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Discussion

Amazon floodplain fish communities: Habitat connectivity and conservation in a rapidly deteriorating environment

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ABSTRACT

The Amazon River Basin contains the world's highest fish species diversity, with a hydrologic cycle that creates a patchy distribution of floodplain lakes at low water and affords dispersal and colonization opportunities through reconnected lakes, rivers, and flooded forests during high water. This connectivity is increasingly threatened by dam construction and droughts caused by climate change. Although the metapopulation framework has not been widely applied to freshwater ecosystems, it should represent a fruitful approach to conservation of important fish stocks and species diversity in Amazonian floodplains. Our examination of the evidence for metapopulation structure reveals that: (1) Although many economically important migratory species are not currently metapopulations (either demographically or genetically), connectivity is crucial to their life histories and anthropogenic stresses may induce metapopulation structure in these species; (2) Some large migratory pimelodid catfish with homing behavior to natal headwater streams appear to be the most spatially expansive metapopulations in existence among freshwater fish; (3) Non-migratory species are less well studied, but some (perhaps many) such species already exist as metapopulations and are vulnerable to disruptions in patterns of connectivity. Connectivity plays a crucial role in each of these cases, so the most promising conservation strategies involve: (1) reduction in dam building; (2) establishment of large enough protected areas to incorporate high β diversity and maintain patterns of connectivity during anomalous low water events; (3) implementation of governmentally facilitated community-based fishing agreements to curb overexploitation and monitor sustainable population levels and connectivity in protected areas.

1. Introduction

The Amazon River Basin, which encompasses the world's largest remaining tropical rainforest, has the highest diversity of fish species of any region in the world, with more than 2000 species identified so far (Reis et al., 2003). Much of this high fish diversity can be attributed to the physical complexity of the system, including variation in water depth, temperature, acidity, velocity, sediment and nutrient loads, and relative isolation of floodplain lakes from the river and each other (Freitas et al., 2010b). These factors have promoted adaptive radiation into a wide variety of local environments with different selective regimes: large river channels, floodplain lakes and streams, and seasonally flooded forests. The Amazon Basin is quite old, initially formed near the end of the Cretaceous, with diversification of major Amazonian freshwater fish lineages such as characins, cichlids and catfish occurring during the Paleogene, between 65 and 23 million years ago (Hoorn et al., 2010).

The threats to biodiversity caused by the loss of tropical ecosystems are frequently documented and discussed (e.g., Malhi et al., 2008; Bradshaw et al., 2009), but the emphasis has generally been on the terrestrial component of these systems. Aquatic ecosystems within tropical regions are faced with a number of anthropogenic threats: overfishing (Batista et al., 1998), invasive alien species (Latini and Petrere, 2004; Pelicice and Agostinho, 2008a), hydroelectric dam-building (Finer and Jenkins, 2012; Araújo et al., 2013), deforestation (Phillips et al., 2009, Lobón-Cerviá et al., 2015) and droughts caused by both deforestation

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and global warming (Marengo et al., 2008, Freitas et al., 2013b, Nazareno and Laurance, 2015). Globally, freshwater ecosystems cover less than 1% of the earth's surface but account for a substantial fraction (about 6%) of total described species, and therefore are worthy of greater attention in general (Dudgeon et al., 2006). Regionally, the aquatic portion of the Amazon Basin covers more than 1 million km^2, and produces 18% of the earth's river discharge (Castello et al., 2013). The fish component of this ecosystem represents significant biodiversity, comprising about 7% of the 28,000 known fish species (Hickman et al., 2014). Further, many species have been exploited by human inhabitants of the region as important sources of food for centuries prior to European colonization (Verissimo, 1895).

Fish inhabiting floodplain lakes in the Amazon Basin are subjected to an annual hydrologic cycle alternating between high and low water seasons. These fish depend on temporal variation in accessible connectivity among lakes, rivers, and seasonally flooded forests to complete their life cycles (Fernandes et al., 2009). The movement of fish species among these habitats at different stages of the hydrologic cycle suggests a system within which some species might be distributed over a region as localized populations that experience a limited degree of cross-migration. In contrast, other species may experience the region as a more-or-less continuous habitat in which the rising water that washes over the floodplain during the annual high water stage prevents isolation. Rare species make up a large fraction of total species richness in any large collection (Preston, 1948), including floodplain lake fish (Yamamoto et al., 2014) and so may be particularly vulnerable to extinction if connections among habitat patches are severed by dams, or the period of lake isolation from the river is extended by droughts.

