Distribution and abundance *elephas* (Gastropoda: Pupinidae) in limestone habitats in Perak, Malaysia

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Abstract

This study aimed to reveal the habitat variables that determine the distribution and abundance of the land snail *Pollicaria elephas* in limestone habitats in the state of Perak, Malaysia. Seventeen plots were selected in a limestone hill to determine the effect of environmental variables on the abundance of this land snail. The environmental variables include habitat (canopy cover and leaf litter thickness); topography (elevation, aspect, ruggedness, and slope); microclimate (soil temperature, air temperature, and humidity); and vegetation (abundance of vascular plant species). The correlation analyses suggest that the abundance of the snails is positively correlated with the abundance of the four vascular plant species, *Diospyros toposia* var. *toposoides*, *Croton cascarilloides*, *Kibatalia laurifolia*, and *Mallotus peltatus*. Furthermore, plots with lower soil temperatures have higher numbers of snails than plots with higher soil temperatures. The results show that a few plots in the southern part of the limestone hill, in which *P. elephas* are absent, are similar in habitat, topography, microclimate and vegetation to the plots in the northern part of the limestone hill, where specimens of this land snail are present. The absence of this species in suitable habitat could be due to their low dispersal ability rather than adverse environmental variables. The findings of this short duration study of land snail ecology on single limestone hill can provide a window into more detailed study of other ground-dwelling large snails in the tropical region.

Keywords

Elephant pupinid snails, ecology, karst, Indochina, Malay Peninsula, Perak, Kinta Valley

Introduction

There are around 1000 recognised land snails species in Malaysia (http://malaypeninsularsnail.myspecies.info/, http://opisthostoma.myspecies.info/, http://borneanlandsnails.myspecies.info/). However, the ecology of the land snails species is poorly known. To date, only a handful species from the genera *Plectostoma*, *Georissa*, *Gyliotrachela*, *Diplommatina* have been studied in terms of their growth (Berry, 1962, 1963; Liew et al., 2014b), reproduction (Berry, 1965), and demography (Berry, 1966; Schilthuizen et al., 2003).

Land snails of the genus *Pollicaria,* commonly known as the elephant pupinid snails, belong to the family Pupinidae. All seven *Pollicaria* species and subspecies from Indochina and Peninsular Malaysia are endemic to this region, and *P. elephas* is the only *Pollicaria* species that occurs on Peninsular Malaysia. (Kongim et al., 2013) (Fig. 1A). This species was described by de Morgan (1885) from the state of Perak. So far, specimens of *P. elephas* were recorded from various localities from the limestone hills in the state of Perak, and from two other locations in Pahang (Chan, 1998; Kongim et al., 2013; Foon et al., 2017; Minton et al., 2017; GBIF.org, 2018).

Some aspects of the morphology, taxonomy, karyotypes and geographical distribution of *P. elephas* have been studied (Pain, 1974; Chan, 1997; Kongim et al., 2010; Kongim et al., 2013). However, the ecology and conservation status of this ground-dwelling species remain unknown. During a preliminary survey at a limestone hill in the state of Perak, Malaysia, we found some localities with very high densities of *P. elephas* while just tens of meters away, there are no snails found. This patchy distribution pattern is not unusual as a previous study on another similarly-sized land snail, *Limicolaria martensiana*, also showed a patchy distribution – more than 100 individuals per m^2 at one locality at Uganda (Ovew, 1969).

From the studies of other macro snails from other regions, land snails abundance in a location can be explained by vegetation or habitat features, such as a denser and heterogeneous canopy and understory, higher litter humidity and thickness, older and bigger trees and the presence of rotten logs, and the availability of calcium (Boag, 1985; Martin and Sommer, 2004; Müller et al., 2005; Horsák et al., 2007; Dvořáková and Horsák, 2012). Composition of plant species, which is sometimes difficult to be measured directly, can be a very useful predictor for snail communities (Dvořáková and Horsák, 2012).

Hence, we tested hypotheses of selected environmental parameters that determine the patchy distribution of *P. elephas* on a limestone hill. To date, this is the only location where a sizeable living population of *P. elephas* can be found since several systematic samplings of land snails throughout limestone hills in Peninsular Malaysia (Clements et al., 2008; Foon et al., 2017). First, we assessed the population size and density of *P. elephas* at different localities on a limestone hill in Perak. Second, we examined the vegetation, topographic and microclimatic variables for each locality to characterise the species-specific requirements for this species.

