Spatial patterns of species richness and endemism of Noronhia in Madagascar

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Species of *Noronhia* grow over almost the entire island of Madagascar. To understand the spatial patterns of richness and endemism within this genus, occurrence data for all species in Madagascar were compiled based on field surveys (global positioning system [GPS] records) and georeferenced herbarium specimens. Madagascar was divided into grid cells of 82 × 63 km = 5,166 km^2, the scale at which ecological parameters are suggested to vary on the island (Wollenberg et al., 2008). The choice of grid cell size matters when identifying centers of species richness and endemism due to its biasing effects when either too small or too large (Crisp et al., 2001). For each grid cell, values of species richness and endemism were calculated (Fig. 1). Species richness was taken as the number of species per grid cell whereas endemism is scored to reflect the species range, i.e. the smaller the range, the higher the endemism score. Specifically, a score of 1 was given if the species occurs in a single grid cell, a score of 0.5 was given to each cell if it occurs in two grid cells, and so on. The weighted endemism for each grid cell was then calculated as the sum of the endemism scores for the species occurring in that grid cell. The corrected weighted endemism was obtained by dividing the weighted endemism score of a cell by the total number of species in the cell, thus reducing the sensitivity to the effect of species richness (Crisp et al., 2001). All spatial analyses were done using ArcGIS (ESRI Inc., Redlands, CA) and the ArcView extension "Endemicity Tools".

Centers of species richness occurred mainly in the north and south of Madagascar (Fig. 1A). These centers tended to be confined to mountainous areas, e.g. in the north, Montagne d'Ambre, Montagne des Français, Manongarivo and Marojejy, and in the south, Andohahela and Anosy-Vohimena. By contrast, centers of endemism were more widespread and were found mainly in the north, west and southeast (Fig. 1B) at both high and low elevations. There was also a center of endemism in the Central Highlands, which had the highest value of corrected weighted endemism (0.5). Centers of species richness and centers of endemism corresponded only in the north and south. The west had low species richness but showed comparatively high scores for endemism, whereas the central east (the region around Andasibe) had higher species richness but low endemism (Fig. 1). While centers of species richness coincided mostly with mountainous regions, centers of endemism did not show any apparent topographic pattern (Fig. 1).

The biogeographic pattern indicated that northern Madagascar was the center of species richness for *Noronhia* (Fig. 1A). Although this pattern may reflect a collection bias towards well-sampled localities in the northern biogeographic region (e.g. Montagne d'Ambre, Montagne des Français, Ankarana), other well-sampled areas where the genus has been documented (e.g. Ankarafantsika, Ranomafana, Zahamena) harbored fewer species. The coincidence of species richness with topographically complex areas suggests a substantial role of mountainous areas in the diversification of *Noronhia*. This finding is not at all unique to this genus as similar patterns have been found in other groups of plants and animals such as vascular plants (Hong-Wa et al., 2008), tree ferns (Janssen & Rakotondrainibe, 2008), cophyline frogs (Wollenberg et al., 2008), leaf chameleons (Townsend et al., 2009), *Memecylon* L. (Stone, 2012), palms (Rakotoarinivo et al., 2013), and reptiles and amphibians (Brown et al., 2014). In particular, the northern

massifs of Madagascar, including Tsaratanana, Manongarivo, Marojejy and Montagne d'Ambre, as well as the southeastern massifs of Andohahela and Anosy-Vohimena, have been found to harbor high species richness in those various groups, supporting the idea that these areas act as species pumps, promoting adaptive and vicariant speciation (Raxworthy & Nussbaum, 1995 ; Wollenberg et al., 2008 ; Vences et al., 2009).

The centers of endemism observed in *Noronhia* coincided with only a few centers of species richness, such as in the grid cells containing Montagne d'Ambre in the north, Manongarivo in the northwest, and Andohahela and Anosy-Vohimena in the south (Fig. 1). Overlapping centers of endemism and species richness may represent historical centers of cladogenesis (Ricklefs & Schluter, 1993 ; Jetz et al., 2004). Although it is unclear whether current species distributions reflect the original geography of speciation or post-speciation range shifts (Losos & Glor, 2003), the coincidence of endemism and richness in Montagne d'Ambre, Manongarivo, Andohahela and Anosy-Vohimena supports the idea that these massifs are centers of diversification for *Noronhia*. Centers of endemism were also found in less known areas in the west and northeast of the island where the genus is mostly known from historical collections. Indeed, many species have been collected in only one or a few localities, thus potentially biasing the interpretation of their endemism. Nevertheless, the pattern of microendemism suggests recent and/or rapid evolution resulting from, e.g., isolation, specialization to particular environments or fine-scale environmental variables as with species growing on karst mountains in the north (Ankarana) and the west (Bemaraha), hybridization or polyploidization (Pearson & Raxworthy, 2009 ; Vences et al., 2009 ; Hong-Wa & Besnard, 2014).