The patchy distribution of floodplain lakes during the low water season, and the network of connections that exist among them (the main river channel and seasonally flooded forests), suggest that regional variations in topography, water chemistry and flow may be at least as important as local lake conditions in determining floodplain lake community structure. Because of this, metapopulation dynamics, involving interacting local populations within a larger region of floodplain habitat, may be applicable to floodplain fish. Here we examine this proposition as a foundation for conservation strategies in an environment where connectivity is directly threatened by dams and climate change. We begin by explaining the dynamic structure of the physical environment in the Amazonian floodplain ecosystem, then introduce the background of metapopulation theory and discuss its applicability to fish species, and finally discuss how this conceptual framework relates to conservation efforts aimed at preserving species diversity and sustainably exploiting fish stocks. Specifically, we address three questions: (1) What criteria should we use to judge whether a species is distributed as a metapopulation, and are there fish species in the Amazon Basin that currently meet these criteria? (2) How do we expect the changing aquatic environment of the floodplains to affect species that are, or are not, currently structured as metapopulations? (3) How does the metapopulation point of view contribute to designing effective strategies for conservation of fish populations and preservation of species diversity?

2. Structure of the physical environment

2.1. The hydrologic cycle and habitat connectivity

The Amazon River Basin is physically heterogeneous, being divided in terms of drainage systems of different geological origins and physical characteristics. The principal systems in this region are whitewater and blackwater. Whitewater rivers such as the Solimões, Madeira, and Purus Rivers carry a high load of sediments and nutrients from pre-Andean headwaters. These rivers are therefore highly productive, with a nearly neutral pH, and support high fish species diversity and productive fish stocks (Lowe-McConnell, 1999; Freitas et al., 2010b). In contrast, blackwater rivers such as the Urubu, Uatumã and Negro originate from the old plateaus of Guyana in Northern South America. They carry a lighter sediment load, are more acidic and less productive than whitewater rivers, but have equivalent numbers of fish species (Goulding et al., 1988; Freitas et al., 2010b).

The hydrologic cycle, or "flood pulse" (Junk et al., 1989) in this vast system is characterized by dramatic changes in water level. It consists of four seasons, rising water, high water, receding water, and low water, each of which have different characteristics with regard to interhabitat connectivity (Fig. 1). Depending on specific location within

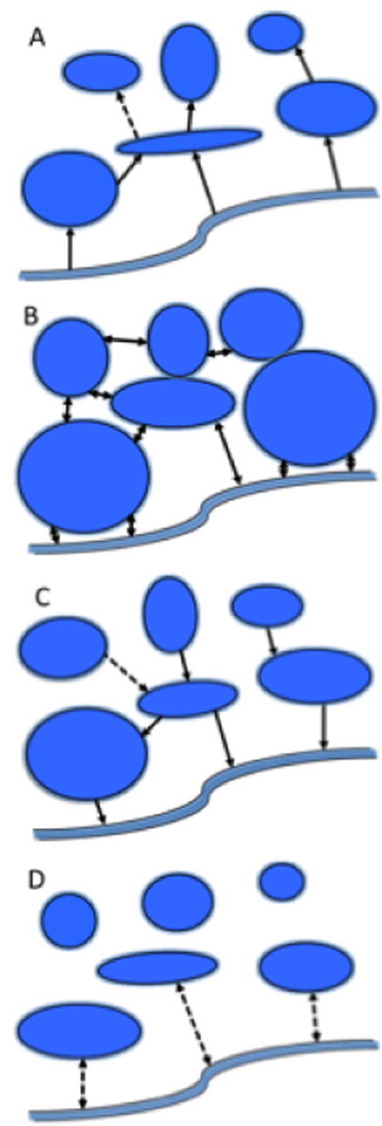

Fig. 1. A portion of a river and its adjacent floodplains, including lakes and connection channels, taking into account the season of the hydrologic cycle: (A) rising water season: the connectivity is increasing so that the water flows from the river to the lakes, increasing their size. The timing of lake connection depends on topography and the distance between the river and lake. Some lakes will be connected only in high water season (dashed lines); (B) high water (flood) season: connectivity is highest and the number of connected lakes at the floodplain will vary with the intensity of the flood pulse. Some lakes could be connected just in years of highest floods. Other lakes could be completely connected as a single aquatic environment; (C) receding water season: connectivity is diminishing as the water flows from lakes to the river, reducing their size. This process is faster than rising water. Some fish species could be retained in the lakes and die during years of extreme drought; (D) low water season: connectivity is lowest and the degree of isolation is a function of the lake position in the floodplain and drought intensity. Extreme drought years could cause a complete disconnection of some floodplain lakes.