



# Multi-gene phylogenetic analysis reveals the multiple origin and evolution of mangrove physiological traits through exaptation



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## ABSTRACT

Mangroves are taxonomically diverse group of salt-tolerant, mainly arboreal, flowering plants that grow in tropical and sub-tropical regions and have adapted themselves to thrive in such obdurate surroundings. While evolution is often understood exclusively in terms of adaptation, innovation often begins when a feature adapted for one function is co-opted for a different purpose and the co-opted features are called exaptations. Thus, one of the fundamental issues is what features of mangroves have evolved through exaptation. We attempt to address these questions through molecular phylogenetic approach using chloroplast and nuclear markers. First, we determined if these mangroves specific traits have evolved multiple times in the phylogeny. Once the multiple origins were established, we then looked at related non-mangrove species for characters that could have been co-opted by mangrove species. We also assessed the efficacy of these molecular sequences in distinguishing mangroves at the species level. This study revealed the multiple origin of mangroves and shed light on the ancestral characters that might have led certain lineages of plants to adapt to estuarine conditions and also traces the evolutionary history of mangroves and hitherto unexplained theory that mangroves traits (aerial roots and viviparous propagules) evolved as a result of exaptation rather than adaptation to saline habitats.

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## 1. Introduction

One of the most profound questions in evolutionary biology is “how evolutionary adaptations and innovations originate?” A narrow focus exclusively on immediate adaptation fails to satisfactorily explain the origin of many important traits (Barve and Wagner, 2013). Darwin (1877) suggested that there are at least two distinct processes that can generate evolutionary novelty. One is natural selection acting directly on genetic variation generated by mutation to create new features and relationships (adaptation). The second is by selection or other processes having generated, in a prior context, features with a different function than at present (exaptation). In other words, exaptation is a feature that performs a function but that was not produced by natural selection for its current use. Perhaps the feature was produced by natural selection

for a function other than the one it currently performs and was then co-opted for its current function. For example, feathers might have originally arisen in the context of selection for insulation, and only later were they co-opted for flight. In this case, the general form of feathers is an adaptation for insulation and an exaptation for flight. This has been called evolution by “exaptation” (Gould and Vrba, 1982; Arnold, 1994). Exaptations have been reported to occur from the macroscopic to the molecular scale, but still the knowledge on the importance of exaptations in the origin of adaptations is obscure (Tomarev and Piatigorsky, 1996; True et al., 1999; Keys et al., 1999; True and Carroll, 2002; Brancalion et al., 2010; Pievani and Serrelli, 2011; Barve and Wagner, 2013). This limitation of case studies could be overcome in those biological systems where it is possible to study systematically many genotypes and phenotypes in which they seem to occur (Ferrada and Wagner, 2012; Samal et al., 2010).

Plants provide unique opportunities to study the mechanistic basis and evolutionary processes of adaptation to diverse environmental conditions. Adaptation of plants is one of the most important areas of study in evolutionary biology especially given

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the fact that they are fixed to a substratum. Among the experimental systems in biology, plants provide excellent opportunities to study the interaction between genetic and environmental variation, which produces the complex traits observed in nature (Anderson et al., 2011). Plants in habitats with periodic or permanent flooding are challenged by several stresses, particularly the rapid depletion of soil oxygen following the onset of flooding (due to the much slower rates of oxygen diffusion in liquid compared to the gas phase (Blom, 1999)). The resulting oxygen deficiency in the root of non-adapted species is considered to be the major factor negatively affecting the survival and growth of submerged plants (Colmer, 2003; Voeselek et al., 2004). Therefore, the possibility exists that the occurrence of mangrove species in unfavorable intertidal zones may have evolved through exaptation, a scenario where a morphological structure evolved in related plant groups have been utilized for a special function in these saline aquatic environments.

