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## perspective

## Challenges, advances and perspectives in island biogeography

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**Abstract.** Island biogeographical research is becoming more and more fashionable, with the continuous identification of new challenges that are critical for the advancement of science. In this contribution we identify biases and limitations associated with island biogeographical studies, and also describe recent advances and propose new perspectives. The main proposals include: 1) downscaling island biogeographical studies to local/plot scale; 2) investigating geographical patterns of intra-specific genetic variation to infer dispersal processes among and within islands; 3) using applied biogeographical research to respond to the current island biodiversity crisis; and 4) applying new computer-intensive methods such as artificial intelligence (AI) approaches.

**Keywords.** Agent-based Models (ABM), dispersal, island biogeography, plot-scale surveys, sample bias

### Introduction

After MacArthur and Wilson's (1963) paper and their book on "The Theory of Island Biogeography" (MacArthur and Wilson 1967), the study of islands received a boost, and they were used as model systems for many purposes, in particular for investigating drivers of species richness and composition. A search of the Web of Science database using "island biogeography" as a topic for the period 1967–2015, generated about 9000 publications that include a diversity of sub-topics and taxonomic units, which largely surpass the island scale and include the application of the original concepts of MacArthur and Wilson's (1963, 1967) works to isolated continental systems, primarily 'habitat islands'.

Traditional island biogeographical studies applied to oceanic islands are based on whole-island diversity indicators collated over decades, using the islands of a particular archipelago as replicates. Although one has to be careful when

using any diversity metric, even at the island scale (Gray and Cavers 2014), for example because unrecorded anthropogenic extinctions may mask current patterns (Cardoso et al. 2010, Faurby and Svenning 2015), there are many recent advances in island biogeography that Fernández-Palacios et al. (2015: 14) described as "a new golden era in island biogeography".

The most recent and important theoretical advance in island biogeography has been the 'General Dynamic Model of Oceanic Island Biogeography' (GDM) (Whittaker et al. 2008), highlighting the relevance of island ontogeny for processes of species diversification in remote volcanic archipelagos. This proposal has inspired many innovative empirical and theoretical studies across a range of archipelagos (reviewed in Borregaard et al. 2016). Another useful concept is that of archipelagos as replicates, which allow the investigation of drivers of diversity in many taxa, at large scales (Triantis et al. 2015). Also, a better under-

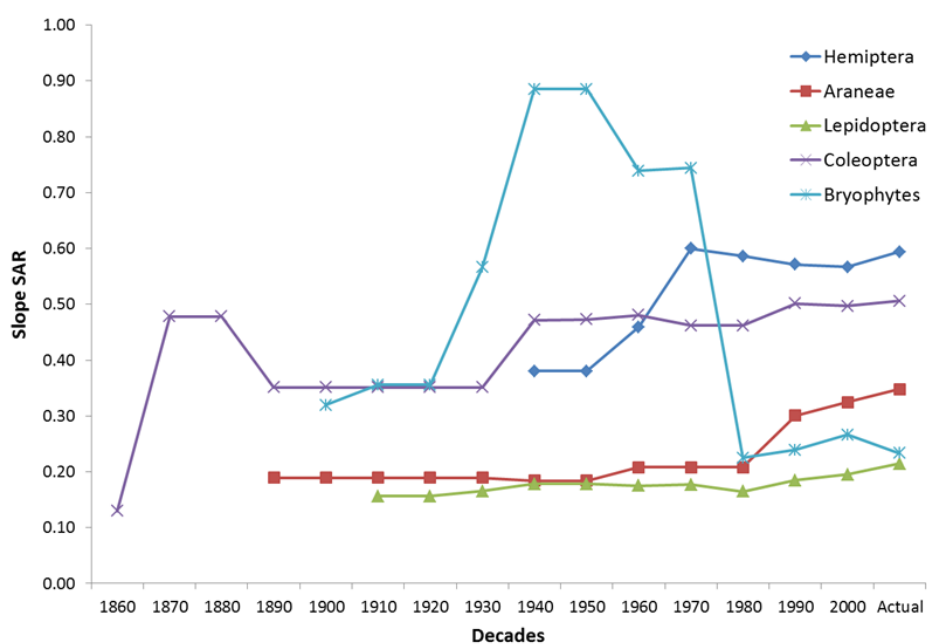
standing of the palaeo-dynamics of remote oceanic archipelagos is particularly relevant for classical biogeographical and evolutionary studies, as shown recently by Fernández-Palacios et al. (2010, 2016) and Rijdsdijk et al. (2014). Methodologically, the use of Bayesian approaches is becoming increasingly important in island biogeography, since it allows the development of dynamic time-constrained models that use results of prior analyses in subsequent modelling (see Gray and Cavers 2014). Considering the relative contribution of ecology (colonization, extinction) and evolution (speciation), these approaches also give flexibility in investigating how the geographical characteristics of island archipelagos and their taxa influence diversity patterns (Patiño et al. 2015, Triantis et al. 2015).

