Comparison of discrete and continuum community models: insights from numerical ecology and Bayesian methods applied to Azorean plant communities

Tese de Mestrado

Diogo Cláudio Pavão

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Comparison of discrete and continuum community models: insights from numerical ecology and Bayesian methods applied to Azorean plant communities

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Diogo Cláudio Pavão

Orientadores

Professor Doutor Luís Filipe Dias e Silva

Professor Doutor Rui Miguel Pires Bento Silva Elias

Tese de mestrado submetida como requisito parcial para obtenção do grau

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“The pattern of variation shown by the distribution of species among quadrats of the earth’s surface chosen at random hovers in a tantalizing manner between the continuous and the discontinuous.”

Webb 1954

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List of Abbreviations

AAN - Accumulated abundance normalized

AAN' – Instantaneous variation of abundance with elevation

DIC - Deviance Information Criterion

NE – Numerical Ecology

NMDS - Non-Metric Multidimensional Scaling

SSI - Simple Structure Index

UPGMA - Unweighted Pair Group Method with Arithmetic Mean

Abstract

Our view of community ecology has evolved over time, beginning with two extreme visions of plant communities which were considered either as species associations driven by random coincidences or as complex organisms with clear interdependencies. The phytosociological approach was mainly linked to the latter, including the development of syntaxonomy. More recently, biological communities tend to be viewed as set of local community assemblages that are linked by dispersal of multiple potentially interacting species (i.e. a metacommunity), a concept that has been used to explain spatio-temporal dynamics. Several models have been proposed to explain the distribution patterns of species and communities along environmental gradients, ranging from discrete, individual community types, to a continuum of plant communities. The Azorean natural vegetation is a good study model to test those hypotheses, since it has been described in detail by several authors therefore creating the opportunity to address theoretical questions within a conceptual metacommunity framework. Through a combination of numerical ecology and Bayesian analyses applied to natural plant community data from the Azores archipelago, the present study evaluated if the present data supports the existence of "discrete community types" or of a "continuum of communities". We used hierarchical clustering (Hellinger distance and UPGMA) and non-hierarchical clustering (k-means clustering), as well as a multinomial model in a Bayesian context to determine the number of plant community groups. A total of 139 plant communities and 85 species were sampled in five islands. The optimum number of plant community groups ranged from 4 to 6 for hierarchical clustering, and neared 43 for non-hierarchical clustering and about 70 for the multinomial analysis. The elevation distribution curves estimated for the vascular plant species suggest that species distributions are determined by physiological limits at the extremes, and by competition under intermediate conditions, but with some niche partitioning between dominant species. Our results would be in agreement with an ecological view of the communities as a continuum, more than with a view considering the existence of discrete community types. Understanding these patterns is an essential ingredient in sustainable vegetation management, especially on this unique natural laboratory, the Azores.

Key Words: Azores; Bayesian methods; community models; metacommunities; natural vegetation; numerical ecology.

Resumo

A nossa visão da ecologia de comunidades tem evoluído ao longo do tempo, partindo de duas visões extremas das comunidades vegetais, uma em que foram consideradas como associações de espécies, conduzidas por coincidências aleatórias, e outra em que foram consideradas como organismos complexos com claras interdependências. A abordagem fitossociológica está principalmente ligada à última abordagem, incluindo o desenvolvimento da sintaxonomia. Mais recentemente, as comunidades biológicas tendem a ser vistas como um conjunto de comunidades locais ligadas através da dispersão de múltiplas espécies que, potencialmente, interagem entre si (i.e., uma metacomunidade). Este conceito de metacomunidade, tem sido usado para explicar dinâmicas espácio-temporais. Têm sido propostos diversos modelos para explicar os padrões de distribuição das espécies e comunidades ao longo de gradientes ambientais, que incluem desde tipos de comunidade individuais e discretas, até um continuum de comunidades vegetais. A vegetação natural dos Açores é um bom modelo de estudo para testar essas hipóteses, pois tem sido descrita em detalhe por diversos autores, possibilitando a abordagem de questões teóricas, no âmbito dos conceitos ligados às metacomunidades. O presente estudo avaliou se os dados relativos às comunidades vegetais naturais do arquipélago dos Açores apoiam a existência de "tipos de comunidades discretas" ou um "continuum de comunidades", através da aplicação de métodos na área da ecologia numérica e de análises bayesianas. Foram usados métodos de aglomeração hierárquica (distância de Hellinger e UPGMA) e não-hierárquica (k-means cluster), bem como um modelo multinomial num contexto bayesiano para determinar o número de grupos de comunidades vegetais. Foram amostradas um total de 139 comunidades vegetais e 85 espécies em cinco ilhas. O número ótimo de grupos de comunidades vegetais variou entre 4 e 6 para os métodos de aglomeração hierárquicos, aproximou-se de 43 para os métodos de aglomeração não hierárquicos, e foi de cerca de 70 para a análise multinomial. As curvas de distribuição em função da altitude, estimadas para as espécies de plantas vasculares, sugerem que a respetiva distribuição é determinada pelos limites fisiológicos nos extremos e pela competição em condições intermédias, mas com uma possível partição de nichos entre as espécies dominantes. Os nossos resultados estão mais de acordo com uma visão ecológica das comunidades ao longo de um continuum, do que com a existência de tipos de comunidades discretas. A compreensão destes padrões é essencial na gestão sustentável da vegetação, especialmente neste laboratório natural único, os Açores.

