ORIGINAL ARTICLE

Colonization of the Philippines from Taiwan: a multi-locus test of the biogeographic and phylogenetic relationships of isolated populations of shrews

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ABSTRACT

Aim Colonization of the Philippines from Taiwan or neighbouring areas of the Asian mainland has been proposed as an important source of diversity for some plant and animal groups in the northern Philippines. Previous inferences, however, were based on taxonomic groupings, which sometimes fail to reflect phylogenetic history. Here, we test for colonization of the Philippines from the north in a group of shrews (Soricomorpha: *Crocidura*) using explicit inferences of evolutionary history.

Location Southeast Asia.

Methods We estimate the phylogenetic relationships of populations of shrews from Batan and Sabtang islands in the northern Philippines using DNA sequences from two mitochondrial genes and three nuclear loci. We employ topology tests to evaluate the possible relationships of these shrews to species from throughout Southeast Asia.

Results We find conclusive evidence that shrews from Batan and Sabtang are closely related to *Crocidura tanakae* from Taiwan and additional specimens from the Asian mainland. Bayesian and frequentist topology tests using alignments of individual loci strongly reject any notion that shrews from Batan and Sabtang are part of the main Philippine radiation of *Crocidura*, indicating that the northernmost Philippine islands were almost certainly colonized by shrews from Taiwan or mainland Asia.

Main conclusions Our results provide the first compelling evidence for colonization of the Philippine archipelago by a terrestrial vertebrate via a northern route. Invasion of the northern Philippines by shrews, however, did not lead to further range expansion to more southerly parts of the Philippines. This study, combined with previous results, documents that *Crocidura* colonized the Philippines at least three times. However, only one of these invasions led to *in situ* speciation and ubiquity across the archipelago. Our findings are part of a growing body of literature suggesting that oceanic archipelagos are often colonized multiple times by groups of closely related species, and occasionally from multiple sources.

Keywords

Batan island, *Crocidura tanakae*, Indochina, island biogeography, Philippines, Sabtang island, Soricomorpha, Taiwan, topology tests.

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INTRODUCTION

The Philippine archipelago represents a potential model system for understanding the effects of various geological, climatic and geographic variables on the diversification trajectories of lineages. Despite this potential, basic features of the evolutionary history of most regional clades, such as the number of times the archipelago was colonized and when and

where the colonizations took place, are mostly unknown (but see Brown & Guttman, 2002; Evans *et al.*, 2003; Jansa *et al.*, 2006; Esselstyn *et al.*, 2009; Oliveros & Moyle, 2010). Colonization is often the initiation point for evolutionary radiations, adaptive or otherwise (Dobzhansky, 1937; Mayr, 1942), suggesting a need to understand the process in detail. Knowledge of how, when and where an invasion took place is crucial to understanding subsequent evolutionary processes in island systems, because this information provides insights into the ages of clades and the extent and tempo of *in situ* diversification.

Several recent phylogenetic and phylogeographic studies have shed light on the process of island colonization (Emerson, 2002). Investigations have demonstrated that groups of closely related species may colonize an island group more than once (Gillespie *et al.*, 1994; Evans *et al.*, 1999; Carranza *et al.*, 2002; Rowe *et al.*, 2008), that the sources of these colonists may vary (Klein & Brown, 1994; Evans *et al.*, 2003) and that continents may be re-invaded by insular lineages (Filardi & Moyle, 2005; Nicholson *et al.*, 2005). Some evidence indicates that successful colonization may be dependent on ecological factors, such as pairwise or diffuse competition (MacArthur, 1972; Diamond, 1975; but see Simberloff, 1978) or on behavioural characteristics of potential colonists, such as the tendency to flock. For instance, in white-eyes (*Zosterops*), flocking may promote colonization by producing large founding populations that have a higher probability of establishing a viable population after arrival (Estoup & Clegg, 2003). Unifying the set of factors that potentially influence both the dispersal patterns (e.g. dispersal ability, ocean currents) and likelihood of success upon arrival (e.g. diffuse competition, founding population size) has the potential to provide the basis of models that predict complex patterns of colonization and community assembly. Nevertheless, at present it is apparent from empirical studies that multiple colonizations of individual archipelagos by closely related species are relatively common, having been documented in groups of plants (Díaz-Pérez *et al.*, 2008), invertebrates (Gillespie *et al.*, 1994) and vertebrates (Ruedi *et al.*, 1998).

