Netherlands Organisation for Scientific Research
Earth and Life Sciences

Open Programme
Proposal form

The maximum length of a proposal is 11 pages

1a. Details of proposal

Title:	Determinants of species diversity at 14 spatial scales in tropical microsnails from endangered limestone habitats
Area:	Geo and Biosphere

1b. Details of applicant

Name:	Menno Schilthuizen
Gender:	Male
Date of birth:	22 April 1965
Institution:	Netherlands Centre for Biodiversity *Naturalis*; CEES, University of Groningen; IBL, Leiden University
Position:	Professor / Permanent Research Scientist
Permanent position:	Yes
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1d. Renewed application? No

1e. Applying for: Post Doc

1f. Composition of the research group

List all staff members involved in the proposed research: provide name, initials, titles and type of involvement, e.g. daily guidance, technician, thesis supervisor, advisor.

Name and title	Specialization	Institution	Involvement
[ALW Postdoc]	community ecology	NCB Naturalis	postdoc
Prof. Dr. M. Schilthuizen	biodiversity	NCB Naturalis, RUG, UMS	daily guidance
Dr. Rampal Etienne	theoretical community ecology	RUG (University of Groningen)	advisor
Dr. Brian McGill	species abundance distributions	University of Arizona, USA	advisor
Dr. Jeff Nekola	land snail community ecology	University of New Mexico, USA	advisor
Dr. Jaap Vermeulen	taxonomy of Southeast Asian snails	NCB Naturalis	data,identification
Mr. T.-S. Liew, MSc	malacofauna of Sabah	UMS (Universiti Malaysia Sabah), NCB	local advisor
Mr. Reuben Clements, MSc	tropical conservation ecology	WWF-Malaysia, James Cook University	local advisor

2. Summary for the general public (preferably in Dutch, max. 100 words)

Biodiversiteitsonderzoekers willen weten waarom van plaats tot plaats andere soorten en andere aantallen soorten voorkomen en waarom sommige soorten zeldzaam, andere algemeen zijn. Dat het antwoord op deze vragen moeilijk te geven is, komt door de schaal waarop je kijkt: van dichtbij zijn het vaak niches die bepalen of een soort ergens voorkomt, terwijl op een grotere schaal "neutrale" processen belangrijker zijn, of andersom. In dit project brengen we de rol van ruimtelijke schaal precies in kaart bij de biodiversiteit van tropische micro-landslakken door uit te zoomen van de allerkleinste schaal (10 x 10 cm) tot de allergrootste (100.000 km^2).

3. Top 5 publications of the research group related to the proposed research

1. **McGill, B.J.**, 2003. A test of the unified neutral theory of biodiversity. ***Nature***, 422: 881-885.

2. **Liew, T.-S.**, **M. Schilthuizen** & M. bin Lakim, 2010. The determinants of land snail diversity along a tropical altitudinal gradient: insularity, geometry, and niches. ***Journal of Biogeography***, 37: 1071-1078.

3. **Schilthuizen, M., T.-S. Liew**, B. Elahan & I. Lackman-Ancrenaz, 2005. Effects of karst forest degradation on Pulmonate and Prosobranch land snail communities in Sabah, Malaysian Borneo. ***Conservation Biology***, 19: 949-954.

4. **Nekola, J.C.** & J.H. Brown, 2007. The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. ***Ecology Letters***, 10: 188-196.

5. J. Chave, D. Alonso & **R.S. Etienne**, 2006. Theoretical biology: comparing models of species abundance. ***Nature***, 441: E1.

