE01749	Subaim-Buli Route (Km 12)	NR	Kabupaten Halmahera Timur	0.9737	128.3010	FJ952301
<i>Oreophryne moluccensis</i>						
BJE01120	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952368
BJE01142	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952369
BJE01143	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952370
BJE01144	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952371
BJE01218	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952372
BJE01240	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952373
BJE01248	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952374
BJE01315	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952375
BJE01370	KM5–KM10 Buli	NR	Kabupaten Halmahera Timur	0.8805	128.2830	FJ952376
BJE01371	KM5–KM10 Buli	NR	Kabupaten Halmahera Timur	0.8805	128.2830	FJ952377
BJE01443	Desa Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952378
BJE01444	Desa Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952379
BJE01673	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952380
BJE01674	Desa Weda Km14	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952381
<i>Platymantis</i> sp.						
BJE01113	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952338
BJE01605	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952339
BJE01606	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952340
BJE01633	Desa Soffif5 (SFPU2)	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7009	127.5915	FJ952341
BJE01698	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952342
BJE01699	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952343
BJE01702	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952344
BJE01703	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952345
BJE01733	Subaim-Buli Route (Km10)	NR	Kabupaten Halmahera Timur	0.9586	128.3020	FJ952346
BJE01773	Subaim-Buli Route (Km12.5)	NR	Kabupaten Halmahera Timur	0.9754	128.3029	FJ952347
<i>Rana papua</i>						
BJE01039	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952348
BJE01040	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952349
BJE01065	Desa Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	1.2889	127.5330	FJ952350

Supplementary Material S1 (continued)
Species and field tag

field tag	Village	Subdistrict	District	Latitude	Longitude	Accession
BJE01121	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952351
BJE01136	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952352
BJE01137	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952353
BJE01278	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952354
BJE01279	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952355
BJE01385	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952356
BJE01415	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952357
BJE01464	Desa Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952358
BJE01467	Desa Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952359
BJE01603	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952360
<i>Litoria infrafronata</i>						
BJE01031	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952304
BJE01032	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952305
BJE01035	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952306
BJE01036	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952307
BJE01043	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952308
BJE01044	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952309
BJE01106	Desa Ruko	Kecamatan Tobelo Utara	Kabupaten Halmahera Utara	1.7833	127.9330	FJ952310
BJE01107	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952311
BJE01109	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8227	127.8300	FJ952312
BJE01192	Desa Voli, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3333	128.1670	FJ952313
BJE01290	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952314
BJE01291	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952315
BJE01293	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952316
BJE01294	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952317
BJE01316	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952318
BJE01352	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952319
BJE01353	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952320
BJE01354	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952321
BJE01358	KM5--KM10 Buli	NR	Kabupaten Halmahera Timur	0.8805	128.2830	FJ952322
BJE01359	KM5--KM10 Buli	NR	Kabupaten Halmahera Timur	0.8806	128.2830	FJ952323
BJE01379	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952324
BJE01380	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952325
BJE01406	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952326
BJE01407	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952327
BJE01437	Desa Musambo	Kecamatan Wasile Selatan	Kabupaten Halmahera Timur	0.8644	127.6798	FJ952328
BJE01439	Desa Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952329
BJE01468	Desa Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952330
BJE01601	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952331
BJE01602	Desa Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952332
BJE01609	Desa Kluting Jaya SP4	Kecamatan Gane Timur	Kabupaten Halmahera Selatan	0.1232	127.8750	FJ952333
BJE01610	Desa Kluting Jaya SP4	Kecamatan Gane Timur	Kabupaten Halmahera Selatan	0.1232	127.8750	FJ952334
BJE01611	Desa Kluting Jaya SP3	Kecamatan Gane Timur	Kabupaten Halmahera Selatan	0.1486	127.8670	FJ952335
BJE01612	Desa Kluting Jaya SP3	Kecamatan Gane Timur	Kabupaten Halmahera Selatan	0.1486	127.8670	FJ952336
BJE01613	Desa Kluting Jaya SP3	Kecamatan Gane Timur	Kabupaten Halmahera Selatan	0.1486	127.8670	FJ952337
<i>Bronchocella cristatella</i>						
BJE01038	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952190
BJE01094	Desa Tabacampaka	Kecamatan Sahu	Kabupaten Halmahera Barat	0.9388	127.5170	FJ952191
BJE01097	Desa Galala	Kecamatan Jailolo	Kabupaten Halmahera Barat	1.1170	127.4670	FJ952192
BJE01098	Desa Galala	Kecamatan Jailolo	Kabupaten Halmahera Barat	1.1170	127.4670	FJ952193
BJE01124	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952194
BJE01125	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952195
BJE01126	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952196
BJE01127	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952197
BJE01222	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952198
BJE01223	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952199
BJE01224	Desa Voli3, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952200
BJE01469	Braha	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952201
BJE01666	Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952202
BJE01677	Weda	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3233	127.7990	FJ952203
BJE01708	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952204
<i>Eutropis multifasciata</i>						
BJE01017	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952228
BJE01025	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952229
BJE01026	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952230
BJE01066	Desa Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	1.2889	127.5330	FJ952231
BJE01100	Desa Galala	Kecamatan Jailolo	Kabupaten Halmahera Barat	1.1170	127.4670	FJ952232
BJE01179	Desa Subaim, SP3	Kecamatan Wasile	Kabupaten Halmahera Timur	1.1089	128.1780	FJ952233
BJE01182	Desa Subaim, SP3	Kecamatan Wasile	Kabupaten Halmahera Timur	1.1089	128.1780	FJ952234
BJE01237	Desa Voli4, TN Lolobata	NR	Kabupaten Halmahera Timur	1.3667	128.2330	FJ952235
BJE01328	Desa Tiwil	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6500	128.3000	FJ952236
BJE01343	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952237

