A macroecological approach to study aquatic macrophyte distribution patterns

Abordagem macroecológica no estudo de macrófitas aquáticas

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Abstract: Aim: Macroecology is a useful tool in the determination of species distribution patterns. Large scale data about the distribution area of aquatic macrophytes in Brazil are scarce. The objective of this study was to analyze the geographic distribution of 56 species, belonging to two families (Potamogetonaceae and Characeae) of aquatic macrophytes in Great Britain and Ireland, examining the relationship of this distribution with the plant size and latitude (Rapoport's rule); **Methods:** Data were obtained from the literature and reorganized in a grid containing 418 quadrats. The ellipse method was used to estimate areographics parameters such as central position, distribution form and extent of occurrence; **Results:** Most species have relatively small range sizes, a pattern found for many assemblages. The broad distribution ranges of some species (e.g. *Potamogeton natans* and *Potamogeton polygonifolius*) have often been taken as compelling evidence of high dispersal rates. The aquatic macrophytes distribution corroborated Brown's model where large sized species must have large areas of occupancy to avoid extinction. Rapoport's rule was observed to hold only for the Characeae; **Conclusions:** Patterns in the geographic distribution of aquatic plants have been ignored in the macroecological literature. However, we did detect some of the patterns that are recurrently detected in other groups of organisms (e.g., Brown's model and Rapoport's Rule). Therefore, our results add to the growing body of research that suggests the importance of mechanisms operating in large spatial scales.

Keywords: areography, aquatic macrophytes, Potamogetonaceae, Characeae, Rapoport's rule.

Resumo: Objetivo: A macroecologia é uma importante ferramenta na determinação de padrões na distribuição das espécies. Dados sobre a distribuição de macrófitas aquáticas em grande escala no Brasil são escassos. Assim, o objetivo deste trabalho foi o de analisar a distribuição geográfica de 56 espécies de macrófitas aquáticas, pertencentes a duas famílias (Potamogetonaceae e Characeae), na Grã Bretanha e Irlanda, examinando a relação da distribuição com o tamanho das espécies e com a latitude ("efeito Rapoport"); **Métodos:** Os dados sobre a distribuição das espécies foram obtidos da literatura e reorganizados em uma gride contendo 418 *quadrats*. O método da elipse foi utilizado para estimar os parâmetros areográficos como posição central, forma da distribuição e extensão de ocorrência; **Resultados:** A maior parte das espécies de macrófitas aquáticas apresentou pequena área de distribuição geográfica, assim como observado para outros grupos de organismos. A ampla distribuição de algumas espécies (e.g. *Potamogeton natans* e *Potamogeton polygonifolius*) provavelmente se deve a um alto potencial de dispersão destas. A relação da área de distribuição das espécies com o tamanho destas corroborou a idéia de Brown, onde espécies de maior tamanho tendem a ocupar áreas maiores, evitando, assim, a extinção. O efeito Rapoport foi observado apenas para as espécies pertencentes à família Characeae; **Conclusões:** Os padrões de distribuição de plantas aquáticas têm sido ignorados na literatura macroecológica. No entanto, nós detectamos alguns dos padrões que são recorrentemente detectados para outros grupos de organismos (e.g., modelo de Brown e regra de Rapoport). Portanto, nossos resultados coadunam com o número crescente de pesquisas que sugere a importância de mecanismos que operam em grandes escalas espaciais.

Palavras-chave: areografia, macrófitas aquáticas, Potamogetonaceae, Characeae, efeito Rapoport.

1. Introduction

Macroecology is the study of relationships between organisms and their environment at large spatial or/and temporal scales, explaining statistical patterns of abundance, distribution and diversity (Brown, 1995). Areography is a branch of macroecology that studies the structure of the geographic range of organisms (Rapoport, 1982). This approach is a useful tool for determining the distribution patterns of a group of species and to gain understanding of the ecological and evolutionary process that explain such patterns (Cordeiro, 2001).

