Zoogeographic patterns on very small spatial scales in rock-dwelling *Plectostoma* snails from Borneo (Gastropoda: Caenogastropoda: Diplommatinidae)

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Abstract

We mapped the fine-scale distribution patterns of *Plectostoma* microsnails on two small, isolated limestone outcrops in Malaysian Borneo. On both hills, two species were present (*Plectostoma simplex* and *Plectostoma concinnum* on Tandu Batu; *Plectostoma fraternum* and *Plectostoma concinnum* on Tomanggong Besar), but the patterns we found were different. On Tomanggong Besar, the two species occupy different parts of the hill and meet along a narrow hybrid zone that is haracterized by a significantly higher rate of predation by *Atopos* slugs. On Tandu Batu, the two species broadly overlap and do not form hybrids. The predation rate here is the same in both species, regardless of whether they occur in monospecific localities or in mixed localities. Our results show that even small limestone outcrops of a few hundred metres in diameter cannot be considered to be uniformly populated by limestone dwelling snails, and a detailed analysis of intra-hill patterns may reveal information on how differences among species evolve and are maintained in the face of hybridization.

Introduction

In elucidating the evolutionary history of species, it is often instructive to analyse geographical patterns of distribution and interactions of closely related species. Such patterns can teach us about the processes that drive and maintain species differences, their coexistence, and reproductive isolation. For example, in sympatric species that are vicariant on a small spatial scale (e.g., the central-European species of *Nicrophorus* burying beetles; Pukowksi, 1933) competition may have driven habitat differentiation. On the other hand, sympatric, ecologically similar species that are not vicariant, may still be experiencing active competition, or may have differentiated ecologically in other, non-geographic ways (e.g., *Yponomeuta* moths specialised on different host plants; Menken, 1996). An even richer image may be obtained when reproductive interactions are included, for example in hybrid zones, i.e., areas where related species meet, mate, and produce hybrids (Barton & Hewitt, 1985; Szymura & Barton, 1986; Harrison, 1993). Such studies have given us insights into: the number of genes involved in reproductive isolation, the strength of selection on each of those genes, the association of hybridization with a habitat interface, the time since hybridization started, whether or not the hybrid zones are primary or secondary in origin (and, therefore, whether the speciation process has been allopatric or not), and their eventual fate (Harrison, 1993). In other words, hybrid zones are "natural laboratories" where the genetic, evolutionary, and ecological forces that drive speciation and maintain species differences can be studied in the field.

Although the literature on hybrid zones has, for historical reasons, been dominated by vertebrates, land snails are particularly suitable organisms for studying hybrid zones. This has to do with their exceedingly low dispersal rate, which results in evolutionary patterns such as clines, endemism, and subspeciation in very small geographic areas (Schilthuizen, 2002). Endemism, parapatric distribution patterns, clinal geographic variation, and hybrid zones in land snails are often displayed on spatial scales of just a few kilometres (Schilthuizen, 1994; Haase et al., 2013; Stankowksi et al., 2020). This means that in land snail studies, an individual researcher can, in one field day, literally walk through evolutionary patterns which, in many other organisms, would be displayed only at the scale of entire continents. For example, the analysis of five areas of contact

between different members of the clausiliid *Albinaria hippolyti* species complex in a 25 × 35 km region in central Crete (Schilthuizen & Lombaerts, 1995; Schilthuizen, 1995; Schilthuizen et al., 1999; Lammers et al., 2013), revealed that the clines in traits are 20–260 m wide, are usually located in seemingly random locations, and involve weak selection against large numbers of genes (in the order of tens to hundreds). In another European clausiliid genus, *Alopia*, Koch et al. (2020) revealed the roles of coiling reversal, sexual selection, and random genetic drift in an entire non-adaptive evolutionary radiation of nine forms (species and lower taxonomic units) within an area in the Southern Carpathians of just a few kilometres across. And within a single square kilometre on Rosemary Island off Northwestern Australia, Stankowski (2013) elucidated the ecological speciation process by which a globose-shelled *Rhagada* species has evolved into a dramatically different flat-shelled form across an ecological transition from a vegetated to a rocky habitat. The distances over which this transition takes place in some places are just a few tens of metres.

Most of the above-mentioned land snail studies were set in more or less extensive and continuous areas of habitat. The situation becomes more complex when the habitat and, therefore, the snail populations are themselves fragmented and patchy. In many parts of Southeast Asia, limestone outcrops exist as small fragments of exposed karst within a "sea" of other types of substratum. In most parts of Borneo, for example, limestone outcrops are each just a few hundred metres across, but are separated from other outcrops by tens of kilometres of sandstone or mudstone. It is known that limestone offers very suitable environmental conditions for calcium-dependent organisms such as land snails (Clements et al., 2006). Nonetheless, most land snail taxa can also occur, albeit at lower densities, on non-limestone soils (Schilthuizen, 2011).

