SHORT COMMUNICATION

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Biogeographic methods identify gymnosperm biodiversity hotspots

Abstract A remarkable congruence among areas of endemism, panbiogeographic nodes, and refugia in western North America, Japan, south-western China, Tasmania, and New Caledonia indicates that these areas deserve special status for conservation. Here we propose that areas identified by different biogeographic methods are significant candidates for designation as hotspots.

Introduction

The current loss of biodiversity places a premium on the task of identifying hotspots (Myers et al. 2000). In addition to the criteria currently used for discovering them, biogeographic methods also have a relevant role to play (Morrone and Espinosa 1998; Luna et al. 2000). We examine herein the application of different biogeographic methods to identify hotspots for gymnosperms, based on the congruence among areas of endemism, panbiogeographic nodes, and Pleistocene refugia.

Currently there are several approaches used in the analysis of the geographic distribution of organisms. In the nineteenth century, it was proposed that the Earth could be divided into biogeographic realms and regions (e.g., De Candolle 1820; Sclater 1858) that were later divided into smaller zones, known as subregions, domains, provinces, and districts. This regionalization, based on the presence of endemic plant and animal taxa, led to the delimitation of areas of endemism, which were defined by several taxa with restricted ranges. Nowadays, areas of endemism represent the basic units in cladistic biogeography and can help determine priorities for biodiversity conservation. These areas of endemism are also known as centers of endemism, distribution centers, core areas, dispersal centers, and centers of evolution (Haffer 1985).

The concept of node is a contribution of the panbiogeographic approach, originally developed by Croizat (1958, 1964). A node represents a geologically and biotically complex area (Craw 1982), which is recognized by the intersection of two or more generalized tracks (Craw 1982), in turn obtained from the overlap of individual tracks of different plant and animal taxa (Morrone and Crisci 1995). Heads (1989) proposed that nodes have four main features: (1) presence of endemic taxa, (2) absence of widespread taxa, (3) phylogenetic and geographic relationships or affinities with several areas at once, and (4) phylogenetic and geographic boundary zones. Based on these biologically significant features, some authors have proposed the identification of nodes as priority areas for biodiversity conservation (Morrone and Crisci 1992; Grehan 1993; Morrone and Espinosa 1998; Luna et al. 2000).

The model of Pleistocene refugia, originally proposed by Haffer (1969), represents a model of allopatric speciation on a subcontinental scale, which was originally developed to explain the high taxonomic diversity of birds in tropical South America, especially in the Amazonian area. Refugia were considered by many authors as areas with stable climatic conditions during dry periods following a reduction of a once more extensive habitat, which allowed some organisms to survive there during adverse climatic conditions. In addition, they are considered areas of taxonomic differentiation for some, but not necessarily all, the taxa inhabiting them (Cracraft 1985). Delimitation of refugia is based primarily on geomorphological, geological, and palynological studies, and secondarily on distributional data of endemic taxa (Haffer 1982, 1985), although there exists some controversy on the criteria for recognizing refugia (Amorim 1987). Refugia have been identified in both tropical and temperate areas of the world (Haffer 1982) and a conservation program based on refugia has been proposed for tropical South America (Brown 1987).

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Gymnosperm distributional patterns

The revision of data from different bibliographic sources led us to recognize the congruence among these three concepts in some geographic areas. Distributional data of gymnosperm genera were obtained from revisionary studies on the orders Cycadales (Jones 1993; Osborne et al. 1999), Coniferales (Silba 1984, 1990; Farjon 1990), and Ginkgoales (Liguo et al. 1999). Distributions of all genera were mapped and this information allowed us to recognize areas of endemism and construct individual and generalized tracks. On these maps, a marked congruence in the geographic distribution was observed for different gymnosperm genera, which led us to recognize 23 areas of endemism (Contreras-Medina 2001) (Fig. 1a).