Materials and Methods

Study Site

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The study site was located on a limestone hill in Perak, Malaysia. A total of 17 plots, each measuring 2 m x 4 m were established; seven in the northern part, nine at the southern part and one at the central part of the limestone hill (Fig. 2). A pilot survey was conducted to ensure that these plots resemble habitats with different environmental variables and identify the plot with *P. elephas* suitable for population density study. The environmental variables of each of the 17 plots were measured during the pilot survey on 11 May 2018.

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Spatial distribution and population density

In the pilot survey, no living *P. elephas* nor empty shells were found in 11 plots. Hence, capture-mark-recapture method (CMR) was used to study the population of *P. elephas* in five of the six plots with living snails. One of the plots (AP-0) with *P. elephas* population cannot be accessed after the pilot survey, and hence CMR study cannot be conducted in the plot. The captured *P. elephas* were marked with nail polish (Fig. 1B and 1C). Different colours of nail polish were used to mark the shells of living *Pollicaria elephas* that were collected during different sampling sessions. The land snails were then released back to their respective plots, and plots were resampled after 10 to 15 days. The CMR was conducted four times for all plots except for one plot (AP-2), where only three CMR sessions took place. The first sampling was conducted on 9 July 2018 whereas the first recapture was on 19 July 2018; the second recapture on 1 August 2018 and the third recapture on 16 August 2018. The number of living individuals collected over the four CMR sessions is shown in Additional File 1.

We calculated the population density of *P. elephas* by counting the living snails during the different CMR sessions in individual plots. Based on the data collected, the population size of *P. elephas* was estimated by using Schnabel index:

- N = total number of snails (unknown)
- C = number of snails captured on the first sampling
- M = number of snails captured on subsequent sampling
- R = number of snails captured on both samplings

Multiple marks and recaptures ensure more accurate estimation of population size. Thus, Schnabel method (Alcoy, 2013), which allows multiple capture-recapture encounters, was applied:

$$N = \frac{\sum_{i=1}^{m} M_i C_i}{\sum_{i=1}^{m} R_i}$$

$$M_i = Total\ number\ of\ previously\ marked\ snails\ at\ time\ i$$

$$C_i = The\ number\ caught\ at\ time\ i$$

$$R_i = The\ number\ of\ marked\ snails\ caught\ at\ time\ i$$

Environmental variables

Four main environmental variables, namely habitat, topography, microclimate, and vegetation, were included in this study. All except for microclimatic variables were measured for the 17 plots. For habitat variables, we measured leaf litter thickness (cm) by averaging litter thickness at eight points within each plot; and estimated the percentage of canopy cover (%). To obtain topographic variables, we created a digital elevation model (DEM) of 4 m^2 cell size based on a 5-meter interval contour map for each of the two study sites by using Triangular interpolation (TIN) in QGIS ver. 2.18.24. (QGIS Development Team, 2018). After that, we used Terrain Analysis Tools to derive topographic features including slope (°), aspect (°, compass direction that a slope faces), and terrain ruggedness index (a quantitative measurement of terrain heterogeneity) (Riley et al., 1999). Topographic parameters were extracted for each of the sampling plots by using 'Add raster values to point' in SAGA (Conrad et al., 2015).

Microclimatic variables

We installed climatic HOBO data loggers to record air temperature and humidity (HOBO MX2301 Temperature/RH) about 1 meter above the ground for seven of the 17 plots. Soil temperature was recorded by using HOBO MX2303 Temperature Sensors, and the external sensors were buried fully under the leaf litter. At two plots at the northern site, living individuals of *P. elephas* were present, namely, plot A-Polli9, which had a high number of snails (15–16 individuals) and plot A-Polli3, which had a lower number of snails (1–2 individuals). At the remaining five plots at the southern part, there were no living individuals of *P. elephas* found. These climatic parameters were logged every 10 minutes in July 2018. However, the data from the two soil temperature loggers and air temperature and humidity loggers cannot be retrieved at all, and the data of some days in other loggers cannot be retrieved because these loggers were damaged by rain and wildlife.