In the Philippine archipelago, potential colonization routes have long been proposed, including southern routes originating from the Sunda Shelf and Wallacea and a northern route from Taiwan or the Asian mainland, through the Batanes and Babuyan island groups (Fig. 1; Wallace, 1902; Dickerson, 1928). Relatively extensive evidence supports the importance of the southern routes of colonization (e.g. Diamond & Gilpin, 1983; Heaney, 1985, 1986; Brown & Guttman, 2002; Evans *et al.*, 2003; Jansa *et al.*, 2006; Jones & Kennedy, 2008; Brown *et al.*, 2009; Esselstyn *et al.*, 2009), but the only information known to us that suggests a northern colonization route to have been important is that from the taxonomy of a few bird, mammal, insect and plant groups (Dickerson, 1928) and a recent phylogenetic analysis of Philippine bulbuls (Oliveros & Moyle, 2010). Generally, these taxa appear to represent only
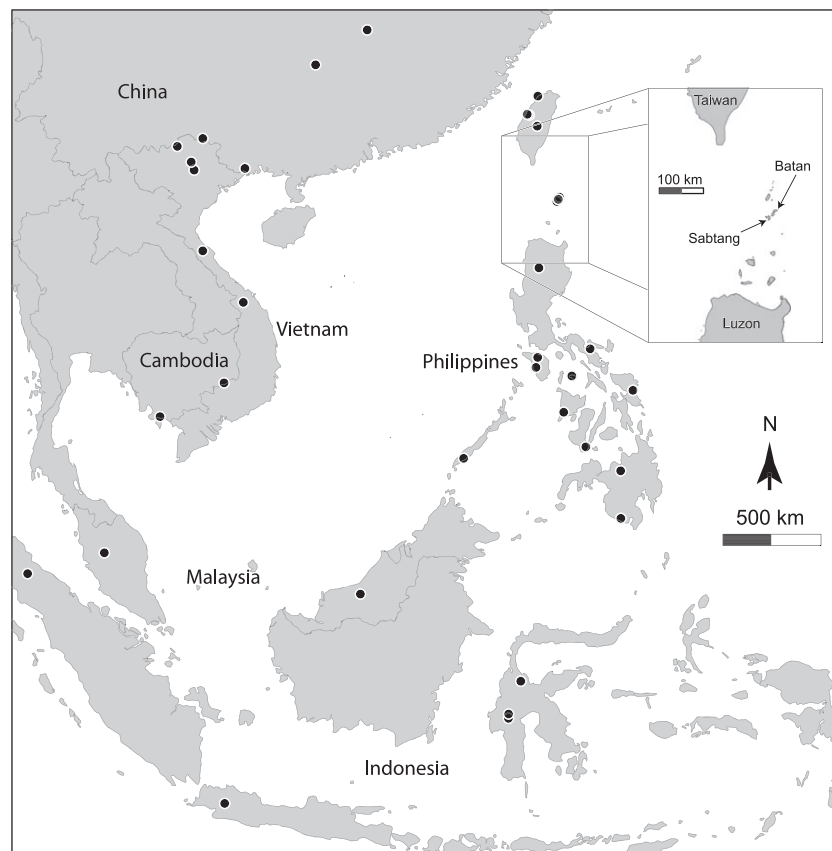
Figure 1 Map of Southeast Asia, showing the geographic distribution of samples used in this study. The inset shows the individual islands of the Batanes group, including Batan and Sabtang, and their position relative to potential source pools on Taiwan and Luzon.

peripheral invasions of the Philippines, in which lineages colonized the Batanes and/or Babuyan islands but did not succeed in invading the larger islands to the south. Some groups, especially among plants and insects, successfully invaded Luzon, but are limited to the highlands of the northern part of the island (Dickerson, 1928). This evidence, of course, is derived from taxonomic associations (excepting Oliveros & Moyle, 2010), which often, but not always, reflect evolutionary history. Thus, although the hypothesized northern colonization route has been proposed and some taxonomies suggest that it is an important source of extant diversity in the northern Philippines, it has yet to be tested with explicit estimates of phylogenetic history.

Shrews (Soricomorpha: *Crocidura*) have proven a useful clade for testing a number of biogeographic hypotheses in East Asia, as they are ubiquitous and diverse throughout the region (e.g. Ruedi *et al.*, 1998; Motokawa *et al.*, 2005; Esselstyn & Brown, 2009). However, the taxonomy of *Crocidura* remains complex and somewhat unresolved, as new species and island populations continue to be discovered (Ruedi, 1995; Lunde *et al.*, 2004; Hutterer, 2007; Jenkins *et al.*, 2007, 2009; Abramov *et al.*, 2008) and molecular evidence has revealed several cases where taxonomy does not fully account for evolutionary history, as inferred from DNA sequence data (Ohdachi *et al.*, 2004; Dubey *et al.*, 2008; Esselstyn *et al.*, 2009).