Palavras-chave: Açores; ecologia numérica; metacomunidades; métodos bayesianos; modelos de comunidades; vegetação natural.

Introduction

The phytosociological approach

During the past 100 years, plant ecologists have been devoted to devising and systematizing methods for the description and classification of plant communities. This modern way of classifying vegetation was established by Braun-Blanquet, the scientist who developed phytosociology in Europe, in the early years. On his early papers (Braun-Blanquet 1921) he recognized the clear distinction between abstract units, particularly associations, and concrete representative stands in the field. In his studies, plant communities were conceived as types of vegetation, recognized by their floristic composition where, amongst the listed species, some are more sensitive expressions of a given relationship than others (i.e. differential species).

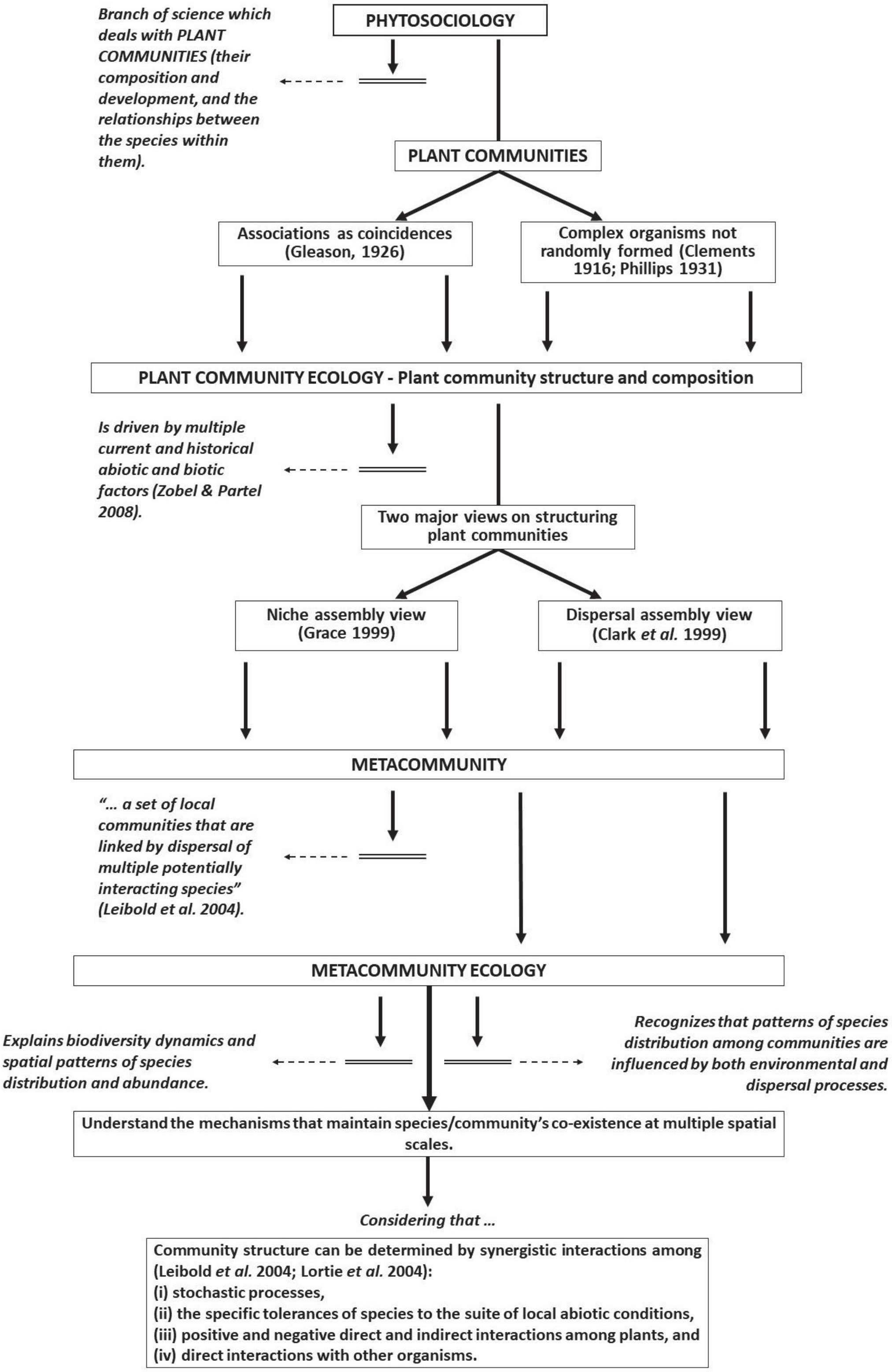
Plant community ecology

In the early days of plant community ecology there have been contrasting views concerning the processes that assemble plant communities. Thus, authors such as Clements (1916) and Phillips (1931), viewed plant communities as complex organisms, suggesting that these communities (organisms) were not randomly formed and only existed in certain combinations (e.g. resulted from co-evolution). On the other hand, Gleason (1926) led the opposite thinking, that is, that the species associations that led to the formation of plant communities were not organisms, but resulted from random coincidences of environmental selection (i.e. the lichens on a tree-trunk enjoy a different environment from the adjacent herbs growing on the forest floor). These two theories have been addressed by more recent authors (e.g. Lortie *et al*. 2004) and are considered as extremes in a conceptual gradient, where both stochastic and deterministic processes contribute to the formation of community assemblages (figure 1).

Meanwhile, other views have emerged, namely an increasing focus on the use of individual-based models in ecology (e.g. Huston *et al.* 1988), where properties of individual organisms and the mechanisms by which they interact with the environment can be measured. Theories based on the competition within communities and on the predictive capabilities of such mechanistic competition models were discussed (Tilman 1982), while the importance of fluctuations in species abundances (base on resource competition models) was also considered (Huisman & Weissing 1999).

