



DEPARTAMENTO DE ZOOLOGIA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

**Spatial predictive distribution modelling of Madeira's
endemic land snail species**

Dinarte Nuno Freitas Teixeira

2009



REGIÃO AUTÓNOMA DA
MADEIRA



REPÚBLICA PORTUGUESA



UNIÃO EUROPEIA
FSE



DEPARTAMENTO DE ZOOLOGIA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

Spatial predictive distribution modelling of Madeira's endemic land snail species

Dissertação apresentada à Universidade de Coimbra
para cumprimento dos requisitos necessários à
obtenção do grau de Mestre em Ecologia, realizada sob
a orientação científica do Professor Doutor José Paulo
Sousa (Universidade de Coimbra) e do Professor
Doutor José Manuel Jesus (Universidade da Madeira).

Dinarte Nuno Freitas Teixeira

2009

O presente trabalho foi financiado pelo Centro de Ciência e Tecnologia da Madeira (CITMA), através da bolsa de Mestrado FSE BM I/2008 – 531, ao abrigo do Programa Operacional de Valorização do Potencial Humano e Coesão Social da RAM (RUMOS).



REGIÃO AUTÓNOMA DA MADEIRA



REPÚBLICA PORTUGUESA



UNIÃO EUROPEIA
FSE

À *Susana*

AGRADECIMENTOS

Esta tese é o resultado de um trabalho conjunto para o qual muitos contribuíram e aos quais desejo reconhecer e deixar o meu agradecimento.

Ao professor Doutor José Paulo Sousa, meu orientador, pela indispensável ajuda, paciência e orientação científica.

Ao professor Doutor José Manuel Jesus, meu orientador, pela amizade e apoio desde os primeiros momentos. Pelo seu empenho, conselhos transmitidos, chamadas à razão e orientação científica o meu muito obrigado.

Ao Doutor Pedro Cardoso, meu orientador e a quem muito devo, pelo constante acompanhamento e disponibilidade, amizade e orientação científica. Por tudo o que me ensinou, pela motivação e animo que sempre me transmitiu, e, acima de tudo, pela manutenção da objectividade do trabalho.

À professora Doutora Regina Cunha, pela amizade, constante incentivo, disponibilidade e revisão do trabalho científico. A sua boa disposição, aliada aos ensinamentos transmitidos muito contribuíram para o *terminus* deste projecto.

À UMa, por ter disponibilizado o laboratório e os meios técnicos que tornaram possível a identificação do material malacológico.

Ao CITA-A, na pessoa do professor Doutor Paulo Borges, por facultar os meios técnicos e logísticos que possibilitaram a realização de parte importante do presente trabalho.

Ao professor Doutor Brito de Azevedo, pela cedência dos dados do CLIMAAT.

À Direcção Regional do Ambiente, pelo acesso à Base de Dados da Biodiversidade do arquipélago da Madeira.

À DRIGOT, pela cedência da cartografia digital e imagens de satélite.

AO CITMA, pela bolsa de Mestrado concedida (FSE BM I/2008 – 531), permitindo o financiamento do presente trabalho.

À Priscila e à Sónia, colegas de mestrado, irrequietas parceiras de grupo e eternas amigas. A boa disposição contagiante, a amizade sincera e a entropia criada ajudaram a manter a sanidade mental. Os momentos passados ficarão gravados para sempre.

À Joana por todo o apoio e amizade.

Ao Duarte Nunes, amigo e companheiro de horas intermináveis de carregamento dos dados biológicos na base de dados da biodiversidade.

Ao Virgílio Gomes, pela amizade e sabedoria transmitida. A sua presença tornou o trabalho de campo numa lição de vida.

Ao meu tio Luciano, sem o qual esta tese não viria a luz do dia.

Aos meus pais, pedras basilares da minha vida, pelo apoio, incentivo e energia transmitidas.

Ao meu mano, por ter permitido a realização de parte de um sonho.

À Susana, essência do meu mundo e companheira de todas as horas. O seu constante estímulo e ajuda imprescindível em todas as fases deste trabalho permitiram a sua conclusão. Por todo o apoio, carinho e encorajamento transmitidos o meu muito obrigado.

ABSTRACT

The present work aims to identify patterns, variables and processes that shape the distribution of endemic molluscs of Madeira Island. We try to recognize new potential species distribution areas and to verify the adequacy of predictive models as a tool for conservation.

The geographic distribution of 68 terrestrial endemic molluscs species from the island of Madeira, Portugal was modeled. The modeling was carried out with a software that utilizes the maximum entropy algorithm (MAXENT), using data extracted from the BIOBASE database and those resulting from sampling elapsed between 2007 and 2008. Twenty-two variables were used to identify the distribution of endemic molluscs species, related to climate, geology, land use, hydrology, disturbance, geographic location and altitude.

The model identified a marked geographical differentiation among faunas from coastal, forest and alpine. The coastal zone comprises three sub-areas of distribution: South coast (main determinants of species distribution: longitude, precipitation and altitude), North coast (latitude) and S. Lourenço Eastern cape (longitude and precipitation), contradicting the assumption of Cameron & Cook (2001) which suggests that forest species distribution are dependent on land use (laurel forest), relative humidity, precipitation, soil permeability and disturbance. Alpine species distribution is determined by precipitation, altimetry and geographical patterns such as longitude and latitude.

Disculella maderensis taeniana and *Disculella maderensis maderensis* distributions are positively correlated with the human settlements on the Madeira's south coast.

The model also allowed validating the importance of altitude and slope on the distribution of species with fusiform shell as postulated by Cameron & Cook (1989).

It was also possible to identify new potential distribution areas for vulnerable *taxa* such as *Discus guerinianus guerinianus*, *Craspedaria moniziana* and *Leiostyla cassidula*, enhancing the high of models as management and conservation tools.

Future work should include predictive modeling with historical data, ecological and species life histories, as well as future climate scenarios in order to fulfill information gaps related to environmental variables.

RESUMO

Com o presente trabalho pretendeu-se identificar os padrões, variáveis e processos que moldam a distribuição da malacofauna endémica da Ilha da Madeira. Procurou-se reconhecer novas áreas potenciais para a prospecção de espécies bem como verificar a adequabilidade dos modelos preditivos enquanto ferramenta de conservação.

Efectuou-se a modelação da distribuição geográfica de 68 espécies endémicas de moluscos terrestres da Ilha da Madeira, Portugal. A modelação foi efectuada com recurso ao software que utiliza o algoritmo da máxima entropia (MAXENT), utilizando-se os dados extraídos da base de dados BIOBASE e aqueles resultantes da amostragem decorrida entre 2007 e 2008. Utilizaram-se vinte e duas variáveis explicativas para a aferição da distribuição da malacofauna endémica divididas entre clima, geologia, uso de solo, hidrologia, perturbação, posição geográfica e altitude.

O modelo permitiu identificar uma marcada diferenciação geográfica entre a malacofauna das áreas costeiras, florestais e alpinas. A zona costeira engloba 3 sub-áreas de distribuição: costa sul (longitude, precipitação e altitude), costa norte (latitude) e Ponta de S. Lourenço (longitude e precipitação), contrariando o postulado por Cameron & Cook (2001). Já a distribuição das espécies com afinidades à floresta está dependente do uso de solo (Floresta Laurissilva), humidade relativa, precipitação, permeabilidade do solo e distância às áreas de perturbação. No que às zonas alpinas diz respeito, a distribuição das espécies está dependente da precipitação, altitude e das variáveis geográficas (longitude e latitude).

A distribuição de *Disculella maderensis taeniana* e *Disculella maderensis maderensis* tem origem antrópica, encontrando-se positivamente correlacionadas com os aglomerados populacionais da costa sul da Madeira.

O modelo possibilitou também a validação da importância de altitude e inclinação do terreno para a distribuição de espécies com concha fusiforme postulado por Cameron & Cook (1989).

Identificou-se igualmente novas potenciais áreas de distribuição de espécies vulneráveis como *Discus guerinianus guerinianus*, *Craspedaria moniziana* e *Leiostryla cassidula*, tendo o modelo revelado elevado potencial enquanto ferramenta de apoio à gestão e conservação de moluscos terrestres.

Os trabalhos futuros de modelação preditiva deverão contemplar dados históricos, aspectos ecológicos, histórias de vida das espécies, bem como utilizar os cenários climáticos futuros, a fim de colmatar as lacunas de informação que as variáveis ambientais parecem encerrar.

CONTENTS

AGRADECIMENTOS	VI
ABSTRACT	IX
RESUMO	XI
1. GENERAL INTRODUCTION	2
1.1 Oceanic Islands biodiversity decline	2
1.2 Oceanic Islands as biodiversity hotspots: Madeira Island as a study case	3
1.3 Molluscan Fauna of Madeira Island	6
1.4 Predictive models as a conservation tool	8
1.5 Study objectives	10
1.6 References	10
2. SPATIAL PREDICTIVE DISTRIBUTION MODELLING OF MADEIRA'S ENDEMIC LAND SNAILS SPECIES	21
2.1 Introduction	21
2.2 Material and methods	25
2.3 Results	32
2.4 Discussion	42
2.5 References	46
3. FINAL REMARKS	60

CHAPTER 1

General Introduction

1. –GENERAL INTRODUCTION

1.1 Biodiversity decline in oceanic Islands

Global biodiversity is declining at an alarming rate and species extinction is an undeniable reality (Pimm et al. 1995, Lawton & May 1995, Dye & Tuggle 1998, Chapin et al. 2000, Biber 2002, Cowie & Robinson 2003).

The magnitude of the loss of species is now so important that some authors argue that we are witnessing the sixth great extinction in the history of life (Leakey & Lewin 1996). In fact, at the current time, the Human driving force is changing habitats, endangering ecosystems and eliminating numerous species, many of them unknown to science (Lawton & May 1995, Pimm et al. 1995, 1996, Chapin et al. 2000, Steadman 2006).

This is more concerning on oceanic Islands, as they are well-known centers of range-restricted species and thus have high levels of endemism on diminute areas. During the last centuries, species extinction has been very significant in several oceanic archipelagos (Reid & Miller 1989, Lawton & May 1995, Sadler 1999, Steadman & Martin 2003, Cardoso et al. 2010), including land snails (Hadfield 1986, Solem 1990, Tomiyana & Kurozumi 1992, Cowie 2001). Terrestrial molluscs belong to the second most diverse animal phylum, occupying an important trophic level in the ecological pyramid of energy and providing basic ecosystem services (Kratz 1991, Lyderd et al. 2004, Seddon 2008). They have a strong impact on macronutrient cycling, diverting fluxes and changing availabilities in terrestrial ecosystems. Furthermore, they have an exceptional affinity on the cycling of essential/non-essential trace elements such as copper, zinc, cadmium and lead (Dallinger et al. 2001).

Despite their diversity, land snails have the dubious honor of comprising the highest number of documented extinctions of any major taxonomic group (Van Bruggen 1995, Lyderd et al 2004, IUCN 2009). Of the 761 records of animal species extinct, 37% are terrestrial molluscs. Furthermore, a total of 939 species of terrestrial molluscs are threatened (IUCN 2009). To prevent their extinction, and that of other small, understudied and undervalued *taxa*, became one of the greatest challenges for conservation science.

1.2 Oceanic Islands as biodiversity hotspots: Madeira as a study case

1.2.1 The archipelago and its environmental history

Madeira archipelago is located in the Atlantic Ocean between latitudes 32°24' and 33°07' N and longitudes 16°16' and 17°16' W, at a distance of about 1000km from mainland Europe (Ponta de Sagres, Portugal) and around 600 km from the western coast of Morocco (Figure 1). The archipelago consists of two larger Islands, Madeira (742 km²) and Porto Santo (43 km²), and a group of three small Islands, the Desertas (13.5 km²).

The Madeira archipelago was originated by "hotspots" between the Miocene/ late Oligocene to the Quaternary, as the sedimentary formations from Madeira and Porto Santo places them between 5.2 MA and 14MA, respectively (Prada & Serralheiro 2000, Geldmacher et al. 2000, 2005, 2006; Brehm et al. 2003, Ribeiro et al. 2005). The hotspot that originated Madeira and Porto Santo, also originated sea mounts, some of which were Islands few millions of years ago.

There were at least four main volcanic phases on Madeira Island, being the eastern peninsula of Ponta de São Lourenço and the Desertas younger than the central

mass of Madeira (Prada & Serralheiro, 2000, Ramalho et al. 2005). From morphological point of view, Madeira Island is composed by seven geological units and made up mostly by a series of peaks, alongside huge and deep depressions or ravines. Pico Ruivo (1.861 m above sea level) is the highest point of the corresponding volcanic peak and rises about 5.300 m above the Madeira abyssal plain from which this entire complex volcanic group has been built (Prada & Serralheiro 2000).