Distribution and composition of plant species

To obtain vegetation data, we counted and identified the vascular plant species with diameter at breast height (DBH) above 1 cm within a 5-meter radius from the centre of the 17 plots. Voucher specimens were collected for each species and were subsequently identified by P.K. Hoo at the Herbarium of Forest Research Institute Malaysia (FRIM).

Data analysis

A principal component analysis (PCA) was conducted to assess the degree of habitat heterogeneity among the 17 plots based on the two habitat variables (leaf litter thickness, and canopy cover), four topographic variables (elevation, slope, aspect, and ruggedness index) and two vegetation variables (number of vascular plant individuals and number of vascular plant species). The abundance of vascular plant species was not included in the PCA analysis because of too many missing values in the dataset (due to the absence of certain plant species in plots). We explored PCA plot for habitat heterogeneity visually according to the plots' locations on the limestone hill (northern part, southern part, and central part). The analysis was done by using R (see Additional File 2 for the script).

Correction tests were performed to examine any significant relationships between the abundance of snails and each of the habitat, vegetation, and topographic variables. For vegetation data, we excluded 43 vascular plant species that were recorded only in one plot before statistical analysis. The final dataset consisted of the abundance data for 20 vascular plant species from 17 plots.

As the dataset was not normally distributed, we used Spearman correlation test based on both null-hypothesis significance testing and corroborated the analysis by using the Bayes factor (BF10) (Kass & Raftery, 1995). Hence, the conclusion is based on the inference of both frequentist (p values) and Bayesian (Bayes factor). All analyses were performed by using the JASP software version 0.12.2 (JASP Team, 2020; Additional File 3).

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As there were missing microclimatic data at some of the plots, either totally or partly in July, we cannot calculate the mean values of each of the microclimatic variables for the month. Hence, we cannot perform rigorous statistical analysis to test the relationship between the microclimatic variables and the abundance of snails in the plot. Nevertheless, we explore the relationships between the abundance of snails and microclimatic variables by plotting the mean of each sampled plot's daily microclimatic variables patterns. We calculated daily mean air humidity, minimum air humidity, mean air temperature, maximum air temperature, mean soil temperature, and maximum soil temperature.

Results

Spatial distribution and population density of the snails

Individuals were found in six out of seven plots on the northern part of the hill; none were found in plots on the central and southern parts (Additional File 1). The smallest marked specimen is 9 mm (shell width), and the majority of the marked snails were subadult (between 3 whorls and before the growth of aperture lip) and adult (Additional File 1). Previous studies on other land snails have shown that the capture rate for CMR technique can be very high – up to 85% recapture rate after one year (Kleewein, 1999). In our study, the recapture rates varied at different plots. For the three plots with more than ten snails recorded during the pilot sampling and the first capture session of CMR, the following three recapture session rates were above 80%, except for two recapture sessions in plot A-Polli2 (23% and 67%). The recapture rates were between 50% and 100% for the two plots with less than ten snails.

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Of the five plots examined in the CMR study, plot A-Polli2 had the highest population size of *Pollicaria elephas* (Table 1), and the calculated population density was estimated to be around 57 individuals for that plot and its surrounding area. The maximum population density in the sampled area of 8 m^2 was around 26 individuals (Table 2 in Additional File 1). The snails' population density in the sampling plots varies only slightly during the different sampling sessions for each plot (Additional File 1).

Effect of environment variables to snail occurrence and abundance

The first three PCA axes explained 78.7% of the habitat, topography and vegetation variations between plots (Fig. 3, Additional File 4, Additional File 5). As shown in Fig. 3, the PCA plot did not show apparent differences between the plots in the northern part (most of the plots with living *P. elephas)* and the southern part (all plots without living *P. elephas)* on the limestone hill. The abundance of *P. elephas* per plot was not correlated with canopy cover, leaf litter thickness, elevation, aspect, slope, and the ruggedness of the habitat (Table 2).