However, there are a few snail taxa that are strictly obligate limestone-dwellers. In Borneo, the most extreme example of this is the genus *Plectostoma* H. Adams, 1865. This diplommatinid genus with approximately 2 mm-tall, often unusually coiled and ornamented shells, is purely restricted to limestone outcrops (Schilthuizen et al., 2003a). The concomitant geographical isolation, local adaptation, and rarity of long-distance dispersal has resulted in high numbers of, often locally endemic, species (Vermeulen, 1991, 1994).

In the Lower Kinabatangan river valley of Sabah, Malaysian Borneo, Schilthuizen et al. (2006) and Hendriks et al. (2019) studied a system of around 20 isolated limestone hills within a region of 10 × 35 km. These outcrops are on average 0.5 km in diameter and separated from the nearest outcrop by about 5 km of unsuitable (i.e., non-limestone) habitat. The dominant *Plectostoma* clade in this area is the *Plectostoma concinnum* complex. Molecular phylogenetic analysis of this complex (Schilthuizen et al., 2006) has shown that it consists of the paraphyletic, highly variable

species *P. concinnum* (Fulton, 1901), as well as several short-range endemic species with distinct morphological autapomorphies, namely *Plectostoma simplex* (Fulton, 1901), *Plectostoma mirabile* (Smith, 1893), and *Plectostoma fraternum* (Smith, 1905) (Vermeulen & Liew, 2022). Most of the limestone hills in the Lower Kinabatangan Valley are inhabited by a single form from the *Plectostoma concinnum* species complex, but three hills are home to two separate forms of the species complex. Each population is distinct genetically and in shell shape and ornamentation. Genetic analysis revealed that the species complex is an old (several million years) radiation and that the allopatric speciation process involves both genetic drift and local adaptation (Schilthuizen et al., 2006), primarily in response to predation by *Atopos rapax* Vermeulen & Liew, 2022 (Rathouissidae), a molluscivorous slug (Liew & Schilthuizen, 2014; Vermeulen & Liew, 2022). Specifically, it appears that the attack behaviour of the slug differs geographically and that the snails' ornamentation has evolved in response to these behaviours, and vice versa (Schilthuizen et al., 2006).

Here, we focus on the microgeographical situation on two of those hills where on each hill two species from this complex occur: Tomanggong Besar (*P. fraternum* and *P. concinnum*; Fig. 1a, b) and Tandu Batu Hill (*P. simplex* and *P. concinnum*; Fig. 1c, d). Genetic studies (Schilthuizen et al., 2006) have already shown that in neither of these cases, the two sympatric species are each other's closest relatives, which suggests that each of these hills must have been colonised twice independently. In this paper, we map the geographic distribution of the sympatric species on both hills in detail, and we also assess (by conchological inference) the presence or absence of hybridisation. Finally, we investigate to what extent the species differ in suffering from slug predation.

Materials and Methods

The two hills in the Lower Kinabatangan Valley, Sabah, Malaysian Borneo (Tandu Batu, 118°20′34.3″E 5°35′47.5″N, and Tomanggong Besar, 118°18′17.3″E 5°30′56.3″N) were visited from October to December 2003. On both hills (250 × 700 m and 200 × 300 m, respectively), 45 localities of 5 × 5 m were chosen that lay within suitable *Plectostoma* habitat (exposed vertical limestone rock surfaces) but otherwise were randomly distributed over the hill. At each locality, coordinates were recorded with a Garmin hand-held GPS device, and 50 adult *Plectostoma* individuals were removed from the rock and placed into a 2.0 mL vial with 100% ethanol, and labelled. In the laboratory, each individual was identified to species. Individuals with clearly intermediate morphology were assumed to be hybrids and separately recorded (Fig. 2).