Mangroves are an ideal system to study adaptations in plants. Mangroves are a taxonomically diverse group of flowering plants that grow primarily in tropical and sub-tropical regions in the intertidal zone (Kathiresan and Bingham, 2001; Alongi, 2008). Mangrove forests are among the most productive and biologically important ecosystems of the world (Polidoro et al., 2010). Mangroves are spread in about 20 families, 27 genera, and 69 species among flowering plants (Spalding, 2010; Polidoro et al., 2010). Mangrove plants grow in soils which are highly waterlogged and with a salinity as high as that of the open sea (Kathiresan et al., 2013). They provide an impressive instance of trait evolution and a combination of diverse morphological and physiological adaptations (Shi et al., 2005). The adaptations of these mangrove plants' root system well-defined types of aerial roots namely stilt roots, pneumatophores, knee roots, cable roots and buttress/plank roots which play three distinct roles: aeration, anchorage, and nutrient absorption (Gill and Tomlinson, 1975; Tomlinson, 1986). These morphological components apparently have different origins in different species (Tomlinson, 1986). Black mangroves (*Avicennia* sp.) live on higher ground and have large numbers of pneumatophores (specialized root-like structures which emerge out of the soil like straws for breathing) which are also covered with pores (lenticels). All species in the genera *Aegiceras*, *Avicennia*, *Acanthus* and *Aegialitis* have salt glands and species in *Laguncularia* and *Conocarpus* have structures analogous to salt glands (Tomlinson, 1986). Among seed plants, vivipary is most well developed in mangroves (Tomlinson, 1986). Vivipary can be divided into two types known as "true vivipary" and "cryptovivipary," representing the two situations in which the embryo grows to break through the fruit wall or the seed coat, respectively (Tomlinson and Cox, 2000). Thus, one of the fundamental issues is what features of mangroves have evolved through exaptation? We attempt to address this by building a broad phylogeny of the mangrove species along with their sister taxa among their respective families. First, we determined if these mangroves specific traits have evolved multiple times in the multigene phylogeny. Once the multiple origins were established, we then looked at related non-mangrove species for characters that could have been co-opted by mangrove species for specialization in estuarine habitats.

Previously the independent evolutionary origins of vivipary and salt secretion has been postulated in mangroves based on 18S rRNA, *rbcL*, and *matR* sequences of mangroves plants only (Shi et al., 2005). However, the evolution and origin of other adaptive features like aerial roots and salinity tolerant mechanisms among mangrove are still unexplored. Therefore, in the present study by taking advantage of molecular systematics and the recent methodological advances in analyzing character evolution in a given phylogeny, we have tried to address the following questions: (1)

Whether molecular phylogeny supports the multiple origins of various adaptive features (aerial roots, viviparity and salt tolerant mechanisms) among mangroves?; (2) Whether different types of aerial roots, and vivipary in mangroves is an exaptation, and are these traits also seen in non-mangrove sister species?; (3) How efficient are these chloroplast (*matK* and *rbcL*) and nuclear (ITS) markers in differentiating mangroves at species level?

## 2. Materials and methods

### 2.1. Ethics statement

The study does not require an ethics statement. However, for mangrove leaf sampling prior written permissions were taken from the district forest officer (DFO) of the respective mangrove forests.

### 2.2. Taxon sampling and study area

The leaf samples of mangroves species belonging to 14 families (17 genera and 37 species) were collected from various estuarine habitats of east and west coast of India (Fig. 1). The field identifications were made by morphological observation by referring the mangrove identification manuals (Naskar and Mandal, 1999; Banerjee et al., 1989).

### 2.3. DNA extraction, PCR and sequencing

Genomic DNA from mangrove leaves was isolated by using the CTAB (Cetyl Trimethyl Ammonium Bromide) DNA extraction method (Sahu et al., 2012). Two chloroplast gene *matK* and *rbcL* were amplified using the universal primers (Wicke and Quandt, 2009) and the nuclear ITS locus (Internal Transcribed spacers) was amplified by using the primers described by White et al. (1990) (Table 2). Polymerase chain reactions (PCR) were performed in the following condition in TechGene™, thermal cycler. PCR reactions included 1–2 µl of template DNA (10–100 ng), 2.5 µl 10× MgCl<sub>2</sub> Buffer (15 mM), 2 µl dNTPs (2.5 mM), 0.5 µl Taq DNA polymerase (1.0 U), 0.5 µl of each primer (10 mM), and 18 µl H<sub>2</sub>O (total volume, 25 µl). The PCR reaction for the *matK* gene was carried out in a one-step touchdown PCR-program (1 cycle at 90 °C, 60 s at 50 °C, 120 s at 68 °C, 35 cycles at 30 s at 95 °C, 60 s at 48 °C, 120 s at 68 °C, subsequent final elongation of 20 min at 68 °C). However, the PCR cycling profile for *rbcL* and ITS locus included initial denaturation at 94 °C for 5 min, followed by 35 cycles of 30 s at 94 °C, 60 s at 60 °C (*rbcL*)/60 s at 54 °C (ITS) and 90 s at 72 °C. The successfully



Fig. 1. Map showing the mangrove sampling sites.

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