Microclimatic variations were observed among different plots, only soil temperature showed an association with the abundance of the snails, while air temperature and humidity showed no effect (raw data in Additional File 6). Soil temperature seems to have some effects on the occurrence of *Pollicaria elephas* (Fig. 4). Although two of the plots at the southern part of the hill (no snails recorded) have a similar mean and maximum soil temperature (~25°C) to one of the plots (A-Polli9) at the northern side with a relatively high number of living snails, a comparison of plot A-Polli9 with a higher number of living snails (15–16 individuals) and plot A-Polli3 with fewer living snails (1–2 individuals) suggests that the abundance of the snail could be affected by the soil temperature. The plot with the higher number of living snails had a soil mean temperature lower than 25°C, and maximum temperature lower than 26°C.

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Air temperature alone does not play a critical role in determining the occurrence of *Pollicaria elephas* (Fig. 5). All of the plots at the southern and northern parts of the hill have a similar mean temperature with differences smaller than 1°C during most of the days, except plot D-P3. A comparison of plot A-Polli9 with a high number of living snails (15–16 individuals) and plot A-Polli3 (1–2 individuals) suggests that the abundance of the snail is not affected by the air temperature as both plots have a similar mean and maximum air temperature.

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It seems humidity alone does not play a critical role in determining the occurrence of *Pollicaria elephas*. However, we could not retrieve the data from the plots with a high population density to confirm it further. The plots with a higher humidity mean (85% –100%) at the southern part of the hill did not harbour *P. elephas* as compared to plots with lower humidity (75%–93%) at the northern part of the hill (Fig. 6).

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Association between the abundance of *P. elephas* and vegetation

A total of 63 taxa of vascular plants were recorded in the 17 plots and species names were obtained for 46 species. The identity of 14 species could only be confirmed at the genus level, and the remaining three species could not be identified to the family level. Altogether 43 vascular plant species were recorded only in one plot, of which 27 species are singletons (Table 3). The number of species per plot ranged between three and 11 species, and the number of individuals ranged between four to 42 (Additional File 4).

Based on the null-hypothesis significance testing ($p < 0.05$) and Bayes factor (BF10), the abundance of four vascular plant species were positively correlated with the abundance of the land snails (Table 4, Additional File 7). Of these four species, *Diospyros toposia* var. *toposoides* (Ebenaceae) was the only plant species found in plots with and without living snails. Two plant species, namely, *Croton cascarilloides* (Euphorbiaceae) and *Kibatalia laurifolia* (Apocynaceae) were recorded only in two plots (A-P0 and A-Polli9). Another plant species, *Mallotus peltatus* (Euphorbiaceae), was recorded only in three plots (A-P0, A-P2 and A-Polli2). All these three plant species were only found in plots with living snails. However, the total number of vascular plants and plant species was not correlated with the abundance of snails in the plots (Table 2).

Discussion

There are synecology studies that focus on the association of habitat features and the composition of communities of land snails (Müller et al., 2005). However, autecology studies on single species in their natural habitat are scarce. The two different approaches of ecology have developed independently, although, the knowledge of both is necessary to understand the ecology of an individual population within a species or the whole ecosystem. A broader understanding of the biogeography of a species starts with the knowledge of the species' autecology on a local scale (e.g. Hugall, et al., 2002). Unfortunately, studies of individual species responses to its environmental variables, in particular, for large land snails in the tropical ecosystem, are still lacking (Horsák et al., 2007).

Spatial distribution and population density of *P. elephas*

To date, there is very little known for the ecology of Malaysian land snails. Furthermore, sampling approaches in previous studies on the biogeography and ecology of land snails may limit the questions that can be addressed regarding the factors that influence small-scale distribution and abundance. Site-specific habitat characteristics can influence the population size and spatial distribution of land snails, forming clustered distributions in suitable habitats fragments (Baur and Baur 1993, 1995; Martin and Sommer 2004; Müller et al. 2005). To date, there is only one report of a living population of *P. elephas* and records of the empty shell of this species in a dozen limestone hills in Malaysia (Chan, 1997; Foon et al., 2017).

The capture-mark-recapture technique has been used for estimation of population size and density for land snails (Blinn, 1963; Hänsel et al., 1999; Standish et al., 2002; Parkyn et al., 2014). Using this technique, we found that *P. elephas* can achieve high population densities, between three and four individuals per square meter, in suitable habitats at the northern part of the examined limestone hill. We could not find other population density studies on similar sized caenogastropod land snails for comparison. However, studies on similar sized pulmonate land snails showed that snails could occur at very much higher densities: up to 100 individuals per m^2 for *Limicolaria martensiana* (Owen, 1969).