Supplementary Material S1 (continued)

Species and field	Village	Subdistrict	District	Latitude	Longitude	Accession
BJE01449	Desa Sofifi3	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7319	127.5530	FJ952238
BJE01676	Desa Weda (Km14)	Kecamatan Weda	Kabupaten Halmahera Tengah	0.3235	127.7837	FJ952239
<i>Gekko vittatus</i>						
BJE01027	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952240
BJE01028	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952241
BJE01095	Desa Tabacampaka	Kecamatan Sahu	Kabupaten Halmahera Barat	0.9388	127.5170	FJ952242
BJE01122	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952243
BJE01275	Desa Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952244
BJE1440	Desa Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952245
BJE01731	Buli-Subaim KM10	NR	Kabupaten Halmahera Timur	0.9586	128.3020	FJ952246
BJE01767	Buli-Subaim KM12	NR	Kabupaten Halmahera Timur	0.9754	128.3029	FJ952247
<i>Hydrosaurus weberi</i>						
BJE01135	Desa Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7899	127.8910	FJ952248
BJE01198	Desa Voli2, TN Lolobata	NR	Kabupaten Halmahera Timur	1.2416	128.2830	FJ952249
BJE01318	Desa Tiwil	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6500	128.3000	FJ952250
BJE01331	Desa Tiwil	NR	Kabupaten Halmahera Timur	0.6500	128.3000	FJ952251
BJE01332	Desa Tiwil	NR	Kabupaten Halmahera Timur	0.6500	128.3000	FJ952252
BJE01388	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952253
BJE01394	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952254
BJE01441	Desa Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952255
BJE01447	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952256
BJE01448	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952257
<i>Lamprolepis smaragdina</i>						
BJE01019	Desa Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952258
BJE01118	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952259
BJE01119	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952260
BJE01397	Desa Sofifi2	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7386	127.5580	FJ952261
BJE01399	Desa Sofifi2	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7386	127.5580	FJ952262
BJE01450	Desa Sofifi3	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7319	127.5530	FJ952263
BJE01451	Desa Sofifi3	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7319	127.5530	FJ952264
BJE01452	Desa Sofifi3	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7319	127.5530	FJ952265
<i>Boiga irregularis</i>						
BJE01069	Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Utara	1.2889	127.5330	FJ952184
BJE01070	Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Utara	1.2889	127.5330	FJ952185
BJE01258	Desa Voli5, TN Lolobata (KM24)	NR	Kabupaten Halmahera Timur	1.3167	128.3356	FJ952186
BJE01638	Sofifi4 (SFPU3)	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.6992	127.5930	FJ952187
BJE01639	Sofifi4 (SFPU3)	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.6992	127.5930	FJ952188
BJE01750	Buli-Subaim Route (km12)	NR	Kabupaten Halmahera Timur	0.9586	128.3020	FJ952189
<i>Candoia paulsoni</i>						
BJE01020	Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952205
BJE01052	Tafale	Kecamatan Jailolo	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952206
BJE01056	Goal	Kecamatan Susupu	Kabupaten Halmahera Barat	1.2500	127.5420	FJ952207
BJE01071	Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	1.2889	127.5330	FJ952208
BJE01140	Mamuya	Kecamatan Galela Selatan	Kabupaten Halmahera Utara	1.7900	127.8910	FJ952209
BJE01145	Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952210
BJE01149	SP3 Subaim	Kecamatan Wasile	Kabupaten Halmahera Timur	1.1089	128.1780	FJ952211
BJE01191	Voli	NR	Kabupaten Halmahera Timur	1.2571	128.1840	FJ952212
BJE01249	Voli3	NR	Kabupaten Halmahera Timur	1.3667	128.3000	FJ952213
BJE01306	Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952214
BJE01307	Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952215
BJE01347	Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952216
BJE01348	Soagimalaha	Kecamatan Maba Selatan	Kabupaten Halmahera Timur	0.6169	128.3800	FJ952217
BJE01389	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952218
BJE01390	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952219
BJE01400	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952220
BJE01401	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952221
BJE01403	Sofifi	Kecamatan Oba Utara	Kabupaten Tidore Kepulauan	0.7198	127.5652	FJ952222
BJE01434	Pintatu	Kecamatan Wasile Selatan	Kabupaten Halmahera Timur	0.8344	127.7170	FJ952223
BJE01436	Musambo	Kecamatan Wasile Selatan	Kabupaten Halmahera Timur	0.8644	127.6798	FJ952224
BJE01438	Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8514	127.6620	FJ952225
BJE01471	Dodinga	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.8072	127.6820	FJ952226
BJE01619	Foya	Kecamatan Toam Timur	Kabupaten Halmahera Selatan	0.0654	127.8773	FJ952227
<i>Stegonotus batjanensis</i>						
BJE01042	Desa Tafale	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	0.9333	127.5170	FJ952361
BJE01068	Desa Tosoa	Kecamatan Jailolo Selatan	Kabupaten Halmahera Barat	1.2889	127.5330	FJ952362
BJE01110	Desa Seki	Kecamatan Galela	Kabupaten Halmahera Utara	1.8228	127.8300	FJ952363
BJE01274	Subaim-Buli Route	NR	Kabupaten Halmahera Timur	0.9416	128.2670	FJ952364
BJE01404	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Halmahera Timur	0.7198	127.5652	FJ952365
BJE01475	Desa Sofifi	Kecamatan Oba Utara	Kabupaten Halmahera Timur	0.7198	127.5652	FJ952366
BJE01623	Desa Nusliko	Kecamatan Weda	Kabupaten Halmahera Tengah	0.2867	127.8857	FJ952367