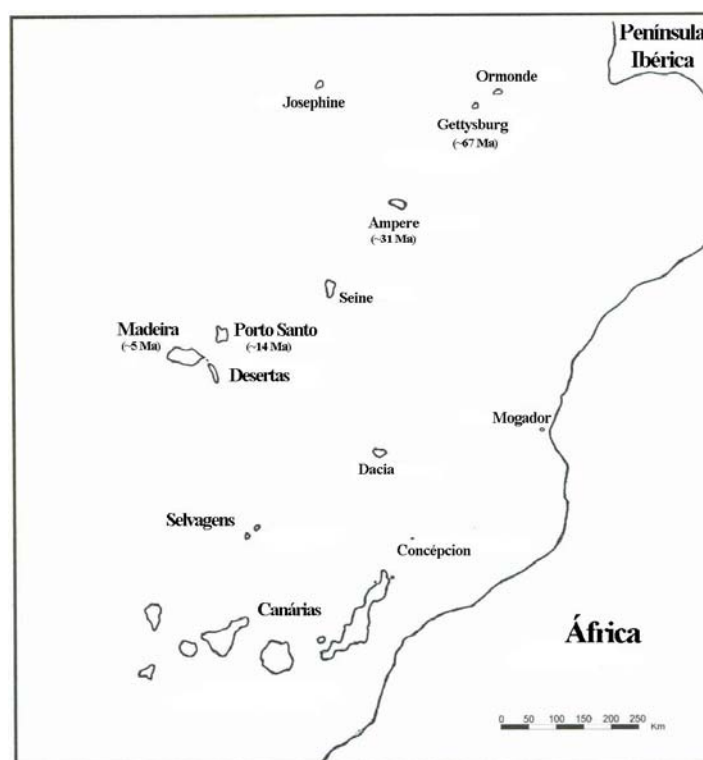


Figure 1. The Macaronesian archipelagos of Madeira and Selvagens and their location on the Atlantic Ocean. The most significant sea mounts, with depths varying from -150m (Sena) to -42m (Goring) are also shown (García-Talavera 1999).

The sea mounts, like Madeira archipelago, have a SW-NE orientation, forming a chain of Islands and submarine banks (e.g. Goring (-42m), Gettysburg (-60m) or Sena (-

150m) between the Portuguese coast and Madeira Island (Figure 1). Probably these submarine peaks were important on organisms' dispersal and colonization processes affecting Madeira Archipelago, following a "stepping stone" model.

The island climate is dominated by winds from NE and by the Canary Islands current, resulting in two major climate types, temperate and mediterranean, reflecting the location and the topography (Capelo et al. 2004, 2007). Regarding the average annual temperature, this Island has a temperate climate above 1500 m (between 0 ° C and 10 ° C) and a mild climate in the remaining area (10 °C to 20 °C).

Rainfall is well distributed throughout the year (Quintal & Vieira, 1985). The climate is occasionally semi-arid in the Eastern cape of S. Lourenço (250 mm to 400 mm), moderate rain occurs across much of the southern coastline (500 mm to 1000 mm), wet at intermediate altitudes (1000 mm to 2000 mm) and excessively wet (above 2000 mm) at higher altitudes. Relative humidity is high throughout the year (75% to 90%), except in the south coast where it is lower (55% to 75%), with a minimum low at Eastern cape of S. Lourenço (35 to 50 %).

Madeira has a high forest density, occupying 34.224 ha (46%) of the island, 16.143 ha (47%) of which is natural forest (IFRAM 2008). The endemic vegetation of Madeira has a relict (paleo-endemic) origin, as a result of the profound environmental crisis of the late Tertiary and later Pleistocene that affected the continental vegetation (Sjogren 1973, Capelo et al. 2004). Madeira's forest corresponds, in most parts of its territory, to pre-climax forest (e.g. endemic species of the genera *Laurus*, *Ocoetea*, *Apollonias*), its replacement steps and the vegetation associated with human presence. At higher altitudes, especially in the north coast of the island, remains the largest areas of pristine forest in Europe (*Clethro-Ocoteetum-foetentis*), while at lower elevations,

with more fertile soil and the densely populated island's southern slope, landscape has a humanized nature (Capelo et al. 2004).

1.2.2. Biodiversity

The Macaronesian archipelagos of Madeira, Selvagens, Azores and Canary Islands are included in the Mediterranean bioclimatic region, being one of the 25 biodiversity hotspots worldwide (Myers et al., 2000). The number of species and subspecies of endemic terrestrial organisms for all Macaronesia is estimated at around 5000, with Madeira and Selvagens contributing with 1419 (22%) *taxa* (Izquierdo et al. 2004, Arechavaleta et al. 2005, Borges et al. 2008).

Madeira and Selvagens archipelagos *per se* include a total of 7571 *taxa* (7452 species and 421 subspecies), belonging to 1003 families and 3648 genera (Borges et al., 2008). The 1419 endemic *taxa* (1286 species and 182 subspecies) represent 19% of the overall species richness. Invertebrates are the most diverse endemic *taxa*, namely Mollusca (168) and Arthropoda (979), comprising about 84% of the Madeiran endemics. The percentage of endemism within Mollusca is particularly remarkable, reaching 67 % (Abreu & Teixeira 2008).

1.3 Molluscan Fauna of Madeira Island

Madeira land snail fauna has a Palearctic and Macaronesian origin (Waldén 1983). Probably, colonizers arrived by island-hopping from Europe to Porto Santo, the oldest Island available to colonizers for perhaps 14 Myr without major volcanic activity, through the chain now remaining as sea mounts (Figure 1). There may be 300 endemic *taxa* in total on all the islands, including extinct forms, derived from at least 20

colonization events (Cameron & Cook 1992). After the molluscan fauna was established, other Islands became available. Migration and speciation took place, as some new species recolonized the original island, diverging from their parental populations (Cook 2008). The topography and habitability of all islands altered periodically, as glaciations promoted sea-level changes, joining islets and exposing new territory or reducing continuous land to isolation. It is the threefold interaction of production of isolates, migration and speciation rates that has been the critical determinant for Madeiran archipelago's high diversity (Cook 2008).

At present, the Madeiran archipelago is inhabited by 254 species and subspecies distributed in 83 genera (17 endemic), and 34 families (Cameron & Cook 1989, 1992, Bank et al. 2002, Abreu & Teixeira 2008). As observed in other oceanic Islands, Madeiran land snails are taxonomically unbalanced (Cameron & Cook 1992). Hygromiidae dominate the endemic fauna, and with Pupillidae, Ferussaciidae, Clausiliidae and Cyclophoridae encompass 90% of the current fauna, a contrast with the closely-related fauna of Western Europe (Waldén 1983, Cameron & Cook 1992, 1996, 1998 Goodfriend et al. 1994, Cook 1996).

The variety of habitats, from the dry seaside to the extremely humid laurel forest, is cited as a key factor on the ecological processes responsible for the speciation and diversity of Madeira island molluscan fauna (Cook et al. 1990, Cameron & Cook 1992, 1998, Cook 1996). Native fauna shows a pronounced geographical differentiation, with clear differences between high mountains, north and south coasts, and the Eastern cape of S. Lourenço (Cook et al. 1990, Cameron & Cook 1992).

Fossil records revealed that Madeiran terrestrial molluscs fauna have engaged substantial changes in its composition consistent with severe climate changes (Cook et al. 1993). Cameron & Cook (1996) suggest that Madeiran species have evolved to live

in dry, rocky and open environments, rather than being arboreal and dependent on damp litter from native trees. These conditions may pre-adapted them to resist clearance, as forest habitats have been subjected to the greatest fluctuations in size and fragmentation before human colonization, building up tolerance to change. Nonetheless, human activities, directly or indirectly, had catastrophic consequences for Madeiran land snail faunas, exceeding the climatic fluctuations of the last several glacial cycles (Cameron & Cook, 1996). Of the fourteen recorded extinctions of land snail species identified in the Quaternary fossil sand patch of Piedade's (S. Lourenço eastern cape), nine occurred after human settlement - 500 years ago (Cook et al. 1993, Goodfriend et al. 1994). This justifies no complacency over conservation, as Madeira archipelago alone contributes with 68 species (27% of current fauna) to the IUCN Red List of Threatened Species, 21% of the total European threatened terrestrial molluscs (IUCN 2009).

1.4 Predictive models as a conservation tool

An essential prerequisite for biodiversity conservation is the ability to define and measure it. The primary scientific requirements are knowledge of species distribution (Dobson et al. 1997, Howard et al. 1998, Van Jaarsveld et al. 1998, Araújo & Williams 2000), identification of trends in this distribution, and understanding the causes of these trends. This allows nature conservation to be based on a solid comprehension of both the phenomenon of biodiversity and its current crisis. However, the distribution of organisms is a complex and dynamic phenomenon determined by various processes and factors, the relevance of which varies along geographical gradients and according to the spatial scale under analysis.

The use of empirical models of occurrence in conservation planning has been increasingly advocated (e.g. Araújo & Williams 2000, 2002, Polasky & Solow 2001). Species distribution models constitute an attractive possibility to overcome our lack of reliable information about the distribution of species, and attempt to provide detailed predictions of distribution by relating presence or abundance of species to environmental predictors. As such, models exploring the relationships between species' occurrence and sets of predictor variables produce two kinds of useful outputs. The first are estimates of the probability of species occurrence at given unrecorded locations. The second are estimates of an area's suitability for species. These mathematical functions and the predicted geographic patterns of distribution can help to understand some of the underlying processes that shape a species' distribution. Model results have also been used to identify areas without information where future studies should be carried out, starting from poor and biased distributional data (Jiménez-Valverde et al. 2006, Richardson et al. 2006).

In support of their widespread use, prediction maps have sometimes been found to provide a more reliable picture of species distributions than maps published in atlas, field guides (Bustamante & Seoane 2004) and expert-based models (Seoane et al. 2005, Pearce et al. 2001, McPherson & Jetz 2007). However, these statistical models are strictly correlative and, as such, supply no explanations; rather, they only suggest them. In spite of their problems, species distribution models are a useful tool to generate testable hypotheses and to explore distribution patterns from incomplete data, provided that they are used with caution and awareness of their limitations.

1.5 Study objectives

Despite 300 years of field work on Madeiran land snails, there is still a lack of knowledge on distribution information (mostly on endemic and threatened species) as well as on the significant factors, processes and variables driving this distribution.

Therefore, the aims in the present study were to:

- a) Develop potential distribution models for selected Madeiran endemic species according to their habitat and niche preferences.
- b) Recognize the underlying processes, variables and parameters that shape the distribution patterns of the selected species.
- c) Test the applicability of MAXENT as a tool for identifying new distribution areas for Madeira's threatened land snail species.

1.6 References

- Abreu C. & D. Teixeira (2008). List of Molluscs. In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M. & Vieira, P. (eds.). A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. pp. 237-244. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo.
- Araújo M.B. & P.H. Williams (2000). Selecting areas for species persistence using occurrence data, *Biological Conservation*, 96: 331-45.

- Arechavaleta M., Martín J.L., Marrero N, Zurita I.M. & Izquierdo (2005). Biodiversidade en gráficas. Espécies silvestres de las Islas Canarias. Consejería de Medio Ambiente y Ordenacion Territorial, Gobierno de Canarias, 56 pp.
- Bank R. A., Groh K. & T.E.J. Ripken (2002). Catalogue and bibliography of the non-marine Mollusca of Macaronesia. In: Falkner, M., K. Groh & M. C. D. Speight (eds.), *Collectanea Malacologica*, Festschrift für Gerhard Falkner: 89-235. ConchBooks, Hackenheim, Germany.
- Biber E. (2002). Patterns of endemic extinctions among Island bird species. *Ecography*, 25: 661-676.
- Borges P.A.V., Abreu C., Aguiar A.M.F., Carvalho P., Jardim R., Melo I., Oliveira P., Sérgio C., Serrano A.R.M. & P. Vieira (eds.) (2008). A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos, Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo. pp. 13-26.
- Brehm A., Pereira L., Kivisild T. & A. Amorim (2003). Mitochondrial portraits of the Madeira and Açores archipelagos witness different genetic pools of its settlers. *Human Genetics* **114** : 77–86.
- Bustamante J. & J. Seoane (2004). Predicting the distribution of four species of raptors (Accipitridae) in southern Spain: statistical models work better than existing maps. *Journal of Biogeography* , 31:295-306.
- Cameron R.A.D. & L.M. Cook (1989). Shell size and shape in Madeiran land snails: do niches remain unfilled ? *Biological Journal of the Linnean Society*, **36**, 79 -96.

- Cameron R.A.D. & L.M. Cook (1992). The development of diversity in the land snail fauna of the Madeira archipelago, *Biological Journal of Linnean Society*, 46: 105-114.
- Cameron R.A.D. & L.M. Cook (1996). Diversity and durability: responses of the Madeiran and Porto-Santan snail faunas to natural and human-induced environmental change. *American Malacological Bulletin*, 12 (1/2): 3-12.
- Cameron R.A.D. & L.M. Cook (1998). Forest and scrub snail faunas from northern Madeira, *Malacologia*, 39 (1-2): 29-38.
- Capelo J., Menezes De Sequeira M., Jardim R. & J.C. Costa (2004). Guia da excursão geobotânica dos V Encontros ALFA 2004 à ilha da Madeira. in Capelo, J. A paisagem vegetal da ilha da Madeira. pp. 5 -45. *Quercetea*, 6, 3 -200.
- Capelo J., Menezes de Sequeira M., Jardim R. & S. Mesquita (2007). Biologia e ecologia das florestas das ilhas – Madeira. In *Árvores e Florestas de Portugal*. Volume 6, Açores e Madeira – A Floresta das Ilhas (ed. J. Sande Silva), pp. 81 -134. Edição da Fundação Luso Americana para o Desenvolvimento, Público e Liga para a Protecção da Natureza. Lisboa.
- Cardoso P., Arnedo M.A., Triantis K.A. & P.A.V. Borges (2010). Drivers of diversity in Macaronesian spiders and the role of species extinctions. *Journal of Biogeography* in press.
- Chapin F. S., Zavaleta E.S., Eviner V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hoyer D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.V. & S. Diaz (2000). Consequences of changing biodiversity. *Nature*, 405:234-242.