In addition, from each locality, a 5 L soil sample was taken, if possible from underneath vertical limestone sur-
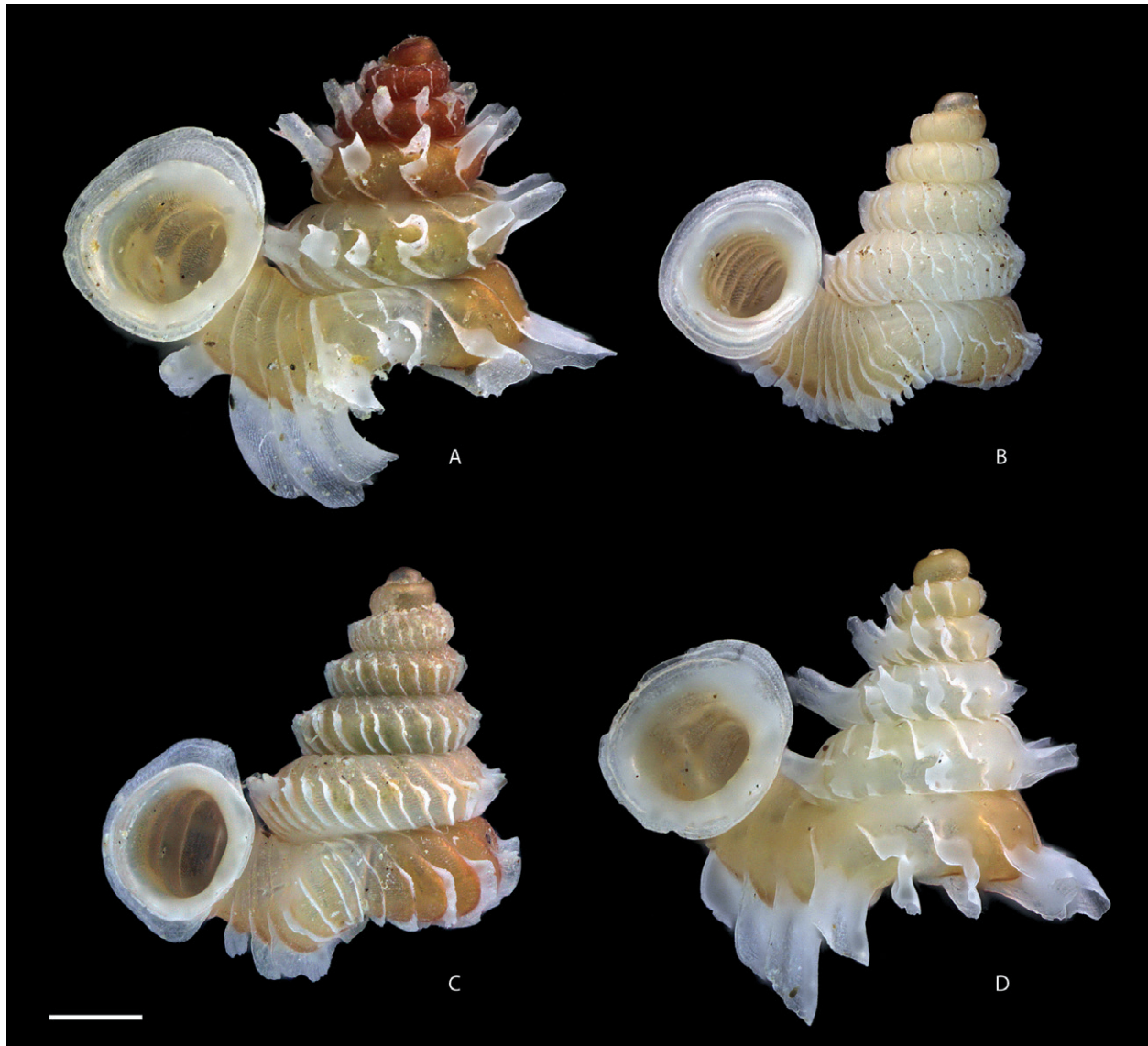
Figure 1. *Plectostoma* shells. **A.** *P. fraternum* (Tomanggong Besar). **B.** *P. concinnum* (Tomanggong Besar). **C.** *P. simplex* (Tandu Batu). **D.** *P. concinnum* (Tandu Batu). Scale bar = 0.5 mm.

faces. The soil was sieved with 5 mm mesh width, and the sieved fraction stored in a labelled plastic bag. In the laboratory, empty adult *Plectostoma* shells were extracted from these soil samples by placing the soil in water, removing all floating debris, drying the floating debris, and using a dissection microscope to pick out the shells (Tweedie, 1961). The shell of each individual was identified to species based on conchological features given by Vermeulen (1991, 1994), and the presence or absence of the typical holes produced during predation by *Atopos rapax* slugs (Schilthuizen et al., 2003b, 2006; Liew & Schilthuizen, 2014) were recorded. Again, individuals with clearly intermediate morphology were marked as hybrids and separately recorded. As with all land snail studies based on empty shells, issues relating to the processes affecting shell accumulation in the soil apply (see Schilthuizen, 2011 for a general treatment of these

issues). Samples are held in the Institute for Tropical Biology and Conservation at Universiti Malaysia Sabah; duplicate specimens from most samples are in Leiden University.

