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Metapopulation models predict the temporal response of two macrophytes to drought in a subtropical water reservoir

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ABSTRACT

Water level fluctuations are among the main drivers of the temporal dynamics of aquatic species, and droughts represent a major disturbance that can affect aquatic populations. We applied a metapopulation perspective to model the temporal variation in the patch occupancy of local populations of two species of submerged macrophytes (*Egeria densa* and *E. najas*) that colonise a large reservoir (Itaipu, Paraguay/Brazil border) and suffered an intense drought disturbance. The severe water drawdown caused a decrease in the numbers of patches that were colonised by both macrophyte species. This disturbance decreased the fractions of patches occupied by *E. densa* and *E. najas* from 13% and 38% to 0.9% and 8.5%, respectively. The recovery of the fraction of patches colonised by populations of these two species had similar responses to the disturbance: a time lag phase, followed by an exponential increase and finally stabilization of the number of occupied patches. Recovery of the fractions of patches that were colonised by *E. densa* and by *E. najas* took 80 and 38 months, respectively. A time lag in the temporal metapopulation, followed by an exponential increase in patch occupancy, strongly indicates that both populations recovered by passive dispersal of fragments between patches. Indeed, a metapopulation model that accounts for the fraction occupied and the water level (as an indication of disturbance) explained the temporal dynamics of both species (coefficients of determination = 78% for *E. densa* and 43% for *E. najas*) relatively well. Our results indicate that aquatic species that follow a metapopulation dynamic and depend on dispersal among sites to recover may be severely affected in a future climate change scenario, in which extreme events (including droughts) will tend to be more frequent.

1. Introduction

Many species form local populations that occur in discrete habitats (patches) distributed over a landscape. Due to environmental and demographic stochasticity, these local populations are prone to extinction in response to disturbances (Hanski, 1998; Husband and Barrett, 1998). The dynamics and persistence of patchily distributed populations may depend on the existence of an array of interconnected populations that are affected by regional processes, such as migration and the recolonisation of empty habitat patches. The dynamics of local, interconnected populations and their links with disturbances are encompassed by the concept of the metapopulation, which emerged in the 1970s (Levins, 1969, 1970).

The spatial scales over which disturbances operate tend to be inversely correlated with their frequencies. Small disturbances are frequent, whereas large disturbances simultaneously affecting different local populations are sporadic (Schroeder, 1991). Depending on their spatial extent and temporal frequency, disturbances may affect an entire metapopulation or only local populations. Large disturbances occurring on broad spatial scales can decrease the number of local populations to such a small number that the entire metapopulation may become extinct (Thomas and Hanski, 2004; Wilcox et al., 2006).

Droughts represent a disturbance that can directly affect aquatic local populations by increasing mortality rates or decreasing birth

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rates due to a decrease in habitat quality (Matthews and Marsh-Matthews, 2003; Chen et al., 2015). Even short-term droughts can affect the persistence of aquatic populations (e.g., Gubiani et al., 2007). However, despite the paucity of data on the effects of droughts in aquatic ecosystems (Lake, 2003; Barros and Albernaz, 2014), a few comprehensive investigations have been conducted in river-floodplain ecosystems (Freitas et al., 2013; Espínola et al., 2014). Improving our understanding of the effects of drought on the persistence of aquatic populations is even more important considering the predicted global changes, which will enhance drought events in some areas (Milly et al., 2005; Marengo et al., 2012) and will affect the aquatic biota, including macrophytes (Jeppesen et al., 2015).

In reservoirs, water level fluctuations follow variations in precipitation rates and the human demand for energy, flood control or drinking water. In these ecosystems, dam operation may markedly decrease the water level, increasing the likelihood of local extinctions of aquatic plants, mainly in the littoral zone (Thomaz et al., 2006). Thus, reservoirs provide excellent opportunities for studying the effects of drought disturbances on aquatic populations.

Metapopulation models are important tools for understanding the distribution and abundance of organisms on large spatial and temporal scales (Levins, 1969; Hanski, 1998). Currently, many metapopulation models can be fitted using either relatively simple (Levins, 1969) or complex (Todd et al., 2016) datasets. Recently, Piana et al. (2014) extended the metapopulation models to account for situations in which patches change in size over time and can be temporarily isolated, affecting both the colonisation and extinction rates. However, the metapopulation approach has been strongly criticized because it is mostly theoretical and rarely matches natural systems (Harrison and Hastings, 1996; Driscoll et al., 2010; Fronhofer et al., 2012). In addition, the application of metapopulation theory for plants subjected to disturbances (e.g., droughts) encounters limitations. For example, the extinction of local populations is a key aspect of metapopulations, but it is difficult to assess plant extinctions because of seed dormancy and propagule banks (Husband and Barrett, 1996; Blindow et al., 2016). Even so, the metapopulation perspective has satisfactorily explained genetic diversity and genetic differentiation of plant populations in river corridors (Tero et al., 2003; Honnay et al., 2010). Studies using molecular tools have shown that riparian and aquatic macrophyte species may have metapopulation dynamics and that water currents and zoochory play key roles in the exchange of individuals among habitat patches (Liu et al., 2006; Pollux et al., 2009; Honnay et al., 2010). These findings suggest that the persistence of some plant populations on large spatial scales depends on exchanges of propagules among colonised and non-colonised habitat patches.