Species range size is a function of the equilibrium between the adaptation capability and the potential of dispersion (Kirkpatrick and Barton, 1997). In this way, the distribution range could be associated to morphological size, population density, dispersion and latitudinal variations (Brown et al., 1996; Gaston et al., 1998; Duncan et al., 1999). Range size estimates have also been applied as criteria in prioritizing species and areas for conservation, and are also important in assessing the impact of changing environmental conditions on species distributions (Mace, 1994; Quinn et al., 1996).

There is a tendency for the geographical ranges of species to increase with latitude (Rapoport, 1982). Evidence for narrower environmental tolerances of low-latitude species associated with an increase of latitudinal ranges of species from low to high latitudes is a phenomenon which Stevens (1989) called Rapoport's rule. Rapoport's rule has been mainly tested on animal groups (Rohde, 1996; Mourelle and Ezcurra, 1997; Ruggiero and Lawton, 1998). A comprehensive analysis of the geographic distribution of aquatic plants can offer a further test for the generality of latitudinal Rapoport effects. Besides, Stevens (1992) has also pointed out that mean altitudinal range size tend to increase with elevation, as a consequence of species with broader climatic tolerances occurring at higher altitudes.

The goal of this study was to highlight the potential of macroecological analysis applied to limnology. The specific objective was to i) analyze the geographic distribution of 56 species of aquatic macrophytes in Great Britain and Ireland and, the relationship with the aquatic macrophyte morphological size, and ii) to examine the validity of Rapoport's rule for aquatic macrophytes, and the relationship between the geographic distribution and altitude.

2. Material and Methods

Since large scale data about the area of occupancy of aquatic macrophytes in Brazil are scarce, we used data on the distribution of aquatic macrophytes in Great Britain and Ireland. The distribution of species in Great Britain and Ireland was obtained from maps in the literature (Moore, 1986 and Preston, 1995, for the Characeae and Potamogetonaceae, respectively). These distribution maps

were redrawn in a grid map with 418 quadrats, 26 x 26 km square. In total 56 species belonging to three different families (Potamogetonaceae, Ruppiaceae and Characeae) were analyzed.

The Potamogetonaceae (which contains the genera *Potamogeton* and *Groenlandia*) is closely related to the Ruppiaceae (which comprises a single genus, *Ruppia*), and many recent authors (e.g. Jacobs and Brock, 1982; Dahlgren et al., 1985; Cook, 1990; Preston, 1995) have treated the Ruppiaceae as a subfamily of the Potamogetonaceae. Thus, for this study, these two families (Potamogetonaceae and Ruppiaceae) are analyzed together as a single evolutionary unit.

The area of occupancy (A_o) of aquatic macrophytes was defined using a single measure, the number of occupied quadrats of the grid. This variable is an estimate of the area where the species actually occur (Gaston, 1994).

The ellipse method (Maurer, 1994) was used to estimate the areographic parameters such as central position, distribution form, and extent of occurrence (E_o) (i.e. the ellipse area that is limited by the points where the species occurred). This extent of occurrence was calculated by the Equation 1:

$$E_o = \pi\sqrt{\lambda_1\lambda_2} \tag{1}$$

where each eigenvalue λ was obtained through a Principal Component Analysis (PCA) of geographical coordinates (latitude and longitude) of the quadrats in which each species occurs and $\pi = 3.142$.

A Pearson coefficient of correlation was calculated to test the relationship between area of occupancy (A_o) and extent of occurrence (E_o).