Besides taking samples, while traversing the hills, we also recorded it if at a certain spot we failed to find any living or dead *Plectostoma*, and we also mapped the presence or absence of microhabitat features known to be important for *Plectostoma*, i.e., limestone boulders and cliffs.

Predation was determined by the presence of a typical hole made by *Atopos rapax* in the shell of the prey. Such holes are made only when access through the aperture is not successful (Liew & Schilthuizen, 2014) so the proportion of perforated shells provides only an underestimation of predation rate. For Tomanggong Besar, under *P. concinnum* and *P. fraternum*, all shells were combined that could unambiguously be assigned to these species, respectively;

Figure 2. Morphologically intermediate shells of *Plectostoma*, mainly judged by the development and spacing of the radial ribs, which lie in between those for typical individuals of the parental species (see Fig. 1), from the *P. concinnum* × *P. fraternum* hybrid populations 11, 42, and 44 on Tomanggong Besar (images from Van Til, 2004).

under "hybrids" all morphologically intermediate shells were combined. Predation rates (Table 1) were then calculated as the number of shells with a predation hole divided by the total number of shells. Significances of predation rate differences were calculated manually in Microsoft Excel with 2×2 χ^2 tests.

Results

Distribution patterns

On Tomanggong Besar (Fig. 3), we found that most of the localities are occupied by a small-shelled population of *P. concinnum*. Only the northwestern flank of the hill, as well as the small "satellite" hillock, are occupied by the larger-shelled *P. fraternum* (14 localities). Unexpectedly, in one locality (locality 1, on the far western side of the hill, close to

the river's edge) among *P. concinnum*, we also found several individuals of *P. brevituba* (Vermeulen, 1994), which is not closely related to the *P. concinnum* complex. The distribution areas of *P. concinnum* and *P. fraternum* adjoin along a zone that mostly coincides with a steep limestone cliff of 5–10 m in height. At four localities that lie along this zone, no pure individuals of either species were found; instead these localities are populated by what, based on inspection of the shell morphology, especially the spacing and size of the radial ribs, appear to be individuals that are genetic mixtures (primary and secondary hybrids as well as back-crosses) of both species. On the summit of the hill, very little suitable habitat is available, and *Plectostoma* is absent or very scarce across most of this area.

On Tandu Batu, the situation is different (Fig. 4). Here, *P. concinnum* is mostly found on the northwestern side of the hill (14 localities), *P. simplex* (18 localities) mostly on the southeastern side (as well as on the small satellite hillock to

Table 1. Predator perforation rates of *Plectostoma* snails on both hills. For Tandu Batu, under "allopatric", all samples were combined where each species was found in isolation. Under "sympatric", all samples were combined where both species were found. Predation was determined by the presence of a typical hole made by *Atopos rapax* in the shell of the prey. For Tomanggong Besar, under *P. concinnum* and *P. fraternum*, all shells were combined and classified under each species if they could unambiguously be assigned to these species. Under "hybrids" all morphologically intermediate shells were combined. "Predation rate" is a minimum value, because some animals are successfully preyed upon by entry through the aperture, which does not leave a mark on the empty shell. Different superscript letters denote predation rates that are significantly different (within their own locality); see Results for details.