- Cook L.M., Cameron R.A.D. & L.A. Lace (1990). Land snails of eastern Madeira: speciation, persistence and colonization. *Proceedings of the Royal Society of London B*, 239, 35-79.
- Cook L.M., Goodfriend G.A. & R.A.D. Cameron (1993). Changes in the land snail fauna of eastern Madeira during the Quaternary, *Philosophical Transactions of Royal Society of London*, 339, 83-103.
- Cook L.M. (1996). Habitat, isolation and the evolution of Madeiran Landsnails, *Biological Journal of Linnean Society*, 59: 457-470.
- Cook L.M. (2008). Species richness in Madeiran land snails, and its causes. *Journal of Biogeography*, 35, 647 -653.
- Cowie R.H. (2001). Decline and homogenization of Pacific faunas: The land snails of American Samoa. *Biological Conservation*, 99:207–222.
- Cowie R.H. & A.C. Robinson (2003). The decline of native Pacific Island faunas: Changes in status of the land snails of Samoa through the 20th century. *Biological Conservation*, 110:55–65.
- Dallinger R., Berger B., Triebkorn-Ikoller R. & H. Kohler (2001). Soil Biology and Ecotoxicology, 489-525 pp. In: Barker, G. M. 2001. *The Biology of Terrestrial Molluscs*, CABI Publishing, Wallingford.
- Dobson A.P., Rodriguez J.P., Roberts W.M. & D.S. Wilcove (1997). *Science*, Vol. 275. no. 5299, pp. 550 – 553.
- Dye T.S. & H.D. Tuggle (1998). Land snail extinctions at Kalaeloa, O‘ahu. *Pacific Science*, 52(2):111–140.

- Garcia-Talavera F. (1999). La macaronseia. Consideraciones geológicas, biogeográficas e paleoecológicas. In: Fernández-Palacios, J. M., Bacallado, J. J. & Belmonte, J. A. (eds.), *Ecología y Cultura en Canarias*, Museo de la Ciencia y el Cosmos, La Laguna, 39-63.
- Geldmacher J., Bogaard P., Hoernle K. & H. Schmincke (2000). An age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems*, **1**(2) (DOI 10.1029/1999GC000018).
- Geldmacher J., Hoernle K., Bogaard P.V.D., Duggen S. & R. Werner (2005). New $^{40}\text{Ar}/^{39}\text{Ar}$ age and geochemical data from seamounts in the Canary and Madeira Volcanic Provinces: A contribution to the “Great Plume Debate”. *Earth and Planetary Science Letters* **237**: 85-101.
- Geldmacher J., Hoernle K., Klügel A., Bogaard P.V.D. & S. Duggen (2006). A geochemical transect across a heterogeneous mantle upwelling: implications for the evolution of the Madeira hotspot in space and time. *Lithos* **90**: 131-144.
- Goodfriend G.A., Cameron R.A.D. & L.M. Cook (1994). Fossil evidence of recent human impact on the land snail fauna of Madeira, *Journal of biogeography*, **21**, 309-320.
- Hadfield M.G. (1986). Extinctions in Hawaiian achatinelline snails. *Malacologia*, **27**:67-81.
- Howard P.C., Viskanac P., Davenport T.R.B., Kigeny F.W., Baltzer M., Dickinson C.J., Lwanga J.S., Matthews R.A. & A. Balmford (1998). Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472 -475.

IFRAM (2008). Inventário Florestal do arquipélago da Madeira. Secretaria Regional do Ambiente e dos Recursos Naturais, Funchal.

IUCN (2009). IUCN Red List of Threatened Species. Version 2009.2.
<www.iucnredlist.org>

Izquierdo I., Martin J.L., Zurita N. & M. Arechavaleta (eds.) (2004). Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). 2nd, Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias

Jiménez -Valverde A., Lobo J.M. & M.L. López Martos (2006). Listado de especies actualizado de los araneidos y tomisidos (Araneae, Araneidae & Thomisidae) de la Comunidad de Madrid: mapas de distribución conocida, potencial y patrones de riqueza. *Graellsia*, **62**, 461 -481.

Kratz W. (1991). Cycling of nutrients and pollutants during litter decomposition in pine forests in the Grunewald, Berlin. In: Nakagoshi, N. and Golley, F. B. (eds). *Coniferous Forest Ecology from an International Perspective*. SPB Academic Publishing bv. The Hague, 151-160 pp.

Lawton H. & May R. M. (1995). *Extinction rates*, Oxford University Press, Oxford.

Leakey R.; Lewin R. (1996). *The Sixth Extinction: Patterns of Life and the Future of Humankind*. New York: Anchor Books.

Lydeard C., Cowie R.H., Ponder W.F., Bogan A.E., Bouche T.P., Clark S.A., Cummings K.S., Frest T.J., Gargomin, O., Herbert D.G., Hershler R., Perez K.E., Roth B., Seddon M., Strong E.E. and F.G. Thompson (2004). The global decline of nonmarine mollusks. *BioSci* 54: 321-330.

- McPherson J.M. & W. Jetz (2007). Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30**, 135 -151.
- Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & J. Kent (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.
- Pearce J.L., Cherry K., Drielsma M., Ferrier S. & G. Whish (2001). Incorporating expert opinion and fine -scale vegetation mapping into statistical models of faunal distribution. *Journal of Applied Ecology*, **38**, 412 -424.
- Pimm S.L., Russel G.J., Gittleman J.L. & T.M. Brooks (1995). The future of biodiversity. *Science*, 269, 347-350.
- Pimm S.L., Gittleman J.L., Russel G.J., T.M. Brooks (1996). Extinction rates. *Science*, 273, 293-297.
- Polasky S & A. Solow (2001). The value of information in reserve site selection. *Biodiversity and Conservation*, 10(7):1051-1058
- Prada S. & A. Serralheiro (2000). Stratigraphy and evolutionary model of Madeira Island. *Bocagiana* nº 200: 1-13.
- Quintal R. & M. J. Vieira (1985). Ilha da Madeira. Esboço de geografia física. Secretaria Regional do Turismo e Cultura. Madeira, Portugal.
- Ramalho R., Madeira J., Fonseca P.E., Silveira A., Prada S., C.F Rodrigues (2005). Tectonics of Ponta de são Lourenço, Madeira Island, *Cadernos Laboratoriais Xeolóxico de Laxe*, 30:223-234.

- Reid W.V. & K.R. Miller (1989). Keeping options alive: The scientific basis for conservation biodiversity. World Resources Institute.
- Ribeiro L., Ech-Chakroun S., Mata J., Boven A., Mattielli N., Hus J. & C. Maerschalk (2005). Elemental and lead isotopic evidence for coeval heterogeneities at Madeira/Desertas mantle source. Acts of VIII Congresso de Geoquímica dos Países de Língua Portuguesa (Portugal) (ed. Anonymous), pp. 485 -488.
- Richardson B.J., Zabka, M. Gray, M.R. & G. Milledge (2006). Distributional patterns of jumping spiders (Araneae: Salticidae) in Australia. *Journal of Biogeography*, **33**, 707 -719.
- Sadler J.P. (1999). Biodiversity on oceanic Islands: a paleoecological assessment. *Journal of biogeography*, 26: 75-87.
- Seddon M.B. (1995). Endangered land snails of Porto Santo (Madeiran Island Archipelago): monitoring changes in species diversity and implications for their conservation. In: van Bruggen, A. C., Wells, S.M. & Kemperman, Th. C. M. (eds.). Biodiversity and Conservation of the Mollusca. Backhuys Publishers, Oegteest-leiden, the Netherlands. (Proceedings of the Alan Solem Memorial Symposium on the biodiversity and conservation of the Mollusca at the 11th International malacological Congress, Siena, Italy, 1992), 171- 185.
- Seddon M.B. (2008). The landsnails of Madeira – an illustrated compendium of the landsnails and slugs of the Madeiran archipelago, National Museum of Wales, Cardiff.

- Seoane J., Bustamante J. & R. Díaz-Delgado (2005). Effect of expert opinion on the predictive ability of environmental models of bird distribution. *Conservation Biology*, **19**, 512 -522.
- Sjogren E. (1972). Vascular plant communities of Madeira. *Boletim do Museu Municipal do funchal*, 26: 46-125.
- Solem A. (1990). How many Hawaiian land snails are left? And what we can do for them. *Bishop Museum Occasional Papers* 30:27-40.
- Steadman D.W. & P.S. Martin (2003). The late Quaternary extinction and future resurrection of birds on Pacific Islands. *Earth-Science Reviews*, 61: 133-147.
- Steadman D.W. (2006). *Extinction and biogeography of tropical Pacific birds*. University of Chicago Press, Chicago.
- Tomiyana K. & T. Kurozumi (1992). Terrestrial mollusks and conservation of their environmental in the Ogasawara Islands. *Regional Views* 5:39-81.
- Van Bruggen A.C. (1995). Biodiversity of Mollusca: Time for a new approach. In *Biodiversity and Conservation of the Mollusca* (eds. A.C. van Bruggen, S.M. Wells & T.C.M. Kemperman), pp. 1–19. Backhuys, Oegstgeest -Leiden, The Netherlands.
- Van Jaarsveld A.S., Freitag S., Chown S.L., Muller C., Koch S., Hull H., Bellamy C., Krüger M., Endrödy-Younga S., Mansell M.W. & C.H. Scholtz (1998). Biodiversity assessment and conservation strategies. *Science*, **279**, 2106 -2108.

Waldén H.W. (1983). Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated Check -list. Annales Zoological Fennici, **20**, 255 -275.

Williams P.H. & M.B. Araújo (2002). Apples, oranges and probabilities: integrating multiple factors into biodiversity conservation with consistency. Environmental Modeling and Assessment 7: 139-151

Wisz M.S., Hijmans R.J., Li J., Peterson A.T., Graham C.H., Guisan A. & NCEAS Working Group (2008). Effects of sample size on the performance of species distribution models. Diversity and Distributions, 14: 763-773.

CHAPTER 2

Case study

2. SPATIAL PREDICTIVE DISTRIBUTION MODELLING OF MADEIRA'S ENDEMIC LAND SNAIL SPECIES

2.1 Introduction

One of the central problems in ecology is to understand how organisms are distributed. This is more important with endemic species that inhabit oceanic islands and show low dispersal capability such as terrestrial molluscs. The Madeiran archipelago comprises one of the most hiperdiverse land snail faunas of oceanic Islands (254 species and subspecies, 67 % of which endemic), with many single Island endemics distributed in a wide range of habitats (Waldén 1983; Cameron & Cook 1989, 1992; Bank et al. 2002; Abreu & Teixeira 2008).

2.1.1 Distribution patterns and diversity

The Madeira land snail fauna shows a geographical differentiation, as coastal habitats include a higher proportion of unique endemic species, restricted to a limited region, when compared to the more homogeneous forest habitats (Cameron & Cook 1996a, 1998). This suggests that the patterns of local geographic replacement or disjunct distributions resulted from a repeated range fragmentation and rejoining, leading to allopatric speciation (Cameron & Cook 2001).

There are at least seven regions (six coastal, one forestry) with recognized distinct faunal compositions that seem to be effectively isolated and undergone a largely independent development (Cameron & Cook 1998, 2001; Cook 2008; Figure 2).

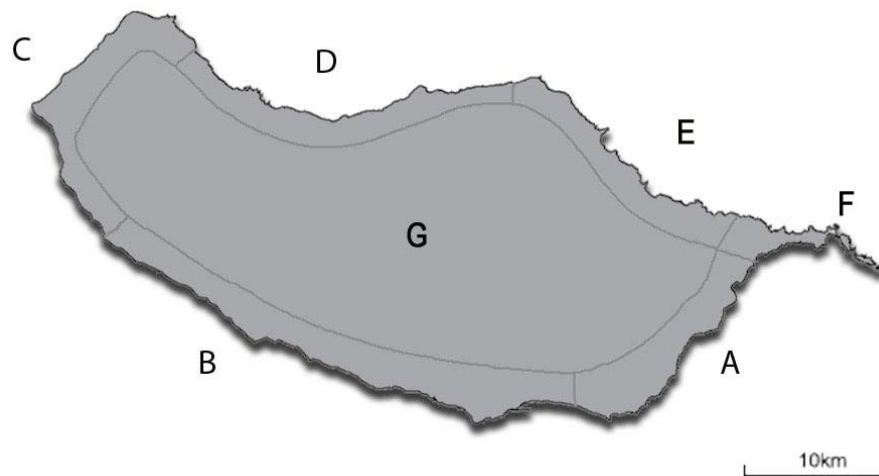


Figure 2. Madeira Island, showing regions found to have differing faunas (Adapted from Cook, 2008). Regions A-F are coastal areas under 500 meters. Region G is endemic laurel forest at higher altitudes.

The Southeast coast (Figure 2 – Region A), with micro sclerophyllous and xerophytic shrubs forests (Capelo 2004), between Caniço and Santa Cruz, present past agricultural disturbance and a high construction index.

The South to southwest dry cliff grassland slopes, from Funchal to Calheta (Figure 2 – Region B) and Calheta - Porto Moniz (Figure 2 – Region C), with agriculture (monocultures) and abandoned fields, presenting shrub forests (dominated by *Maytenus umbellata* and *Olea maderensis*) and irregular elements of endemic forest (*Apollonias barbujana*).

The Northwest coast from Porto Moniz to São Jorge, with some shrub areas and substantial elements of the Laurel Forest found at sea-level, encompassing high rainfall and humidity levels when compared with south coast (Figure 2 – Region D).

Coastal cliff and slopes of northeast coast, between São Jorge and Caniçal, dominated by shrubs with a native forest influence (Capelo et al 2004; Figure 2 – Region E).

The São Lourenço's eastern cape (Figure 2 – Region F), with xerophytic elements (Hampshire 1984, Capelo et al. 2004) and a distinct faunal composition, by means of local ecofenotypes and relict woodland species.

The Laurel Forest group is dominated by *Clethra arborae* and *Ocotea foetentis sigmentum*, above 600 meters, in habitats characterized by high levels of humidity, precipitation and low disturbance (Figure 2a – Region G).

Besides the defined habitats presented above, there are also terrestrial mollusc species with unknown habitat preferences, ranging from coastal areas through water channels, intermediate and disturbed habitats, to Laurel forest influence.