~~Based on t~~The total number of living *P. elephas* snails recorded during the pilot survey—73 snails in seven plots (total area of 48 m^2~~). Hence,~~ indicates that the population size of *P. elephas* at the northern part of this hill could reach several thousands. To date, this is the largest known living population of *P. elephas* in Perak. However, there are still more than 80 hills in Perak remained to be discovered that may harbour the living population of this species.

There were no *P. elephas* in the southern part of the limestone hill, while large populations of *P. elephas* have been found at the northern part of the limestone hill. All examined plots were on the same limestone outcrop, with a similar climatic condition, soil conditions, land snail communities (Foon et al., 2017). Furthermore, there were no apparent differences in environmental variables in microclimate, topography, habitat, and vegetation between the northern and southern part of the limestone hill.

However, it is unclear why the snails from high-density spots do not migrate to the other spots at the same hill with similar habitat. Due to this study's short duration, the dispersal ability of *P. elephas* could not be determined. Nevertheless, the dispersal distances for other similar-sized land snails are very short, ranging from meters to tens of meters per year (Baur, 1986;

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Detailed information from one hill, demonstrating a clustered occurrence, and incidental finds of empty shells elsewhere do not allow conclusions about the present occurrence of the species. This is because we do not know to what extent incidental finds of empty shells indicate occurrence of clustered populations nearby.

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Schilthuizen et al., 2005; Edmorthy et al., 2012; Ozgo and Bogucki, 2011; Kramarenko, 2014). One possible explanation could be the homing behaviour of certain ~~snails~~ species (Rollo & WellingtonIf, 1981, Tomiyama, 1992; Stringer et al., 2018) ~~where the snails have~~with highly specialised habitat requirements, ~~in~~ which these snails would not migrate far from their favoured spot. ~~Hence, t~~These ~~snails~~ species could be narrow-ranged endemics occurring patchily across a large landscape. Another possible explanation could be unfavourable habitat that prevents the snails disperse to isolated spots with preferred habitat.

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Although the environmental variables included in this study were unlikely to determine the absence and presence of this species in different parts of the hill, the heterogeneity of population densities in the plots at the northern part of the hill showed that higher abundance of *P. elephas* could be associated with very local-scale lower soil temperature. This is expected as *P. elephas* is a ground-dwelling land snail. From our observation on the snails' behaviour in the field and in captive populations, snails were active during the night where they were seen feeding on leaf litter. In the daytime, the snails could be found burying themselves underneath the leaf litter. Besides, no vertical movement of this species has been observed during fieldwork. Hence, we assume that a constant and relatively low soil ground temperature is important for the population to thrive.

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Association between snail abundance and abundance of plant species

Previous studies on the association between plants and specific land snail species were conducted outside of the tropical regions (Blinn, 1963; Pollard, 1975; Cowie, 1985; Hänsel et al., 1999; Standish et al., 2002; Burrell et al., 2007; Horsák et al., 2011; Parkyn et al., 2013, 2014). Most of these studies suggested that plants act as shelters for land snails (Blinn, 1963; Pollard, 1975; Cowie, 1985; Standish et al., 2002; Burrell et al., 2007; Parkyn et al., 2014).

Most importantly, the abundance of *P. elephas* is positively associated with a relatively common vascular plant, *Diospyros toposia* var. *toposoides*, on the limestone hill. The other three comparatively uncommon species, namely, *Croton cascarilloides*, *Kibatalia laurifolia*, and *Mallotus peltatus* were somehow positively correlated to the snails' abundance. We think that a plausible explanation for this relationship could be that the leaf litter from these plant species is suitable for the snails' diet. However, it is also possible that rather than a direct causal relationship, both plants and snails prefer the same aspect of the local environment. Hence, a specially designed experiment is needed in order to test this hypothesis. To our knowledge, there were no *in situ* experiments on food preferences of land snails that were conducted in the field, though there are some experiments done in the laboratory setting for decaying leaves of selected plant species (Puslednik, 2002; Proćków et al., 2013). *In situ* experiments on food preferences in a tropical rainforest are challenging because identifying leaf litter from plants is difficult, as plants are very diverse even within a small area, as was shown in this study (see also Crowther, 1982, 1987a, 1987b).