More recent studies have shown that the processes that promote diversity may change across communities (Cavender-Bares *et al.* 2009). Therefore, plant community composition and structure are driven by multiple current and historical abiotic and biotic factors. Recent empirical evidence suggests that historic factors (Zobel & Pärtel 2008) and dispersal limitation (Zobel & Kalamees 2005) may be important determinants for community composition and ecology (figure 1). There are two major, complementary, views on the rules at work in structuring plant communities.

Considering all these factors, the need to explain the assembly of local communities remains a major focus in plant community ecology. More recently, some ecologists, realized that some theories emphasizing competition or predation paint an incomplete, and in some cases misleading picture of our understanding of the structure and organization of ecological systems.



Branch of science which deals with PLANT COMMUNITIES (their composition and development, and the relationships between the species within them).

Is driven by multiple current and historical abiotic and biotic factors (Zobel & Partel 2008).

"... a set of local communities that are linked by dispersal of multiple potentially interacting species" (Leibold et al. 2004).

Explains biodiversity dynamics and spatial patterns of species distribution and abundance.

Recognizes that patterns of species distribution among communities are influenced by both environmental and dispersal processes.

Understand the mechanisms that maintain species/community's co-existence at multiple spatial scales.

Community structure can be determined by synergistic interactions among (Leibold *et al.* 2004; Lortie *et al.* 2004):
(i) stochastic processes,
(ii) the specific tolerances of species to the suite of local abiotic conditions,
(iii) positive and negative direct and indirect interactions among plants, and
(iv) direct interactions with other organisms.

Figure 1. An historical conceptualization of plant communities. Each definition/aim is represented by a pair of horizontal lines which are illustrated by hatched lines and the corresponding description is in bold italics adjacent to the symbol. Solid arrows depict the conceptualization of plant communities over the years.

In fact, there are different possible explanations for species absences or disappearances from a site (Kraft *et al.* 2015): either they are unable to tolerate the new abiotic conditions (i.e. trade-offs resulting in reduced allocation to growth and reproduction) or the changing conditions result in altered biotic interactions (i.e. leading to increased fitness differences with competitors).