Niche requirements

Differences in shell shape and size in endemic land snails are associated with different microhabitats and surface preferences. High-spined species tend to be active on vertical surfaces (e.g. *Boettgeria depauperata*), while low-spined species use horizontal substrates (e.g. *Janulus bifrons*) or burrows in soft material (e.g. *Amphorella tornatellina*). There are species less discriminating (e.g. *Leiostyla* sp.), that inhabits a variety of niches from damp places to dry coastal cliffs, burrowing under leaf litter, tree trunks or rock faces (Cameron & Cook 1989, Cook 2008, Seddon 2008).

Overall, Madeiran land snail species are undoubtedly adapted to the environments in which they live on, as forest species, with high humidity requirements, and have reduced (e.g. *Plutonia* sp) or delicate shells (e.g. *Leptaxis membranacea*), in comparison to robust dry-facies species of the coastal areas (e.g. *Discula polymorpha*).

Nonetheless, fossil records revealed that the land snail fauna of the Island has engaged substantial changes in its composition consistent with severe climate changes (Cook et al. 1993). Furthermore, Quaternary fossil records from Piedade's sand patch (S. Lourenço eastern cape) suggests a 30% extinction rate of Madeiran fauna, having two-thirds of this occurred after past human settlement (500 years ago), as a consequence of severe ecosystem change and disturbance. As a result, 68 of Madeira endemic land snail species are listed as threatened (IUCN 2009).

2.1.2 Predictive models

Although there are more than 300 years of land snail field studies on Madeira Island, there are still gaps on distribution patterns on Madeira's terrestrial molluscs. As a common practice, researchers have proposed geographical distributions of different Madeira Island land snail species based on a limited number of collecting localities and extrapolating to include a region delimited by assumed geographical barriers such as mountains and watercourses (Waldén 1983, Cook et al. 1990). In the absence of a complete inventory of species distribution, predictive models arise as useful tools to generate testable hypotheses and to explore distribution patterns from incomplete data, using algorithms to interpolate and extrapolate from the observed distribution of the species into territories without information (Ferrier et al. 2002 a,b). Recently, numerous mathematical techniques have been developed to estimate the geographical distribution of a species, producing detailed information about distribution and habitat suitability maps (Soberón & Peterson 2005).

Maximum entropy (MAXENT) modeling arises as one of the best predictive tools (Elith et al. 2006), with a great potential to identify distributions and habitat selection of wildlife given its reliance on presence only data locations (Baldwin 2009).

These predictive models have been generally developed for plants and vertebrate species (Guisan & Thuiller 2005). Only a few studies have modeled the potential distribution of invertebrate species, and these have dealt mostly with vectors of human diseases (López-Cárdenas et al. 2005, Peterson et al. 1999) and introduced species (Roura-Pascual et al. 2006).

2.1.3 Study objectives

At the present study we aim to:

- a) Develop potential distribution models for selected Madeiran endemic species according to their habitat and niche preferences.
- b) Recognize the underlying processes, variables and parameters that shape the distribution patterns of the selected species.
- c) Test the applicability of MAXENT as a tool for identifying new distribution areas for Madeira's threatened land snail species.

2.2 Material and methods

2.2.1 Study area and its environments

The Madeiran archipelago is situated in the Atlantic Ocean, 1000 Km southwest of mainland Portugal (Ponta de Sagres) and 600 km west of Morocco, at 33°07' N 17°16' W (Figure 3). This volcanic and oceanic archipelago is constituted by 3 clusters of Islands and islets, with Madeira Island as the biggest of them (742 km²), rising to 1861m of altitude.

With an estimated geological age of 5.2 MA (Prada & Serralheiro 2000), Madeira Island has a very rugged topography dominated by high-altitude mountains, separated by deep ravines. The substrate is almost exclusively volcanic in origin, and coasts are generally rocky and steep. Only at the eastern extremity of the island (S. Lourenço's cape) there are soils of sea-sand origin on a low peninsula which is the driest part of the Island.



Figure 3. The Madeiran archipelago and its geographic location on the North Atlantic Ocean (Adapted from Cook 2008).

Madeira Island comprises a wide range of habitats and climatic zones, including subalpine regions, extensive laurel forests and lower coastal areas with Mediterranean climate (Capelo et al. 2004). Its topography, with relatively high altitudes, favors the occurrence of orographic precipitation, originating very humid areas and allowing the existence of significant water resources. As vegetation is concerned, there are two major natural vegetation types: a damp forest association at higher altitudes and below it a dry

association of grasses, herbs and low scrubs encompassing 4 vegetation series (Capelo et al. 2004).

2.2.2 Data compilation

Prior to conducting field surveys, published, grey literature and private collections were studied in order to compile a list of Madeira's endemic terrestrial mollusc species and their distribution. Raw species distribution data was obtained from 30 published articles and 2 private malacological collections. The Madeira's Biodiversity Database (BIOBASE) was used for data storage, being species distribution records geographically referred to a 500x500 m UTM square grid (sq), covering a greater or lesser number of possible squares. Based on this number, the precision level indicates the accuracy of data: 1-3 sq (precision level 1), 4-50 sq (precision level 2), 50-300 sq (precision level 3) and Island level (precision level 4). Levels 3 and 4 were used when literature data records were unspecific, indicating a distribution area around a region (e.g. Funchal) or simple indicating a presence on the Madeira Island, respectively. Only species with precision level of 1 (1-3 sq) or 2 (4-50 sq) and confirmed status (with one or more species record within the last 10 years) were selected (Figure 4).

In order to cover all habitats and fill the distribution gaps observed, 24 sampling areas were selected through IDRISI Kilimanjaro image calculator function (Clark Labs 2004), using the three environmental variables thought *a priori* to be most important to land snails distribution: land use, mean annual precipitation and altimetry (Figure 4).

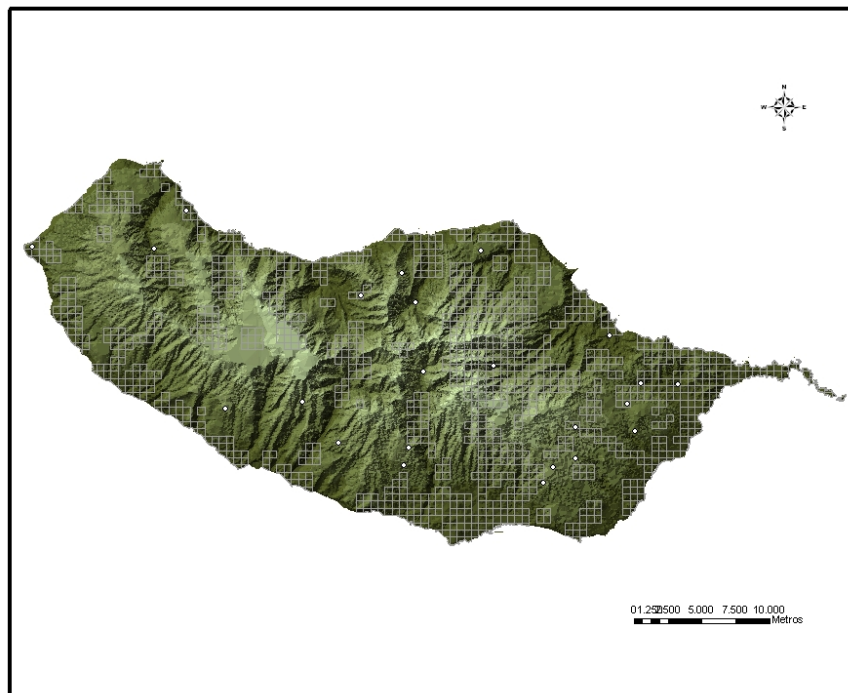


Figure 4. Database species distribution (squares) and sample areas used in the present work (dots).

The land use variable was used according to these categories: 1 – abandoned agriculture fields; 2 – social areas; 3 – agriculture fields; 4 – natural areas (meadow and riparian vegetation); 5 – exotic forest areas; 6 – laurel forest. For the mean annual precipitation two intervals were used: 1: 0-1450 mm; 2: 1450-2900 mm. The former were calculated on the basis of the identified geographical differences of the selected habitats. The altimetry variable was divided in two intervals (1: 0-500 m; 2: 500-2000 m), using as cutoff the different altitudinal requirements of land snail faunas. Laurel Forest fauna are located above 500 m, and the coastal and São Lourenço's cape fauna's occurs from coastal areas to 500 m (Figure 4).

Samplings were made through 2007 and 2008, from October to March, when the weather was most suitable at lower elevations (cool and moist), increasing the probability to find active snails and semi-slugs. Land snails were surveyed on areas of

30 x 30 meters, searched by two people through 1 hour per site, as two replicates were made per year per site (Cameron & Cook 1998). For soil fauna determination, two litres of litter and soil were removed for sieving and sorting in laboratory. The representative specimens are stored at University of Madeira, Biology Department. Determinations were made based on conchological characteristics. Nomenclature follows Bank et al. (2002). A full faunal list for each site presented on Figure 4 is given in Table III (Appendix I).

2.2.3 Species selection

According to distribution patterns (forest, grassland and unknown habitat preferences), niche occupancy, ecological constraints and conservation vulnerability, 68 species were considered suitable for modeling, as they were distributed in 10 or more localities. Although in some cases only five locations are required to develop a useful model (Hernandez et al. 2006, Pearson et al. 2007), the localities were not spatially independent to enable model testing, even using the jackknife approach.

For distribution modelling analysis, individual species richness maps were exported to GIS shapefile and the centroid of each grid cell was calculated using DIVA-GIS 7.1.1 software (Hijmans et al. 2004).

2.2.4 Environmental coverage variables

A comprehensive database of spatially explicit information for Madeira island was collected and transformed in a GIS environment using Idrisi software (Clark Labs 2004) and DIVA-GIS 7.1.1. Twenty two environmental predictors were assembled to model the land snail distribution. The layers were related to seven principal traits: climate, geology, land use, hydrology, disturbance, geographic position and elevation

(Table I). Raster files were produced and resized to a 0.25 km² grid layer to fit the model.

Table I - Environmental variables used in the model.

Abbreviature	Description	Type	Source
prec_annual	Annual mean precipitation	continuous	CLIMAAT ^a
tmax	Maximal temperature of the warmest month	continuous	CLIMAAT
tmin	Minimal temperature of the coldest month	continuous	CLIMAAT
rhmax	Annual maximal relative humidity	continuous	CLIMAAT
rhmin	Annual minimal relative humidity	continuous	CLIMAAT
house_dist	Distance to houses	continuous	PEA ^b
road_dist	Distance to roads	continuous	PEA
wcour_dist	Distance to watercourses	continuous	PEA
mmwc_dist	Distance to man made water channels	continuous	PEA
houses	Houses	continuous	DRIGOT ^c
Roads	Roads	continuous	DRIGOT
wcour	Water courses	continuous	PEA
mmwc	Man made water courses	continuous	PEA
luse	Land use	categorical	SRA ^d
geol	Geology	categorical	SRA
soil	Soil type	categorical	SRA
perm	Soil permeability	continuous	PEA
alt	Altitude: elevation above sea level in meters derived from PEA	continuous	PEA
slope	Slope derived from PEA	continuous	PEA
asp	Aspect derived from PEA	continuous	PEA
lat	Latitude	continuous	PEA
long	Longitude	continuous	PEA

^aCLIMAAT Project (Azevedo, 1996)

^bPEA: Portuguese Environmental Agency

^cDRIGOT: Direcção Regional de Informação Geográfica e Ordenamento do Território;

^dSRA: Secretaria Regional do Ambiente e dos Recursos Naturais;

2.2.5 Modelling development

To predict our species geographical distribution we used the maximum entropy algorithm available in *MAXENT 3.3.1* (Phillips et al. 2004, 2006). This software has

been recommended in recent model comparisons (e.g. Elith et al. 2006), and has been found to produce useful results with small sample sizes (Hernández et al. 2006).

MAXENT is a machine learning method that fits the probability distribution of maximum entropy for presences, constrained by the values of the pixels where the species has been found (Grendar & Grendar 2001, Phillips et al. 2004, 2006). Requiring presence-only data, allows the use of both continuous and categorical variables, as the convergence to the optimal probability is guaranteed by the deterministic algorithms (Phillips et al. 2006). Therefore, the resultant output represents how much better the model fits the location data than would an uniform distribution (Grendar & Grendar 2001, Phillips et al. 2006).

For each species, default settings were used except for iterations that were set for 1000. Suitable regularization values, included to reduce over fitting, were selected automatically by the program. To evaluate the models we used a receiver operating characteristic (ROC) analysis, which has been widely used for model evaluation, and is part of the MAXENT output (Elith et al. 2006). The ROC generates a single measure of model performance, area under the curve (AUC), providing information on the usefulness of the model (*i.e.*, AUC: >0.9 = very good; AUC: 0.7–0.9 = good, AUC: <0.7 = uninformative; Liu et al. 2005). We ran 10 random partitions per species, compared AUC values, and chose the best model, *i.e.*, the model with an AUC value closest to 1.

A *jackknife* was run to estimate the relative importance of each variable in determining the potential distribution of the species. Each variable was excluded in turn, and a model was created with the remaining variables. Then a model was produced using each variable in isolation. Additionally, a model was created using all variables (see Phillips et al. 2006). The evaluation of model accuracy predictions was performed

using 20% of species distribution data as random test percentage, as these datasets allowed to successfully validate the variables presented in this work. Only the variables that contributed more than 10% to the species distribution models were selected and discussed.