	Total	Perforated	Predation rate
Tandu Batu			
P. concinnum allopatric	150	18	0.12[a]
P. simplex allopatric	1050	173	0.16[a]
sympatric	1077	181	0.17[a]
Tomanggong Besar			
P. concinnum	2969	423	0.14[a]
P. fraternum	1495	287	0.19[b]
hybrids	429	111	0.26[c]
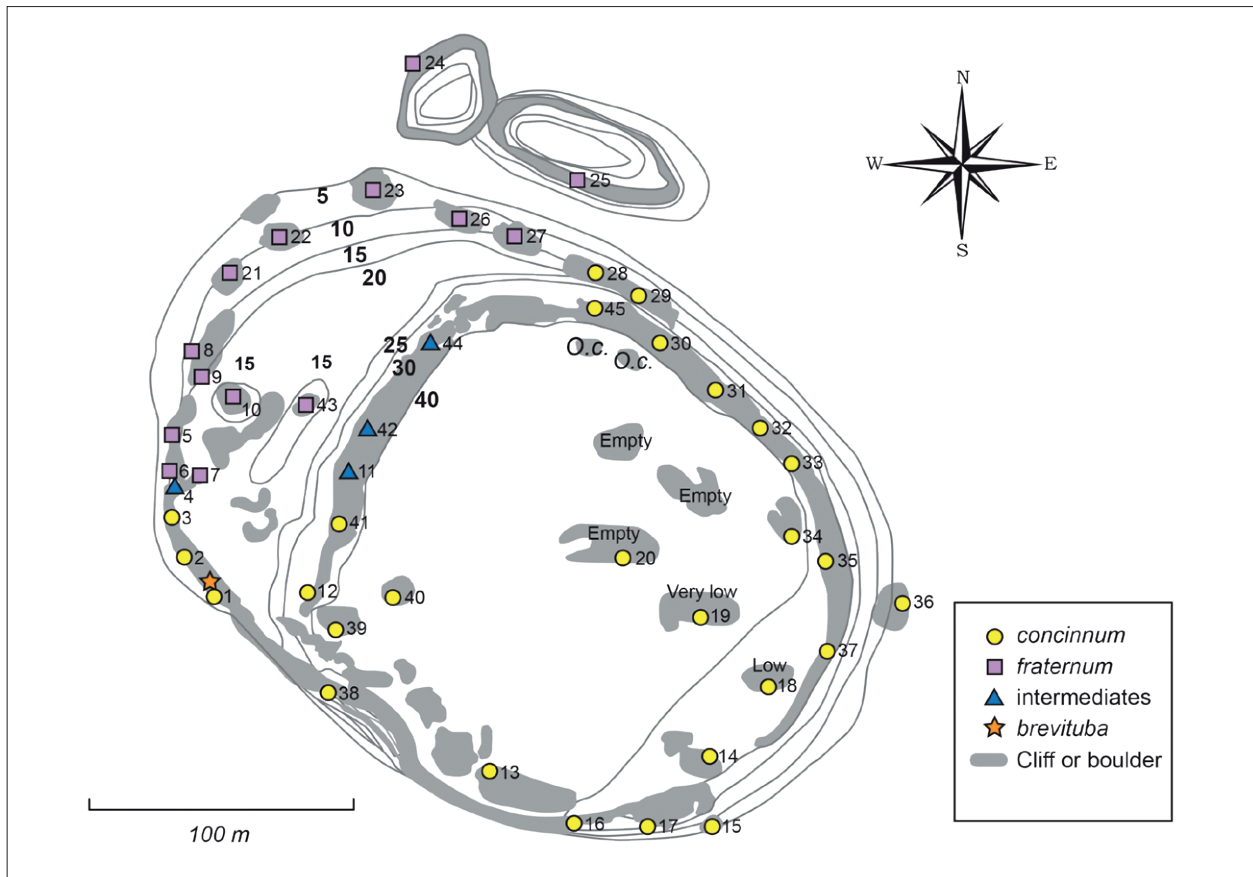
Figure 3. Distribution map of *P. concinnum*, *P. fraternum*, *P. brevituba*, and *P. concinnum* x *P. fraternum* hybrid populations on Tomanggong Besar. The indications "low," "very low", and "empty" refer to assessed population densities and absences. The indication "O. c." refers to the presence of *Plectostoma concinnum* observed in the field, but not sampled. The contours are drawn with 5-m elevation intervals (see the numbers in bold).

the south), but in between and scattered throughout the hill are many (13) localities where both species co-occur, without any sign of hybridization. In these mixed populations, *P. simplex* was the most abundant overall.

The above results are based only on the living population. Looking at the samples of empty shells from the forest floor (which may include specimens from decades ago; Schilthuizen, 2011), we found the following regarding distributions. On Tomanggong Besar, the empty shells showed the same distributions as the living population. On Tandu Batu, there were several localities where the living population consisted entirely of *P. concinnum*, whereas the shells in the soil showed a mixture of both species.

Predation

The patterns of predation are based on the empty shells taken from the forest floor and may therefore be an average across multiple years. On Tomanggong Besar, we found a mean *Atopos rapax* predation rate of 0.17 across all species. The rate in *P. fraternum* was significantly higher than in *P. concinnum* (0.19 vs 0.14, respectively; $P < 0.001$; χ^2 test). Interestingly,

the hybrids showed a significantly higher predation rate than either of the pure populations, namely 0.26 ($P = 0.002$; χ^2 test). On Tandu Batu, the mean *Atopos* predation rate was 0.16. The rate in *P. simplex* was somewhat lower than in *P. concinnum* but not statistically significantly so (0.12 vs 0.16, respectively; $P = 0.16$; χ^2 test). In the localities with sympatric *P. concinnum* and *P. simplex*, predation rate was 0.17; this was also not significantly different from the predation rates in either of the monospecific populations. Although predation rates on both hills vary greatly between localities and, in the case of Tomanggong Besar, between *Plectostoma* species, there were no indications of further geographic patterns in predation rate across each of the two hills.

