

Mangrove Conservation Genetics

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Abstract

Mangrove forests occupy a narrow intertidal zone of tropical and subtropical regions, an area that has been drastically reduced in the past decades. Therefore, there is a need to conserve effectively the remaining mangrove ecosystems. In this mini-review, we discuss how recent genetic studies may contribute to the conservation of these forests across its distribution range at different geographic scales. We highlight the role of mangrove dispersal abilities, marine currents, mating system, hybridization and climate change shaping these species' genetic diversity and provide some insights for managers and conservation practitioners.

Introduction

Humans are changing the world at an alarming rate and at the global scale. These changes are sufficient to leave their stratigraphic, geochemical and radiogenic signatures in the geological records (Waters et al. 2016). Additionally, the biosphere also presents signs of human activities such as human-driven vertebrates extinction rates, which are much higher than conservative “background” rates (Ceballos et al. 2015). Understanding and addressing problems concerning the loss of biodiversity are the main goals of conservation biology. It focuses on the application of different fields of knowledge, from sociology to ecology and evolutionary biology, to preserve the biological diversity from the genetic to the biome level (Soulé and Soulé 1985; Wilcove 2009). The variation at the DNA level is particularly important because it is the foundation of the evolutionary processes. With that in mind, conservation geneticists use a vast arsenal of techniques to describe patterns of genetic variation or to make inferences about evolutionary

processes concerning different organisms, mainly rare and endangered species. This is particularly relevant when an entire community is under threat, as is the case of mangroves.

Mangrove forests occupy the intertidal zones of tropical and sub-tropical regions (Tomlinson 1986), and its distribution has been drastically reduced in the past decades (Valiela et al. 2001; Duke et al. 2007). These tree communities are naturally composed by fewer species than other tropical and subtropical forests (Tomlinson 1986). 11 of the 70 true mangrove species (*sensu* Tomlinson 1986) are considered Critically Endangered (CE), Endangered, or Vulnerable according to the International Union for Conservation of Nature (IUCN) Red List categories of threat, whereas seven species are considered Near Threatened species (Polidoro et al. 2010). By describing the genetic diversity and understanding the natural or “human-made” evolutionary processes that generated this variation, it may be possible to detect early signs of population reductions and then reduce the changes of species extinction. This is only one of the many contributions of genetics to the conservation of mangrove ecosystems.

In this mini-review, our main objective is to discuss some of the recent mangrove conservation genetics related papers and highlight species differences and commonalities of evolutionary patterns and processes to provide some insights concerning mangrove conservation. Our focus on recent efforts is justified by the existence of an inspiring review (Triest 2008).

Mangroves as colonizer species

Colonization, as the establishment of a given species in a site that it has not previously occupied, is a general feature of all organisms. However, the extent

and scale that this process occurs varies among organisms and mangrove species are specially adapted for colonizing new regions (Tomlinson 1986). As a likely adaptation to an intertidal habitat between land and sea, most mangrove species share three traits: buoyant and salt-water resistant propagules (i.e. dispersal units), and embryos that develop while they are still attached to the mother tree without dormant periods (Tomlinson 1986). These features allow mangrove plants to travel long distances through water so that transoceanic dispersal has been reported for different genera both in the western (Nettel and Dodd 2007; Takayama et al. 2013; Cerón-Souza et al. 2015; Mori et al. 2015a) and eastern hemispheres (Takayama et al. 2013; Lo et al. 2014). From the management point of view, incorporating long distance dispersal qualitatively or quantitatively into population models would likely improve conservation programs' success (Trakhtenbrot et al. 2005).

Additionally, considering these 'dispersal' traits, one would also expect that mangrove propagules would majorly flow through prevailing ocean surface currents. It implies that, on the geographic scales from hundreds to thousands of kilometers, the seawater surface movement would act as both gene flow maintainer and barrier depending on the populations' geographic location. In the complex land and seascape of South-East Asia, the congruence between gene flow patterns and the predominant ocean current was reported for different genera (Chiang et al. 2001; Su et al. 2006; Liao et al. 2006; Yahya et al. 2014; Wee et al. 2014; Wee et al. 2015). Similarly, in the eastern coast of the Neotropical region, the bifurcation of the South Equatorial Current into North Brazil and Brazil currents seems to be a key driver of population subdivision (Pil et al. 2011; Mori et al. 2015b). Accordingly, land masses play an important role as barriers to the gene flow in mangrove species both between the western and eastern hemisphere and within each of these biogeographic regions (Triest 2008; Takayama et al. 2013; Lo et al. 2014; Sandoval-Castro et al. 2014; Wee et al. 2014; Cerón-Souza et al. 2015). Therefore, due to this apparent general feature among mangrove species, conservation programs that focus on this geographic scale should not ignore the population genetic connectivity driven by ocean currents and land masses. Inputting these factor in metapopulation models (Ouborg et al. 2010), for example, would be particularly interesting.