During the late 1980s, a population of *Crocidura* was discovered on the small, isolated island of Batan, which lies approximately halfway between southern Taiwan and northern Luzon (Fig. 1). Heaney & Ruedi (1994) noted the morphological similarity of these specimens from Batan to a series from Taiwan, and tentatively placed the newly discovered population within *Crocidura attenuata* (Milne-Edwards, 1872), a widespread species then reported from south-central China and Indochina to Taiwan. The Taiwanese population of *C. attenuata* that Heaney & Ruedi (1994) used in their comparisons was originally described as an endemic species (*Crocidura tanakae* Kuroda, 1938), later synonymized with *C. attenuata* (Ellerman & Morrison-Scott, 1951; Fang *et al.*, 1997), and then resurrected as a Taiwanese endemic (Fang & Lee, 2002). Thus, the Taiwanese specimens Heaney & Ruedi (1994) associated with shrews from Batan are now referred to *C. tanakae* (Smith & Xie, 2008). Further complicating this history, Esselstyn *et al.* (2009) tentatively referred a series of specimens from Vietnam and China to *C. tanakae* because they had very similar DNA sequences to specimens from Taiwan. Therefore, it now appears that *C. attenuata* and *C. tanakae* are widespread forms that are morphologically similar, but only distantly related to each other (Smith & Xie, 2008; Esselstyn & Brown, 2009; Esselstyn *et al.*, 2009).

Recently, fieldwork conducted by C.H.O. in the Batanes group of islands provided fresh tissue samples of *Crocidura* from Batan and revealed the presence of shrews on the neighbouring island of Sabtang (Fig. 1). Here, we use these new specimens to test Heaney & Ruedi's (1994) hypothesis that shrews from Batan (and Sabtang) are closely related to *C. tanakae* from Taiwan, which implies invasion of the

Philippines from the north. We compare this concept with the alternative, in which shrews from the Batanes are part of a widespread clade found throughout the more southern parts of the Philippines.

Geological history and faunal diversity of the Batanes islands

The islands of Batan and Sabtang are part of a double island arc system, consisting of an eastern and a western chain of islands spanning the Bashi Strait between southern Taiwan and northern Luzon (Yang *et al.*, 1996). The western arc is old, derived from Miocene volcanic activity, and includes Sabtang (Yang *et al.*, 1996). The eastern arc includes Batan and is geologically young, with all volcanic activity having occurred after *c.* 2 Ma (Yang *et al.*, 1996). Luzon and Taiwan are substantially older than Batan and Sabtang (Hall, 2002). Taiwan was connected repeatedly to the Asian mainland during periods of low sea level, but deep water separates the Batanes islands from both Taiwan and Luzon (Heaney, 1985; Voris, 2000). We are not aware of any evidence that might suggest that subsidence has reduced the extent of landmasses in the Bashi Strait. The southern shore of Taiwan and the northern shore of Luzon are approximately equidistant from the islands of Batan and Sabtang (*c.* 200 km).

The mammal fauna of the Batanes islands is extremely depauperate. Heaney *et al.* (1998) reported only four species (a shrew and three bats) from the islands. Among these four species, the shrew and one bat (*Pteropus dasymallus*) are considered most closely related to more northerly forms from Taiwan or the Ryukyu Islands (Heaney & Ruedi, 1994; Heaney *et al.*, 1998).

MATERIALS AND METHODS

We supplement the multi-locus alignment of Esselstyn *et al.* (2009) with new sequences from shrews sampled from the Batanes islands, Taiwan, Vietnam and Cambodia (Fig. 1). We include one sequence per species or divergent lineage from published data and all newly generated sequences. The resulting alignments sample all three species known from Taiwan, eight of nine species known from the Philippines, three to six (varies among loci) of nine species from Sulawesi, five to eight of *c.* 25 species from Indochina and the Sunda Shelf, plus several lineages from Indochina and the Philippines that may warrant recognition as distinct species.

We use four single-locus alignments to test Heaney & Ruedi's (1994) hypothesis that shrews from Batan (and Sabtang) are more closely related to *C. tanakae* from Taiwan than to any of the species from the more southerly islands of the Philippines. Three of these alignments are derived from fragments of nuclear loci, represented by apolipoprotein B (*ApoB*), DEAD box Y intron 14 (*DBY*) and mast cell growth factor introns 5–6 (*MCGF*). A fourth alignment is a concatenation of the complete sequences of the mitochondrial protein coding genes cytochrome b (cyt *b*) and NADH

Table 1 Summary of alignment features and models of sequence evolution estimated with Akaike's information criterion (AIC) and implemented in maximum likelihood (ML) and Bayesian phylogenetic analyses of Southeast Asian *Crocidura*.

Locus	Number of nucleotides	Number of ingroup taxa	AIC model	ML model	Bayesian model
ApoB	577	58	HKY + G	GTR + G	HKY + G
DBY	477	30	K81uf + G	GTR + G	GTR + G
MCGF	635	59	TVM + G	GTR + G	GTR + G
mtDNA	2184	59	GTR + I + G	GTR + I + G	GTR + I + G

mtDNA, mitochondrial DNA.

dehydrogenase subunit 2 (*ND2*; Table 1). We sought to make each of the alignments as similar to the others and as complete as possible (in terms of sampled diversity). Accordingly, we excluded some species from the Asian mainland that are available only as published mitochondrial sequences. Nevertheless, all major clades inferred in a previous molecular phylogenetic investigation of Southeast Asian *Crocidura* (Esselstyn *et al.*, 2009) are broadly represented. Taxon sampling in the *DBY* matrix is less extensive than in the others, because some species were available to us only as female specimens.

DNA isolation, amplification and sequencing protocols follow Esselstyn *et al.* (2008, 2009). New sequences of the three nuclear and two mitochondrial genes were generated from specimens from Batan and Sabtang islands, Taiwan, Vietnam and Cambodia. All new sequences were deposited in GenBank, under accession numbers GU358489–GU358604. Locality data and museum catalogue numbers are given in Appendix S1 in Supporting Information.

Each of the four single locus alignments was analysed under Bayesian and maximum likelihood optimality criteria. We used *Suncus murinus* (Linnaeus, 1766) as the outgroup for all alignments except *DBY*, where we substituted *Crocidura batakorum* (Hutterer, 2007) because of difficulties obtaining sequences of this fragment from *S. murinus*. Appropriate models of sequence evolution were estimated using Akaike's information criterion (AIC) in MODELTEST 3.7 (Posada & Crandall, 1998). If the model favoured by AIC was not available in our chosen phylogenetic software, we used the next available, more parameter-rich model. Bayesian analyses were conducted in MRBAYES 3.1 (Ronquist & Huelsenbeck, 2003) and relied on four runs, each with four chains run for 5×10^{6} generations. Samples were drawn from Markov chain Monte Carlo (MCMC) inferences every 1000 generations. We selected an appropriate burn-in based on examination of the trends and distributions of log-likelihoods and parameter values using TRACER 1.4 (Rambaut & Drummond, 2007). To assess convergence among MCMC runs, we also examined the correlations of split frequencies among runs in the program Are We There Yet? (AWTY; Nylander *et al.*, 2008).

Maximum likelihood estimates of gene trees were generated in RAxML 7.0 (Stamatakis, 2006). One hundred replicate searches were conducted per locus using the default search algorithm. Each search was initiated with a random starting tree. One hundred bootstrap pseudoreplicates were completed and bootstrap support was plotted on the maximum likelihood topology.

To test the hypothesized relationships of *Crocidura* from Batan and Sabtang, we employed Bayesian and frequentist approaches to tests of alternative phylogenetic topologies. After completion of phylogenetic inferences, we created constraint trees that included specimens from Batan and Sabtang as members of the main Philippine radiation of shrews (including all available Philippine species of *Crocidura* except *C. batakorum*). For the Bayesian approach, we then used PAUP* 4.0b (Swofford, 1999) to filter the posterior distribution of trees from each single locus analysis for consistency with the constraint tree. The proportion of trees in the posterior distribution consistent with the constraint tree provides an estimate of the posterior probability that the hypothesis is true. For the frequentist approach, we employed the approximately unbiased (AU) test (Shimodaira, 2002). We used RAxML to identify the best tree consistent with the constrained topology (100 searches) before generating per-site log likelihood scores on the best tree under constrained and unconstrained searches. Per-site likelihood scores were then used in CONSEL (Shimodaira & Hasegawa, 2001; Shimodaira, 2002) to complete the AU test.

Our phylogenetic analyses revealed a very close relationship between shrews from the Batanes islands and *C. tanakae* from Taiwan. We therefore computed a statistical parsimony network among mitochondrial haplotypes for all available individuals of *C. tanakae*, and several specimens tentatively referred to this species. The network was calculated in TCS 1.21 (Clement *et al.*, 2000) with a 95% confidence limit on haplotype connections and used a matrix of concatenated cyt *b* and *ND2* sequences. We eliminated all missing characters from the mitochondrial matrix for this analysis, reducing the number of nucleotides to 1906. Twenty-four individuals from the Batanes islands, Taiwan, Vietnam and China were included in this analysis (Appendix S1). The network is presented as a means of visualizing the mitochondrial diversity found in this lineage, and as an exploratory tool for evaluating the possibility that *C. tanakae* was recently introduced to Batan and Sabtang by humans.

RESULTS

Final alignments contain 477–2184 nucleotides and 30–59 ingroup taxa (Table 1); each alignment is available on TreeBase under accession S2581. Matrices are mostly complete, with 7% or fewer missing characters. Models of sequence evolution chosen by AIC for the three nuclear loci were simpler than the available options in MRBAYES and RAxML (Table 1).

In Bayesian phylogenetic inference, all evidence suggests that MCMC chains converged in all analyses, as likelihood scores were stable after 2×10^6 generations (or earlier) for all runs and correlations of split frequencies were high. We therefore discarded the first 2×10^6 generations as burn-in for all Bayesian analyses, leaving 12,000 trees (3000 trees per run × 4 runs) in the posterior distribution resulting from each alignment. When pooled among runs, effective sample sizes were estimated at >1000 for all parameters, in all MCMC analyses.