In this contribution, we first look at biases and limitations associated with island biogeographical studies, and then describe recent advances and propose new perspectives: 1) applying island biogeographical models to local/plot scale; 2) investigating geographical patterns of intra-specific genetic variation to infer dispersal processes among and within islands; 3) using the emergence of applied biogeographical research to respond to the current island biodiversity crisis; and 4) implementing new computer-intensive methods such as artificial intelligence (AI).

## Biases and limitations associated with island biogeographical studies

### Biases

Biases associated with sampling effort are important in any ecological or biogeographical study. We undertook a search of the Azores Bioportal<sup>1</sup> to investigate the impact of the knowledge of species diversity in the nine Azorean islands on species–area relationship (SAR) slope on a temporal scale. For this, we computed a SAR curve of each decade for the nine islands using the power function  $S = CA^z$  linearized in the double logarithmic form  $\log S = \log C + z \log A$ . For Lepidoptera and Coleoptera, the slope value was stable in the last eight decades (Fig. 1), which reflects the fact that a large proportion of the entomological surveys and taxonomic work in the Azores in the first decades of the 20<sup>th</sup> century was concentrated in those two taxonomic groups (see a literature review in Borges and Vieira 1994). However, only recently does the sampling effort across the nine islands seem to be good enough to generate stable SAR slopes for Bryophytes, Hemiptera and Araneae. This means that the sampling effort across multiple islands of an archipelago should be controlled for, when performing complex statistical analyses. Changes in the slope may also be due to changes in habitat area and/or paying the extinction debt (Cardoso et al. 2010, Triantis et al. 2010).



**Figure 1.** Temporal variation of the SAR slopes for a log–log model relating the nine Azorean island areas with species richness for their mosses, liverworts and hornworts (Bryophyta), spiders (Araneae), true bugs (Hemiptera), beetles (Coleoptera) and moths and butterflies (Lepidoptera).

<sup>1</sup> <http://www.atlantia.angra.uac.pt/>, last accessed 30<sup>th</sup> June 2016

### *Limitations*

We can divide limitations related to island biogeographical studies into two types: i) those intrinsic to island systems, and ii) those that may also apply to continental biogeographical studies.

#### Limitations intrinsic to islands

The first main limitation is the Linnaean shortfall: the faunas and floras of many islands and small archipelagos are not well known. Moreover, as shown in Fig. 1, even for well surveyed archipelagos, bias can arise owing to uneven sampling effort between islands (see also Gray and Cavers 2014), and endemic species inventories are still largely incomplete (see Lobo and Borges 2010).

The fact that few islands are available to apply robust statistical models that involve multiple regression and variable selection is a serious limitation. As an alternative, the use of mixed-effects models was recently proposed (Bunnefeld and Phillimore 2012), as they incorporate in the same analysis islands from multiple archipelagos and/or taxa, while controlling for data structure and idiosyncrasies derived from fixed factors not under study (e.g. archipelagos and taxa for studying SAR or the GDM). These have been successfully applied in recent studies, for example for bryophytes (Patiño et al. 2013) and land-snails (Cameron et al. 2013).