Discussion

The geographical patterns that we have revealed in this study are of a very small spatial scale. This is especially the case for Tomanggong Besar, where the endemic *Plectostoma fraternum* occupies its global territory (at an estimated population size of half a million; Schilthuizen et al., 2003b), an area of
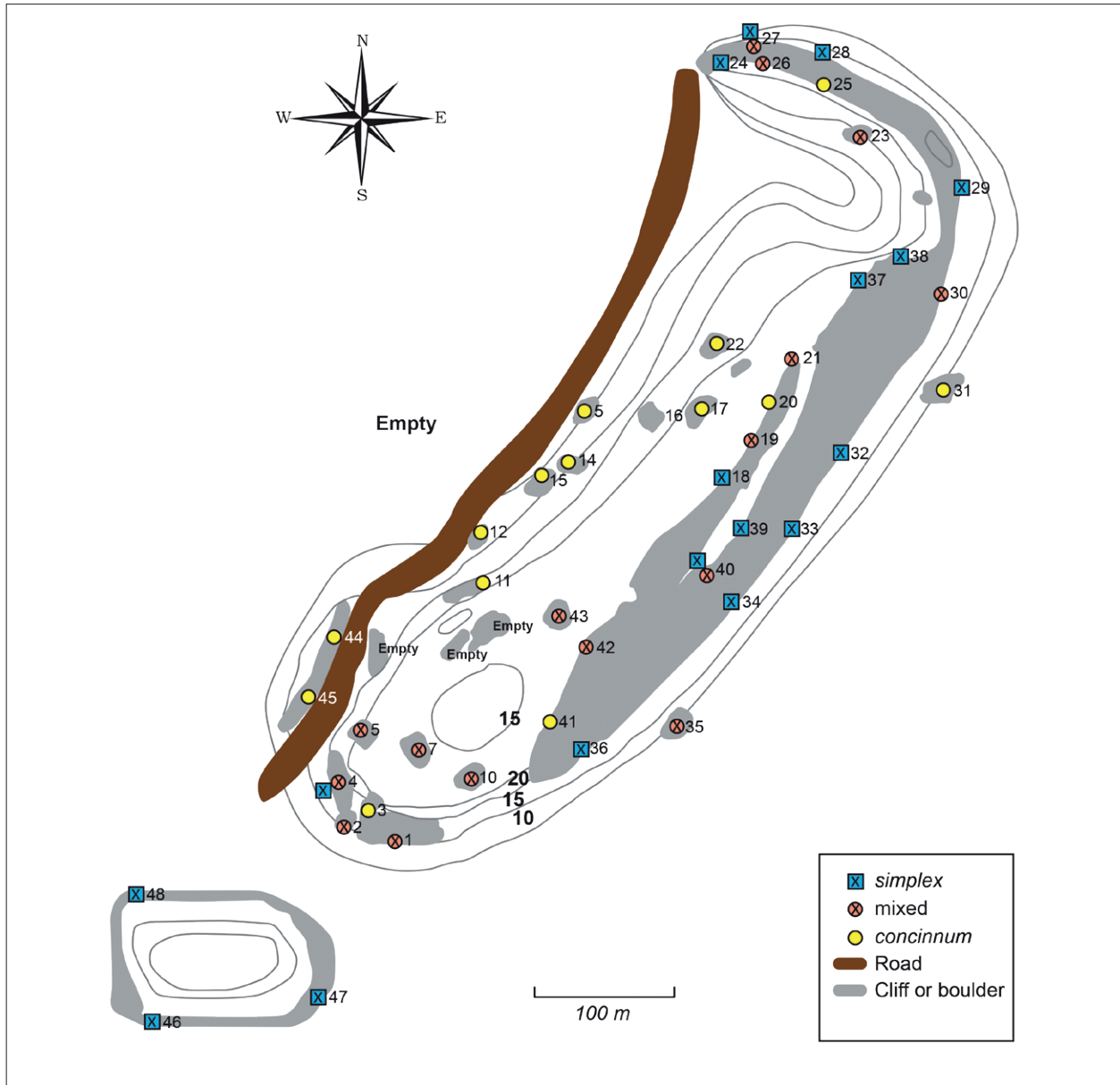
Figure 4. Distribution map of *P. concinnum* and *P. simplex* on Tandu Batu. The indications "empty" refer to absences of *Plectostoma*. The contours are drawn with 5-m elevation intervals (see the numbers in bold).

approximately 200 × 75 m, and even manages to maintain a 100 m long, 10 m wide hybrid zone with the more widely distributed *P. concinnum*. Patterns of such a small spatial scale are not unheard of in land snails and have been recorded in, for example *Albinaria* (Schilthuizen, 1994) and *Rhagada* (Stankowski, 2013); nonetheless, even for land snails they are notable. The fact that the hybrid zone appears to be "trapped" at a geographical feature (a cliff) and is characterised by high rates of predation, suggest that it is a so-called "tension zone" (Barton & Hewitt, 1985): a hybrid zone that is maintained by a balance between reduced hybrid fitness (which removes hybrid gene combinations from the zone) and dispersal (which generates new hybrid gene combinations in the zone).