Shrews from Batan and Sabtang are more closely related to *C. tanakae* from Taiwan and other taxa from the Asian mainland than to any species from the Philippines (Figs 2 & 3). All our inferences and topology tests strongly support Heaney & Ruedi's (1994) hypothesis that shrews invaded the northernmost Philippines from Taiwan or the Asian mainland rather than from the more southerly Philippine islands. Although some loci provide greater resolution and support than others, topologies are mostly consistent, and independent analyses of each of the four loci result in the inference of a close relationship among the Batan and Sabtang shrews and *C. tanakae* from Taiwan (Figs 2 & 3). The Bayesian approach to topology tests yields an estimated posterior probability of zero for inclusion of shrews from Batan and Sabtang in the main Philippine clade for all loci and 1.0 for a clade including shrews from Batan and Sabtang and *C. tanakae* from Taiwan, in three of four loci (Table 2). Similarly, the AU tests soundly reject any notion that shrews from Batan are a component of the main Philippine radiation, with all locus-specific *P*-values ≤0.001 (Table 2).

We found three mitochondrial haplotypes in the six shrews available from the Batanes islands (Fig. 4). Populations on Batan and Sabtang are separated from the nearest individual (from Taiwan) by 15 steps in the statistical parsimony network (Fig. 4), suggesting that they are currently isolated from other populations of *C. tanakae*.

DISCUSSION

Our phylogenetic inferences and topology tests provide conclusive evidence of shrews colonizing the northern Philippines from Taiwan or its immediate vicinity. Although *C. tanakae* successfully invaded the Batanes group of islands, there is no evidence that it has established populations south of this area. Shrews were discovered recently in the Babuyan islands, south of the Batanes, but this population is closely related to *Crocidura grayi* from Luzon (Esselstyn *et al.*, 2009), suggesting that *C. tanakae* in the Philippines is restricted to the Batanes islands.

The extremely close relationship of shrews from Batanes and Taiwan (0.0079 uncorrected *p*-distance in mitochondrial DNA) raises the question of whether the presence of *C. tanakae* on Batan and Sabtang is natural or the result of human-mediated dispersal. Available evidence is insufficient to allow an explicit test of these alternative hypotheses (natural versus human-mediated colonization), but it does

permit examination of some plausible scenarios. For example, if shrews colonized Batanes naturally, we expect this population to be established by a very small number of individuals — perhaps even by a single pregnant female. If this were the case, monophyly of single-copy genes (e.g. mitochondrial) would be achieved rapidly, if not instantly (in the case of a single pregnant colonist) within the new population. On the other hand, if human-mediated dispersal were responsible for the presence of *C. tanakae* on Batan and Sabtang, we might expect to find multiple, unrelated haplotypes on the islands, and each haplotype might be shared with, or very closely related to, haplotypes from the source population. This pattern would result from regular, or more frequent, arrivals of colonists via an ever-present mechanism (e.g. ship traffic) and would result in our inference of polyphyly among individuals in the exotic population. Among the five specimens from Batan and one from Sabtang, we found three mitochondrial haplotypes, involving two substitutions in *ND2*. Monophyly of these six individuals was strongly supported in Bayesian (estimated posterior probability = 1) and maximum likelihood (bootstrap support = 99) inferences (Fig. 3), suggesting a founding colonization by one or a few individuals and implying that the population's presence is natural. Similarly, the parsimony network shows that shrews from the Batanes islands are isolated by 15 mutational steps from all other individuals of *C. tanakae* (Fig. 4), suggesting they are the result of a recent (by geological standards) colonization by a small founding population and that they are currently isolated from other populations of *C. tanakae*. Finally, if one were willing to assume a molecular clock, even with a fast rate of 0.05 substitutions/site/Myr (Bannikova *et al.*, 2006), the divergence between the Taiwan and Batan populations would date to *c*. 79 ka, well before people began travelling between Taiwan and the northern Philippines *c*. 6 ka (Gray *et al.*, 2009). A recent natural colonization event is not unexpected given that many of the islands between Taiwan and Luzon, including Batan, have origins in the Quaternary (Yang *et al.*, 1996). We presume that most colonizations of oceanic islands by shrews, including this case, are the result of one or a few individuals riding on floating vegetation.