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There were single-species land snail studies to investigate the effects of vegetation on the population density in non-tropical (Hänsel et al., 1999; Horsák et al., 2011; Barrientos, 2000, 2019; Caldwell et al., 2014) and tropical regions (Barrientos, 2000). However, so far, for tropical regions, very few studies focused on introduced land snail species (e.g. Barrientos, 2000). Even though we cannot confirm the in-depth association between the vascular plant species and snail feeding ecology, we have identified the candidate plants to be included in further experiments.

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Conclusion

Pollicaria elephas is a ground-dwelling species of land snail, but its ecology was poorly known. Our study provided some basic understanding of how each habitat, topography, microclimate, and vegetation variables play some roles in determining the species' occurrence at different parts of a limestone hill. This study also shows that ground temperature and a few vascular plant species show a positive association with the abundance of snails. However, there are two caveats ~~of~~ to the conclusions: the short duration of the study and no replicate sites on other hills. Nevertheless, this study's findings can be used to formulate hypotheses to be tested when another living population of this snail can be found in the other new sites. In summary, the absence of *P. elephas* in certain parts of the hill could be caused by low dispersal ability rather than adverse environmental conditions, and once the population of this species is established on a site, the abundance of the living snails is associated with the abundance of the four vascular plant species, namely *Diospyros toposia* var *toposoides*, *Croton cascarilloides*, *Kibatalia laurifolia*, and *Mallotus peltatus*. Also, plots with a lower soil temperature will have a higher number of living snails than plots with a higher soil temperature.

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Acknowledgements

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References

Alcoy, J. C. O. (2013). The Schnabel Method: An ecological approach to productive vocabulary size estimation. *International Proceedings of Economics Development and Research*, 68, 19.

Barrientos, Z. (2000). Population dynamics and spatial distribution of the terrestrial snail *Ovachlamys fulgens* (Stylommatophora: Helicarionidae) in a tropical environment. *Revista de Biología Tropical*, 48(1), 71-87.

Barrientos, Z. (2019). Demography of the land snail *Tikoconus* (*Tikoconus*) *costarricanus* (Stylommatophora: Euconulidae) in tropical low montane and premontane forests, Costa Rica. *Revista de Biología Tropical*, 67(6). 1449-1460.

Baur, B. (1986). Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). Ecography, 9(2), 117-125.

Berry, A. J. (1962). The growth of *Opisthostoma* (*Plectostoma*) *retrovertens* Tomlin, a minute cyclophorid from a Malayan limestone hill. Journal of Molluscan Studies, 35(1), 46-49.

Berry, A. J. (1963). Growth and variation of the shell in certain Malayan limestone hill snails. Journal of Molluscan Studies, 35(5), 203-206.

Berry, A. J. (1965). reproduction and breeding fluctuations in *Hydrocena monterosatiana* a Malayan limestone archaeogastropod. In Proceedings of the Zoological Society of London, 144(2), 219-228.

Berry, A. J. (1966). Population structure and fluctuations in the snail fauna of a Malayan limestone hill. Journal of zoology, 150(1), 11-27.

Blinn, W. C. (1963). Ecology of the land snails *Mesodon thyroidus* and *Allogona profunda*. Ecology, 44(3), 498-505.

Boag, D. A. (1985). Microdistribution of three genera of small terrestrial snails (Stylommatophora: Pulmonata). Canadian Journal of Zoology, 63(5), 1089-1095.

Burrell, C., Scott, B., & Yen, A. L. (2007). Habitat Preferences of the Otway Black snail *Victaphanta Compacta* (Cox and Hedley, 1912) (Rhytididae). The Victorian Naturalist, 124(4), 204-209.

Caldwell, R. S., Copeland, J. E., Mears, G. L., & Douglas, D. A. (2014). Notes on the natural history and ecology of *Inflectarius magazinensis* (Pilsbry and Ferriss, 1907) (Gastropoda: Polygyridae), the Magazine Mountain Shagreen. American Malacological Bulletin, 32(2), 211-216.