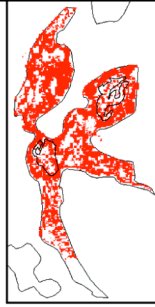
Supplementary Material S2. Halmahera-wide projections of ecological niche models for each species. Red indicates locations where species are predicted to occur given the geographical locations of samples in this study. Borders of Aketajawe-Lolobata park are indicated with black lines.

Frogs

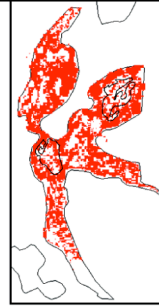
*Litoria
infrafnata*



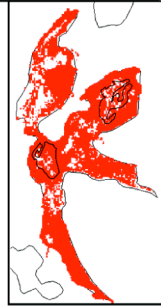
*Limnonectes
grunniens*



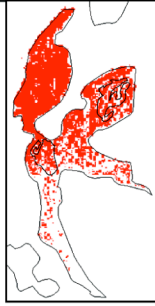
*Rana
papua*



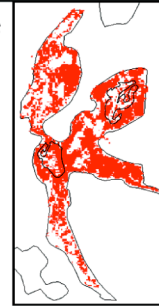
*Oreophryne
moluccensis*



*Litoria
nigropunctata*



*Platymantis
sp.*



Snakes

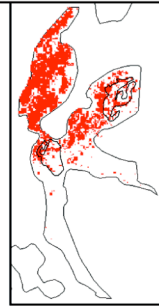
*Stegonotus
batjanensis*



*Candoia
paulsoni*



*Boiga
irregularis*



Lizards

*Eutropis
multifasciata*



*Bronchocella
cristatella*



*Lamprolepis
smaragdina*



*Hydrosaurus
weberi*



*Gecko
vittatus*



Supplementary Material S3. Partial correlation and probability of type I error of partial Mantel test between four environmental distances for each species. Labels follow Table 1 and for each species. Significance after Bonferonni correction for six tests is indicated (*), except *Lamprolepis* where correction is for three tests.