A panbiogeographic analysis of gymnosperm genera showed the existence of some generalized tracks and nodes (Fig. 1b) in New Caledonia, New Zealand, southern China, south-eastern Australia, western North America, Tasmania, and Japan (Contreras-Medina et al. 1999).

If we compare the above results with the world distribution of refugia according to Haffer (1982) (Fig. 1c), congruence among some areas of endemism, nodes, and refugia is evident for the gymnosperm taxa analyzed, which is remarkable because these methods are generally viewed as competing approaches. The concept of refuge is closely related to the notion of area of endemism, although not identical. Areas with high concentrations of endemic taxa have been considered as refugia by many authors (e.g., Toledo 1982); however, Cracraft (1985) argued that some of them represent areas of high speciation but are not necessarily refugia. A similar caveat was stated by Brown (1987) in the overlap between endemic centers and forest refuges. The relationship between areas of endemism and nodes was somehow allowed by Craw's (1989) definition of a node: as "an area of endemism where two or more generalized tracks overlap".

Congruence between areas of endemism and nodes does not exist in all cases for gymnosperms, but some nodes may represent areas of endemism for other groups of organisms. Similarly, areas of endemism that do not coincide with nodes for gymnosperms may represent nodes for other taxa.

Five areas are identified by all three biogeographic approaches: Tasmania, New Caledonia, Japan, southwestern China, and western North America (Fig. 1d). The remaining areas are only congruent among two of the three approaches: for example the Valdivian and Mesoamerican areas represent both areas of endemism and refugia; north-eastern Australia represents a node and a refuge; and New Zealand represents an area of endemism and a panbiogeographic node. Notwithstanding, some of the areas proposed are supported by the three approaches if we consider other sets of taxa, e.g., Mesoamerica is a node based on animal and plant distributions (Croizat 1958; Luna and Contreras-Medina 2000), whereas north-eastern Australia represents an
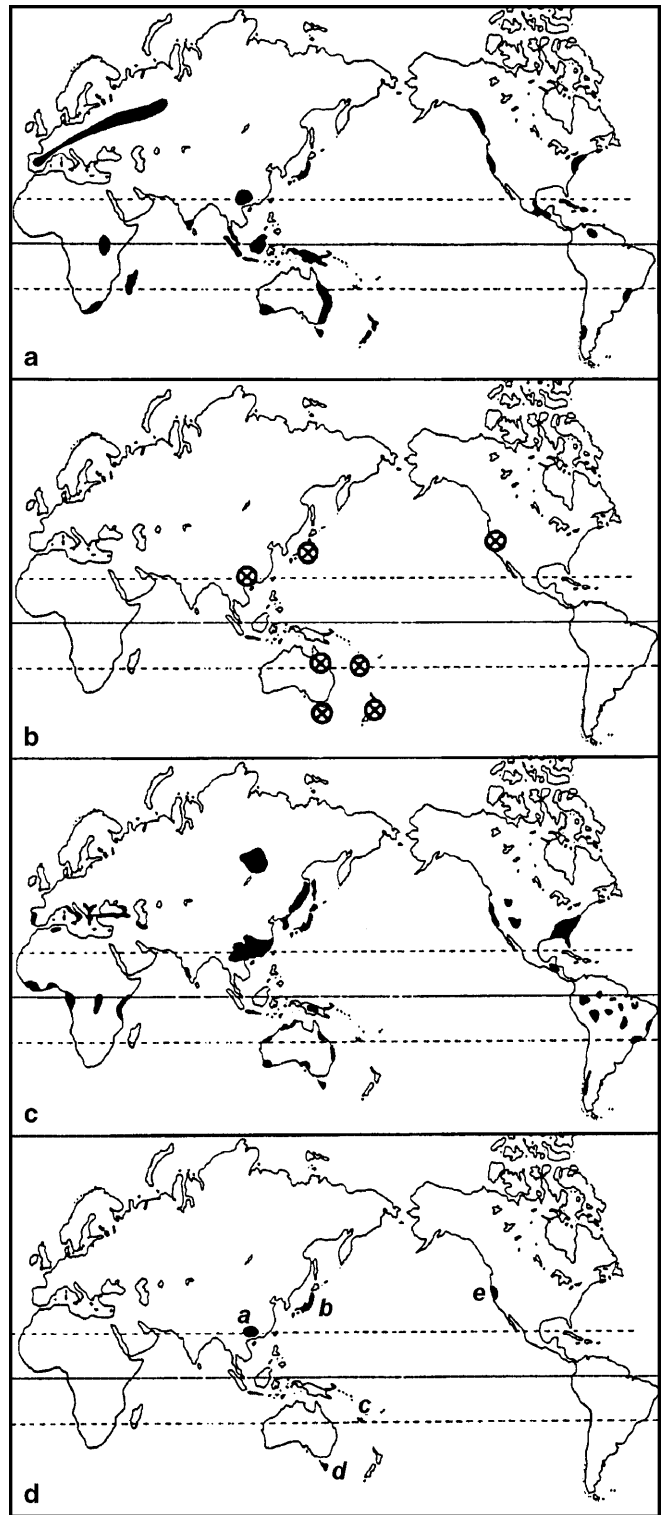