MAXENT produces in ASCII format a continuous prediction of specific presence of the suitability of the habitat for the species through a suitability map that ranges from 0 to 1, with values near 1 corresponding to large habitat suitability for the presence of the species in analysis. It is often desirable to show a binary map of predicted presence/absence, using a "breaking point" beyond which it is considered that the species may exist (e.g. Liu et al. 2005). However, in this work, we have chosen to only use the original charts of probability.

For a concise mathematical definition of MAXENT, discussion of its application to species distribution modelling and initial testing of the approach see Phillips et al. (2006).

2.3 Results

2.3.1 Survey data

Thirty eight species (35 land snails and 3 semi-slugs) were collected, belonging to 8 families (Table III – Table XX Appendix I). The Higromiidae have a large distribution range, being present in 21 of 24 sampling areas encompassing the highest number of species recorded (14).

An average of 3.8 species were collected per site, being the maximum number of species registered on site 226 (13 sp; Figure 4) and the minimum on the sites 223, 224 and 225 (1 sp; Figure 4).

Table II. Species collected on field surveys throughout 2007-2008 using 24 sites. Family and number of species are indicated, as well as the number of sample areas where species were collected.

Family	Species	Sample Areas
Clausilidae	4	12
Craspedomatidae	2	5
Ferussacidae	3	12
Gastrodontidae	1	4
Hygromiidae	14	21
Lauridae	9	9
Vertiginidae	2	5
Vitrinidae	3	6
	38	24

2.3.2. *Modelling land snails distribution*

Predictive models were developed for 68 endemic land snail species, comprising the literature and survey data. Distribution models of the species were validated using the AUC scores, providing a ranked approach for assessing differences in species distributions for developed models compared to a random distribution. 83.4% of the predictive models were considered very good ($AUC \geq 0.90$), being the remaining defined as good (AUC 0.7-0.9).

For each species, the predictive variables' importance was evaluated, based on the jackknife values (leave-one-out). Only those that presented values above 10% were accounted for discussing the main drivers of land snails' distribution.

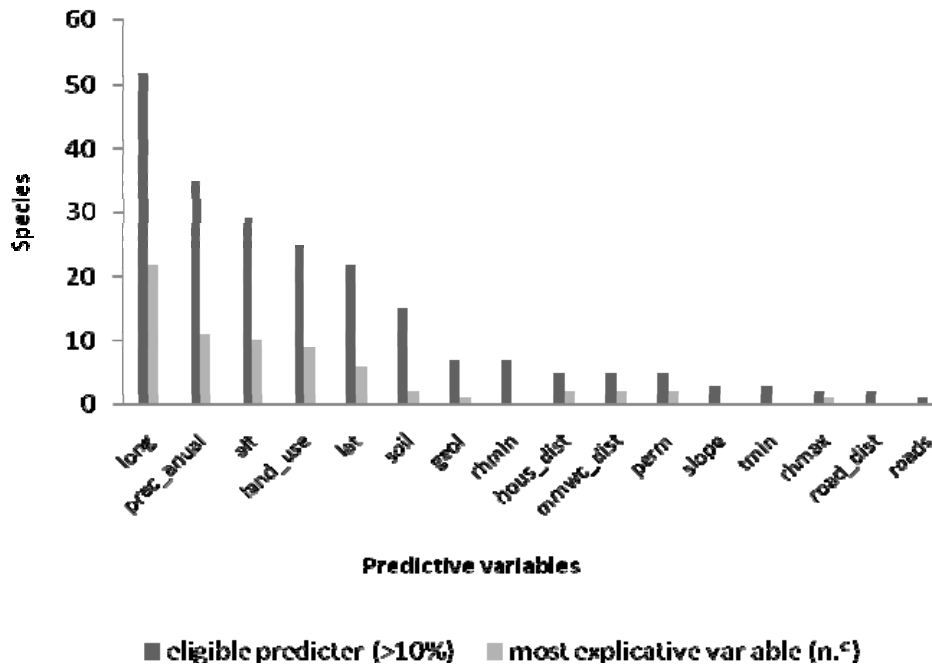


Figure 5. Predictive variables that explain the distribution of the modeled endemic species. The variables selected explained more than 10% of species distribution.

2.3.2.1 Habitat type and ecological niches

According to results provided by the model, land snail species distribution is determined by 16 different predictor variables, with five of them, i.e., geographic position (longitude and latitude), elevation, climate (annual precipitation) and land use, constituting more than 85% of the most important variables in all models combined (Figure 5). Those variables can be translated in distribution barriers shaping species ability to disperse, mostly longitude (as it is the most explicative variable for 22 species), marking a clear differentiation between coastal, forest and alpine faunas (Figures 6 a-c).

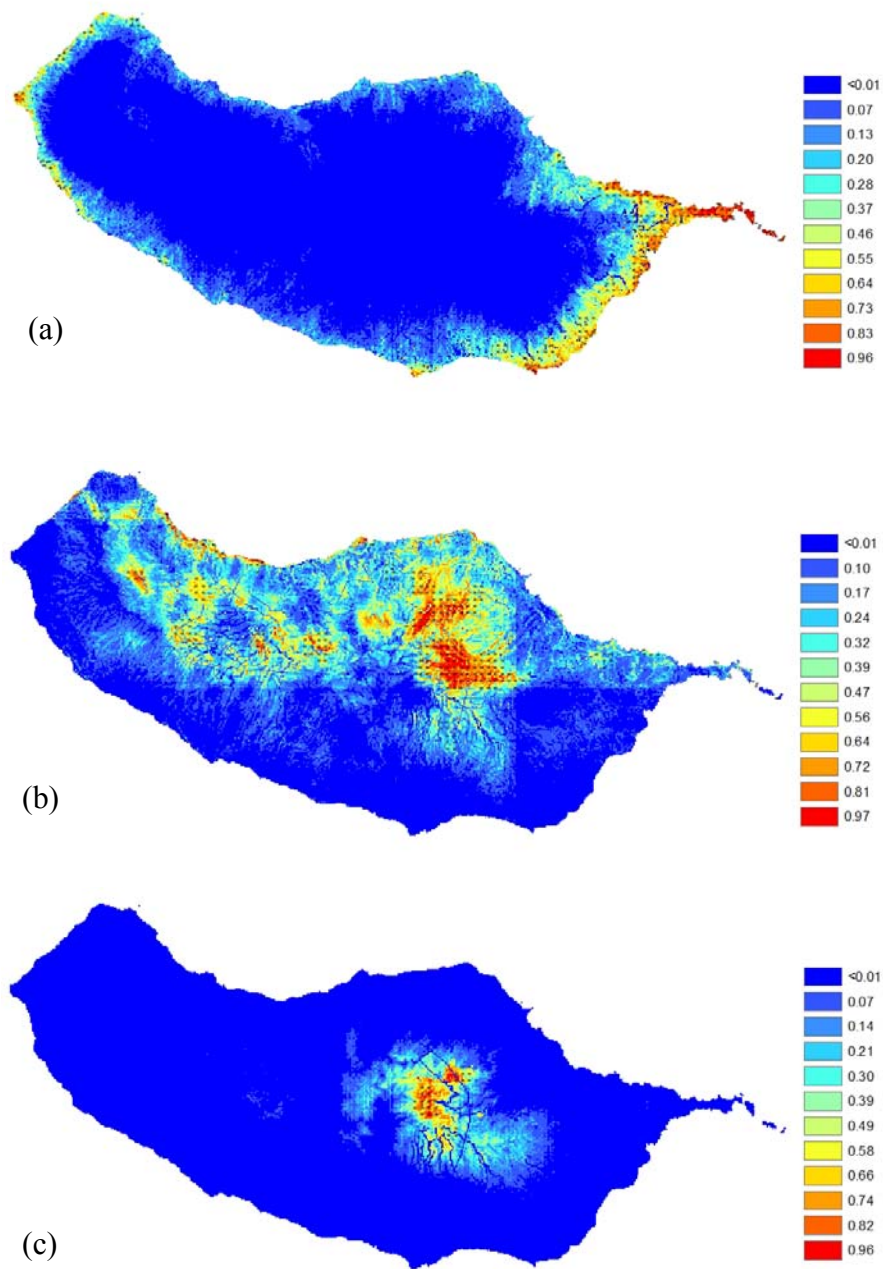


Figure 6. Predictive species distribution maps for (a) coastal *taxa*, e.g. *D. p. polymorpha*; (b) forest species, e.g. *L. membranacea* and (c) alpine species, e.g. *A. armitageana*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

Model results for coastal fauna representatives such as *Discula polymorpha polymorpha* indicates a pronounced geographical dependence (longitude), when distribution also limited by altimetry (occurring up to the barrier of 400 meters) and confined by a precipitation barrier up to 1450 mm (Figure 6a). In contrast, distribution of forest species like *Leptaxis membranacea* is determined mostly by land use in the form of presence of natural forest and by geographical position as they are circumscribed to *Clethro arborae* – *Ocoteo foetentis sigmetum* alliance group above 600 meters (Figure 6b). Alpine species distribution is dependent of precipitation (above 2000 mm), altimetry (above 1600 meters) and geographical patterns such as longitude and latitude, as they inhabit the central highlands of Madeira (Figure 6c).

Model results indicate that the Madeira's coastal area has a pronounced faunal differentiation resulting in three distinct sub-areas: north coast, south coast and S. Lourenço's eastern cape. Each of these sub-areas encloses endemic species whose distribution is restricted to these areas. The Higromiid *Disculella spirulina* occurs only at the western part of the island, being restricted by longitude and relative humidity (Figure 7a), showing suitable habitat at the vicinity of its current location. As the Lauridae *Leiostyla vincta watsoniana* is concerned, its distribution is circumscribed by latitude to the north coast of the island, between Porto Moniz and S. Jorge (Figure 7b). On the eastern cape of S. Lourenço, the distribution of the Ferrussacidae *Amphorella iridens* is determined by longitude and (low) precipitation, as this area is the driest part of Madeira Island (Figure 7c).

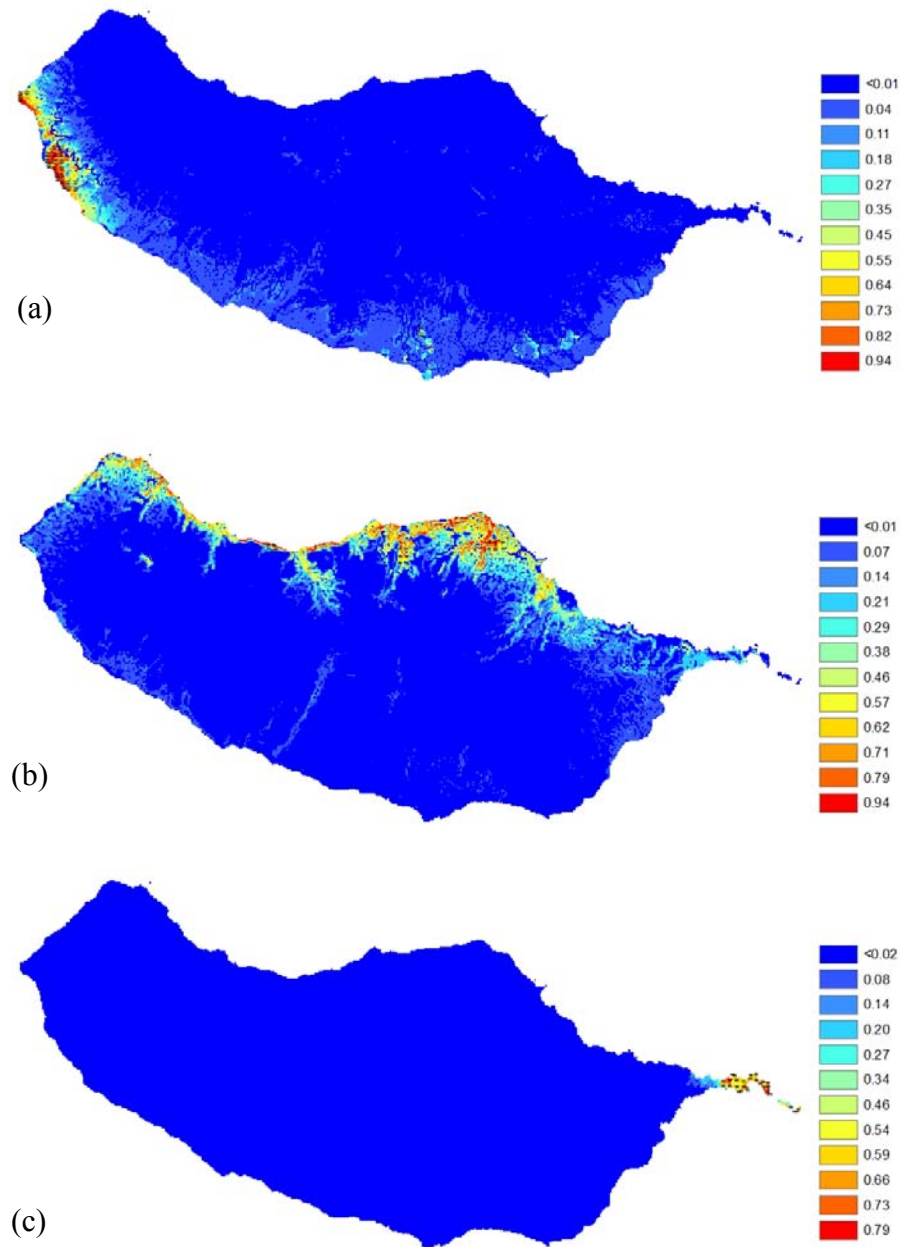


Figure 7. Predictive species distribution maps for coastal habitats *taxa*, e.g. (a) *D. spirulina*, (b) *L. v. watsoniana* and (c) *A. iridens*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

The model indicates that forest species distribution are more homogeneous, as 61% of their distribution is dependent of land use (presence of Laurel forest) and sensibility to disturbance (semi-slug *Plutonia behni*, Figure 8a), or to soil permeability (*Leiostyla colvillei*, Figure 8b). Semi-slug species seem to have larger distributional areas while the *Leiostyla* genera seem spatial restricted and niche confined.