The ellipse form (F) (also called range shape) was also obtained based on the two eigenvalues through the following index (Equation 2):

$$F = \frac{\lambda_1 - \lambda_2}{\lambda_1 + \lambda_2} \tag{2}$$

An estimate of the central geographical distribution was calculated through the latitudinal midpoint and longitudinal midpoint of the occurrence points of each species, as (Equations 3 and 4)

$$\text{Longmid point} = \frac{\max\text{long} - \min\text{long}}{2} \tag{3}$$

$$\text{Latmid point} = \frac{\max\text{lat} - \min\text{lat}}{2} \tag{4}$$

where maxlat and minlat are the latitudinal maximum and minimum values, respectively, and maxlong and minlong are the longitudinal maximum and minimum values, respectively.

The relationship between geographic distribution (given by area of occupancy - A_o) and macrophytes size was tested to investigate whether Brown's model can be applied to aquatic plants. According to this model, small size species could have different area o occupancy while the large ones must have large areas of occupancy (Brown and Maurer, 1987; Brown, 1995). The data about macrophyte size was obtained from the literature (Moore, 1986; Preston, 1995) representing the stem length of the plants.

To validate Rapoport's rule, the latitudinal midpoint of each species was correlated with their area of occupancy (A_o). This latitudinal effect was just tested in the Great Britain region, due to it represents a continuum and greater continent. A Pearson coefficient of correlation was calculated to test the relationship between these estimates. It is important to consider that the geographical limitation of the continent at higher latitudes may influence the geographical range of the species. In this way, with the objective to exclude this influence, we also calculated the proportional number of quadrats occupied by the species considering the total number of quadrats between the latitudinal maximum and minimum point of the species.

Given the importance of altitude in this environment, we applied a multiple regression considering latitude, longitude and altitude as independent variables. A mean altitudinal range of species at a given site was calculated by averaging the altitudinal range of each species present. Species recorded at some land below 1,000 ft were classified as 0, over 1,000 ft were classified as 1, over 2,500 ft were classified as 2 and over 3,500 ft were classified as 3.

3. Results

We found a positive and significant relationship between the log-transformed values of A_o and E_o (r = 0.623: Figure 1). The frequency distribution of the geographical range sizes of species tends to be unimodal, with a strong right-skew (Figure 2). That is, most species have relatively small range sizes (corresponding to around 50 quadrats), and a few have relatively large ones (approximately 6 species have their area of occupancy represented by more than 200 quadrats). Most of these species with large geographic distribution belong to the Potamogetonaceae (*Potamogeton natans, P. polygonifolius, P. perfoliatus, P. berchtoldii, P. crispus, P. pectinatus*). The species of the Characeae with wide distributions are *Chara vulgaris* var. *vulgaris* (116 quadrats) and *Nitella flexilis* var. *flexilis* (112 quadrats).

Most of the species have circular distributions, mainly species with large area of occupancy, with *F*-values ranged from 0.2 to 0.4 (Figure 3). The small-sized species of both families have large variation in distribution area (Figure 4). Only two widely distributed species have large stem length (*P. natans* and *Potamogeton lucens*). The data corroborated the Brown model where small species can have different
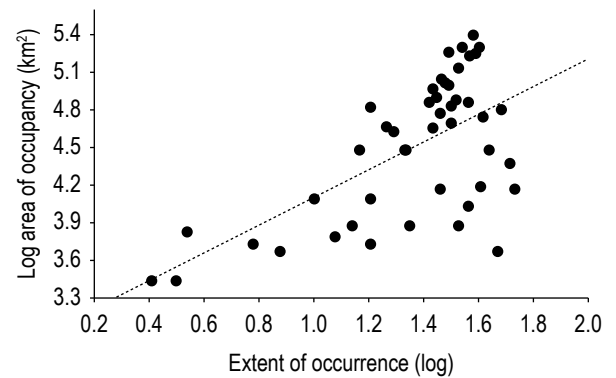
Figure 1. Relationship between the logarithm of extent of occurrence (Eo) and the area of occupancy (Ao) of the aquatic macrophyte species of Great Britain and Ireland.
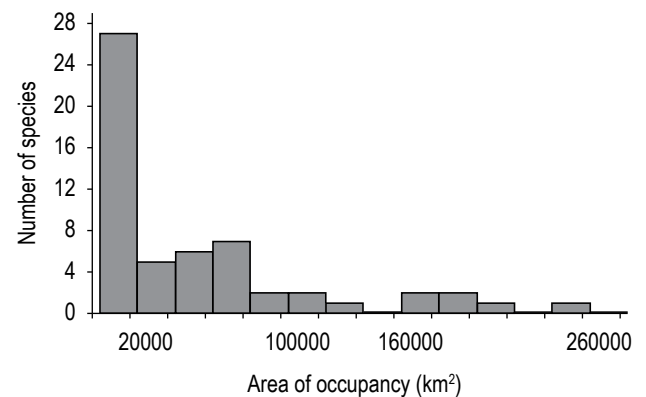

