



Original article

Using species abundance distribution models and diversity indices for biogeographical analyses

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ABSTRACT

We examine whether Species Abundance Distribution models (SADs) and diversity indices can describe how species colonization status influences species community assembly on oceanic islands. Our hypothesis is that, because of the lack of source-sink dynamics at the archipelago scale, Single Island Endemics (SIEs), i.e. endemic species restricted to only one island, should be represented by few rare species and consequently have abundance patterns that differ from those of more widespread species. To test our hypothesis, we used arthropod data from the Azorean archipelago (North Atlantic). We divided the species into three colonization categories: SIEs, archipelagic endemics (AZEs, present in at least two islands) and native non-endemics (NATs). For each category, we modelled rank-abundance plots using both the geometric series and the Gambin model, a measure of distributional amplitude. We also calculated Shannon entropy and Buzas and Gibson's evenness. We show that the slopes of the regression lines modelling SADs were significantly higher for SIEs, which indicates a relative predominance of a few highly abundant species and a lack of rare species, which also depresses diversity indices. This may be a consequence of two factors: (i) some forest specialist SIEs may be at advantage over other, less adapted species; (ii) the entire populations of SIEs are by definition concentrated on a single island, without possibility for inter-island source-sink dynamics; hence all populations must have a minimum number of individuals to survive natural, often unpredictable, fluctuations. These findings are supported by higher values of the α parameter of the Gambin mode for SIEs. In contrast, AZEs and NATs had lower regression slopes, lower α but higher diversity indices, resulting from their widespread distribution over several islands. We conclude that these differences in the SAD models and diversity indices demonstrate that the study of these metrics is useful for biogeographical purposes.

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1. Introduction

Community ecology is dominated by idiosyncratic results and few general laws (Lawton, 1996; Storch et al., 2008; Beck et al., 2012; Passy, 2012). Many ecological processes are contingent on the temporal and spatial scale in which they operate (Gaston and Lawton, 1990; Gaston and Blackburn, 1996; Fraterrigo and Rusak, 2008), which makes it difficult to identify recurrent patterns and processes. Moreover, completely different processes can lead to

very similar patterns (Gaston et al., 2000; Starzomski et al., 2008), which can impede inferring processes from patterns.

Most work that has been done in community ecology to characterize species assemblages according to their abundance relied on the study of patterns of species abundance distributions (SADs), because they are considered one of the most basic descriptors of a community (Magurran, 2004; McGill et al., 2007). In general, local communities tend to have mostly rare and only few common species (Magurran, 2004; McGill et al., 2007), and there are many proposed explanations for the underlying processes, ranging from niche-based competition to neutral processes (Hubbell, 2001; Gravel et al., 2006; Vergnon et al., 2009; Matthews and Whittaker, 2014a).

The study of species abundances in community ecology has led

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to the development of two main approaches that are now routinely used to describe communities: species abundance distribution models, typically represented by rank-abundance plots, and diversity indices (Hayek and Buzas, 2010). Although the mechanisms leading to particular distribution models or diversity values are difficult to be established, the study of community structure by species abundance distribution models and diversity indices has proven useful in shedding light on a variety of community characteristics, including how they are affected by environmental disturbances (Magurran, 1988, 2004; Hayek and Buzas, 2010; Dornelas, 2010).

The same statistical tools used in community ecology could be profitably used to investigate SADs of assemblages defined by criteria different from those used to define communities, i.e. groups of organisms occupying a particular area, usually interacting with each other and their environment. For example, species can be grouped according to their persistence (such as core versus satellite, or native versus vagrant species; see Holloway, 1996; Magurran and Henderson, 2003; Matthews et al., 2014a) or colonization history (e.g., endemic versus non endemic), and one can ask how species abundances change within and among these categories. This may be important to develop hypotheses about the effect of species' history, dispersal and colonization ability on community structure. However, as far as we know, no research has attempted to use species abundance distribution models and diversity indices to compare species groups defined on the basis of broad biogeographical categories such as those that express their level of endemism.

Oceanic islands are good models to examine whether SADs and diversity indices can clarify how biogeographical categories can influence relative species abundances. Indeed, oceanic islands form discrete isolated spaces where the biogeographical status of their species can be established easier than in continental systems, where continuous ecological gradients make biogeographical characterization more subjective (after all, any species can be considered as endemic to a certain area, depending on the way the area is defined, i.e. it is a question of scale, Laffan and Crisp, 2003). In general, oceanic islands contain a large number of endemic species, either through *in situ* speciation (neoendemism), or through the extinction of species outside the islands (palaeoendemism) (Lomolino et al., 2010). These endemic species may occupy several islands (Archipelagic Endemics, hereafter AREs) or be restricted to one particular island (Single Island Endemics, hereafter SIEs). Such species, together with other native but non-endemics (hereafter NATs) form the three distinct biogeographical categories into which the species inhabiting an archipelago can be grouped. A further category may be represented by exotic (introduced) species, which are however not considered here because their presence is due to human introduction.