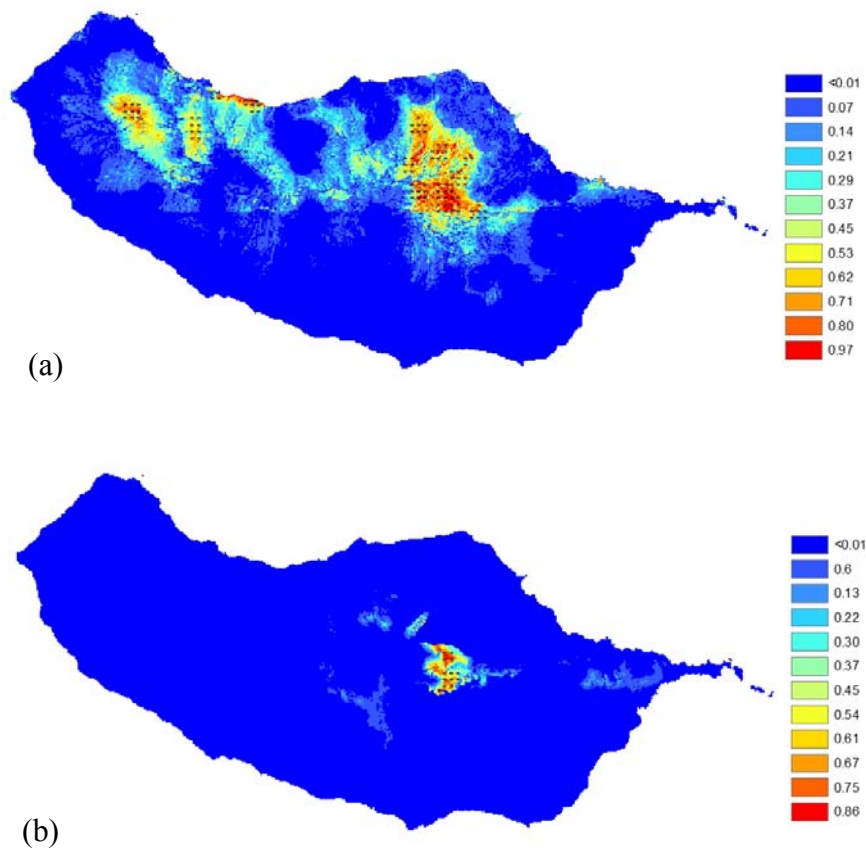


Figure 8. Predictive species distribution maps for forest habitats species, e.g. a) *P. behni* and b) *L. colvillei*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

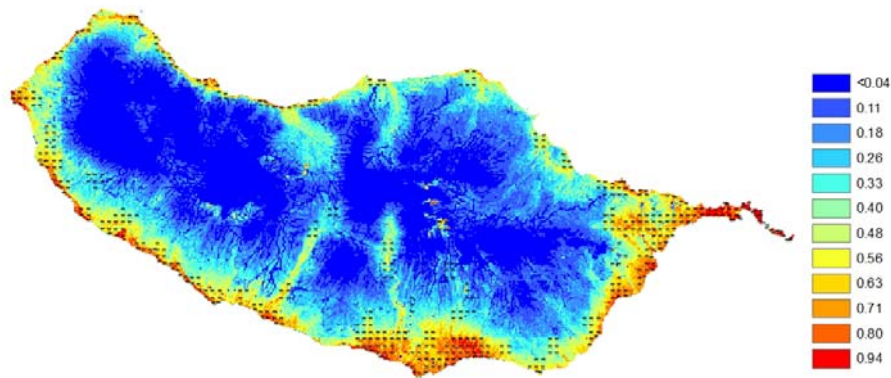


Figure 9. Predictive species distribution maps for unknown habitat preferences species *A. nitidiuscula*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

Species with undefined habitat preferences such as the Higromiidae *Actinella nitidiuscula* show a defined distribution pattern (Figure 9). Altimetry, longitude and annual precipitation are the driving forces of their distribution.

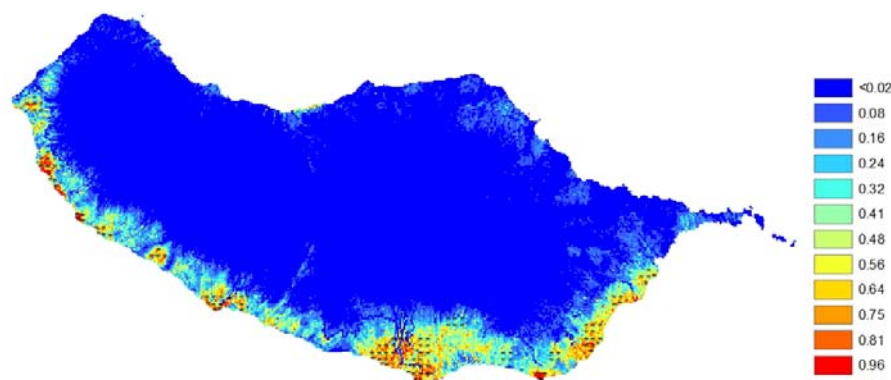


Figure 10. Predictive species distribution maps for anthropic taxa *D. m. taeniana*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

Model shows that *taxa* like *Discula maderensis taeniana* (Figure 10) seems to benefit from human presence, where distance to houses was the explanatory variable better describing their predicted distribution pattern.

We also tested the distribution of land snail species according to phenotypic characteristics (shell form). Our model confirms that the distribution of the low spired Ferrussacidae *Amphorella tornatellina* and the high spired species like *Boettgeria deltostoma* is mainly determined by altimetry (Figure 11 a-b).

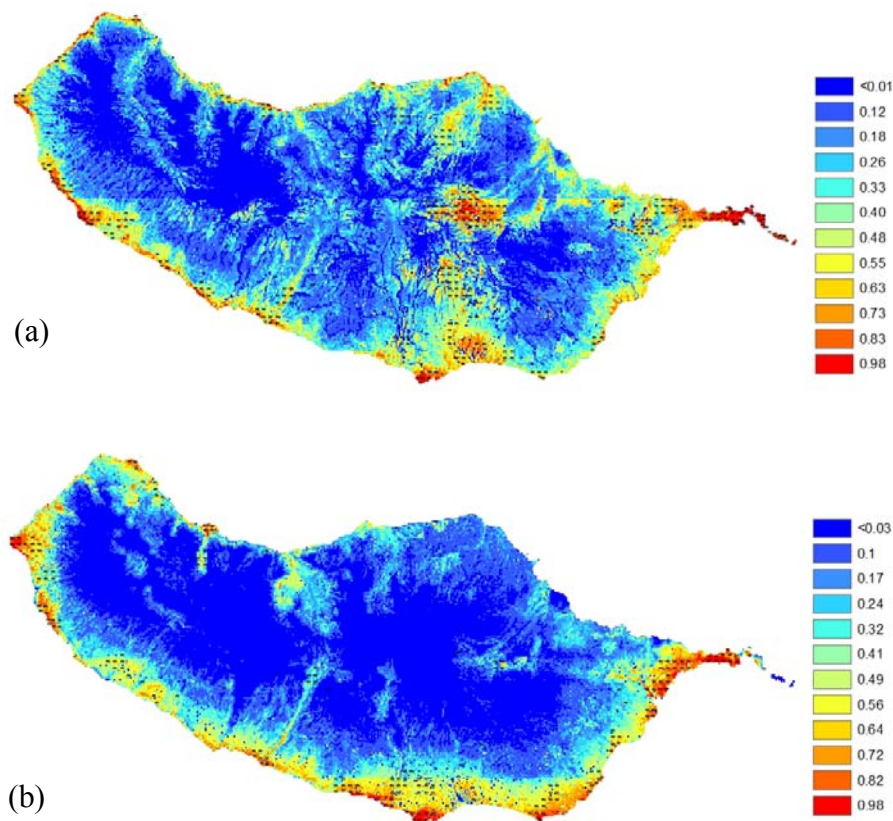


Figure 11. Predictive distribution maps for species according to phenotypic characteristics (shell form), e.g. (a) *A. tornatellina* and (b) *B. deltostoma*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

2.3.2.2 Threatened species

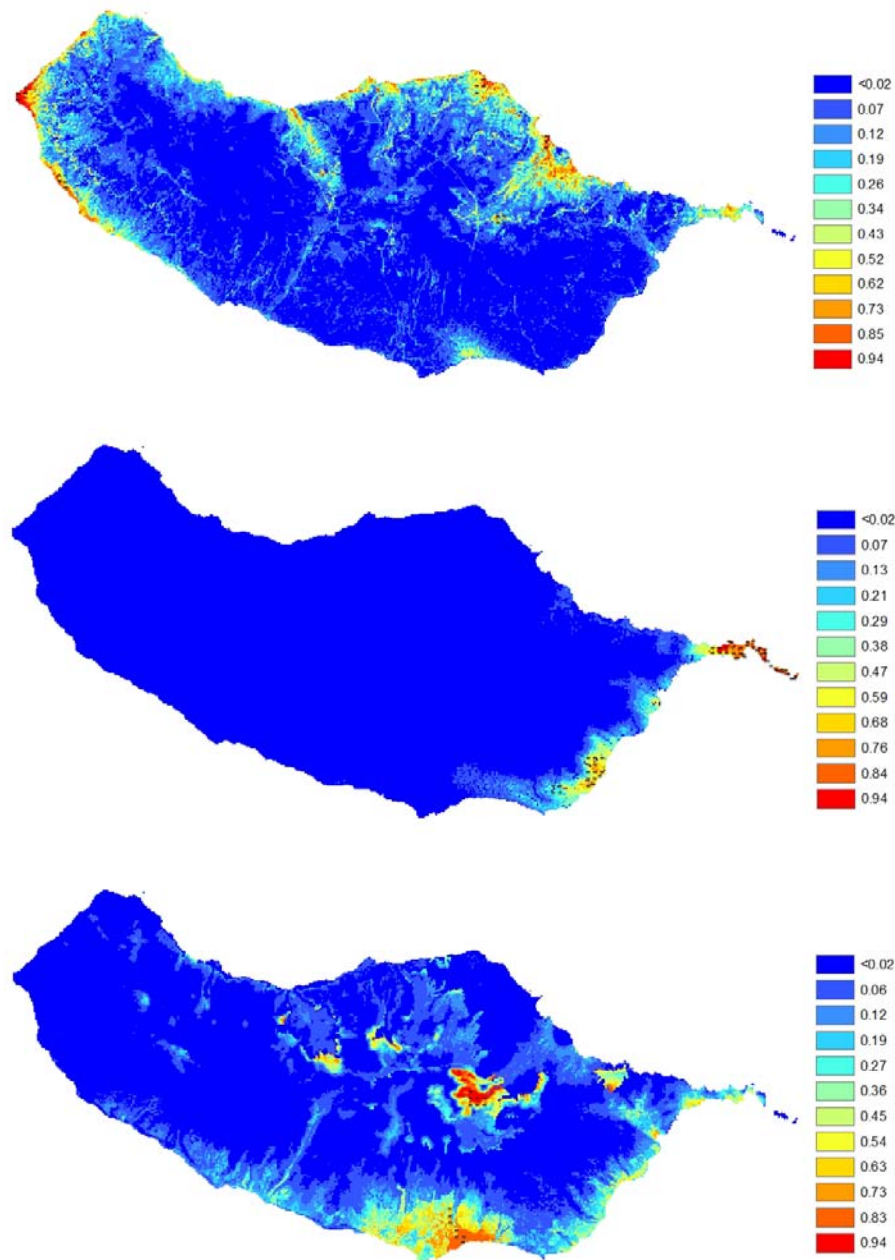


Figure 12. Predictive distribution maps for threatened *taxa*, e.g. (a) *Discus guerinianus guerinianus*, (b) *Craspedaria moniziana*, (c) *Leiostyla cassidula*. Shades of blue to red represent MAXENT prediction values ranging from 0 to 1, with 1 representing the areas with maximum suitability and 0 minimum suitable for species distribution, respectively. The observed locations are showed as black stars.

We have tested the predictive power of species model distribution as a possible conservation tool for Madeira's land snail species/subspecies for threatened *taxa* according to their IUCN threatened status (IUCN 2009): *Discus guerinianus guerinianus* (endangered), eastern ranged *Craspedaria moniziana* (endangered) and the range circumscribed *Leiostyla cassidula* (critically endangered).

D. g. guerinianus distribution seem to be dependent of longitude, as the predictive model was able to identify *taxon* suitable areas on the northwest (Ponta do Pargo) and central north (São Jorge) of the Island and also at S. Lourenço's eastern cape.

G. moniziana distribution also appears to be restricted by longitude, as also strongly associated with annual precipitation and altimetry. Distribution maps show the species distribution is range confined to the southeast of Madeira Island, as the model seems to fail to predict new suitable areas for this specie.

In the case of *L. cassidula*, soil type seems to determine the distribution areas suitable for this Lauridae, followed by land use and minimal annual relative humidity. The model was able to identify three new suitable distribution areas for the species: central area of the Island, in laurel forest core; northeast of the Island, on a disturbed habitat area near Porto da Cruz; and on the vicinity of urban area of Funchal.

2.4 Discussion

Our model suggests a marked land snail faunal differentiation between coastal (grassland), forest and alpine habitats. The coastal species distribution has a pronounced geographical pattern, limited by longitude, altimetry and precipitation. A similar pattern is verified on alpine species distribution. Although model results stress a wider distribution capability of forest species, they are limited in range to Laurel forest areas

and also highly dependent of humidity and precipitation levels, soil permeability and lack of disturbance.