The colonization of oceanic islands by organisms of limited dispersal capacity initiates diversification processes via genetic drift, adaptive radiation and allopatric speciation. Colonization generates isolation and occasionally puts organisms in places with abundant ecological opportunity (e.g. Harmon *et al.*, 2008). Thus the frequency, directionality and stochasticity of colonization warrant renewed attention from evolutionary biologists (Cowie & Holland, 2006; Heaney, 2007). Here, we provide the first compelling test of hypothesized colonization of the Philippines from a northern source by a terrestrial vertebrate. We find that *C. tanakae* colonized the Batanes islands from Taiwan or the Asian mainland, but this shrew has not succeeded in invading other parts of the Philippine archipelago, where distantly related lineages of *Crocidura* reside (Figs 2 & 3). The colonization of Batan and
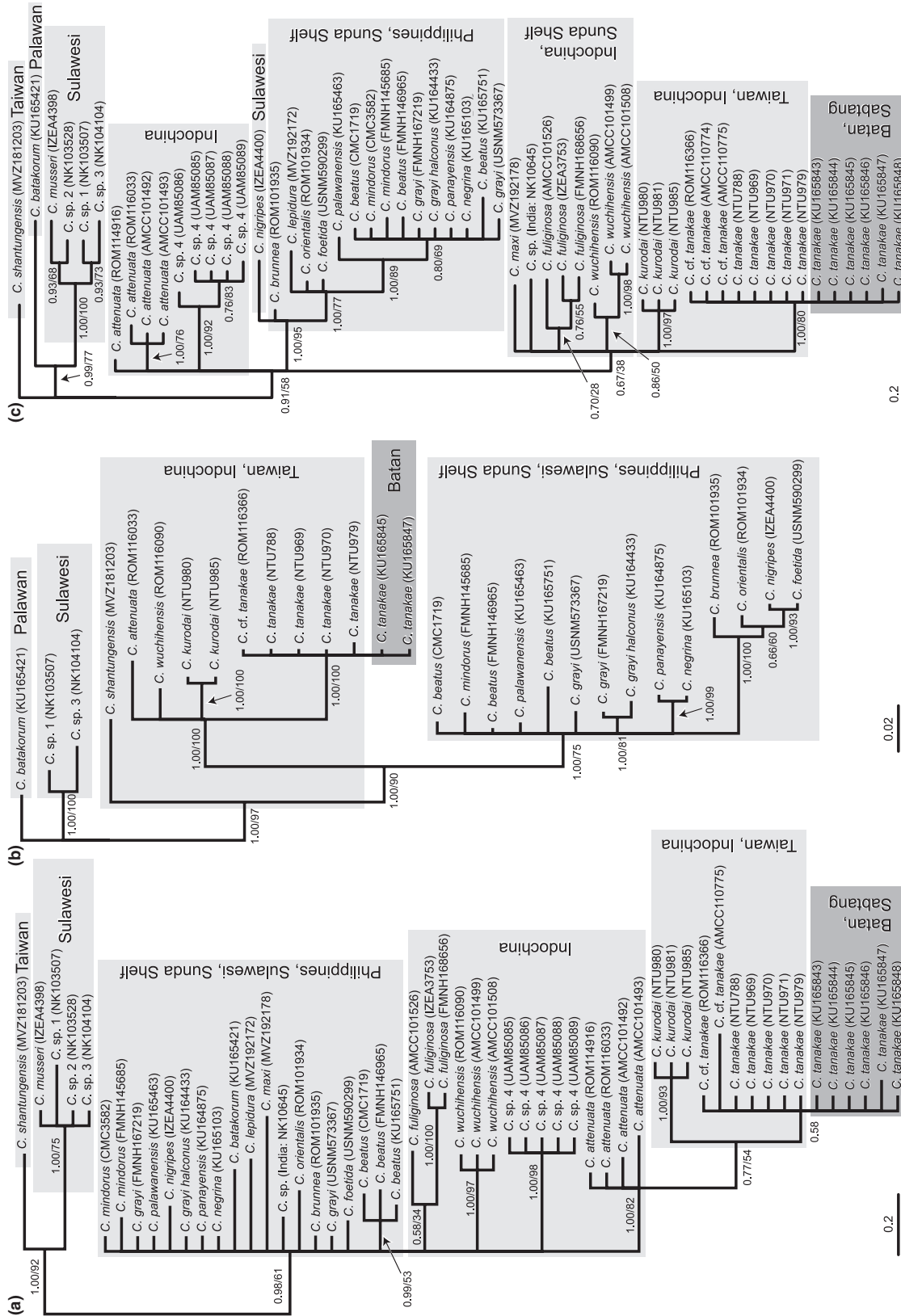
Figure 2 Bayesian majority-rule consensus trees of Southeast Asian *Crocidura* derived from sequences of the nuclear genes: (a) apolipoprotein B, (b) DEAD box Y intron 14 and (c) mast cell growth factor introns 5–6. The