Nature conservation in Amazonia: the role of biological theory in reserve delimitation

Conservación de la naturaleza en la Amazonía: El rol de la teoría biológica en la delimitación de las reservas

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Abstract
Large-scale conservation programmes were not implemented in Amazonia until the 1970s. In Peru and Brazil, most conservation areas were established in the -70s through -90s. Delimitation of reserves relied on theories on the distribution of Amazonian biodiversity, developed since the -60s. This paper analyses the credibility of those theories, and recommends new conservation strategies.

The most influential theories in Brazil were Prance's phytogeographical scheme and Haffer's refuge hypothesis. They explained uneven distribution of species with supposed fragmentation of the rainforest in the Pleistocene. Phytogeographical representativeness and protection of the refuges were recommended as conservation goals. In Peru, the aim has been to conserve all ecosystem types.

Holdridge's 'life zone' theory used in Peru to identify ecosystem types is too crude for Amazonia. The refuge hypothesis has received heavy criticism. The Amazonian forest apparently was not fragmented in the Pleistocene. Data on species distributions are severely inadequate.

The new biological paradigm emphasises geological-hydrological disturbance, and fine-scale ecological heterogeneity. Habitat types discernible in satellite images could be used as surrogates for species in reserve selection.

The new paradigm should rapidly be implemented. Currently conservation is based on erroneous scientific theories and, hence, arbitrary in its ability to protect Amazonian biodiversity.

keywords: Brazil; Ecological heterogeneity; Life zone ecology; Peru; Refuge hypothesis

Resumen
La Amazonía abarca el bosque húmedo tropical más grande del mundo. Esta área ha sido por mucho tiempo considerada uno de los centros más importantes de biodiversidad a nivel global. Sin embargo, iniciativas a gran escala con miras a la protección de los bosques de la Amazonía, no fueron implementadas hasta los finales de los años setenta. En el Perú y Brasil, los países amazónicos principales, la mayoría de las reservas naturales fueron establecidas en 1970–1990. Estas fueron delimitadas en base a las recomendaciones derivadas de teorías sobre la distribución

espacial de la biodiversidad en la Amazonía, postuladas desde los años sesenta. En otras palabras, la conservación de la naturaleza en la Amazonía está casi exclusivamente basada en teoría biológica de la segunda mitad del siglo XX. Este artículo analiza la credibilidad de esa teoría y recomienda nuevas estratégias de conservación.

Las teorías de mayor trascendencia en Brasil son el esquema fitogeográfico de Prance y la hipótesis de refugios de Haffer. Esas teorías explican la distribución heterogénea de las especies como producto de la fragmentación del bosque húmedo-tropical, durante períodos de clima árido en el Pleistoceno. Las recomendaciones para la conservación amazónica subrayaron representatividad fitogeográfica y la protección de los refugios. En el Perú, la red de reservas ha sido diseñada para cubrir todos los tipos de ecosistemas identificados.

La teoría ecológica de las zonas de vida de Holdridge, la que se ha utilizado en el Perú para identificar tipos de ecosistemas, es demasiado cruda para la Amazonía. La hipótesis de refugios ha recibido críticas severas. El bosque amazónico aparentemente no estuvo fragmentado en el Pleistoceno. Además, los datos sobre la distribución de las especies son gravemente inadecuados.

El nuevo paradigma biológico de la Amazonía remarca perturbación geológica e hidrológica, y heterogeneidad ecológica a una escala detallada. Al menos en la Amazonía Occidental, el gran número de especies parece deberse a una diversidad de hábitats tipo mosaico, originado por procesos modificadores históricos y contemporáneos. Tipos de hábitats perceptibles en imágenes de satélite podrían ser utilizadas como sustitutivos de las especies en la delimitación de las reservas.

El nuevo paradigma debería ser implementado rápidamente, si se desea mejorar la conservación de las especies amazónicas. Actualmente, la conservación está basada en teorías científicas erradas, y por lo tanto, está arbitraria en lo referente a su eficacia de proteger la biodiversidad de la Amazonía.

palabras claves: Brasil; Heterogeneidad ecológica; Zonas de vida; Peru; Hipótesis de refugios

Introduction

Amazonia harbours the world's largest tropical rainforest. The region has long been considered one of the globally most important biodiversity centres. However, serious initiatives towards protecting Amazonian forests were not implemented until the late 1970s, when large-scale plans were prepared for a nature reserve network of the entire region. In Peru and Brazil, the principal Amazonian countries, most nature reserves were established in the 70s through 90s. Most of the reserves were delimited on the basis of recommendations derived from theories on the distribution of Amazonian biodiversity. These theories had been developed since the 60s. Nowhere else on the globe has contemporary scientific understanding affected conservation programme design as directly as in Amazonia (Foresta 1991). The scientific community has the responsibility to evaluate that understanding, because if it proves wrong, it renders inappropriate most actions taken towards the conservation of Amazonian biodiversity.