Figure 2. The frequency distribution of the geographical range sizes of aquatic macrophyte species of Great Britain and Ireland. Geographical range size is normally distributed when log transformed.
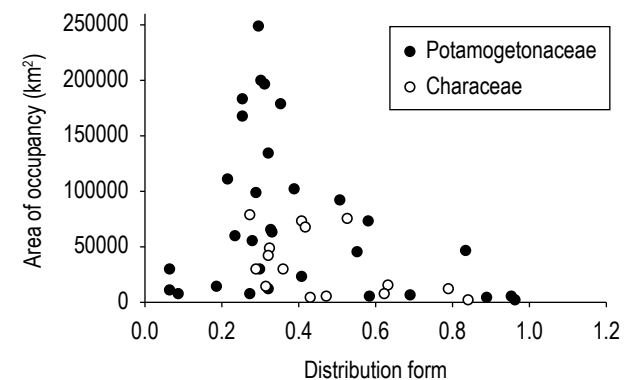
Figure 3. Relationship between the distribution form and the area of occupancy (A_o) of both families of aquatic macrophytes. The form varies from 0 (circular) to 1 (elongate).

areas of occupancy while the large size species must have large areas of occupancy

A significant and positive correlation was found between the area of occupancy (log) and latitudinal midpoint for the species belonging to the Characeae (r = 0.80; p < 0.001:
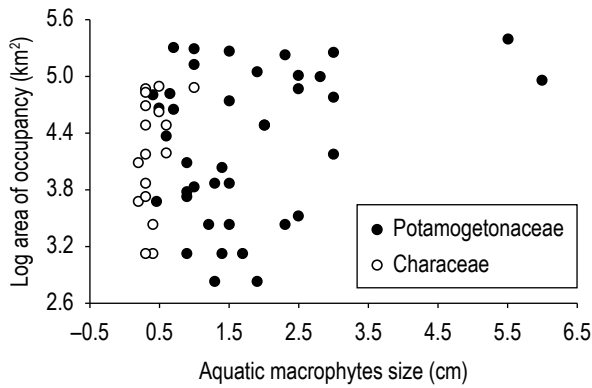
Figure 4. Relationship between the aquatic macrophytes size and the area of occurrence (A_o).

Figure 5a). Even when we considered the geographical limitation of the continent at higher latitudes, only the Characeae show a positive correlation between geographic range and latitude (r = 0.55; p = 0.028) (Figure 5b).

We also applied a multiple regression considering latitude, longitude and altitude as independent variables. There is no influence of altitude on the area of occupancy (log) of Potamogetonaceae (p = 0.88) and Characeae (p = 0.27). Considering the proportional number of quadrats occupied, we also observed the same pattern for Potamogetonaceae (p = 0.87) and for Characeae (p = 0.75).

4. Discussion

There is an increasing interest in the role of large scale processes in determining the structure of local communities, based on quantitative aspects of species distributions, and in assessing the impact of changing environmental conditions on these distributions (Mace, 1994; Quinn et al., 1996). The large scale study of aquatic plants is interesting in the sense to find some patterns that can explain the geographical range of some species and to observe how the influence of environmental impacts could be the responsible for the changes in the distribution of these species (Chambers et al., 2008).