Previously (Schilthuizen et al., 2006) it was found that shell ornamentation in *Plectostoma* may be engaged in an evolutionary arms race with the attack behaviour of *Atopos* slugs. This could explain why the hybrid population suffers greater predation rate: the shell shape of a hybrid is composed of elements of both parental species, which may render the hybrids imperfectly defended. However, without observations of the predation behaviour of slugs targeting hybrids, we cannot be sure in what way the attack behaviour responds to the intermediate morphology. Also, since the proportion of snails killed by entry through the aperture, which does not leave a visible mark on the empty shell (Liew & Schilthuizen, 2014), the total predation rate cannot

be ascertained. It cannot be predicted whether the zone will be stable in the long run, but given that the population size and area of *P. concinnum* are greater, it is conceivable that the zone will eventually move at the expense of *P. fraternum* and the latter species will go extinct. We should stress the caveat here, that hybrid status of individuals was based only on intermediate conchology and was not supported by genetic data. Also, we stress that the above ideas regarding the hybrid zone are merely hypotheses and do require further studies.

Interestingly, the situation on Tandu Batu is different. Here, *P. simplex* and *P. concinnum* appear to be partly parapatric, partly sympatric, while showing very little, if any, hybridization. The difference in hybridization rate with Tomanggong Besar cannot only be due to different degrees of relatedness, because both species pairs have similar phylogenetic distances (Schilthuizen et al., 2006). Another difference with the situation on Tomanggong Besar is that the predation rates across the different taxa are not distinguishable on Tandu Batu, suggesting that both species are equally well defended against *Atopos* attack.

In summary, our results show that, even on small limestone hills, microgeographic patterns in distribution, hybridization, and predation can be discerned that reveal aspects of the evolution and maintenance of species differences. This may be of relevance for the many zoologists working on the malacofauna of these small, isolated limestone outcrops. Sometimes, especially for small hills of just a few hundred metres in diameter, a single large sample is taken on a hill to represent the entire population of a species (Hoekstra & Schilthuizen, 2011; Khalik et al., 2018; Schilthuizen et al., 2006). Our results show that this simplified approach would mean that small-scale evolutionary patterns remain unknown.

References

Barton, N.H., & Hewitt, G.M., 1985. Analysis of hybrid zones. — Annual Review of Ecology and Systematics, 16: 113–148.

Haase, M., Esch, S., & Misof, B., 2013. Local adaptation, refugial isolation and secondary contact of alpine populations of the land snail *Arianta arbustorum*. — Journal of Molluscan Studies, 79: 241–248.

Harrison, R.G., 1993. Hybrid zones and the evolutionary process: 1–376. Oxford University Press, Oxford.

Hendriks, K.P., Alciatore, G., Schilthuizen, M., & Etienne, R.S., 2019. Phylogeography of Bornean land snails suggests long-distance dispersal as a cause of endemism. — Journal of Biogeography, 46: 932–944.

Hoekstra, P., & Schilthuizen, M., 2011. Phylogenetic relationships between isolated populations of the limestone-dwelling microsnail *Gyliotrachela hungerfordiana* (Gastropoda: Vertiginidae). — Journal of Zoological Systematics and Evolutionary Research, 49: 266–272.

Khalik, M.Z., Hendriks, K., Vermeulen, J.J., & Schilthuizen, M., 2018. A molecular and conchological dissection of the "scaly" *Georissa* of Malaysian Borneo (Gastropoda, Neritimorpha, Hydrocenidae). — ZooKeys, 773: 1–55.

Koch, E.L., Neiber, M.T., Walther, F., & Hausdorf, B., 2020. Patterns and processes in a non-adaptive radiation: *Alopia* (Gastropoda, Clausiliidae) in the Bucegi Mountains. — Zoologica Scripta, 49: 280–294.

Lammers, Y., Kremer, D., Brakefield, P.M., Groenenberg, D.S.J., Pirovano, W., & Schilthuizen, M., 2013. SNP genotyping for detecting the "rare allele phenomenon" in hybrid zones. — Molecular Ecology Resources, 13: 237–242.