Frogs	Comparison	Correlation	P value
<i>Limnonectes grunniens</i>	Surface:Ecology	0.92204	<0.001*
	Surface:Flow	0.71882	0.057
	Surface:Paleoisland	0.56957	0.045
	Ecology:Flow	-0.54376	0.961
	Ecology:Paleoisland	-0.44553	0.915
	Flow:Paleoisland	-0.16748	0.938
<i>Litoria infrafrenata</i>	Surface:Ecology	0.79193	<0.001*
	Surface:Flow	-0.34977	0.990
	Surface:Paleoisland	0.32867	0.006*
	Ecology:Flow	0.61708	0.005*
	Ecology:Paleoisland	-0.05475	0.573
	Flow:Paleoisland	-0.14141	0.871
<i>Litoria nigropunctata</i>	Surface:Ecology	0.72548	<0.001*
	Surface:Flow	-0.06277	0.497
	Surface:Paleoisland	0.17943	0.196
	Ecology:Flow	0.52575	0.162
	Ecology:Paleoisland	0.25289	0.196
	Flow:Paleoisland	-0.13927	0.730
<i>Oreophryne moluccensis</i>	Surface:Ecology	0.97418	0.003*
	Surface:Flow	0.45525	0.206
	Surface:Paleoisland	0.46367	0.172
	Ecology:Flow	-0.35146	0.776
	Ecology:Paleoisland	-0.37792	0.758
	Flow:Paleoisland	-0.14354	0.828
<i>Platymantis</i> sp.	Surface:Ecology	0.98811	0.004*
	Surface:Flow	-0.01446	0.313
	Surface:Paleoisland	0.72498	0.231
	Ecology:Flow	0.11686	0.344
	Ecology:Paleoisland	-0.75331	0.792
	Flow:Paleoisland	0.49863	0.058
<i>Rana papua</i>	Surface:Ecology	0.90751	<0.001*
	Surface:Flow	-0.28083	0.648
	Surface:Paleoisland	-0.55611	0.901
	Ecology:Flow	0.52437	0.254
	Ecology:Paleoisland	0.73529	0.063
	Flow:Paleoisland	-0.41344	0.866
Snakes			
<i>Boiga irregularis</i> ^a	Surface:Ecology	0.98914	0.208
	Surface:Flow	0.89439	0.449
	Surface:Paleoisland	0.58143	0.505
	Ecology:Flow	-0.82631	0.674
	Ecology:Paleoisland	-0.46240	0.598
	Flow:Paleoisland	-0.81267	0.833
<i>Candoia paulsoni</i>	Surface:Ecology	0.76186	<0.001*
	Surface:Flow	-0.09482	0.624
	Surface:Paleoisland	0.48431	0.005*
	Ecology:Flow	0.29872	0.138
	Ecology:Paleoisland	-0.15305	0.797
	Flow:Paleoisland	-0.09319	0.806
<i>Stegonotus batjanensis</i>	Surface:Ecology	0.79389	0.017
	Surface:Flow	0.27345	0.336
	Surface:Paleoisland	-0.27929	0.632
	Ecology:Flow	-0.06096	0.484
	Ecology:Paleoisland	0.55750	0.241
	Flow:Paleoisland	-0.06893	0.592
Lizards			
<i>Bronchocella cristatella</i>	Surface:Ecology	0.92670	<0.001*
	Surface:Flow	0.14531	0.515
	Surface:Paleoisland	-0.38646	0.844
	Ecology:Flow	-0.14852	0.582
	Ecology:Paleoisland	0.60892	0.087
	Flow:Paleoisland	0.11691	0.233
<i>Eutropis multifasciata</i>	Surface:Ecology	0.90924	0.004*
	Surface:Flow	-0.30398	0.728
	Surface:Paleoisland	0.12857	0.357
	Ecology:Flow	0.44619	0.129
	Ecology:Paleoisland	0.20040	0.287
	Flow:Paleoisland	-0.20169	0.950
<i>Gekko vittatus</i>	Surface:Ecology	0.96574	<0.001*
	Surface:Flow	0.06960	0.368
	Surface:Paleoisland	0.40307	0.380
	Ecology:Flow	-0.05701	0.353
	Ecology:Paleoisland	-0.23004	0.656
	Flow:Paleoisland	-0.01756	0.568
<i>Hydrosaurus weberi</i>	Surface:Ecology	0.93465	0.114
	Surface:Flow	0.53273	0.318
	Surface:Paleoisland	0.80217	0.273
	Ecology:Flow	-0.21085	0.585
	Ecology:Paleoisland	-0.89465	0.845
	Flow:Paleoisland	-0.03340	0.538
<i>Lamprolepis smaragdina</i>	Surface:Ecology	0.92719	0.009*
	Surface:Flow	0.26055	0.293
	Surface:Paleoisland	NP	NP
	Ecology:Flow	-0.21023	0.438
	Ecology:Paleoisland	NP	NP
	Flow:Paleoisland	NP	NP

^a Small sample size; see note in Table 1.