A significant and positive correlation between the extent of occurrence (E_o) and area of occupancy (A_o) is necessary for consistency of areographical parameters (calculated through the ellipse method). Species with wide extents of occurrence are likely to have large areas of occupancy, whilst species with narrow extents of occurrence are likely to have small areas of occupancy (Gaston, 1991). Of more interest is the magnitude of the correlation between the two measures, indicating that it is possible to use the estimates calculated through the ellipse method to determine the general tendencies in the geographical patterns of the aquatic macrophytes.

The frequency distribution of the geographical range sizes of species revealed an approximately log-normal curve.
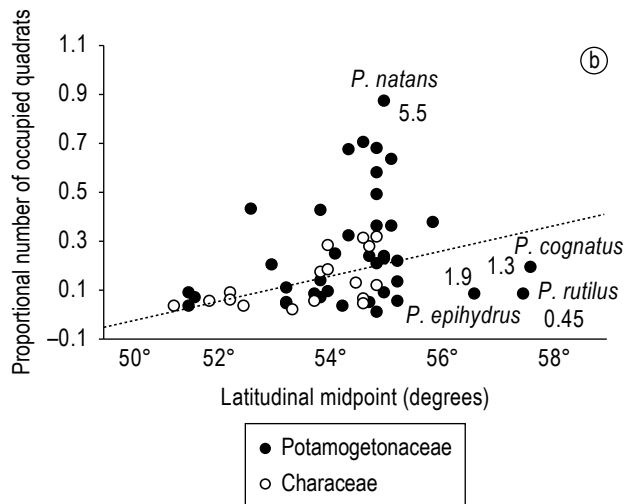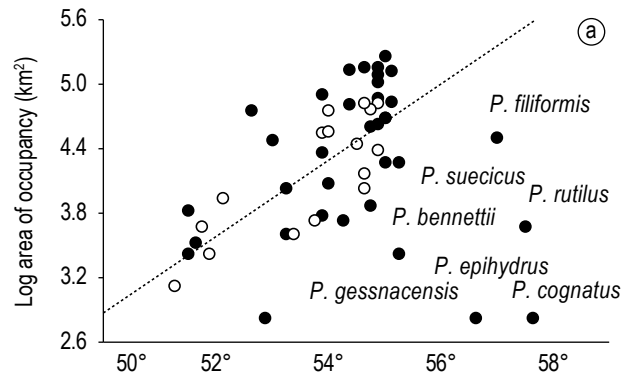
Figure 5. a) Relationship between the area of occupancy (log) and the latitudinal midpoint of aquatic macrophytes species in Great Britain and Ireland (r = 0.80; p < 0.001, for Characeae) b) Relationship between the proportional area of occupancy and the latitudinal midpoint of the aquatic macrophytes species (r = 0.55; p = 0.028, for Characeae).

This is a pattern found for many assemblages (Brown, 1995; Blackburn and Gaston, 1996; Gaston, 1998). The relative small range size of most species of aquatic macrophytes appears to be another of those very general emergent statistical characteristics of taxonomic assemblages. It appears to reflect another fundamental way that species within taxonomic groups have divided up the earth's resources, in this way by inhabiting different amounts of geographic space (Brown, 1995). The pattern also implies that related species differ widely in their ecological requirements.

The broad distribution ranges of some aquatic macrophytes have often been taken as compelling evidence of high dispersal rates (Santamaría, 2002). According to Jacobs and Wilson (1996) the distributional patterns are best explained by a combination of dispersal, vicariance and local speciation. The dispersal of stems and fruits is probably aided by their buoyancy. Preston (1995) found that the fruits of *Potamogeton perfoliatus* could float for one to

six months, those of *P. lucens* and *P. polygonifolius* for six to 12 months and those of *P. natans* for over 12 months. Thus, the large distribution range of *P. natans, P. polygonifolius, P. perfoliatus* can probably be attributed to high dispersal rates (buoyancy of their fruits), and higher tolerance to eutrophication, when compared to Charophytes.