Another important limitation associated with biogeographical studies on islands is related to the availability of present and future climate data. Islands are often small, while global climate models are necessarily made at relatively coarse resolutions (1x1 km or larger). In addition, the specificities of oceanic island topography and consequent climate can hardly be reflected using global or large-scale circulation models. To overcome such a shortfall a simple layer model was proposed by Azevedo et al. (1998), based on the transformations experienced by an air mass crossing over a mountain, simulating the evolution of an air parcel's physical properties starting from the sea level. This model has been applied successfully within Macaronesian islands at very small scales, namely in Azores (see e.g. Borges et al. 2006, Hortal et al. 2010), and Madeira (Boeiro et

al. 2013), and Guadeloupe (Azevedo et al. unpublished) and we call for more widespread use of this type of small-scale physical climate model. Alternatively, for small islands authors can: (a) use the local-scale dynamical climate model MUKLI-MO\_3 parameterized with data from local meteorological stations (Mifka and Aloise 2014); (b) run local climate models using approaches like multiple regressions with residual kriging and universal kriging, based on weather stations in combination with predictors from GCMs.

#### Limitations not exclusive to islands

The number of resident researchers in islands is rather small and their universities usually rather recent in origin (less than 50 years), which leads to inconsistencies and asymmetries in the knowledge of the distributions of different taxonomic groups among islands and archipelagos. This taxonomic shortfall is not exclusive to islands (see e.g. Cardoso et al. 2011, Meyer et al. 2015), but is particularly important, as revealed by the few large-scale multi-archipelago biogeographical studies which are restricted to either land plants (e.g. Patiño et al. 2014, Weigelt et al. 2015) or birds (e.g. Kalmar and Currie 2006).

Long-term biodiversity data are either rare or almost absent for islands, which hampers the study of the biogeography of extinctions (but see Triantis et al. 2010) and temporal dynamics of island biota. Satellite cover is also comparably poor in islands – in terms of both quality of image because of high percentages of cloud cover (see e.g. Gil et al. 2013), and the lower frequency of satellite visits compared to continental areas. This clearly limits the acquisition of data for island ecosystems. The limited availability of data on land uses, vegetation types, and geological and edaphic features is not exclusive to islands but is frequently a problem for many island systems. For instance, CORINE or the IUCN habitat categories are mostly useless in the Azores, Madeira or Canary Islands. They are good only for large scales.

Given these biases and limitations, island biogeographical studies are challenging. Here we propose four further avenues to develop studies of biogeography on islands.

### Toward local scale biogeography: recent examples mostly from Macaronesia

Downscaling regional island biogeographical studies to the local scale facilitates the generation of hypotheses using diversity metrics that are based on intensive fieldwork using standardized sampling strategies in different sites within different islands and within different archipelagos. Studies using plot-scale surveys for testing island biogeographical models are generally lacking (but see Borges and Brown 1999, Gruner 2007, Karger et al. 2014). However, some ongoing projects in Macaronesia and other archipelagos address this limitation with plot-level data to understand island ecological processes across archipelagos, which may also shed light on island biogeographical patterns and processes. The first study, which started in 1999, is the BALA project (**B**iodiversity of **A**rthropods from the **L**aurisilva of **A**zores). This has yielded a wealth of publications for the Azores (see Borges et al. 2005, Ribeiro et al. 2005 and Borges et al. 2011 for a review; also see the BALA project website<sup>2</sup>). The BALA project generated standardized plot data for 100 sites across seven islands of the Azores for epigeal and canopy arthropods, and these are still being exploited (see e.g. Rigal et al. 2013, Cardoso et al. 2014, Matthews et al. 2014).

Two recent projects, implemented within the 2011 European FP7 NetBiome call, investigate diversity and biogeographical patterns in islands across archipelagos: ISLANDBIODIV<sup>3</sup> and MOVECLIM<sup>4</sup> (see also Gabriel et al. 2014 and Coelho et al. 2016). In the case of ISLANDBIODIV, the intensive sampling and surveying of 30 plots (ten in each island) for vascular plants, springtails, spiders and beetles in Terceira Island (Azores), Tenerife (Canary Islands) and La Réunion (Mascarenes) allows, for the first time, tests of the emergent properties of island species' community structures across archipelagos. In the case of MOVECLIM, an elevation-stratified protocol (Ah-Peng et al. 2012) was applied within several islands (Pico in Azores;

La Palma in Canary Islands; Réunion in the Mascarenes; Tahiti in French Polynesia; and Guadeloupe in the Caribbean) to understand bryophytes' and ferns' ecological and biogeographical processes across elevational transects and islands.