Our basic hypothesis is that these three biogeographical categories (SIEs, AREs, and NATs) are characterized by different patterns of relative abundance of individuals. In particular, we hypothesize that rare species (i.e. species having small size populations) should be less common among the SIEs than in other categories, because their distribution restricted to single islands determines the lack of source-sink dynamics necessary for maintaining viable populations of species with reduced population size (i.e. rescue effects, see Hanski, 1994; Sutherland et al., 2012). Because of the small number of individuals that form their populations, rare species are more sensitive to demographic accidents that increase the likelihood of local extinction (e.g. Allee's effect; Lande et al., 2003; Freckleton et al., 2005), which leads, in turn, to a lower probability of persistence on single islands, i.e. as SIEs. Therefore, the SADs of SIEs should be characterized mainly by a predominance of abundant species, well adapted to specific island environmental conditions,

and few rare species (see, for example, Borges et al., 2006). The few rare SIEs species may be signatures of past extinctions of archipelagic endemics formerly distributed on more islands but now restricted to only one island, or SIEs really evolved on single islands (see Borges et al., 2006; Gaston et al., 2006). By contrast, since AREs and most NATs are distributed on different islands of an archipelago, inter-island source-sink dynamics should maintain a substantial amount of rare species (Freckleton et al., 2005; Matthews et al., 2014a). In addition, it is well known that there is a correlation between species range size and abundance, with widespread species being also more abundant (a pattern known as the positive interspecific abundance-occupancy relationship, Gaston and Lawton, 1990; Gaston et al., 2000, 2006). Therefore, AREs and NATs should include both rare species, which occur on few islands and have low mean abundance, and common species, which occur on most islands and are abundant on most of them. Following Taylor's Power Law (see Gaston et al., 2006), this should generate, for AREs and NATs, SADs less strongly affected by the dominance of few, extremely abundant species and, hence, less steep rank abundance patterns.

To test these predictions, we analysed the rank-abundance distribution and diversity patterns of the arthropods inhabiting the Azorean Islands, a volcanic archipelago located in the North Atlantic. Using the Azores as a model system, we expect to demonstrate the utility of SADs and diversity indices to disentangle fundamental ecological processes among groups of species having different biogeographical origins.

2. Materials and methods

2.1. Fieldwork

The Azorean archipelago is located in the North Atlantic, 37°–40° N and 25°–31° W. It comprises nine main islands and some small islets aligned along a roughly WNW-ESE trend. All islands are of volcanic origin (ranging from 250,000 years B.P. in Pico - Demand et al., 1982 - to 8.12 Myr B.P. in Santa Maria - Abdel-Monem et al., 1975). Documents from the 15th century suggest that native vegetation almost completely covered all of the islands until when the first human settlements were established. Clearing for wood, agriculture and pasture have markedly reduced the native forests, which are now largely restricted to high and steep areas (Martins, 1993; Gaspar et al., 2008). Here, we focused on arthropod species, which are the most diverse animal group in the Azores (Borges et al., 2010) and for which we have large sets of species standardized abundance data. Species abundance data used in the present study were collected during several field surveys carried out from 1999 to 2007. Arthropods were collected using standardized protocols targeting both soil and canopy communities. Sampling was conducted in 100 sites in 18 native forest fragments in seven islands (BALA project; Borges et al., 2005, 2006; Ribeiro et al., 2005; Gaston et al., 2006; Gaspar et al., 2008). We laid out a minimum of four independent 150-m long, 5-m wide transects in each forest fragment, with more transects in larger fragments. We sampled the epigeal arthropod fauna using 30 pitfall traps (100 ml each) per transect for at least a two-week period during summer months. Half of the pitfall traps contained an attractive solution (Turquin solution, Turquin, 1973), while the remaining had a non-attractive solution with a small proportion of ethylene glycol. The two types of traps were placed alternately. Canopy arthropods from woody shrub and tree species were sampled using a beating tray in the same period of trap functioning. Ten beating samples were taken at 10-m intervals from each of the three most dominant woody plant species in the site (Ribeiro et al., 2005) covering part of the original 150-m transect.

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