4. Description of the proposed research (4 pages maximum, including figures, excluding literature references, font size at least 10 points)

BACKGROUND.—Although the study of biodiversity has progressed greatly over the past 50 years, we are still a long way from a comprehensive understanding of the processes that determine species diversity in space. In fact, "What Determines Species Diversity" was considered one of 25 great unanswered questions which the journal *Science* highlighted on its 125th anniversary[33]. Despite admirable attempts at reaching some form of consensus[25,37,14], many aspects are still unclear[28]. Among the uncertainties are, e.g., (a) the degree to which community diversity is determined primarily by the available niches or by "neutral" processes[11]; (b) the degree to which competitive exclusion of redundant species can be rendered ineffective by predators and parasites[17,2,32] and community instability[15,30]; (c) the degree to which species diversity is driven by the food web's primary productivity[50]; and (d) the causes for the frequently-observed rare-species skew in empirical species abundance distributions (SADs)[12]. A major obstacle in resolving some of these questions is the fact that different processes act at different spatial scales. Various authors[45,37,14] have highlighted the multiphasic shape of the species-area curve when extended over all possible spatial scales, with different processes responsible for the shapes of different parts of the total curve (Fig. 1). Yet, most studies of species diversity within a certain taxon tend to focus on just a small part of this multiphasic curve, and since taxa as well as geographic regions differ in the scales at which their species-area curves change shape, different studies on the same taxon but at different spatial scales or in different parts of the world often result in conflicting outcomes.

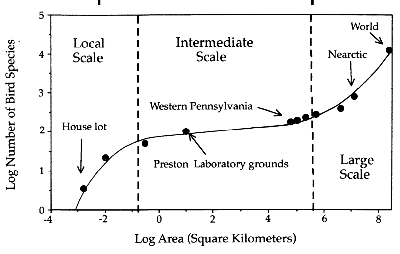

Figure 1. the triphasic species-area curve for birds (from Hubbell, 2001)

Land snails are a case in point. In principle, this is a very useful animal group for testing several hypotheses about species diversity[47], especially when compared and complemented with a far more popular group, terrestrial Arthropoda, to whom they are second in species numbers[3]. Like insects, they can be sampled exhaustively and in an unbiased fashion, not by trapping or fogging but by collecting empty shells from the ground[44]. Their much lower vagility prevents the problem[12] of distinguishing between resident populations and migrants, and causes high beta-diversity and short-range endemism, allowing a larger range of relevant spatial scales and probably all relevant ecological and evolutionary processes to be encompassed in a single study[1].

Unfortunately, though, studies of land snail community ecology have not led to any consensus. E.g., land snail point diversities show no latitudinal gradient in species richness, which suggests that the processes which produce this gradient in most other organisms[4] only work in land snails at larger spatial scales[47,37]. Yet elevation, often considered to affect the same processes as latitude[19], does show gradients in species richness[51,22]. Island-biogeographical studies on land snails, on the other hand, suggest that neutral processes such as dispersal and extinction are much more important than habitat structuring[29,37]. In addition to these conceptual paradoxes, many methodological issues remain unresolved[44]: Are empty shells a good proxy for the contemporary populations (and, if not, how do we avoid sampling bias and sampling error)? Are the standard 20 x 20 m quadrat sizes sufficiently small to capture point diversity? Are land snails, especially when of different body size, ecologically sufficiently similar to be studied as a single guild?

AIMS.—This project has the following aims:

1. to carry out the first-ever study of species diversity in a tropical land snail community which makes full use of the advantages of working with this animal group and which may serve as a point of comparison for results from other groups of terrestrial invertebrates.
2. to resolve or circumvent, for the first time, the above-mentioned methodological issues
3. to answer the following questions:
    a. what is the shape of the species-area curve across 14 orders of magnitude of spatial scale?
    b. which model best explains the shapes of the species-abundance distributions found at each of the spatial scales simultaneously?
    c. is habitat differentiation or niche differentiation demonstrable at the smallest of spatial scales?
    d. what are the spatial scales at which speciation contributes to patterns of species diversity?
    e. is it possible to incorporate all relevant biological processes into a model that explains the curve found under (a)?
    f. how could the model under (e) be applied to generate management recommendations for tropical forest conservation?

INNOVATIVE ASPECTS.—First, our proposed study will settle two long-standing methodological debates in tropical mollusc community ecology, namely: (i) whether empty shells are a good proxy for contemporary snail communities in karst forests and (ii) the appropriate quadrat size for measuring point diversity. Second, it will be the first-ever study of non-arthropod terrestrial invertebrates where diversity is studied in an effort-controlled manner across a multitude of spatial scales that range from pure point diversity to Rosenzweig's[37] "biogeographical provinces", Third, contrary to earlier studies of mollusc communities, it does so while ensuring that all species studied are within a single guild and separated for body-size classes. Consequently, the study will enable us, for the first time, to determine the processes responsible for species diversity in this terrestrial animal phylum at all relevant spatial scales.

Figure 2. A small sample of microsnails from the soil beneath a Malaysian limestone surface (photo: Reuben Gopalasamy Clements)

STUDY SYSTEM.—We will work with communities of microsnails (body size < 5 mm) on limestone surfaces in forests in Malaysian Borneo. This guild is chosen because

(i) the species are almost fully described[52-55,57], ample reference material is available, and our team has long-standing experience with their phylogenetics, ecology, and evolution[5-7,20-22,39-41,43]; (ii) while communities are similar, land snail populations on limestone substrate are much denser than on other substrates, allowing statistically meaningful samples to be gathered in relatively little time[20] (Fig. 2); (iii) the habitat structure is relatively simple, consisting of microvegetation on limestone surfaces that are in principle two-dimensional, but weathered in a fractal pattern of pits of varying size[44]; (iv) there is currently a rise in interest in the conservation of tropical limestone biotas[5], which means our result may be applied in conservation directly.
Some 300 limestone hills (ranging in size from 100 m^2 to 50 km^2) are evenly scattered over Malaysian Borneo, harbouring an estimated 500 species of limestone-dwelling terrestrial gastropods. Most hills have been mapped[60,23,18] and many have been sampled exhaustively for land snails by ourselves and others[56,7,61].

SAMPLING.—Since our sampling relies heavily on empty shells from the forest floor, we will begin with radiocarbon dating of shells of varying degrees of shell weathering, including specimens collected alive from the same locality. We will use one or several species of Euconulidae for this, since this family is known to have particularly low rates of "old" carbon uptake from the limestone sediment[34,35]. The results will show over which time range the majority of the death assemblage stretches and will help deciding a long-standing question in land snail ecology, namely whether empty shells can be expected to represent the contemporary populations or whether sampling needs to be limited to fresh shells.
Once this issue is resolved, we will perform the following nested sampling of our study system, which stretches over 14 spatial scales from 10 x 10 cm (10^{-2} m^2) to the 300 x 800 km area of entire Malaysian Borneo (2.4 x 10^{11} m^2). We will cover the five largest spatial scales by using existing data: from previous studies, we have quantitative inventories for *c.* 85 separate limestone locations, evenly scattered over Malaysian Borneo[56,20,7,Vermeulen, Liew, and Schilthuizen, unpublished data]. Rarefaction over locations with multiple quadrats[20] has shown that these inventories have a very high degree of completeness (completeness ratio = 0.90 ± 0.08). These inventories will be pooled for duplicate sets of limestone sites covering areas of 10, 100, 1000, and 10,000 km^2, and a single set for the total study area of 240,000 km^2.
For the nine smallest spatial scales (1 km^2 and below), we will select two mostly undisturbed limestone hills of approximately 1 km^2. Each will be divided into ten 0.1 km^2 sections, of which one will be further divided into ten 0.01 km^2 sections, of which one again will be further subdivided into ten 0.001 km^2 sections, and so on until the smallest spatial scale of 10 x 10 cm. For each hill, this gives us ten quadrats at each spatial scale (except for the 1 km^2 scale of the entire hill, for which there are two), giving a total of 162 quadrats. Throughout each quadrat (except perhaps the two smallest scales, where the quadrat size may be limiting), five litres of litter and top soil will be randomly assembled and enriched by flotation[42]. The flotsam will be dried and taken through a sieve cascade of 6.70, 2.24, 1.00, and 0.67 mm mesh widths. Each of the four sample-fractions will be stored separately, sorted for shells (if necessary—depending on the radiocarbon data—only fresh shells), and the total volume of the shell sample determined (for a more exact estimation of mean body size), Shells will be identified to species level using identification keys[57] and reference collections of UMS, Jaap Vermeulen, and NCB Naturalis. Species will be separated into endemic and widespread ones, on the basis of their world range being smaller or larger,

Figure 3. A cluster of microsnails (shell height c. 2 mm) in a pit on a limestone surface

respectively, than our study area (2.4 x 10^{11} m^2); in reference to our earlier papers[56], the former category incorporates mostly range size classes 1 and 2, the latter classes 3 - 5. Also, all Diapheridae will be removed from the data, as these are carnivores and cannot be considered part of the guild of microvegetation-feeding herbivores[38].
In each quadrat of 10^2 m^2 or larger, we will also select ten 25 x 25 cm sections of vegetated limestone surface, take high-resolution photographs of them, use a coarse brush to remove all snails and vegetation and store these samples in pure ethanol. The snails will be separated into the same size classes as the empty shells and identified to species level. The microvegetation will be identified to the smallest possible taxonomic unit with the assistance of botanists at NCB Naturalis. The photographs will be analysed by determining for every living snail both the microvegetation type it is found on and the size of the depression in the rock surface in which it was observed (Fig. 3).

ANALYSES.—We will analyse the data for each sample and for each sample-fraction with the software package *EstimateS 8.2.0*[8]. We will first plot log estimated species richness (determined by rarefaction) against log sampling area and determine spatial scales at which the curve shape changes, giving a first indication of the scales at which different processes come into play. Using Rosenzweig's[37] method of non-linear regression on the untransformed species richness vs. area data, we will determine the true "point diversity", i.e., the number of species that co-occur when area effects have been filtered out. The largest spatial scale at which the species richness is not significantly different from true point diversity may be assumed as the appropriate quadrat size for future studies of land snail diversity and an important way to settle the long-standing debate on this matter[20,44]. For the expected linear, central portion of the curve, we will use regression to determine the value for *z*, expecting a relatively high value associated with island-biogeographic processes given snails' generally strongly fragmented metapopulations[13]. Finally, since patterns of allopatric speciation and short-range endemism are commonly observed in tropical land snails on the scale of tens of kilometres or even less[47,48], we expect evolutionary effects to begin playing a role on the scale of 10^6 m^2 and above. This will be assessed by analysing the data with and without the endemics included.

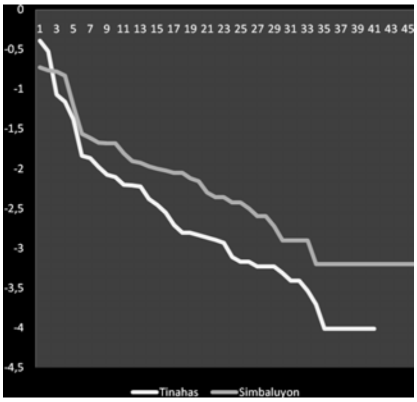

Figure 4. SADs (Whittaker plots) for two samples from a single quadrat (unpublished data)

We will then compute SADs[26,31] (Fig. 4) for complete samples and fraction-samples at each spatial scale. Using the software packages Palamedes[27] and PowerNiche[10] we will determine the goodness-of-fit for each SAD with a selected range of (to use Magurran's[26] terminology) statistical, niche-based, non-niche based, and neutral models, such as the lognormal[36], the broken stick[24], the sequential niche-breakage[49] and the unified neutral theory[14]. (Unpublished work by Nekola [pers. comm..] suggests that this may require constraining sample size at a value below 5,000 individuals, which, if necessary, we will do by resampling our data sets.) An alternative approach we may apply is the ISAD (individual species abundance distribution) method[59], in which niche effects are identified by positive or negative relationships between sample diversity and individual species abundances. We will thus test several (partly mutually exclusive) hypotheses, namely:

1) that the SADs will fit niche-based models only at the smallest spatial scales, and only within the same body size class, since ecological interactions will take place mainly among equal-sized animals within cruising range of one another[44]

2) that samples from larger spatial scales and including more body size classes will converge to the canonical lognormal as a result of the central limit theorem effects[26,46].
3) that the community behaves as a classical neutral metacommunity at the smallest spatial scales, because the organisms are sessile and compete for roughly the same resource on a two-dimensional plane where space is limited[14].

We will use the ecological data from our photographs as an independent test for niche differentiation or the lack thereof to complement the results of testing the SADs for conformance to niche–based models.

IMPACT AND FUTURE WORK.—The study described above will lay the foundations for building a model that incorporates the relative effects of niche differentiation, competition, dispersal, extinction, and speciation on the land snail communities at all relevant spatial scales. Such a model will not only be extremely valuable for understanding biodiversity patterns in this study system (and act as a point of reference for similar studies in other systems) but will also allow direct application in conservation. Karst forests world-wide and in Southeast Asia in particular, are under severe threat of destructive exploitation by quarrying for cement and disturbance by fire, logging, and cave-tourism[16,58,9,5]. This is particularly worrying for taxa such as terrestrial Gastropoda that have high population densities on calcareous substrates, and for which limestone hills could form important targets for conservation of entire communities[5]. However, conservation planning for karst systems have sofar been fraught with confusion over the relevant spatial scales. Conserving a few large hills and sacrificing other smaller ones has been mentioned as one possible option[7], whereas others have suggested that it is wiser to exploit many hills, but only a certain portion of each[58]. Our study will result in a set of data which may be used as a baseline by which to estimate the loss of biodiversity of destructions at each spatial scale. In collaboration with the Sabah Wildlife Department, the Minerals and Geoscience Department, and the NGO HUTAN, with all of whom we have a long-standing working relation, we will integrate the results from this study in the management of the Kinabatangan Wildlife Reserve, an area in Sabah with a rich land snail fauna, thanks to the presence of many limestone hills, some of which are, however, under threat from quarrying, logging, and fire.

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61. Yong, H.S., Ng, F.S.P & Lee, E.Y.E., 2004. Sarawak Bau Limestone Biodiversity. *Sarawak Museum Journal Special Issue*, 6.

5. Timetable of the project

1. **preparatory phase: 01-01-2011 – 30-06-2011**, as follows:
   a. literature study: 2 months
   b. exploring existing data sets: 2 months
   c. applying for research permits: 1 month
   d. exploratory visit to Malaysia: 1 month
2. **field work: 01-08-2011 – 30-11-2011**, as follows:
   a. preparations, meeting officials and collaborators: 3 weeks
   b. surveying and setting up the 10^4 – 10^6 m^2 sections: 1 week
   c. sampling the 10^4 – 10^6 m^2 sections: 3 weeks
   d. setting up, photographing and sampling 820 25 x 25 cm sections: 4 weeks
   e. setting up and sampling the 10^{-2} – 10^3 m^2 sections: 2 weeks
   f. flotation, preparing for drying, and curation of samples (in the field): 1 week
   g. sieving and storing of size-fractioned samples: 2 weeks
3. **sorting shells from all dry samples: 01-12-2011 – 01-08-2012**
4. **identifications and counting: 01-08-2012 – 31-10-2012**
5. **analysis of samples: 01-11-2012 – 28-02-2013**
6. **writing of papers and visit to Malaysia for final reporting: 01-03-2013 – 31-12-2013**

6. Scientific embedding of the proposed research

a. Community and Conservation Ecology. This project will bolster the ongoing collaboration between the research group COCON of Prof. Dr. Han Olff at the Centre for Ecological and Evolutionary Studies of the University of Groningen and researchers at NCB Naturalis (i.e., Schilthuizen [also extra-ordinary professor in Groningen], Vermeulen, Maassen, Liew, Miller, Rijsdijk). Within this collaboration, the Groningen group's expertise in theoretical and computational ecology, particularly their recent work on species abundance distributions, and NCB's expertise in taxonomy, phylogenetics, and field ecology of tropical invertebrate communities are beginning to stand out as a fruitful match. In addition, both groups have collaborative links with Univ. Arizona (McGill).

b. Tropical land snail ecology. Malacologists at NCB Naturalis (i.e., Liew, Schilthuizen, Vermeulen, de Winter) form an important core in the field of tropical land snail community ecology and maintain active links with similar groups, particularly in the UK (Natural History Museum: Cameron, Naggs, Raheem; the Univ. of Nottingham: Wade, Davison; Cardiff Univ.: Rowson, Tattersfield), in the US (Univ. New Mexico: Nekola), in Thailand (Chulalongkorn University: Panha, Tongkerd, and co-workers), in Malaysia and Singapore (WWF-Malaysia: Clements; National Parks Singapore: Davison; UNIMAS: Mohammad Effendi Marzuki), and in Japan (Tohoku Univ.: Chiba, de Chavez). Aspects of this project proposal were discussed and debated by all these collaborators during the recent symposium on "community ecology of tropical forest snails" at the World Congress of Malacology.

c. NCB Naturalis research theme "Biodiversity". The here proposed project forms part of an ongoing NCB Naturalis research project (led by Schilthuizen) on Southeast-Asian land snail biodiversity. This research project falls within the NCB Naturalis research theme "Global Change Biology", one of the aims of which is: "To understand the rain forest history in order to assess present day impact of global change on tropical forest biodiversity, to model future impact of GCC on rain forest ecosystems and to assist politicians and NGOs in taking biodiversity conservation decisions." (NCB Research and Infrastructure Implementation Plan, 2009). This theme is one of the research areas that the NCB hopes to develop and for this reason is giving special funding. The embedding of the here proposed project within this theme will strengthen both the theme and foster further collaboration among the theme participants.

7. Societal significance

The proposed project aims at understanding biodiversity patterns in tropical land snails in rainforests on limestone. This habitat type is under severe threat from human-induced disturbance and destruction, and mollusks are one of the groups that will be most affected by this, due to their high rates of endemism, high species turnover, and high population densities. Besides our scientific work on this interesting fauna, we have been running a campaign to apply our knowledge in the preservation of these karst ecosystems and the present project will feed into this by providing us with a set of data on species diversity spanning all spatial scales. Activities of our campaign until now have included the listing of endangered snail species on the IUCN Red List (www.redlist.org), close collaboration with Malaysian conservation agencies (WWF-Malaysia and the NGO HUTAN), and the *Institute for Tropical Biology and Conservation* at Universiti Malaysia Sabah, participating in and organizing karst conservation workshops (e.g., UNESCO-workshop *Karst Biodiversity and World Heritage in East and Southeast Asia*, Mulu, 2001), publishing karst conservation manuals (e.g., Vermeulen & Whitten, 1999. *Biodiversity and cultural heritage in the management of limestone resources: lessons from East Asia*. The World Bank) and generating media attention, both locally in Malaysia and internationally, e.g.:
The Star (Malaysian national newspaper), 11 September 2006, *Evolution in Action in Valley* http://thestar.com.my/news/story.asp?file=/2006/9/11/nation/15393171&sec=nation
Daily Express (East Malaysian newspaper), 11 September 2006, *Kinabatangan Hills Offer Vital Lessons on Evolution* http://www.dailyexpress.com.my/news.cfm?NewsID=44340
National Geographic, 12 September 2006, *Animal-rich Limestone Towers Face Rocky Future in Asia* http://news.nationalgeographic.com/news/2006/09/060912-stone-karst.html
BBC Wildlife Magazine, December 2006, *Protected by Design*
United Nations Environmental Programme (UNEP), 12 September 2006, *Environment in the News* http://www.unep.org/cpi/briefs/2006Sept12.doc.

Agrarisch Dagblad (Dutch daily), 5 November 2008, *Grote kalksteenheuvels beter beschermen* http://www.agd.nl/1063867/Nieuws/Artikel/Grote-kalksteenheuvels-beter-beschermen.htm
Vroege Vogels (Dutch radio show), 5 November 2008, *Biodiversiteitsbescherming op tropische kalksteenheuvels: hoe groter, hoe beter* http://vroegevogels.vara.nl/nieuwsitem-.167.0.html?&tx_ttnews%5Btt_news%5D=347692&tx_ttnews%5BbackPid%5D=123&cHash=a47cbdfb17
Maleisië.be (Dutch-language weblog on Malaysia), 5 November 2008, *Kalksteenheuvels in Maleisië "Arken van Biodiversiteit"* http://nieuws.maleisie.be/2008/20081105_kalksteenheuvels_in_-maleisie_arken_van_biodiversiteit.html

8. Legal requirements

Has been complied with the law and legal requirements with respect to the proposed research, such as '*Wet op Dierproeven*', '*DNA-recombinant legislation*' and/or '*Code of conduct on Biosecurity*'?

X Yes O No

9. Budget

		Year 1	Year 2	Year 3	Year 4
Personnel (mm)		1 postdoc	1 postdoc	1 postdoc	
Research costs (k€)					
	Equipment	3350	9750	0	
	Consumables*	1300	0	0	
	Fieldwork	21350	0	2950	

* max. € 10.000,- p/year

Specification of the requested funds:

Equipment:
- digital camera[1] € 650
- field notebook computer (Toughbook)[1] € 2500
- high-end GPS[2] € 400
- Matlab software[3] € 750
- high-resolution satellite photographs[4] € 1500
- automated soil sorting machine[11] € 7500

Consumables:
- vials € 500
- boxes € 500
- bags € 150
- alcohol € 150

Fieldwork/Travel:
1. exploratory visit to Malaysia (1 month)
   - flights[5]: € 2500
   - land transportation costs: € 350
   - lodging costs: € 1500
2. field work in Malaysia (4 months)
   - flights[6]: € 3500
   - land transportation costs[7]: € 5000
   - lodging costs[8]: € 3000
   - field assistants / guides[9]: € 5000
   - permits (administration costs and fees): € 500
3. reporting in Malaysia (2 weeks)
   - flights[10]: € 2000
   - land transportation costs: € 200
   - lodging costs: € 750

Justifications:
1. *necessary for documenting the quadrats and the 25 x 25 cm microhabitats, as well as storing and pre-analysing data.*
2. *essential for mapping the quadrats*

3. *required for running Palamedes*
4. *for mapping quadrats; high-resolution photographs are not available for Malaysia in Google Maps or Google Earth*
5. *one return ticket Amsterdam – Kuala Lumpur, and domestic legs as follows: Kuala Lumpur – Kota Kinabalu; Kota Kinabalu – Lahad Datu; Lahad Datu – Sandakan; Sandakan – Kota Kinabalu; Kota Kinabalu – Mulu; Mulu – Kuching; Kuching – Kuala Lumpur*, incl. carbon credits.
6. *one return ticket Amsterdam – Kuala Lumpur, and domestic legs as follows: Kuala Lumpur – Kota Kinabalu (return); Kota Kinabalu – Lahad Datu (return); Lahad Datu – Sandakan (return); Kota Kinabalu – Mulu (2 returns); Kota Kinabalu – Kuching (return)* , incl. carbon credits.
7. *4-wheel drive vehicle rent: € 245 / week; fuel: € 800*
8. *€ 25 / day*
9. *one local guide, € 20 / day; one local field assistant, € 30 / day*
10. *one return ticket Amsterdam – Kuala Lumpur, and domestic legs as follows: Kuala Lumpur – Kota Kinabalu (return); Kota Kinabalu – Mulu (return); Kota Kinabalu – Kuching (return)* , incl. carbon credits
11. *for processing soil samples--reducing manual sorting time*

10. Financial assistance from other sources

None requested. However, NCB naturalis will cover travel and expenses for daily advisor (Menno Schilthuizen) and publication costs under NCB naturalis's open access policy.