Based on species distribution, a clear faunal differentiation was present on coastal faunas from south, north and São Lourenço eastern cape, as our model did not confirm the 6 different faunal partitions stated by Cook (2008). Even though coastal species seem more range confined, as longitude and latitude arise as the most important predictive variables for 28 species, model results do not indicate a micro geographical differentiation within northern and southern coastal faunas. Furthermore, as *L. r. macilenta* and *L. abbreviata* distribution models shows new suitable areas were identified on the zones described by Cameron & Cook (1997, 2001).

Like *D. spirulina* and *D. tabellata* models indicate, southern coastal species distribution has a clear longitudinal pattern when compared with northern coastal species. In spite of their apparent geographical pattern, mainly explained by latitude, northern coastal species distributional areas tend to be less range restricted and ecological constrained as shown by the models related to *L. v. watsoniana* and *L. abbreviata*. These species seem to be pre-adapted to new environments, enabling them to occupy disturbed forest areas. Furthermore, north coast Laurel forest reaches lower altitudes (300 m) than in the south coast (800 m), as this *taxa* seem to be able to inhabit those areas between coastal and forest (Cameron & Cook 1998, Capelo 2004). On the other hand, southern coastal species have human and biological barriers separating them from forest areas. This is a more humanized area, with a high construction rate until the 600 meters quota. Additionally, there is a vegetation belt (600-800 m) formed mainly by *Eucaliptus* sp. and *Pinus* sp as a result of reforestation, functioning as land snail deserts as endemics are concerned (IFRAM 2008). Cameron & Cook (1996) suggest that Madeiran species have evolved to live in dry, rocky and open environments, rather than

being arboreal and dependent on damp litter from native trees. These conditions pre-adapt them to resist clearance, as habitats have been subjected to the greatest fluctuations in size and continuity before human colonization, building up allopatric diversity and tolerance to change. These patterns are not clearly associated with ecological differences, as fossil records related to climatic and sea-level changes in the late Pleistocene/Holocene, suggest that these coastal areas have been subject to isolation and reconnection. That seems to be the case at the eastern cape of S. Lourenço. This area is home to relict species with woodland affinities such as *Craspedaria tiarella* and *Craspedopoma mucronatum*, an heritage of the last 10 MA glaciations (Cook et al, 1990).

São Lourenço's *A. iridens* and *H. pauperculum* predicted models reveals that species distribution is dependent of longitude and precipitation, with the distinct ecological, geological, climatic and vegetation parameters making this a distinctive area on Madeira Island faunal scene.

According to the woodland species distribution pattern, levels of relative humidity, soil permeability and disturbance appear to act as boundaries to species distribution. *Leptaxis membranacea* and *Plutonia behni* distributional model identify, among other Vitrinidae models, a vast quantity of suitable habitat areas, ranging from forest to the near shore areas of the north of Madeira Island. This result seems to confirm Cameron & Cook (1989) indication that forested areas show little geographical variation in species composition compared to open coastal habitats, with Lauridae *Leiostyla colvillei* distribution model suggesting a different scenario. The distribution pattern of the species is based on land use and geological characteristics. Furthermore, this species is associated to *Erica arborea* shrub, being only found at the core of Laurel forest at Fajã da Nogueira (Seddon, 2008). Nonetheless, even though ecological

parameters like land use, disturbance (e.g. measured as distance to houses), soil permeability, precipitation and geology were identified as playing an important role on the species distribution requirements modeled, it could also mean that species distribution patterns are not exclusively based on environmental and ecological factors. Maybe the interactions between environment and species are not satisfactorily measured, as historical factors and specific niche vegetation data are needed for a clearer view.

Species that inhabit the transitional and disturbed areas seems to have a identified distribution pattern. Altitude seems to lose strength as a predictive distribution variable for the fauna associated to this area, as climatic variables arise. Precipitation, relative humidity and temperature are suggested as being the driving forces behind species distributions. Regarding *A. giramica*, relative humidity seems to be the driving force of its modeled distribution. This species inhabits areas that have been subjected to changes in land-use practice as a result of touristic developments and increasing urbanization, and as such, the quality of habitats has declined. With the present model, new potential distributional areas were identified, making possible a species relocation in the future. Although the widespread *A. l. lentiginosa* could be found in many localities, it had a small range. The present model identified new potential distribution areas on localities with high habitat disturbance.

Our model also suggests that disturbance is not always a limiting factor in *taxa* distribution. Predicted distributional areas for *D. m. taeniana* and *D. m. maderensis* are positively correlated with the southern Madeira human population clusters. This fact enhances the apparent anthropogenic character of these endemic species, as it was already recognized for two other endemics *D. p. polymorpha* and *H. pauperculum* by Cameron & Cook (1996), but was not confirmed in the present work.

Other potential significant contribution of our model was the recognition of the importance of altitude and slope for the distribution of high spired shell species of *B. deltostoma* as previous stated by Cameron & Cook (1989).

Our model of endangered species predictive distributions gave good results, enabling the identification of the explanatory variables that better predict their distribution, as well as new projected suitable areas for all three selected species, showing the model usefulness as a conservation tool. Although models identified suitable areas for the *taxon*, it does not mean that species will be able to occupy them, as constrictions such as low dispersal capability, environmental barriers (mountains, water courses) or competition with the already existing species in those habitats could limit their success as colonizers. As to *C. moniziana*, a new model incorporating two new variables niche types and historical species data could increase the model fitness and better predict its distribution.

2.5 References

Abreu C. & D. Teixeira (2008). List of Molluscs. In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M. & Vieira, P. (eds.). A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. pp. 237-244. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo.

- Albers J.C. (1854). *Malacographia Maderensia sive enumeratio molluscorum quae in insulis Maderae et Portus Sancti aut vive extant aut fossilis reperiuntur*. Reimer. Berlin. 264. pp. American Malacological Bulletin 12:3–12.
- Azevedo E. B. (1996). *Modelação do Clima Insular à Escala Local. Modelo CIELO aplicado à ilha Terceira – Tese de Doutoramento*. Universidade dos Açores, 247pp.
- Baldwin R.A. (2009). Use of Maximum Entropy Modeling in Wildlife Research. *Entropy*, 11, 854-866.
- Bank R.A., Groh K. & T.E.J. Ripken (2002). Catalogue and bibliography of the non-marine Mollusca of Macaronesia. In: Falkner, M., K. Groh & M. C. D. Speight (eds.), *Collectanea Malacologica, Festschrift für Gerhard Falkner*: 89-235. ConchBooks, Hackenheim, Germany.
- Bustamante J. & J. Seoane (2004). Predicting the distribution of four species of raptors (Accipitridae) in southern Spain: statistical models work better than existing maps. *Journal of Biogeography*, 31:295-306.
- Cameron R.A.D. & L.M. Cook (1989). Shell size and shape in Madeiran land snails: do niches remain unfilled ? *Biological Journal of the Linnean Society*, **36**, 79 -96.
- Cameron R.A.D. & L.M. Cook (1992). The development of diversity in the land snail fauna of the Madeira archipelago, *Biological Journal of Linnean Society*, 46: 105-114.

- Cameron R.A.D. & L.M. Cook (1996)a. Diversity and durability: responses of the Madeiran and Porto-Santan snail faunas to natural and human-induced environmental change. *American Malacological Bulletin*, 12 (1/2): 3-12.
- Cameron R.A.D., Cook L.M. & J.D. Hallows (1996)b. Land snails on Porto Santo- adaptive and non-adaptive radiation, *Proceedings of Royal Society of London B* 351:309-327.
- Cameron R.A.D., Cook L.M. & G. Gao (1996) b. Variation in snail species widespread on Porto Santo, Madeiran archipelago. *Journal of Molluscan Studies* 62:143–150.
- Cameron R.A.D. & L.M. Cook (1998). Forest and scrub snail faunas from northern Madeira. *Malacologia*, 39, 29 -38.
- Cameron R.A.D. & L.M. Cook (1999). Land snail faunas of the Deserta islands, Madeiran archipelago, past and present. *Journal of Conchology*, 26, 1 -15.
- Cameron R.A.D. & L.M. Cook (2001). Madeiran Snails: Faunal differentiation on a small island. *Journal of Molluscan Studies*, **67**, 257 -267.
- Cameron R.A.D., Cook L.M., Goodfriend G.A. & M.B. Seddon (2006). Fossil Land Snail Faunas of Porto Santo, Madeiran Archipelago: Change and Stasis in Pleistocene to Recent Times, *Malacologia*, 49:1, 25-60 pp.
- Capelo J., Menezes De Sequeira M., Jardim R. & J.C. Costa (2004). Guia da excursão geobotânica dos V Encontros ALFA 2004 à ilha da Madeira. in Capelo, J. A paisagem vegetal da ilha da Madeira. pp. 5 -45. *Quercetea*, **6**, 3 -200.
- Capelo J., Menezes de Sequeira M., Jardim R. & S. Mesquita (2007). Biologia e ecologia das florestas das ilhas – Madeira. In *Árvores e Florestas de Portugal*.

Volume 6, Açores e Madeira – A Floresta das Ilhas (ed. J. Sande Silva), pp. 81 - 134. Edição da Fundação Luso Americana para o Desenvolvimento, Público e Liga para a Protecção da Natureza. Lisboa.

Cardoso P., Arnedo M.A., Triantis K.A. & P.A.V. Borges (2010). Drivers of diversity in Macaronesian spiders and the role of species extinctions. *Journal of Biogeography* in press.

Chapin F. S., Zavaleta E.S., Eviner V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hoper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.V. & S. Diaz (2000). Consequences of changing biodiversity. *Nature*, 405:234-242.

Cook L.M., Jack T. & C. Pettit (1972). The distribution of land molluscs in the Madeiran archipelago. *Boletim do Museu Municipal do Funchal*, 26, 1 -29.

Cook L.M, Cameron R.A.D. & L.A. Lace (1990). Land snails of eastern Madeira: speciation, persistence and colonization. *Proceedings of the Royal Society of London B*, 239, 35-79.

Cook L.M., Goodfriend G.A. & R.A.D. Cameron (1993). Changes in the land snail fauna of eastern Madeira during the Quaternary, *Philosophical Transactions of Royal Society of London*, 339, 83-103.

Cook L.M. (1996). Habitat, isolation and the evolution of Madeiran Landsnails, *Biological Journal of Linnean Society*, 59: 457-470.

Cook L.M. (2008). Species richness in Madeiran land snails, and its causes. *Journal of Biogeography*, 35, 647 -653.

- Craze P.G. & L.A. Lace (2002). Differences in physiological tolerance between co-existing taxa of the Madeiran land snail genus *Heterostoma* measured under controlled humidity and simulated rainfall. *Journal of Zoology* 256:17–24.
- Dallinger R., Berger B., Triebskorn-Ikoller R. & H. Kohler (2001). Soil Biology and Ecotoxicology, 489-525 pp. In: Barker, G. M. 2001. *The Biology of Terrestrial Molluscs*, CABI Publishing, Wallingford.
- Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & N.E Zimmermann (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Ferrier S., Watson G., Pearce J. & M. Drielsma (2002)a. Extended statistical approaches to modeling spatial pattern in biodiversity: the north-east New South Wales experience. I. Species-level modeling. *Biodiversity Conservation*, 11: 2275–2307.
- Ferrier S., Watson G., Pearce J. & M. Drielsma (2002)b. Extended statistical approaches to modelling spatial pattern in biodiversity: the north-east New South Wales experience. II. Community-level modelling. *Biodiversity Conservation* 11: 2309-2338.
- Garcia-Talavera F. (1999). La macaronseia. Consideraciones geológicas, biogeográficas e paleoecológicas. In: Fernández-Palacios, J. M., Bacallado, J. J. & Belmonte, J.

- A. (eds.), *Ecología y Cultura en Canarias*, Museo de la Ciencia y el Cosmos, La Laguna, 39-63.
- Geldmacher J., Bogaard P., Hoernle K. & H. Schmincke (2000). An age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems*, 1(2).
- Geldmacher J., Hoernle K., Bogaard P.V.D., Duggen S. & R. Werner (2005). New $^{40}\text{Ar}/^{39}\text{Ar}$ age and geochemical data from seamounts in the Canary and Madeira Volcanic Provinces: A contribution to the “Great Plume Debate”. *Earth and Planetary Science Letters*, 237: 85-101.
- Geldmacher J., Hoernle K., Klügel A., Bogaard P.V.D. & S. Duggen (2006). A geochemical transect across a heterogeneous mantle upwelling: implications for the evolution of the Madeira hotspot in space and time. *Lithos* 90: 131-144.
- Goodfriend G.A., Cameron R.A.D. & L.M. Cook (1994). Fossil evidence of recent human impact on the land snail fauna of Madeira, *Journal of biogeography*, 21, 309-320.
- Goodfriend G.A., Cameron, R.A.D., Cook, L M., Courty M.A., Federoff N., Kaufman, N., Livett E. & J. Tallis (1996). The Quaternary eolianite sequence of Madeira: stratigraphy, chronology, and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 120:195–234.
- Grendar M. & M. Grendar (2001). What is the question that MaxEnt answers? A probabilistic interpretation, in A. Mohammad-Djafari (ed.) *Bayesian Inference and Maximum Entropy Methods in Science and Engineering*, AIP (Melville), 83.