A project recently approved by the Portuguese Foundation for Science and Technology, MACDIV<sup>5</sup>, aims to characterize cross-scale variation of taxonomic, functional and phylogenetic diversities (alpha and beta), from plot to archipelago scales, sampling spiders from 10 islands in the Azores, Madeira, Canary Islands and Cape Verde. In Hawaii, the project Dimensions in Biodiversity<sup>6</sup> was initiated in 2014, aiming to understand processes at the interface between ecology and evolution in four islands, by studying small plots in *Metrosideros* mesic and wet forest (see Gillespie 2016).

The results obtained with studying regional–local processes allow the implementation of advanced statistical methods to reveal mechanisms driving the distribution of species and observed diversity patterns. With these kinds of plot-based studies, replicated in many islands and archipelagos, we expect to identify regional spatial, historical and environmental factors that may influence local diversity (taxonomic, functional and phylogenetic) patterns and processes in islands. Results of the projects BALA, ISLANDBIODIV, MOVECLIM, Dimensions in Biodiversity and MACDIV will also contribute to understanding long-term ecological processes, since permanent plots can be resampled over time.

### Dispersal within and among islands

Island biogeographical theory, when reduced to its fundamental components, leaves us with three key biological processes: colonization, extinction and speciation. Colonization and speciation contribute to the accumulation of species on islands, while extinction has the opposite effect. Classic island theory describes a hypothesized theoretical relationship between colonization and extinction

<sup>2</sup> <http://islandlab.uac.pt/projectos/ver.php?id=65>, last accessed 30<sup>th</sup> June 2016

<sup>3</sup> <http://island-biodiv.org/>, last accessed 30<sup>th</sup> June 2016

<sup>4</sup> <http://moveclim.blogspot.com/>, last accessed 30<sup>th</sup> June 2016

<sup>5</sup> <http://ce3c.ciencias.ulisboa.pt/research/projects/ver.php?id=61>, last accessed 30<sup>th</sup> June 2016

<sup>6</sup> <http://nature.berkeley.edu/hawaiidimensions/>, last accessed 30<sup>th</sup> June 2016



(MacArthur and Wilson 1963, 1967), and empirical data reveal that speciation may also be embedded within this model (Emerson and Kolm 2005). Colonization history among islands over long evolutionary timescales is recorded within the phylogenetic relationships of species, although it must be taken into account that extinction removes species and thus it also removes colonization history, which is likely to be more problematic for deeper phylogenies (Emerson 2002). Many studies have sought to use phylogeny to extrapolate colonization history among islands, and Bayesian methods have been developed to summarize these at the community level (Sanmartín et al. 2008). In contrast to phylogenetic sampling, there has been less emphasis on population-level sampling within species or species complexes to investigate dispersal over more recent timescales, both among and within islands. If one starts with a simple null hypothesis that most speciation within an island is of allopatric origin, then a sampling framework can be implemented to ask “do species sampled from taxa with a history of *in situ* speciation show higher genetic structuring than species sampled from non-diversified lineages?” Because geographically referenced intraspecific genetic data can be used to estimate gene flow and genetic connectivity among individuals, this question may be rephrased as “does dispersal limitation promote speciation within islands?”

A second null hypothesis that can be tested within this framework is that dispersal promotes speciation via colonization, by asking the question “do species sampled from taxa with a history of speciation via colonization show less genetic structure than species sampled from taxa where *in situ* speciation has been more important?” For the same reason provided above, this question may be rephrased as “does dispersal promote speciation between islands?” These two null hypotheses provide a framework to test the extent to which the distribution of biodiversity within and among islands fits a neutral model where the dynamics of colonization and speciation are mediated by individual species’ dispersal limitations. There are parallels here to recent continental studies where the sampling and DNA sequencing

of beetle communities have revealed that variation in community composition is strongly explained by individual species’ dispersal limitation (Baselga et al. 2013). It will be interesting to see whether this extends to speciation on islands, where one might expect selective pressures to hold more explanatory power. The kind of community-level ecological sampling protocols described in the previous section provide an exploitable framework for the application of intraspecific genetic sampling to test the hypotheses presented here.