Fig. 1 a Areas of endemism proposed for gymnosperm genera; **b** nodes proposed from a panbiogeographic analysis of gymnosperm genera (modified from Contreras-Medina et al. 1999); **c** refugia proposed in the world (modified from Haffer 1985); **d** hotspots resulted from overlap among areas of endemism, panbiogeographic nodes, and Pleistocene refugia: *a* south-western China, *b* Japan, *c* New Caledonia, *d* Tasmania, *e* western North America

area of endemism for birds (Cracraft 1991) and beetles (Wang et al. 1996).

Hotspots

Biogeographic studies can contribute useful information to conservation policies, e.g., areas of endemism may represent a key in a solid conservation plan and panbiogeographic nodes may represent biotically complex areas which deserve conservation (Morrone and Crisci 1992). The application of panbiogeographic methods in conservation biology has been proposed in New Zealand (Grehan 1989) and Mexico (Morrone and Espinosa 1998; Luna et al. 2000). Nodes have also been considered as hotspots (Grehan 1993; Luna et al. 1999); these areas may be also particularly important for conservation biology purposes, because they contain biotic elements from different origins. Refugia have been considered as areas with the highest species richness (Toledo 1982), and for this reason they could be considered in a conservation plan (Brown 1987).

The term 'hostpots' has been used by Prendergast et al. (1993) and Gaston and Williams (1996) to refer to areas of extreme taxonomic richness. It should be noted, however, that this term was originally used to refer to areas where high levels of richness, endemism, and human threat coincide (Myers 1988, 1990). There is a significant congruence among the five areas discussed and the hotspots of the world identified by Myers et al. (2000). In this latter study, 25 hotspots were proposed for the world; we add to this list two new areas, namely Tasmania and Japan, based on the overlap of methods applied in this study from gymnosperm distribution.

The coincidence among different approaches invites an explanation, which may be either methodological or ontological. From a methodological viewpoint, it might be possible that the different methods, although radically different, share some basic procedures which may lead to the same results, especially considering that endemism plays a role in all of the approaches. In contrast, it is also possible that areas with high diversity values may be detected by the different approaches. We think that the latter option is the most plausible explanation for our finding, although further studies are still required to test the congruence between the patterns here observed in relation to other taxa.

At present, it seems that the fundamental question in conservation biology is: what to protect? From this perspective, biogeography can and should play a key role (Morrone and Espinosa 1998; Luna et al. 2000). Areas identified by all three approaches are of conservation importance due to: (1) their appropriate climatic conditions (refugia); (2) the historical factors that have been important in their evolution (nodes); and (3) the restricted distributions of some taxa that inhabit them (areas of endemism). In this sense, ecological and historical biogeographic studies focused in these areas can be used to formulate conservation plans in the countries where they are located.

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