On smaller scales, conversely, mangrove dispersal is comparatively limited considering gene flow by both pollen and propagules. Although there are differences among species due to their natural history and ecological traits (Cerón-Souza et al. 2012), generally there is genetic structure on a local scale even when no obvious constraints exists (Geng et al. 2008; Islam et al. 2012; Cerón-Souza et al. 2012; Mori et al. 2015b). It may lead to a pattern of spatial genetic structure (Geng et al. 2008; Islam et al. 2012; Cerón-Souza et al. 2012). One impressive example of how limited mangrove pollen and propagule dispersal may be on a local scale is the dispersal distance of only tens of meters as estimated for a viviparous species from the eastern hemisphere (Geng et al. 2008). This limited dispersal is likely linked to the self-compatibility and mixed mating system that some mangrove species present (Landry and Rathcke 2007; Geng et al. 2008; Cerón-Souza et al. 2012; Nadia et al. 2013; Landry 2013; Mori et al. 2015b). Collectively, these results have many conservation implications; for instance, in view of the limited pollen and propagule dispersal on local scales, deforestation of an area may imply an irreversible genetic diversity loss even within a single estuary (Cerón-Souza et al. 2012).

Hybridization is a major evolutionary process in mangrove species

Gene flow occurs not only among populations but also among species, and its consequences are quite diverse (Hoffmann and Sgrò 2011; Abbott et al. 2013). In mangroves, ongoing and/or ancient hybridization has been reported for most of true mangrove genera: *Acrostichum* (Zhang et al. 2013), *Avicennia* (Mori et al. 2015a; Mori et al. 2015b), *Bruguiera* (Sun and Lo 2011), *Ceriops* (Tsai et al. 2012), *Lumnitzera* (Guo et al. 2011), *Rhizophora* (Cerón-Souza et al. 2010; Duke 2010; Lo 2010; Takayama et al. 2013), and *Sonneratia* (Zhou et al. 2005; Qiu et al. 2008; Zhou et al. 2008). The widespread occurrence of so many hybrids in mangrove lineages poses challenges to managers and policy makers. First, it is difficult to classify individuals identified as hybrids according to criteria of origin (natural or anthropogenic) and the presence or extent of introgression (Allendorf et al. 2001). Moreover, it is often difficult to determine the direction of hybridization, which influences on the species extinction risks (Todesco et al. 2016). Despite the call for the protection of non-anthropogenic hy-

brids of some authors (Allendorf et al. 2001), hybrids should not be included in the IUCN Red List whatever their origins may be, to avoid making things even more complicated to managers and stakeholders. For mangrove conservation professionals, the case of *Bruguiera hainesii*, currently under the critically endangered (CE) IUCN category, is quite interesting. According to genetic data, it is a hybrid between two widespread species: *B. gymnorhiza* and *B. cylindrical* (Ono et al., 2016). Although removing the label of CE may reduce this species/hybrid protection, it may also allocate any available budget to the protection of its parental species and this decision is definitely not trivial to make.

Climate change

Although hybridization is a natural process that occurs among mangrove species lineages, its occurrence may increase as the climate changes and geographic distribution of related species shifts (Hoffmann and Sgrò 2011). This is only one of the consequences of global climatic alterations to mangrove forests. Despite the ability of mangrove forest to adjust to the sea level rise (Krauss et al. 2013), in many areas, the rate at which seas are rising exceeds the soil elevation gain (Lovelock et al. 2015). Moreover, the velocity of climate change is projected to be the particular high in mangrove forests (Loarie et al. 2009) and extreme changes are expected to happen earlier in mangroves than in other environments (Beaumont et al. 2011). Consequently, evidences of geographic expansion abound in the recent literature (Osland et al. 2013; Cavanaugh et al. 2014; Saintilan et al. 2014; Crase et al. 2015; Cavanaugh et al. 2015). Predicting how mangroves will respond to the current climate changes in medium and long terms is a huge challenge. Genetic studies may contribute to this matter by understanding how selective neutral and non-neutral variations are distributed in populations. This is currently feasible due to relatively recent DNA sequencing revolution, which made possible the use of the genome-wide information and even whole-genome sequencing of non-model organisms (Ellegren 2014; Andrews et al. 2016). The information regarding species gene functions may be assessed by transcriptome analyses and, for some mangrove species, this is already available (Dassanayake et al. 2009; Liang et al. 2012; Huang et al. 2012; Huang et al. 2014; Yang et al. 2015).

Perspectives

For decades, the body of knowledge concerning the mangrove species genetic variation has attracted the attention of many researchers from different groups all around the world (Triest 2008). We expect that this trend will continue and there will be much more genetic information from more mangrove taxa and, possibly, fully sequenced genomes in the near future. However, the translation of this growing field of research into management projects and conservation policies is still a great concern (Laikre 2010; Shafer et al. 2015). For species that occur in many different political units (countries, states, municipalities), such as mangrove trees, the link between policy and research seems even weaker. Despite the existence of political instruments and treaties that appeal to the mangrove conservation (Polidoro et al. 2010), the area covered with mangrove forests still decreases (Richards and Friess 2015). Moreover, the list of 15 countries that contain 74.3% of the world's mangrove areas is composed of 14 developing countries, where environmental policies are often neglected or disregarded (Giri et al. 2011). Therefore, we urge an equal focus on both “genetics” and “conservation” in mangrove conservation genetics.

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