Chan, S. Y. (1997) On *Pollicaria elephas* (de Morgan,1885) from Perak, West Malaysia. The Papustyla, 11 (3) 11-12.

Chan, S. Y. (1998) A brief collecting trip to Perak, West Malaysia. part two. The Papustyla, 12 (2) 1-2.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., and Böhner, J. (2015): System for Automated Geoscientific Analyses (SAGA) v. 2.1.4, Geosci. Model Dev., 8, 1991-2007.

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Cowie, R. H. (1985). Microhabitat choice and high temperature tolerance in the land snail *Theba pisana* (Mollusca: Gastropoda). Journal of Zoology, 207(2), 201-211.

Crowther, J. (1982). Ecological observations in a tropical karst terrain, West Malaysia. I. Variations in topography, soils and vegetation. Journal of Biogeography, 65-78.

Crowther, J. (1987a). Ecological observations in tropical karst terrain, West Malaysia. II. Rainfall interception, litterfall and nutrient cycling. Journal of Biogeography, 145-155.

Crowther, J. (1987b). Ecological observations in tropical karst terrain, West Malaysia. III. Dynamics of the vegetation-soil-bedrock system. Journal of biogeography, 157-164.

Dvořáková, J., & Horsák, M. (2012). Variation of snail assemblages in hay meadows disentangling the predictive power of abiotic environment and vegetation. Malacologia, 55(1), 151-162.

Edworthy, A. B., Steensma, K. M. M., Zandberg, H. M., & Lilley, P. L. (2012). Dispersal, home-range size, and habitat use of an endangered land snail, the Oregon forestsnail (*Allogona townsendiana*). Canadian journal of zoology, 90(7), 875-884.

Foon, J. K., Clements, G. R., & Liew, T. S. (2017). Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. ZooKeys, (682), 1-94.

GBIF.org (12 October 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.wajiyx

Hänsel, N., Walther, C., & Plachter, H. (1999). Influence of land use and habitat parameters on populations of *Candidula unifasciata* and *Helicella itala* (Gastropoda, Helicidae) on calcareous grassland. Verhandlungen-Gesellschaft fur Okologie, 29, 363-372.

Horsák, M., Hájek, M., Tichý, L., & Juřičková, L. (2007). Plant indicator values as a tool for land mollusc autecology assessment. Acta Oecologica, 32(2), 161-171.

Horsák, M., Škodová, J., & Cernohorsky, N. H. (2011). Ecological and historical determinants of Western Carpathian populations of *Pupilla alpicola* (Charpentier, 1837) in relation to its present range and conservation. Journal of Molluscan Studies, 77(3), 248-254.

Hugall, A., Moritz, C., Moussalli, A., & Stanisic, J. (2002). Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). Proceedings of the National Academy of Sciences, 99(9), 6112-6117.JASP Team (2020). JASP (Version 0.12.2) (https://jasp-stats.org/)

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. Journal of the American Statistical association, 90(430), 773-795.

Kleewein, D. (1999). Population size, density, spatial distribution and dispersal in an Austrian population of the land snail *Arianta arbustorum styriaca* (Gastropoda: Helicidae). Journal of Molluscan Studies, 65(3), 303-315.

Kongim, B., Sutcharit, C., Tongkerd, P., Tan, S. H. A., Quynh, N. X., Naggs, F., & Panha, S. (2010). Karyotype variation in the genus *Pollicaria* (Caenogastropoda: Pupinidae). Zoological Studies, 49(1), 125-131.

Kongim, B., Sutcharit, C., Naggs, F. & Panha, S. (2013). Taxonomic revision of the elephant pupinid snail genus *Pollicaria* Gould, 1856 (Prosobranchia, Pupinidae)". ZooKeys 287: 19-40. doi:10.3897/zookeys.287.4617.

Kramarenko, S. (2014). Active and passive dispersal of terrestrial mollusks a review. Ruthenica, 24(1).

Liew, T. S., Kok, A. C., Schilthuizen, M., & Urdy, S. (2014b). On growth and form of irregular coiled-shell of a terrestrial snail: *Plectostoma concinnum* (Fulton, 1901) (Mollusca: Caenogastropoda: Diplommatinidae). PeerJ, 2, e383.