The fundamental question is, whether the present conservation area network even in theory has the potential of protecting all Amazonian species. To answer this question, I shall outline the

biological theories that have been most influential in the delimitation of reserves, and how the theories have been applied in Brazil and Peru. I then describe critique presented against these theories, and give an account on more recent biological and geological studies that have given rise to a new biological paradigm for Amazonia. I conclude with some recommendations for future refinement of the Amazonian conservation area network.

Reserve delimitation in Brazil and Peru

Two biological theories formed the basis for the nature reserve network established between the late 70s and early 90s in Brazilian Amazonia. One was Prance's (1977) phytogeographical scheme, the other Haffer's (1969) Pleistocene refuge hypothesis. Prance derived eight floristically distinct provinces in Amazonia from distribution patterns in five plant families. Haffer explained observations of bird distribution patterns with repeated fragmentation of the Amazonian rainforest into refuges during Pleistocene climatic cycles. The refuges would have acted as species repositories, and speciation and repopulation centres. Consequently, the hypothesis holds, we can still find centres of high species richness and endemism where the forest survived throughout the Pleistocene. Distribution patterns congruent with this hypothesis were observed in, i.a., lizards (Vanzolini & Williams 1970), plants (Prance 1973), and butterflies (Brown 1975).

The two theories were applied to conservation in an assessment called "An analysis of Nature Conservation Priorities in the Amazon" (Wetterberg et al. 1976; hereafter referred to as "the Amazon Analysis"). A conservation area network was recommended that would include sufficient representation of all eight phytogeographical provinces. The reserves were recommended to be placed in the supposed refuges. A third biological theory was utilised in giving second priority to locations where several vegetation types occurred. These were identified, i.a., using the vegetation map by Pires (1974, cited after Jorge Pádua & Bernardes Quintão 1982). The selection of over 75% of the strictly protected area in Brazilian Amazonia has relied on the Amazon Analysis (IUCN 1992).

Although Peruvian authorities recognised the recommendations of the Amazon Analysis (Jorge Pádua & Bernardes Quintão 1982), conservation in Peru has relied on different theories. The aim has been to create a reserve network that would protect all Peruvian ecosystem types, or 'life zones' (*sensu* Holdridge 1947). These were identified using Tosi's (1960) ecological map and its later biogeographical refinement (Dourojeanni 1990; CDC-UNALM 1991).

Critique of the applied theories

The refuge hypothesis was formulated to explain observed biotic patterns, but it was also backed by lithostratigraphical, geomorphological, and biostratigraphical observations (Damuth & Fairbridge 1970; Absy & Van der Hammen 1976; Brown & Ab'Saber 1979; Simpson 1982). However, all evidence from these fields has been refuted on the basis of inadequacy, irrelevancy, or plain faultiness (Räsänen et al. 1987; Salo 1987; Bush 1994; Colinvaux 1996). On the other hand, new palynological data show that the Amazonian forest block has been continuous throughout the Pleistocene, albeit somewhat smaller and compositionally different during glacial maxima (Bush 1994; Colinvaux 1996).

From a conservationist's point of view, it is all but irrelevant whether the refuge hypothesis as an explanation to observed biogeographical patterns is correct or not. What counts is where the greatest numbers of species are to be found. Unfortunately we do not know even that. Firstly, suggested locations of refuges, based on different organism groups, overlap as little as if they were randomly placed (Beven et al. 1984). Secondly, the more detailed surveys on Amazonian biota are conducted, the more evident becomes the degree of ignorance still prevalent. Some of the observed patterns of endemism in plants are artefacts of severely biased collecting activity (Nelson et al. 1990). In a recent attempt to use biological museum collections to assess conservation priorities in Amazonia, it was noticed that over 25% of the 472 1°×1° grid cells in Amazonia had no records of the 421 plant, arthropod, fish, and primate species analysed in the study (Kress et al. 1998). A dataset of 323 species of pteridophytes and 297 species of the angiosperm family Melastomataceae shows that 39% and 27% of the species, respectively, occurred only in one of four different collecting areas in western Amazonia (Ruokolainen et al. In press). When only unidentified species of the same dataset were considered (16% and 56% of the totals, respectively), the same portions rose to 75% in the pteridophytes and 50% in the melastomes. These results show that restricted-range species are still largely unknown due to lack of collecting. Hence, the understanding of biogeographical patterns is likely to change significantly with the increase of data.

The 'life zone' scheme (Holdridge 1947) is an acceptable theoretical framework for classifying vegetation. But the physical variables used to delimit different vegetation types (precipitation and temperature) do not vary much within the Amazonian lowlands. Consequently, Amazonia comprises only a few different life zones. Conserving samples of these clearly is not enough for conserving all Amazonian species.