The metacommunity approach

Communities will cover a range of different dependencies among species, determined by the relative importance, and variation in space, of each filter (e.g. altitude) that acts upon the species pool, crediting communities with more complexity and dynamics (Götzenberger *et al.* 2012). While community ecology as a field is concerned with explaining the patterns of distribution, abundance and interaction of species in communities, in the past, much of formal community theory was focused on a single scale, assuming that local communities were closed and isolated (i.e. May 1973). However, the interactions and demography of local communities can be influenced by various kinds of spatial dynamics, including interactions among local communities at larger scales (metacommunities) (Chase & Leibold 2002). A metacommunity is a set of local community assemblages that are linked by dispersal of multiple potentially interacting species, with dynamic processes leading to exchange of species among different communities and evolutionary processes occurring within communities (Leibold *et al.* 2004). Therefore, metacommunity ecology is concerned with explaining biodiversity dynamics and spatial patterns of species distribution and abundance while recognizing that those patterns are influenced by both environmental and dispersal processes (e.g. Fernandes *et al.* 2014), that occur across different spatial scales (Meynard *et al.* 2013) (figure 1). Thus, a fundamental goal of metacommunity ecology is to understand the mechanisms that maintain species/community's co-existence at multiple spatial scales, by considering that community structure can be determined by synergistic interactions among (i) stochastic processes, (ii) the specific tolerances of species to the suite of local abiotic conditions, (iii) positive and negative direct and indirect interactions among plants, and (iv) direct interactions with other organisms (Leibold *et al.* 2004; Lortie *et al.* 2004) (figure 1).

Community assemblage patterns along an environmental gradient

Van der Maarel (2005, pp. 60), proposed a spectrum of six hypothetical community patterns and the respective underlying explanatory mechanisms for the composition of the vegetation along an environmental gradient:

- Pattern a) is defined by communities as organisms (i.e., as co-evolved groups of species) arrayed along an environmental gradient – the extreme concept of a community viewed as an organism. Species abundance curves along the gradient are symmetric bell-shaped, with more or less amplitude, depending on how much co-evolution occurred on each community;

- Pattern b) is based on the niche concept of species partitioning of a resource along a gradient, where the species have equal ranges and amplitudes and are equally spaced along the gradient. Species abundance curves along the gradient are symmetric bell-shaped;

- Pattern c) represents independent niche partitioning of species within strata (trees, shrubs, etc.) - basically, the result is a continuum of communities with each species showing a response partially determined by its growth form. Species abundance curves along the gradient are symmetric bell-shaped with range and amplitude depending on strata;

- Pattern d) defines niche partitioning for dominant species (major species, e.g. trees) and individualistic distribution of understory species (minor species) (Gauch & Whittaker 1972). Major species have symmetric bell-shaped abundance curves, while minor species have irregular curves (irregular range and amplitude);

- Pattern e) is specific for tree species: at the extremes, species distributions are determined by physiological limits, but under intermediate conditions, species distributions are determined by competition (Austin 1999). Species abundance curves are symmetric bell-shaped, except on limits where it extends or not (amplitude), depending on physiological limits;

- Pattern f) corresponds to a vegetation continuum determined by the individualistic species distribution and has no pattern along the gradient. All species have irregular abundance curves (irregular range and amplitude).

Testing community assemblage models in the Azores

The primordial vegetation of the Azores was firstly described by Gaspar Frutuoso (1589a,b,c), and later Seubert (1844), Morelet (1860), Guppy (1917), Tutin (1953), Dansereau (1970) and Sjögren (1973a,b) added, field information data about the occurrence of many species, and descriptions about the main altitudinal vegetation belts, often based on a phytosociological approach (see table 5 on Elias *et al.* 2016). More recently, Dias (1996) described the types of natural vegetation in the Azores using a classification based in floristic and structural data (i.e., using biovolume); and 20 years later Elias *et al.* (2016) presented a classification of the zonal vegetation coupled with a modelling approach that allowed estimating the potential distribution of primordial vegetation on the entire archipelago. Meanwhile, Marcelino *et al.* (2014), Queiroz *et al.* (2014) and Silva *et al.* (2017) used Bayesian methods to validate plant community assemblages along environmental gradients, within a metacommunity approach. Therefore, we have conditions in the Azores to study the different models proposed by van der Maarel (2005).

Research aim and hypotheses

Within the conceptual metacommunity framework (i.e. Heino *et al.* 2015) we aim to test the different scenarios proposed by van der Maarel (2005) using a data set consisting of 139 plots (Elias *et al.* 2016), describing the remaining areas covered by primordial plant communities in the Azores. To test the different scenarios, we will use both numerical ecology and Bayesian methods applied to plot data, and also species distribution curves with elevation. We hope therefore to clarify if the target vegetation in the Azores is more closely described by a set of discrete community types, by a continuum of plant communities, or by one of the alternative scenarios described above.