While phylogenetic sampling can tell us which species or lineages originate from colonization events between islands, such studies typically say little about what might have driven subsequent speciation within islands. In contrast, population-level molecular sampling within species complexes distributed across multiple islands offers the potential to explore both dispersal and speciation, and any potential interactions between these two processes (Emerson and Faria 2014). The work of Jordal et al. (2006) provides a clear demonstration of one such interaction. A double colonization of the Canary Island of La Palma from El Hierro by the beetle species *Aphanarthrum glabrum* was followed by limited admixture between the two founding populations, presumably with negative fitness consequences, facilitating character displacement and the completion of reproductive isolation. Recent work by Hendrickx et al. (2015) implicates ongoing dispersal of flighted species among islands in the repeated evolution of flightless ecotypes of *Calasoma* beetles in the Galapagos islands. Molecular sampling within a closely related complex of nine species within the weevil genus *Laparocerus* in the Canary Islands indicates species’ origins from multiple founding events of different species followed by genetic admixture (Faria et al. 2016). All three studies demonstrate a speciation dynamic with a less-than-simple dispersal history that would not be so easily discernable among more distantly related species.

Sampling closely related species complexes reduces the impact of both (i) species extinctions and (ii) the turnover of genetic variation within

species through time that eventually erases signatures of divergence and gene flow in the speciation process. Detailed molecular analyses, combined with geographically representative sampling within closely related species complexes on islands, would appear to be a promising line of investigation for a fine-scale understanding of role of dispersal in the speciation process. The increasing accessibility and rigour of restriction site-associated DNA sequencing for genotyping-by-sequencing (GBS) (e.g. Mastretta-Yanes et al. 2015) should facilitate this. By yielding potentially thousands of loci for analysis, GBS can provide greater statistical power for the discrimination of dispersal and admixture, while also relaxing the need for large sample sizes that are typically associated with population genetic analyses. This may be particularly attractive for island-based studies, where sample sizes are often limited by species being rare or difficult to collect. Recent advances using hybrid capture techniques (Suchan et al. 2016) also open the door for the use of museum or collection material, potentially allowing researchers to investigate temporal trends in dispersal history, and other population genetic phenomena of interest in island settings, such as the population genetic consequences of disturbance effects.

### Conservation biogeography on islands

Island native habitats have great conservation and heritage value, but are facing rapidly increasing human pressure and the negative effects of global change (invasive species, land-use changes and climatic changes). The recent Declaration of Guadeloupe (IUCN – International Conference on Biodiversity and Climate Change, 21–25 October 2014 at Guadeloupe) defined actions to counter biodiversity loss and climate change impacts in EU Outermost Regions and Overseas Countries and Territories (ORs and OCTs). This identified climate change and invasive species as two of the most important threats to Islands. Thus, it is also responsibility of biogeographers to adopt conservation biogeography (Whittaker et al. 2005, Richardson and Whittaker 2010) as a priority in their research agendas.

A fundamental question in island biogeography and ecological studies responding directly to the current island biodiversity crisis could be: “how will human activities (agriculture, forestry, fisheries and touristic activities) plus climate change interact with invasive species and affect the distributions of endemic species, native habitats and ecosystem services?”. Policy-based conservation biogeography should include the human socio-economic dimension for a more complete understanding of how the drivers of taxonomic (species), functional (ecosystems) and phylogenetic (evolutionary) diversity at all spatial and temporal scales interact with socio-economic needs. By performing applied biogeographical research, biogeographers may achieve a more meaningful integrative research programme. We suggest that more research effort should be directed toward: (i) the spatial and temporal dynamics of human socio-economic needs and land use on islands; (ii) the spatial distribution of ecosystem services relevant for human populations; (iii) the impacts of local-scale processes, both social and ecological, on large-scale island ecosystem dynamics; (iv) the role and importance of current protected areas for the spatial distribution and population dynamics of native (and in particular endemic), exotic and invasive species; and (v) the impacts of invasive species and climate change on the distribution of already restricted island endemic species.