- Groh K. (1983). Eine neue *Leptaxis* Art aus den quartären Schneckensanden von Porto Santo (Madeiren) (Pulmonata: Helicidae). Archiv für Molluskenkunde 114:59–64.
- Groh K. & J. Hemmen (1986)a. Zur Kenntnis der Vitriniden des Madeira-Archipels (Pulmonata: Vitrinidae). Archiv für Molluskenkunde 116:183–217.
- Groh K. & J. Hemmen (1986)b. *Geomitra (Serratorotula) gerberi* n. subgen. n. sp. aus dem Quartär von Porto Santo (Pulmonata: Helicidae). Archiv für Molluskenkunde 117:33–38.
- Guisan A. & W. Thuiller (2005). Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993-1009.
- Hadfield M.G. (1986). Extinctions in Hawaiian achatinelline snails. Malacologia, 27:67-81.
- Hampshire, R.J. (1984). A study of the vegetation of the. Ponta de São Lourenço in Madeira, Ilhéu Chão and. Deserta Grande. Boletim do Museu Municipal do Funchal, 36 (164): 207-226.
- Hernandez P.A., Graham C.H., Master L.L. & Albert D.L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29: 773-785.
- Hijmans, R.J., Guarino, L., Bussink, C., Mathur, P., Cruz, M., & I. Barrentes (2004). *DIVA-GIS. Vsn. 5.0*. A geographic information system for the analysis of species distribution data.
- Holyoak D.T. & M.B. Seddon (1986). An undescribed *Leiostyla* (Gastropoda, Pulmonata) from Madeira. Journal of Conchology. London. 31: 191-193.

Howard P.C., Viskanac P., Davenport T.R.B., Kigeny F.W., Baltzer M., Dickinson C.J., Lwanga J.S., Matthews R.A. & A. Balmford (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472 -475.

IFRAM (2008). Inventário Florestal do arquipélago da Madeira. Secretaria Regional do Ambiente e dos Recursos Naturais, Funchal.

IUCN (2009). IUCN Red List of Threatened Species. Version 2009.2. <www.iucnredlist.org>

Izquierdo I., Martin J.L., Zurita N. & M. Arechavaleta (eds.) (2004). Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). 2nd, Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias

Jiménez -Valverde A., Lobo J.M. & M.L. López Martos (2006). Listado de especies actualizado de los araneidos y tomisidos (Araneae, Araneidae & Thomisidae) de la Comunidad de Madrid: mapas de distribución conocida, potencial y patrones de riqueza. *Graellsia*, **62**, 461 -481.

Kratz W. (1991). Cycling of nutrients and pollutants during litter decomposition in pine forests in the Grunewald, Berlin. In: Nakagoshi, N. and Golley, F. B. (eds). *Coniferous Forest Ecology from an International Perspective*. SPB Academic Publishing bv. The Hague, 151-160 pp.

Lace L.A. (1992). Variation in the genitalia of the land snail *Heterostoma paupercula* (Lowe, 1831) (Helicidae) in Madeira. *Biological Journal of the Linnean Society* 46:115–129.

Lawton H. & May R. M. (1995). *Extinction rates*, Oxford University Press, Oxford.

- Leakey R.; Lewin R. (1996). *The Sixth Extinction: Patterns of Life and the Future of Humankind*. New York: Anchor Books.
- Liu, C., Berry P.M., Dawson T.P., & R.G. Pearson (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385- 393.
- Lopez-Cardenas J., González-Bravo F.E., Salazar-Schettino P.M., Gallaga-Solorzano J.C., Ramírez-Barba E., Martínez-Mendez J., Sanchez-Cordero V., Peterson A.T., Ramsey J. (2005). Fine-scale predictions of distributions of Chagas disease vectors in the state of Guanajuato, Mexico. *J Med Entomol* 42: 1068-1081.
- Lowe R.T. (1831). *Primitiae Faunae et florum Maderae et Portus Sancti*. Transactions of the Cambridge Philosophical Society 4:1–70. [Also published as a separate by Van Voorst, London, 1851].
- Lowe R.T. (1852). *Brief diagnostic notices of new Maderan land shells*. *Annals and Magazine of Natural History* (2) 9 (50): 112-120, 275-279. London.
- Lowe R.T. (1854). *Catalogus molluscorum pneumonatorum insularum Maderensium*: or a list of all the land and freshwater shells, recent and fossil, of the Madeiran Islands: arranged in groups according to their natural affinities; with diagnoses of the groups, and of the new or hitherto imperfectly defined species. *Proceedings of the Zoological Society of London* 22:161–218.
- Lydeard C., Cowie R.H., Ponder W.F., Bogan A.E., Bouche T.P., Clark S.A., Cummings K.S., Frest T.J., Gargomin, O., Herbert D.G., Hershler R., Perez K.E., Roth B., Seddon M., Strong E.E. and F.G. Thompson (2004). The global decline of nonmarine mollusks. *BioSci* 54: 321-330.

- McPherson J.M. & W. Jetz (2007). Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30**, 135 -151.
- Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & J. Kent (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.
- Nobre A. (1931). *Moluscos terrestres fluviais e das águas salobras do arquipélago da Madeira*. Porto, 211 pp
- Pearson R.G., Raxworthy C.J., Nakamura M. & A.T. Peterson (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34: 102-117.
- Peterson A.T, Cohoon K.P. (1999). Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecol Model* 117:159–164.
- Phillips S.J., Dudik M. & R.E. Schapire (2004). A maximum entropy approach to species distribution modeling. *Proceedings of the 21st International Conference on Machine Learning*. ACM Press, New York pp. 655–662.
- Phillips S.J., Anderson R.P. & R.E. Schapire (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* 190: 231-259.
- Prada S. & A. Serralheiro (2000). Stratigraphy and evolutionary model of Madeira Island. *Bocagiana* nº 200: 1-13.
- Ramalho R., Madeira J., Fonseca P.E., Silveira A., Prada S., C.F. Rodrigues (2005). Tectonics of Ponta de são Lourenço, Madeira Island, *Cadernos Laboratoriais Xeolóxico de Laxe*, 30:223-234.

- Ramsey S. (2005). Fine-scale predictions of distributions of Chagas disease vectors in the state of Guanajuato, Mexico. *J Med Entomol* 42: 1068-1081.
- Reid W.V. & K.R. Miller (1989). Keeping options alive: The scientific basis for conservation biodiversity. World Resources Institute.
- Ribeiro L., Ech-Chakroun S., Mata J., Boven A., Mattielli N., Hus J. & C. Maerschalk (2005). Elemental and lead isotopic evidence for coeval heterogeneities at Madeira/Desertas mantle source. Acts of VIII Congresso de Geoquímica dos Países de Língua Portuguesa (Portugal) (ed. Anonymous), pp. 485 -488.
- Richardson B.J., Zabka, M. Gray, M.R. & G. Milledge (2006). Distributional patterns of jumping spiders (Araneae: Salticidae) in Australia. *Journal of Biogeography*, **33**, 707 -719.
- Roura-Pascual N., Suarez A.V. & K. McNyset (2006). Niche differentiation and fine-scale projections for Argentine ants based on remotely sensed data. *Ecology Applications*, 16:1832–1841.
- Seddon M. (1995). Endangered land snails of Porto Santo (Madeira Island Archipelago): monitoring changes in species diversity and implications for their conservation. *Biodiversity and Conservation*, 4, 171 -204.
- Seddon M.B. & I.J. Killeen (1996). A new species of the genus *Leiostylia* from the Madeiran archipelago. *Journal of Conchology*. London. 35: 445 - 449.
- Seddon M.B. (2008). The landsnails of Madeira – an illustrated compendium of the landsnails and slugs of the Madeiran archipelago, National Museum of Wales, Cardiff.

- Soberón J. & A.T. Peterson (2005). Interpretation of models of fundamental ecological niches and specie's distributional areas. *Biodiversity Informatics* 2:1-10
- Sjogren E. (1972). Vascular plant communities of Madeira. *Boletim do Museu Municipal do funchal*, 26: 46-125.
- Teixeira D. & C. Abreu (2003). Moluscos terrestres da Ponta de São Lourenço e Ilhéus Adjacentes, *Biodiversidade Madeirense: Avaliação e Conservação*, Direcção Regional do Ambiente, Funchal, 122 pp.
- Van Bruggen A.C. (1995). Biodiversity of Mollusca: Time for a new approach. In *Biodiversity and Conservation of the Mollusca* (eds. A.C. van Bruggen, S.M. Wells & T.C.M. Kemperman), pp. 1–19. Backhuys, Oegstgeest -Leiden, The Netherlands.
- Van Jaarsveld A.S., Freitag S., Chown S.L., Muller C., Koch S., Hull H., Bellamy C., Krüger M., Endrödy-Younga S., Mansell M.W. & C.H. Scholtz (1998). Biodiversity assessment and conservation strategies. *Science*, **279**, 2106 -2108.
- Waldén H.W. (1983). Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated Check -list. *Annales Zoological Fennici*, **20**, 255 -275.
- Waldén H.W. (1984). The land mollusc fauna of Madeira in relation to other Atlantic islands and the Palaearctic region. Pp 38–45. in SOLEM, A. and A. C. VAN BRUGGEN, editors. eds. *World-wide snails*. Brill. Leiden. ix +. 289. pp.

Wisz M.S., Hijmans R.J., Li J., Peterson A.T., Graham C.H., Guisan A. & NCEAS Working Group (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 14: 763-773.

Wollaston, T.V. (1878). *Testacea Atlantica or the land and Freshwater Shells of the Azores, Madeira, Salvages, Canaries, Cape Verdes and Saint Helena*. Reeve. London. xi +. 588. pp.

CHAPTER 3

Final Remarks

3. FINAL REMARKS

Predictive models of species spatial distributions arise as important tools for ecology and conservation applications. From this study we were able to validate the suitability of Maximum Entropy Algorithm as a species distribution predictor for Madeira's endemic land snails *taxa*.

The species distribution models showed a marked habitat differentiation between habitats suitability and revealed dispersal constraints of the tested species. Nonetheless, models identified data gaps that limited their predictive capability. Future work must be done in order to incorporate historical, ecological (species related) and future climate scenarios data as a pathway to a more robust species distribution prediction.

As a final note, MAXENT revealed itself to be a powerful conservation tool for predict spatial distribution on threatened species. We recommend that current and potential distribution maps resulting from the present work should be considered as important tools for conservation purposes by distinct entities in Madeira dedicated to the promotion of biodiversity.

APPENDIX I

Table III. Land snail species captured between 207-2008 field trips.

ID	Species	Family	Sample areas																							
			111	112	113	114	115	116	121	122	123	124	125	126	211	212	213	214	215	216	221	222	223	224	225	226
1	<i>Actinella actinophora</i>	Hygromiidae	1																							1
2	<i>Actinella arcta</i>	Hygromiidae												1												
3	<i>Actinella fausta</i>	Hygromiidae									1															
4	<i>Actinella giramica</i>	Hygromiidae				1																				
5	<i>Actinella lentiginosa lentiginosa</i>	Hygromiidae				1		1							1				1							
6	<i>Actinella lentiginosa stellaris</i>	Hygromiidae		1																						
7	<i>Actinella nitidiuscula</i>	Hygromiidae		1	1													1	1	1						
8	<i>Amphorella mitriformis</i>	Ferussaciidae				1																				
9	<i>Amphorella tornatellina</i>	Ferussaciidae		1			1			1		1						1		1	1	1	1			1
10	<i>Boettgeria crista</i>	Clausilidae											1	1												1
11	<i>Boettgeria deltozona</i>	Clausilidae						1		1								1								
12	<i>Boettgeria depauperata</i>	Clausilidae				1													1							
13	<i>Boettgeria exigua</i>	Clausilidae	1						1												1	1				
14	<i>Caseolus innominatus innominatus</i>	Hygromiidae																					1			
15	<i>Columella microspora</i>	Vertiginidae	1																							1
16	<i>Craspedaria tiarella</i>	Hygromiidae							1																	
17	<i>Craspedopoma mucronatum</i>	Craspedopomatidae					1	1				1								1						1
18	<i>Craspedopoma neritoides</i>	Craspedopomatidae																								1
19	<i>Discullela maderensis</i>	Hygromiidae		1														1								
20	<i>Hemilauria limnaeana</i>	Lauridae																								1
21	<i>Janulus bifrons</i>	Gastrodontidae			1					1								1	1							
22	<i>Leiostryla concinna</i>	Lauridae																								1
23	<i>Leiostryla fusca</i>	Lauridae	1																							
24	<i>Leiostryla irrigua</i>	Lauridae	1					1						1					1							

ID	Species	Family	Sample areas																							
			111	112	113	114	115	116	121	122	123	124	125	126	211	212	213	214	215	216	221	222	223	224	225	226
25	<i>Leiostyla loweana loweana</i>	Lauridae						1				1		1						1						1
26	<i>Leiostyla millegrana</i>	Lauridae									1															
27	<i>Leiostyla sphinctostoma</i>	Lauridae	1				1																			
28	<i>Leiostyla vincta vincta</i>	Lauridae						1																		
29	<i>Leiostyla vincta watsoniana</i>	Lauridae					1																			
30	<i>Leptaxis furva</i>	Hygromiidae												1										1		
31	<i>Leptaxis groviana groviana</i>	Hygromiidae		1	1											1		1								
32	<i>Leptaxis membranacea</i>	Hygromiidae										1		1						1						1
33	<i>Leptaxis simia simia</i>	Hygromiidae				1	1		1		1			1				1	1						1	
34	<i>Plutonia behnii</i>	Vitrinidae												1												
35	<i>Plutonia marcida</i>	Vitrinidae																		1						1
36	<i>Plutonia ruivensis</i>	Vitrinidae							1			1							1							1
37	<i>Pyrgella leacockiana</i>	Ferussaciidae	1			1				1																1
38	<i>Staurodon seminulum</i>	Vertiginidae	1					1				1								1						
N		8	8	5	3	6	5	7	4	4	3	6	2	7	2	2	5	2	7	6	2	2	1	1	1	13



REGIÃO AUTÓNOMA DA
MADEIRA



REPÚBLICA PORTUGUESA



UNIÃO EUROPEIA
FSE