The new Biological Paradigm

The traditional biological view of long-term stability and large-scale environmental homogeneity in Amazonia started to change in the late 1960s towards the paradigm invoking Pleistocene climatic lability as an explanation for regional biotic differences. The idea of present-day ecological homogeneity was, however, largely retained. The new view profoundly affected nature conservation, as described above. It was at its most popular in the mid-80s, when a quite different picture started to emerge.

Not only was the refuge hypothesis heavily criticised, but new information on present-day disturbance regimes and the geological past was also presented. First, profound disturbance through channel changes of rivers was documented for the western parts of Amazonia. An analysis of satellite images showed that 26.6% of the modern lowland forest had characteristics of recent erosional and depositional activity (Salo et al. 1986). This confirmed that habitat heterogeneity was one of the main reasons of high species numbers. Next, new insight on the effect of sub-Andean tectonics showed that fluvial disturbance had occurred from the Tertiary through the Quarternary causing a mosaic of fossil and present floodplains in Amazonia (Räsänen et al. 1987). Finally, evidence accumulated showing that in forests outside current fluvial disturbance (*tierra firme* forests), floristic composition correlates with properties of the soil (Young & León 1989; Poulsen & Balslev 1991; Kahn & de Granville 1992; van der Werff 1992; Tuomisto & Ruokolainen 1994; Tuomisto & Poulsen 1996; Ruokolainen & Tuomisto 1998). As a

result of these findings, it is only fair to state that the biological paradigm has changed once again. Now Amazonia has to be viewed as an area of ancient and ongoing geological and hydrological disturbance—and as an area of considerable ecological heterogeneity. These ideas are summarised by Tuomisto et al. (1995). Their satellite image analyses show that western Amazonia harbours more than 100 biotope types.

While it is of utmost importance to recognise this most recent Amazonian biological paradigm, it must be noted, though, that it is probably more pronounced in the western parts, and that we still do not know much about the central and eastern parts of the region in this regard. There is still a tremendous scientific ignorance concerning the existence of different ecosystem types within Amazonia (see e.g. Schulman et al. 1999). Furthermore, there are very few data on how animal distributions relate to the documented ecological heterogeneity.

Future reserve delimitation

In the introduction to this presentation I stated that the fundamental question in Amazonian conservation today is, whether the existing conservation area network has the potential of protecting all Amazonian species. Due to lack of knowledge of species distribution patterns, it is currently impossible to answer this question. However, it is clear that the biological theories used as a basis for network design, represent an imperfect, if not simply erroneous understanding of the Amazonian nature. Hence, even if the proposed reserve system were established in its entirety, it would, at the very best, be arbitrary in its ability to save Amazonian biodiversity.

The theories applied in Brazil and Peru for conservation area delimitation have a fundamental difference. Those used in Brazil are direct approximations of species occurrences. In Peru, the conservation units are surrogates for species, in the sense that it is assumed, though not explicitly proven, that different species inhabit the different ecosystems. Due to the prevailing scientific ignorance, we cannot directly rely on species distributions in selecting reserves. Hence, using surrogates is the only efficient solution. But the problem is how to choose the appropriate surrogate.

Vegetation mapping in the Amazon basin has progressed since the 1970s. For the Brazilian "Legal Amazon" 28 vegetation types have been identified (IBGE & IBDF 1988). Recent conservation recommendations relied on this classification (Fearnside & Ferraz 1995). However, no vegetation classification of sufficient resolution exists to detect the ecological heterogeneity recognised using remote sensing by Tuomisto et al. (1995). Even without a formal description of vegetation types, patterns visible in satellite images can, nevertheless, be used as surrogates for species distributions in conservation area selection. Floristic differences correlate quite well with reflectance values in Landsat TM images (Ruokolainen & Tuomisto 1998). Therefore I suggest Landsat image analyses be used to map ecological heterogeneity in all of Amazonia. The results should then be used for a gap analysis of the existing reserve network, and the network developed on the basis of the analysis.

Nature conservation should not be a one-time project, but rather an ongoing process. Any conservation area system should be continuously refined to reflect improving scientific understanding. In the case of Amazonia, this was indeed pointed out already by those who formulated conservation recommendations in the 70s (Jorge Pádua & Bernardes Quintão 1982;

Foresta 1991). Science now provides new insight on the Amazonian nature that should already be incorporated into conservation efforts. However, we are still far from a satisfactory understanding of the spatial patterns of Amazonian biodiversity, let alone the processes that created and maintains it. Therefore, basic research must continue. But we must also ensure that there is a continuous dialogue between scientists, policy-makers, and non-governmental organisations that often implement conservation decisions. Today this is more important than ever, since economically and technically oriented, large-scale development programmes, such as the trans-oceanic highway, pose severe threats to pristine Amazonian nature.

Acknowledgements

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List of special symbols

°: degree symbol
×: multiplication sign
–: n-dash
—: m-dash