### New methods for island biogeography

Although islands are in many ways simpler model settings for biogeography and conservation studies, they are still complex systems. Therefore, commonly used statistical modelling techniques are often unable to reflect patterns and processes at multiple spatial and temporal scales. Incorporating the temporal component, which adds an extra layer of complexity, has recently led to great advances through the use of phylogenetic methods (see above), the development of the General Dynamic Model (Whittaker et al. 2008) and the development of methods that are capable of modelling directional spatio-temporal processes determined by island emergence (Carvalho et al. 2015).

However, this is just the beginning.

Ecological systems have been studied using two complementary modelling approaches. The classical top-down approach primarily studies emergent patterns through correlations of varying complexity. Mechanistic bottom-up models (e.g. agent-based mModels, ABMs, also known in biology as individual-based models, IBMs) directly simulate processes, providing biological explanations of how components (biotic or abiotic) work causally together to produce a given pattern. In ABMs, the objects of study are the individuals themselves. Intrinsic to each individual are a number of characteristics modelled by different rules or equations. A given explanatory variable, either intrinsic (e.g. energy accumulated) or extrinsic (e.g. temperature), is used to model the dependent variable (e.g. movement propensity), not only to make predictions but also to find direct causality between variables. From scales as small as a petri dish to the entire globe, ABMs are now extensively used to find mechanistic relations between individuals and the environment, including within island biogeographical studies (e.g. Rosindell and Phillimore 2011), being an ideal way to directly study colonization, speciation and extinction processes. Making them spatially explicit further enhances their power. Several multi-agent programmable modelling environment platforms are available, of which NetLogo<sup>7</sup> is probably the most used, but there are many other possibilities (Nikolai and Madey 2008).

Models, either classical or mechanistic, are usually found and parametrized based on theoretical reasoning. Finding hidden relationships, models and even principles in a collaborative human–machine effort is now possible through the use of massive computational power (Schmidt and Lipson 2009, Cardoso et al. 2015). A particularly interesting approach to island biogeography is the use of artificial intelligence (AI) methods that are able to cope with a range of data form and size, to find both classical and mechanistic models. AI includes the field of evolutionary computation, a large set of methods of which the better studied are genetic algorithms (Holland 1975). Within this

field, symbolic regression (SR; Koza 1992), which searches for both the formal structure of functions and the fitting of parameters simultaneously, was recently proposed as a possible way to evolve free-form equations purely from data, often without prior human inference or hypotheses (Cardoso et al. 2015). Nature is usually not linear and yet, except when some theoretical models are available (e.g. island species–area relationships [ISARs] and GDM), we are still mostly using linear models (GLMs and related techniques). Compared with linear approaches, symbolic regressions (SR) are fully flexible in the shape of the relationships between predictor and dependent variables, allowing a much better fit of data. SR also has several advantages over other, commonly used, highly flexible regression (e.g. GAMs) or machine-learning (e.g. neural networks) techniques. Most importantly, the evolved equations are human-readable and interpretable. Interpretability allows new ideas to formulate general models and theoretical principles. SR was used with success, among other applications, to find new models for the ISARs and the GDM (Cardoso et al. 2015, Vujić et al. 2016).

The application of ABM, SR and other innovative solutions should be explored for their potential to reveal patterns of diversity across multiple taxa and regions and the processes that may explain these. Ideally the data used should be the result of standardized sampling to generate local diversity metrics (alpha diversity) to understand (a) replacement and loss or gain of species in space and time (i.e. true turnover and richness differences in beta diversity; Carvalho et al. 2012), (b) how these influence large-scale patterns in regional pools (gamma diversity), and (c) how to make best use of increasingly available high-quality remote sensing, genetic and functional data.

## Conclusions

Integrative biogeographical studies on islands are lacking. Limitations are sometimes severe and innovative approaches are needed. Here we have identified the need to downscale island biogeog-

<sup>7</sup> <https://ccl.northwestern.edu/netlogo/>, last accessed 30<sup>th</sup> June 2016



raphy to local scale, creating opportunities for long-term ecological and biogeographical research. There is a need for population-level sampling of species or species complexes distributed across multiple islands to investigate dispersal over recent timescales, both among and within islands. The integration of agent-based models and symbolic regression techniques will help biogeographers to explore local- to large-scale ecological patterns and processes within and across islands and archipelagos, eventually leading to better conservation and policy decisions.

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