Liew, T.S., & Schilthuizen, M., 2014. Association between shell morphology of micro-land snails (genus *Plectostoma*) and their predator's predatory behaviour. — PeerJ, 2: e329.

Menken, S.B.J., 1996. Pattern and process in the evolution of insect-plant associations: *Yponomeuta* as an example. — Entomologia Experimentalis et Applicata, 80: 297–305.

Pukowski, E., 1933. Ökologische Untersuchungen an *Necrophorus F.* — Zeitschrift für Morphologie und Ökologie der Tiere, 27: 518–586.

Schilthuizen, M., 1994. Reproductive isolation in snails of

the genus *Albinaria* (Gastropoda: Clausiliidae). — Biological Journal of the Linnean Society, 52: 317–324.

Schilthuizen, M., 1995. A comparative study of hybrid zones in the polytypic land snail *Albinaria hippolyti* (Gastropoda Pulmonata: Clausiliidae). — Netherlands Journal of Zoology, 45: 261–290.

Schilthuizen, M., 2002. Mollusca: an evolutionary cornucopia. — Trends in Ecology and Evolution, 17: 8–9.

Schilthuizen, M., 2011. Community ecology of tropical forest snails: 30 years after Solem. — Contributions to Zoology, 80: 1–15.

Schilthuizen, M., Chai, H.-N., Kimsin, T.E., & Vermeulen, J.J., 2003a. Abundance and diversity of land snails (Mollusca: Gastropoda) on limestone hills in Borneo. — Raffles Bulletin of Zoology, 51: 35–42.

Schilthuizen, M., Rosli, R.B., Muji, A., Ali, B., Salverda, M., van Oosten, H., Bernard, H., Ancrenaz, M., & Lackman-Ancrenaz, I., 2003b. The ecology and demography of *Opisthostoma* (*Plectostoma*) *concinnum* s.l. (Gastropoda: Diplommatinidae) on limestone outcrops along the Kinabatangan River: 55–71. In: Maryati, M., Goossens, B., Ancrenaz, M., & Andau, M. (eds). Kinabatangan Scientific Expedition. Universiti Malaysia Sabah, Kota Kinabalu.

Schilthuizen, M., Hoekstra, R.F., & Gittenberger, E., 1999. Selective increase of a rare haplotype in a land snail hybrid zone. — Proceedings of the Royal Society of London B, 266: 2181–2185.

Schilthuizen, M., & Lombaerts, M., 1995. Life on the edge: a hybrid zone in *Albinaria hippolyti* (Gastropoda: Clausiliidae) from Crete. — Biological Journal of the Linnean Society, 54: 111–138.

Schilthuizen, M., van Til, A., Salverda, M., Liew, T.S., James, S.S., Elahan B., & Vermeulen, J.J., 2006. Micro-geographic evolution of snail shell shape and predator behavior. — Evolution, 60: 1851–1858.

Stankowski, S., 2013. Ecological speciation in an island snail: evidence for the parallel evolution of a novel ecotype and maintenance by ecologically dependent postzygotic isolation. — Molecular Ecology, 22: 2726–2741.

Stankowski, S., Westram, A.M., Zagrodzka, Z.B., Eyres, I., T. Broquet, T., Johannesson, T.K., & Butlin, R.K., 2020. The evolution of strong reproductive isolation between sympatric intertidal snails. — Philosophical Transactions of the Royal Society B, 375: e20190545.

Szymura, J.M., & Barton, N.H., 1986. Genetic analysis of a hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata*, near Cracov in southern Poland. — Evolution, 40: 1141–1159.

Tweedie, M.W.F., 1961. On certain Mollusca of the Malayan limestone hills. — Bulletin of the Raffles Museum, 26: 49–65.

Van Til, A., 2004. *Opisthostoma* snails on limestone outcrops along the lower Kinabatangan River in Sabah, Malaysia. Predation & distribution. — Unpublished student report, Vrije Universiteit, Amsterdam.

Vermeulen, J.J., 1991. Notes on the non-marine molluscs of the island of Borneo 2. The genus *Opisthostoma* (Gastropoda Prosobranchia: Diplommatinidae). — Basteria, 55: 139–163.

Vermeulen, J.J., 1994. Notes on the non-marine molluscs of the island of Borneo 6. The genus *Opisthostoma* (Gastropoda Prosobranchia: Diplommatinidae), part 2. — Basteria, 58: 75–191.

Vermeulen, J.J., & Liew, T.S., 2022. Land snails and slugs of Sabah and Labuan (Malaysia): i–x, 1–432. Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu.