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Land snails on islands: building a global inventory

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Abstract

Land snails are one of the most diverse groups of terrestrial animals and are commonly used as model organisms in ecology, biogeography and conservation biology. Despite being poor dispersers, they form crucial components of island faunas and exhibit high percentages of endemism. Insular land snails are also among the most threatened animals on Earth, already having suffered extensive human-caused extinctions. However, current estimates of global insular land snail diversity are based on sporadic records published at the scale of individual islands and/or archipelagos. To tackle this shortfall, we herein present the major features of a global inventory of island snails. We recovered full species lists from existing literature and available species checklists for 727 islands across the globe and collated a database which currently includes the occurrence of 11,139 species, that is approximately 48% of all known land snail species (of which there are an estimated 23,000). Seventy-five percent of the species are single-island endemics, underlining the exceptional nature of islands as global biodiversity hotspots. Overall, our attempt is one of few to examine insular invertebrate diversity at coarser scales and a crucial step to the study of global patterns in island biodiversity.

Highlights

- Despite much interest in insular snails, it is not known how many island snail species there are, or how many are endemic to single islands and/or specific island regions?
- We address these questions by collating the first global database of insular land snails.
- Although hosting almost 50% of the known land snail species and 82% of the known families, the 727 islands represent just about 3% of global landmass.
- Seven large islands comprise almost 50% of global single-island endemics richness.
- Our database represents one of the few attempts to quantify global invertebrate diversity on islands, and thus serves as a plea to intensify research efforts towards describing and understanding the patterns and processes establishing invertebrate biodiversity at large spatial scales.

Keywords: endemic species richness, invertebrate biodiversity, island biogeography, land snails, macroecology, species database, taxonomic diversity

Introduction

"Land-Molluscs are a great perplexity to me."

C. R. Darwin, 1857.

Land snails constitute one of the most species rich groups of terrestrial animals on Earth. With ~23,000 named species (MolluscaBase 2020) and an estimated amount of 11,000-40,000 as yet undescribed taxa (Lydeard et al. 2004, Rosenberg 2014), they are only superseded by the millions of terrestrial arthropods, i.e. insects with >1,000,000 and arachnids with >110,000 described species (IUCN 2020). Occupying a spectrum of habitat types ranging from arid deserts – e.g., *Sphincterochila boissieri* in Israel and Egypt – and coastal sand dunes – e.g., *Theba tantanensis* in Morocco – through to alpine moraines – e.g., *Limax seticus* in Himalaya – land snails are almost ubiquitous and are found in all continents except Antarctica (Cameron 2016).

Despite their poor ability for active dispersal (e.g. Hausdorf and Hennig 2003, Cameron 2013), their sedentary lifestyle and their minimal tolerance to seawater, several land snail families appear as important components of insular faunas (e.g. Cowie 2004, Cameron et al. 2007, Cameron 2013). Charles

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Darwin was one of the first to notice this seeming contradiction as it appears in one of his letters to A.R. Wallace in 1857: *"One of the subjects on which I have been experimentising and which cost me much trouble, is the means of distribution of all organic beings found on oceanic islands and any facts on this subject would be most gratefully received: Land-Molluscs are a great perplexity to me."* (from Holland 2009). Today, based on phylogenetic studies, we know that certain groups of land snails are capable of dispersing across vast geographic distances and over ocean basins (e.g. Gittenberger et al. 2006, Holland and Cowie 2009) in various ways, including anemochory, zoochory and anthropochory (e.g. Cameron 2016).

Land snails are among the better known and studied groups of invertebrates on islands, especially those of oceanic archipelagos (Cameron et al. 2013). Detailed studies of land snails in such archipelagos started early (Seddon 2008, Cameron et al. 2013) and, in many cases, they are now thought to be effectively complete. Therefore, there is now evidence of some remarkable radiations – e.g. *Partula* in Moorea (Murray et al. 1993), *Mandarina* in the Ogasawara Islands (Chiba 1999), *Bulimulus* in the Galapagos (Parent and Crespi 2009) and Achatinellidae in Hawaii (Cowie 1995) – which display very high levels of endemism (e.g. 89% in the Madeiran islands, 90% in the Mascarene islands, 94% in the Galapagos islands and 99% in the Hawaiian islands, see Triantis et al. 2015, Table 1). The availability of such data, coupled with the multiplicity of life forms – e.g. in terms of size, reproduction and habitat preferences (see Cameron 2016) – that land snails exhibit, makes them ideal models for the study of some of the most fundamental issues in island biogeography (see Patiño et al. 2017 for a review), such as: inferring processes underlying community assembly (e.g. Astor et al. 2014), gaining insights into mechanisms of evolutionary diversification (e.g. Cowie 1995, Holland and Cowie, 2009), or understanding the factors that generate observed macro-scale diversity patterns (e.g. Triantis et al. 2015).

At the same time, land snails constitute one of the most imperiled groups of terrestrial animals (Lydeard et al. 2004). Extinctions of land snails represent the majority of currently known extinctions among all plants and animals (200/950; IUCN 2020), and more than 70% of these have arguably taken place on oceanic islands (Régnier et al. 2009). Accordingly, with an estimated number of >1,000 species extinctions globally (Cowie et al. 2017), land snails have been used as surrogates to describe the status of global biodiversity and to estimate overall human-induced extinction rates amidst the often-claimed contemporary 6th mass extinction event (Régnier et al. 2015).

With only a few exceptions (Cameron et al. 2013, Triantis et al. 2015), however, information about the diversity of island land snails is scattered among accounts of individual island or archipelagic faunas. There is no comprehensive checklist of island land snail faunas with which to test the generality of hypotheses concerning the nature and origin of island biodiversity or the processes involved. We have started to address this gap by collating a global database on insular land snail faunas. For this, we have developed a comprehensive species-by-island presence-absence matrix based on an exhaustive literature review. In terms of the number of species, we believe our database to be currently the largest, for insular invertebrates in general.

Data collation

In defining "land snail", we acknowledge that terrestrial existence in gastropods has evolved more than once (Barker 2001). We took into account all land snail species belonging to the currently recognized 137 gastropod families with representatives on land (four in Neritomorpha, 13 in Caenogastropoda and 120 in Heterobranchia; see MolluscaBase 2020). Slugs and semi-slugs are also included, but we have excluded amphibious or semi-aquatic taxa.

Land snail occurrence was recorded on an island by island basis. Using the keywords "gastropod + island + checklist + land-snail + species-list" (and different combinations of these) we performed a detailed survey of existing literature and species checklists in three major bibliometric databases (Google Scholar, Web of Science, Scopus). The survey was conducted between March 2016 and December 2018. To supplement these checklists, we also used taxonomic studies and studies with various other purposes (e.g. biology or ecology) which focused on single species. In addition, we contacted a series of experts on molluscan taxonomy from various institutes worldwide in order to update checklists and to gain access to faunas of poorly known islands. In this way, we recovered more than 200 bibliographic references (92% published and 8% unpublished records; see Table S1), which we used to develop a species-by-island presence-absence matrix. Lists known – or suspected – to be incomplete based on the information provided in the data sources were excluded. This led to excluding around 50 islands. While theoretically complete lists may, and sometimes do, acquire additional species as a consequence of modern taxonomic revision (e.g. Teixeira et al. 2019), we regard those included in our database as sufficiently robust to be used in future biogeographic and macroecological studies.

In some cases, checklists contained taxa which have not yet received a formal description under the provisions of the International Commission on Zoological Nomenclature (ICZN; https://www.iczn.org). These were included only when local experts confirmed their specific status. Recently extinct species (i.e. species arguably extinguished by human activity and recorded only as subfossils) were also included in our database, whereas species presumed to be introduced – i.e. not forming part of the indigenous island faunas – were excluded (as in Cameron et al. 2013, Triantis et al. 2016).

Our data derive from publications spanning more than a century (128 years, Fig. 1). As taxonomic concepts and practice have changed over this period, we have checked for taxonomic validity and potential

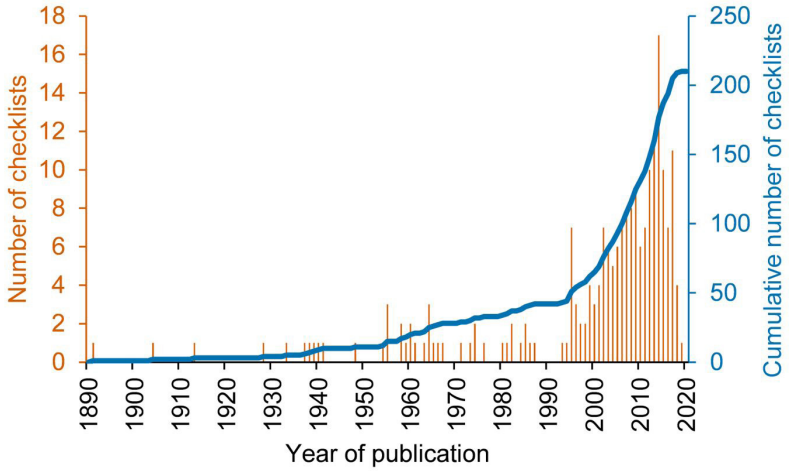

Figure 1. Temporal extent of the recovered insular land snail checklists.

synonyms through a name-parsing approach, as employed in several web-based taxonomic databases; namely the MolluscaBase (option "Match taxa")[1], the Global Biodiversity Information Facility (GBIF; option "Name Parser")[1], the Global Name Index (GNI; option "Name Parser")[1], the Integrated Taxonomic Information System (ITIS; option "Compare Taxonomy/Nomenclature")[1], the Catalogue of Life (CoL; annual checklist 2019)[1], and the Worldwide Mollusc Species Database (WMSD; downloaded and searched with common spreadsheet workflows)[1]. In this way, all specific names were contrasted against multiple taxonomic inventories and exact matches were considered as accepted/valid unless otherwise stated. Where found, spelling mistakes and genus names were corrected, while assignment to families followed the most up-to-date taxonomic nomenclature for Gastropoda, as implemented in MolluscaBase (2020). Infraspecific entities were grouped into their respective specific taxonomic rank, with the location and number of subspecies kept in the database for future reference. Synonymized names were also kept in the database to secure transparency in case of future taxonomic reevaluations.

Database structure

Our database currently contains data on the land snail faunas of 727 islands and 86 island territories (i.e. archipelagos or island groups; see Table S1 for number of islands in each island territory and Proios et al. 2021), comprising a total of 9,056,007 species-by-island/archipelago occurrences. Taxonomic information for each species includes its assignment to family, genus, specific epithet and its full species rank name (genus+specific epithet). Synonyms are also provided in the form of genus+specific epithet. Author names both for the valid names and the synonyms are to be added in a later release, which will have the form of a relational database to meet general biodiversity information standards. The results of the name-parsing approach employed in the six web-based databases listed above are also included to ensure name traceability. So far, the database contains 793 undescribed entities which are herein included as species with unresolved taxonomic status (identified in a dedicated field). The presence of subspecific entities is also taken into account, keeping the location and number of subspecies also in a separate field. This information will be further expanded (i.e. including the actual names of subspecies) in later versions of the database. Other fields indicate the status of each species as either extinct or extant, and as either island endemic or native non-endemic (non-native species are currently excluded from the database). Names of islands are given as mentioned in original publications of species checklists, and names of island territories (i.e. archipelagos or island groups) are also included.

Biogeographic and taxonomic patterns

The 727 islands considered span five continents and 11 biogeographic realms, with the majority located in the Palearctic (262), the Oceanian (161) and the Panamanian (88) realms (defined *sensu* Holt et al. 2013). Regarding the types of islands considered, there was no *a priori* reason to constrain the search to islands of specific geological origin. Therefore, our database encompasses all three major categories of true marine islands *sensu* Whittaker and Fernández-Palacios (2007), i.e. oceanic islands, continental fragments and continental shelf islands. Atolls are also included, with biodiversity data aggregated into single multi-islet geographic entities.

In terms of taxonomic diversity, our database provides presence-absence data for 11,139 species names, of which 10,350 (93%) are formally described taxa and 789 (7%) represent undescribed entities.

1 MolluscaBase: http://www.molluscabase.org/, GBIF: https://www.gbif.org/, GNI: http://gni.globalnames.org/, ITIS: https://www.itis.gov/, CoL: http://www.catalogueoflife.org/, WMSD: http://www.bagniliggia.it/WMSD/WMSDhome.htm. All last accessed 11/2019.

The species included are classified into 113 families and 1,113 genera, that is 82% of known land snail families (113/137) and 24% of known land snail genera (1,113/4,618) (the number of known land snail families and genera are based on MolluscaBase 2020). Among the undescribed specific entities, 429 have not yet been assigned to a genus, while one has not been assigned to either at genus or at family level. The majority of these undescribed taxa are found in the North and South Islands of New Zealand, 259 belonging to the family Punctidae and 149 to Charopidae. Such cases, although yet unresolved, were taken into account in order to avoid underestimations of species richness.

The number of species and genera included in our database vary remarkably across families, the most species- and genus-rich families being Charopidae (106 genera, 725 species), Camaenidae (77 genera, 676 species) and Urocoptidae (51 genera, 682 species). In turn, the number of species vary remarkably across genera, with the vast majority of genera (867) containing up to 10 species and a minority of 12 genera containing more than 100 species. Indicative of the uneven contribution of families and genera to insular land snail species richness is the fact that ~51% of genera pertain to just 14 families (Charopidae, Camaenidae, Urocoptidae, Helicarionidae, Streptaxidae, Clausiliidae, Helicinidae, Annulariidae, Achatinellidae, Cyclophoridae, Geomitridae, Achatinidae, Euconulidae and Helicidae), while ~50% of species are members of just 94 out of the 1,113 retrieved genera.

The most widespread families are Achatinidae (324 islands), Clausiliidae (242 islands), Helicidae (242 islands), Helicinidae (216 islands) and Pristilomatidae (210 islands). The presence of twenty more families ranges between 101 and 195 islands, with the remaining 88 families being present in <100 islands (on average ~30 islands).

Across the 727 islands included in our database, indigenous land snail species richness ranges from one to 1,349 species (Fig. 2a), with the majority of islands (~51%, n=373) hosting up to 13 species. Cuba and Madagascar have the highest species richness, each containing >1000 indigenous species (1,349 and

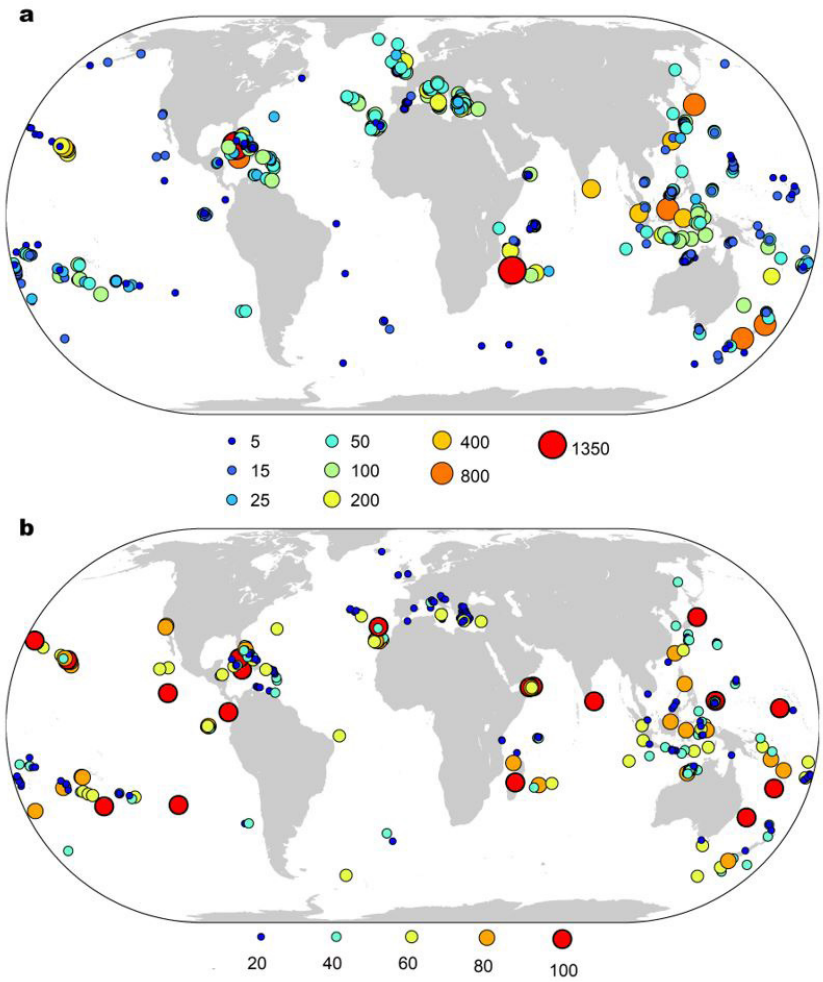

Figure 2. a) Indigenous land snail species richness (n=11,139) on islands included in our database (n=727). Each color denotes the upper bound of the number of species across 9 richness levels. **b)** Percentage of single-island endemic species (SIE; n=8,331) for those islands of our database which contain SIEs (n=330). Each color denotes the upper bound of the proportion of SIEs across 5 proportional levels.

1,147, respectively), followed by the North and South Islands of New Zealand – which host >600 species each (689 and 660, respectively), and Japan, Jamaica and Borneo – each being home to >500 species (582, 518 and 507, respectively). Together, these seven large islands contain ~44% of all retrieved species (4,907/11,139).

About 75% of all species (8,331/11,139) are single-island endemics (SIE). This perhaps is not unexpected given the tendency of land snails *"…to radiate into large numbers from relatively rare initial propagules"* (Holland 2009; pp. 540). The highest SIE richness values are found – in descending order – in Cuba (1,250), Madagascar (1,124), Jamaica (485), Japan (471), Borneo (390), Oahu (249) and Sri Lanka (195). These seven islands – with the replacement of the North and South Islands of New Zealand by Oahu (Hawaii) and Sri Lanka as compared to indigenous richness – comprise ~50% of global SIE richness (4,164/8,331). Eighteen islands displayed remarkable SIE percentages – higher than 80% – together hosting ~51% of SIEs (4,226/8,331) (Fig. 2b). The proportion of SIE (pSIE) in the 330 islands that actually host at least one single-island endemic species ranges from 1% to 100% (mean = 29.9% ± 1.4% s.e.).

Perspectives on global land snail diversity

Land snails on islands are remarkably diverse. Our thorough literature review yielded a striking figure for the presence of ~48% of currently known land snail species (11,139 / ~23,000 species) on just 727 islands. Considering the fact that the total area of 3.82 million km^2 of these islands represents ~2.9% of global landmass (assuming 130.03 million km^2 of total land area, see Ritchie and Roser 2013), the number of retrieved land snail species reveals notable levels of non-marine molluscan representation on islands and marks potential underestimations of global land snail species richness. This is in accordance with Lydeard et al. (2004), who suggested a number between 11,000 and 40,000 undescribed terrestrial species globally. Future comparison with relevant continental catalogues will certainly offer valuable insights in understanding the causes of such spatial disparities. Regardless, a stunning 75% of the species recovered are single-island endemics, highlighting unparallel levels of insular endemism in comparison with other better-known taxa [<20% for birds (Johnson and Stattersfield 1990) and plants (Groombridge 1992, Whittaker and Fernández-Palacios 2007)] and aligning with previous studies asserting the prevalence of islands as global hotspots of endemism (Myers et al. 2000, Whittaker and Fernández-Palacios 2007, Kier et al. 2009).

We are aware that, although exhaustive, our search is by no means conclusive and that the discovery and description of new species will certainly add to current figures, especially if further, yet unexplored island territories (e.g. New Guinea, Cape Verde etc.) are added. It is also likely that we have missed the existence of known island faunas due to inherent limitations in our searching approach, including the time frame of our initial literature search (3/2016 – 12/2018). For example, for the Channel Islands of California the current version of our database only includes information from Magney (2016), while the recent information from Drost et al. (2018) will be incorporated in future revisions. Similarly, species checklists for two islands in the Gulf of Guinea (São Tomé and Príncipe; Holyoak et al. 2020) were not available during the period of our initial search, while the full faunas for the Solomon Islands (Delsaerdt 2010, 2012, 2016) were only recently acquired by the authors, hence are also due to be included in later versions of the database. Therefore, future amendments will include: i) more islands with well-studied faunas, ii) islands where surveys have yielded no species, as absence data – which were not specifically accounted for herein – can be as informative as presence data in studying biodiversity patterns (e.g. Wang et al. 2016), and iii) invasive species (*cf.* Moser et al. 2018) – for which detailed information was lacking in most references examined, hence opted to be skipped at present. In doing so, communal involvement is perhaps the preferable way to proceed so that taxonomic reevaluations and resolution of undescribed species can also be accounted for. We hope that by documenting our effort to initiate this database, the present paper will serve as a plea to direct research efforts towards known or discoverable gaps.

Overall, the collation of our database highlights the prospect of mobilizing disseminated information to substantially improve knowledge on island biodiversity and especially, to facilitate the resolution of important taxonomic gaps for poorly known groups. To this end, our database is one of very few attempts (e.g. AntWeb[2]) to quantify island diversity on a global scale for an invertebrate group that has already yielded insights into ecological and evolutionary processes, as well as providing a stark reminder of the current wave of anthropogenically induced extinction. Future work will use it to test and develop these insights.

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2 https://www.antweb.org/, last accessed 16/09/2020.

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Data Accessibility

For each island and archipelago, the main reference source(s) for the respective species list is given in the Supplementary Material Table S1. Data are deposited on Harvard Dataverse repository at https://doi.org/10.7910/DVN/1KJQWJ (Proios et al. 2021), under an embargo of two years since the publication of the current manuscript. Data are also available upon reasonable request to K.P. (konproios@biol.uoa.gr / konproios@gmail.com).

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Bibliography used to recover land snail species occurrences per island territory.

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