Here, we applied a metapopulation perspective to evaluate the temporal variation in the patch occupancy of populations of two submerged macrophytes (*Egeria densa* Planch and *E. najas* Planch) that suffered an intense drought disturbance. We predicted that (i) the recovery of the metapopulation would take a relatively long time (years) and that (ii) the number of patches that were recolonised overtime would parallel a logistic model. The rationale of the former prediction is that the recolonisation of empty patches would depend on propagules coming from other colonised patches. If recolonisation depended on resistant structures that remained in the previously colonised patches, recovery would occur in months, given the fast regeneration rates of the propagules of *E. densa* and *E. najas* (e.g., Silveira et al., 2009; Umetsu et al., 2012). The rationale of the latter prediction is that increasing the number of colonised patches would result in increased colonisation rates over time (a *quasi*-Alee effect) up to an asymptote at which all patches suitable for colonisation would be occupied.

2. Materials and methods

2.1. Study area

Surveys were performed in the Itaipu Reservoir (Brazil – Paraguay border). It is a large (1350 km^2) and deep (mean depth = 22 m) monomictic reservoir that was filled in 1982 (Fig. S1; Appendix A). Aquatic macrophytes colonise only the shallow (< 5 m) parts of the reservoir arms (Bini and Thomaz, 2005; Thomaz et al., 2006). The water level fluctuated less than one meter per year until 1999, favoring the colonisation of many (approx. 132) species of aquatic and amphibious plants. Nevertheless, a marked decrease in water level (approx. 5 m) in 1999, due to *La Niña* (Fernandes et al., 2009), led to an extensive extirpation of patches that were colonised by submerged macrophytes (for details, see Bini and Thomaz, 2005; Thomaz et al., 2006).

2.2. Life history of the organisms analyzed

The two studied species of macrophytes are rooted submerged and canopy-forming plants, both belonging to the family Hydrocharitaceae. They share similar morphology and have high vegetative growth rates via stem fragments (Silveira et al., 2009; Umetsu et al., 2012).

Long-term studies of *Egeria* in the Itaipu Reservoir show that the temporal dynamics of these species fulfill the assumptions of a metapopulation (Thomaz et al., 2006) because (i) they are distributed in small patches separated by large non-colonised areas; (ii) they disperse mainly by propagules; and (iii) their populations follow an asynchronous dynamic in the reservoir, i.e., the colonisation of new patches and the extinction of existing ones does not follow a seasonal, well-defined pattern. In addition, we assume that patch recolonisation is driven mainly by the passive dispersion of fragments, given that these species rarely reproduce sexually (Cook and Urmi-König, 1984), and that the rate of local population regeneration from resistant fragments (after a disturbance) is minimal.

2.3. Sampling

Sampling was performed from January 1999 to October 2010, at approximately six-month intervals. In each sampling campaign, the presence of macrophytes was surveyed in 235 georeferenced sites in eight large arms on the east side of the reservoir (Fig. S1; Appendix A). In every site, the presence of plants was assessed by two persons for approximately 10–12 min over approximately 100 m of the littoral region in a slow-moving boat. The presence of plants was evaluated by raking the sediment down to a depth of five meters, along with visual inspection of the water surface.

2.4. Metapopulation models

The fundamental idea of metapopulation persistence due to a stochastic balance between extinction and recolonisation of empty patches was developed by Levins (1969, 1970). Levins' model assumes a series of large patches of similar habitats with local populations going extinct and empty patches recolonised by individuals originating from occupied patches, describing the first metapopulation model as follows:

$$df/dt = \text{immigrationrate}(i) - \text{extinctionrate}(e) \quad (1)$$

where f is the fraction of occupied patches by local populations ($0.0 \le f \ge 1.0$). This equation is the simplest Levins' model and can be modified to incorporate the effects of environmental variables, increasing its complexity. The dynamics of *E. densa* and *E. najas* were described using basic metapopulation models (i.e., mainland-island, internal colonisation, rescue effect and a variation between