outgroup (*Suncus murinus*) was pruned from (a) and (c) for ease of presentation. The outgroup (*Crocidura batakorum*) in (b) is included. Numbers at nodes represent posterior probabilities, followed by maximum likelihood bootstrap support. Taxonomic identities and museum catalogue numbers are given at the terminals. Museum acronyms are defined in Appendix S1. Grey boxes indicate the regions from which terminal taxa were collected, with darker grey boxes noting the phylogenetic position of samples from the northern Philippines.
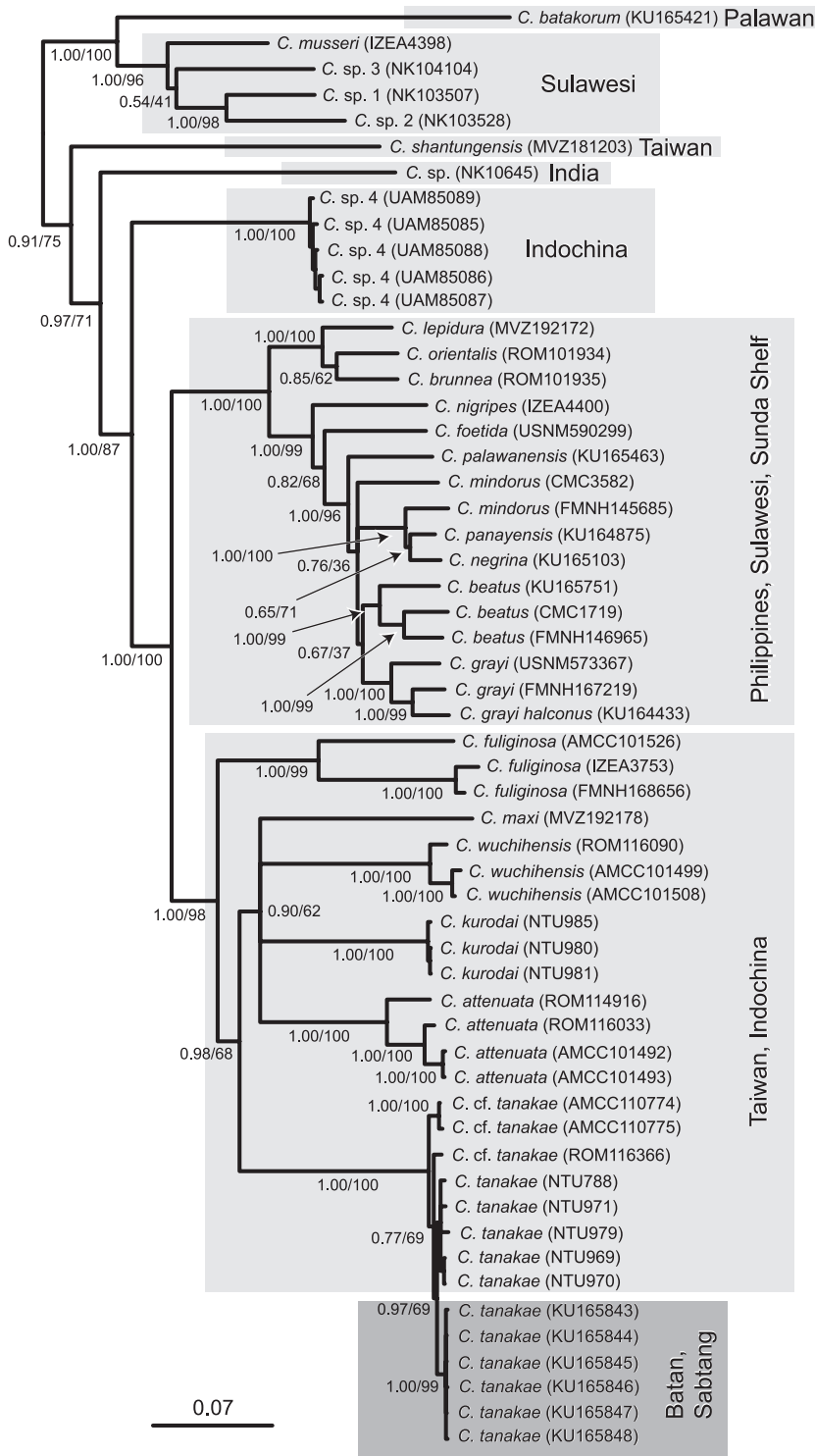
Figure 3 Bayesian majority-rule consensus tree derived from mitochondrial DNA sequences (cyt *b* and *ND2*) from Southeast Asian *Crocidura*. The outgroup (*Suncus murinus*) was removed for ease of presentation. Numbers at nodes represent posterior probabilities, followed by maximum likelihood bootstrap support. Taxonomic identities and museum catalogue numbers are given at the terminals. Museum acronyms are defined in Appendix S1. Grey boxes indicate the regions from which terminal taxa were collected, with darker grey boxes noting the position of samples from the northern Philippines.