Martin, K., & Sommer, M. (2004). Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. Journal of Biogeography, 31(4), 531-545.

Commented [JJV32]: Separate paragraph

Minton, R. L., Harris, P. M., & North, E. (2017). Diversity and taxonomy of Vietnamese *Pollicaria* (Gastropoda, Pupinidae). Zoosystematics and Evolution, 93, 95.

de Morgan, J. (1885) Note sur quelques espèces nouvelles de Mollusques terrestres réceuillis dans le Peninsula Malaise. Le Naturaliste 7: 68-70.

von Moellendorff, O. (1886) The landshells of Perak. Journal of the Asiatic Society of Bengal 55: 299-316.

Müller, J., Strätz, C., & Hothorn, T. (2005). Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. European Journal of Forest Research, 124(3), 233-242.

Owen, D. F. (1969). Ecological aspects of polymorphism in an African land snail, *Limicolaria martensiana*. Journal of Zoology, 159(1), 79-96.

Ozgo, M., Bogucki, Z. (2011). Colonisation, stability, and adaptation in a transplant experiment of the polymorphic land snail *Cepaea nemoralis* (Gastropoda: Pulmonata) at the edge of its geographical range. Biological Journal of the Linnean Society, 104(2), 462-470.

Pain, T. (1974) The land operculate genus *Pollicaria* Gould (Gastropoda), a systematic revision. Journal of Conchology 28: 173-178.

Parkyn, J., & Newell, D. A. (2013). Australian land snails a review of ecological research and conservation approaches. Molluscan research, 33(2), 116-129.

Parkyn, J., Brooks, L., & Newell, D. (2014). Habitat use and movement patterns of the endangered land snail *Thersites mitchellae* (Cox, 1864)(Camaenidae). Malacologia, 57(2), 295-307.

Pollard, E. (1975). Aspects of the ecology of *Helix pomatia* L. The Journal of Animal Ecology, 305-329.

Proćków, M., Drvotová, M., Juřičková, L., & Kuźnik-Kowalska, E. (2013). Field and laboratory studies on the life-cycle, growth and feeding preference in the hairy snail *Trochulus hispidus* (L., 1758)(Gastropoda: Pulmonata: Hygromiidae). Biologia, 68(1), 131-141.

Puslednik, L. (2002). Dietary preferences of two species of *Meridolum* in southeastern Australia. Molluscan Research, 22(1), 17-22.

QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). Index that quantifies topographic heterogeneity. intermountain Journal of sciences, 5(1-4), 23-27.

Rollo, C. D., & Wellington, W. G. (1981). Environmental orientation by terrestrial Mollusca with particular reference to homing behaviour. Canadian Journal of Zoology, 59(2), 225-239.

Schilthuizen M, Rosli R, Ali AMM, Salverda M, van Oosten H, Bernard H, Ancrenaz M, Lackman- Ancrenaz I. 2003. The ecology and demography of *Opisthostoma* (*Plectostoma*) *concinnum* s.l. (Gastropoda: Diplommatinidae) on limestone outcrops along the Kinabatangan river. In: Mohamed M, Goossens B, Ancrenaz M, Andau M, eds. *Lower Kinabatangan* *scientific expedition*. Kota Kinabalu, Universiti Malaysia Sabah, 55-71.Schilthuizen, M., Scott, B. J., Cabanban, A. S., & Craze, P. G. (2005). Population structure and coil dimorphism in a tropical land snail. Heredity, 95(3), 216-220.

Standish, R. J., Bennett, S. J., & Stringer, I. A. (2002). Habitat use of *Tradescantia fluminensis* by *Powelliphanta traversi*. Science for Conservation, 195A, 35.

Stringer, I. A. N., Parrish, G. R., & Sherley, G. H. (2018). Homing, dispersal and mortality after translocation of long-lived land snails *Placostylus ambagiosus* and *P. hongii* (Gastropoda: Bothriembryontidae) in New Zealand. Molluscan Research, 38(1), 56-76.

Tomiyama, K. (1992). Homing behaviour of the giant African snail, *Achatina fulica* (Ferussac)(Gastropoda; Pulmonata). Journal of Ethology, 10(2), 139-146.