The distribution of aquatic macrophytes is affected in the long term by changes in climate and in the shorter term by sucessional processes which modify the habitat of some water bodies, and most heavily, influenced by man (Santamaría, 2002). Many species have extended their range by colonizing artificial habitats such as field ponds, drainage ditches, reservoirs, ornamental lakes and others (Preston, 1995).

The range shape (*F*) of the aquatic macrophytes showed a circular distribution (values nearest to zero) for both families analyzed. Probably, the aquatic macrophytes distribution does not follow any systematic pattern such as north/south and/or east/west.

One of the most obvious variables that affect abundance is size of the organism. Hutchinson and MacArthur (1959) noted that the distributions of land mammals of Michigan and Europe were highly skewed, such that there were many more species of relatively small mammals than of large or extremely small ones. They suggested that this pattern reflect the capacity of the species to be relatively more specialized and hence to subdivide space and resources more finely (Brown, 1995). Any resource available in the environment could seemingly support either many small organisms or a few large ones. Thus, the same resource should support more species of small body size than of large. Groups of organisms as different as bacteria, trees, insects, fishes, and mammals all show the pattern described above (many more species of small size than of large).

The aquatic macrophytes of Great Britain and Ireland corroborate this pattern (Brown's model) with small species having varying area of occupancy while large species such as *Potamogeton natans* and *P. lucens* have large areas of occupancy. The central idea of Brown's model is that geographical range in large-bodied species should be sufficiently large to maintain minimum viable populations and to avoid extinction (Diniz-Filho and Fowler, 1998). In contrast, small-bodied species are not subject to the same constraint and may occupy either small or large geographic ranges. This triangular pattern is called the "range restriction". According to Brown (1995) large-bodied species are extremely unlikely to have small ranges, resulting in a triangular relationship which is truncated at large geographic ranges.

Rapoport's Rule (Stevens, 1989) establishes a positive correlation among the geographic range and the latitude of occurrence of the species. In other words, species with higher latitudinal midpoints have evolved broader tolerances to climatic factors than those species with lower latitudinal midpoints and the broad tolerance has in turn led to wider latitudinal extent in the geographical ranges of high-latitude species than in the ranges of lower-latitude species. This rule was validated in the present study for the species belonging to the Characeae (Figure 5a). When we take off the geographical continental constriction (the proportional number of quadrats occupied by the species considering the total number of quadrats between the latitudinal maximum and minimum point of the species) we observed the same pattern, increase of latitudinal ranges of Characeae from low to high latitudes. Probably, these species have large tolerances to the great climatic variability at higher latitudes. Some Potamogetonaceae species have greater environmental tolerances (i.e. *Potamogeton cognatus, P. rutilus*) but they have smaller areas of occupancy.

Recent global changes in climate and habitats modified by man have caused many changes in species distribution. Many of the documented changes in the pondweed flora (Potamogetonaceae) of local sites are the result of eutrophication (Preston, 1995, Murphy, 2002). This effect favours species which prefer eutrophic conditions, such as *P. crispus* and *P. pectinatus,* and which have wide geographic range. Thus, in eutrophic lakes, erect and canopy-forming angiosperms are superior competitors over bottom-dwelling forms (e.g. the macroalgae charophytes), probably due to the fast growth and shading of other plants (Carpenter and Adams, 1977; Blindow, 1992). In addition, species with restricted distributions may be among the most vulnerable to habitat loss or degradation (Lawton, 1994).

Patterns in the geographical ranges of aquatic plants species have received remarkably little attention and there are very few data sets of extensive area coverage for Brazilian aquatic plants. Further studies should contribute to increase understanding the processes that drive the geographical distribution of these species.

Acknowledgements

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