Sabtang by shrews represents the third known instance of invasion of the Philippines by *Crocidura*. Multiple invasions of the country have been noted in other groups, including murid rodents (Jansa *et al.*, 2006), frogs (Brown & Guttman, 2002; Evans *et al.*, 2003) and bulbuls (Oliveros & Moyle, 2010). An emerging pattern is that some invasions result in substantial diversification while others appear not to generate speciation

events (or extinction eliminates the evidence). The data presented here and by Esselstyn *et al.* (2009) strongly suggest that *Crocidura* invaded the Philippines once from the Sunda Shelf, once from Wallacea or the Sunda Shelf and once from the Taiwan region. However, only one of these colonization events (the one from the Sunda Shelf) led to widespread ubiquity and *in situ* speciation.

Table 2 Results of Bayesian and frequentist tests constraining phylogenetic topology to include shrews from Batan and Sabtang to be members of the main Philippine radiation of *Crocidura*, or a member of *C. tanakae* from Taiwan and the Asian mainland. Posterior probabilities (PP) and *P*-values from approximately unbiased tests are shown.

Alignment	PP (Batanes, Taiwan)	PP (Batanes, Philippines)	*P*-value (Batanes, Taiwan)	*P*-value (Batanes, Philippines)
ApoB	0.58	0.00	1.00	5×10^{-6}
DBY	1.00	0.00	1.00	7×10^{-5}
MCGF	1.00	0.00	0.999	0.001
mtDNA	1.00	0.00	1.00	6×10^{-34}

mtDNA, mitochondrial DNA.
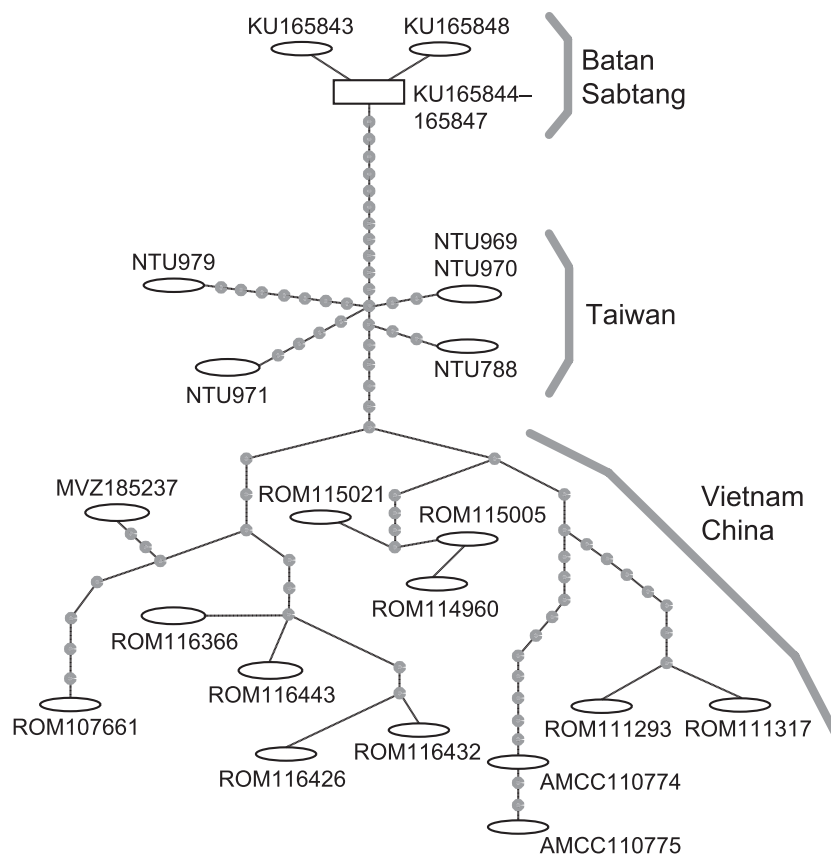
Figure 4 Statistical parsimony network of mitochondrial haplotypes in *Crocidura tanakae* and closely related populations from Vietnam and China tentatively referred to the same species. Grey circles represent individual steps in the network. Museum catalogue numbers are shown at terminals and museum acronyms are defined in Appendix S1. Grey brackets indicate the regions from which terminal taxa were collected.

Several recent studies suggest a need to recognize an inherent complexity in patterns of island colonization over geological time-scales, in which isolated archipelagos may be invaded multiple times from multiple sources by groups of closely related species. Multiple invasions have been noted in several lineages in Southeast Asia (Brown & Guttman, 2002; Evans *et al.*, 2003; Jansa *et al.*, 2006; Oliveros & Moyle, 2010), as well as in other archipelagos, including the Hawaiian islands, West Indies and Macaronesia (Gillespie *et al.*, 1994; Klein & Brown, 1994; Díaz-Pérez *et al.*, 2008). Successful colonization requires both the dispersal of propagules to an island and reproduction after the journey. Good colonizers will thus possess traits that yield a tendency to disperse and a capacity to reproduce upon arrival. Although shrews do not possess features that clearly define them as good colonizers, their ubiquity on islands throughout much of Southeast Asia indicates that they have been quite successful at establishing populations on oceanic islands. The present distribution of *Crocidura* in the oceanic Philippines is highly regular; most islands that have been adequately surveyed (16 islands with records of *Crocidura*: Rickart *et al.*, 1993; Heaney & Ruedi, 1994; Heaney *et al.*, 1998; Esselstyn *et al.*, 2009) hold a single species of *Crocidura*, suggesting a possible role for competition in preventing secondary colonization (e.g. MacArthur, 1972). This distribution implies that shrews are good at colonizing islands that lack shrews, but they may struggle to persist after arrival on an island that is already inhabited by a closely related species. The two exceptions to the one species per island pattern (Mindoro and Mindanao islands) are each inhabited by two species. In both cases, one species appears to be a restricted-range, high-elevation specialist, whereas the other is widespread and common throughout the island, perhaps limiting the interaction between these species. If pairwise competition

does exclude potential colonists, then dispersal events to neighbouring islands may frequently fail to establish populations, and inter-island dispersal may be far more common than is generally appreciated.

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SUPPORTING INFORMATION

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Appendix S1 List of samples used in this study.

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