**General remarks:**

**There is actually very little about this that is “phyloclimatic”. We reference a tree but only to pick pairs of species from it so that the tree no longer matters. The picking of species pairs has not gone so well, which is why we now have to do this sleight of hand with the “clade pairs”. I really recommend you redo the tree, with the extra data that you have, using \*BEAST. This will allow you to i) use multiple sequences per species (as you have available) ii) estimate divergence dates under a relaxed clock model. You can then directly calculate the rate at which distance between niches (i.e. Schoener’s D / MY) was accumulated and compare this between highland and lowland.**

**In addition, it would be good to balance this paper out a bit more. For example, a lot of time is spent on explaining the ENM when this is actually (according to the title) about divergence and diversification. Maybe part of the ENM can go into supplementary materials? Also, maybe the future scenarios can be moved into a different publication?**

**A phyloclimatic analysis of the evolution of niche divergence in tropical pitcher plants**

Rachel Schwallier1,2, Niels Raes1,3, Rogier van Vugt4,5, Rutger Vos1,8 and Barbara Gravendeel1,6,7

1Naturalis Biodiversity Center, Einsteinweg 2, 2333 CC Leiden, The Netherlands

2Rachel.Schwallier@naturalis.nl

3Niels.Raes@naturalis.nl

4Hortus botanicus, Rapenburg 73, 2311 GJ Leiden, The Netherlands

5 r.r.van.vugt@hortusleiden.nl

6University of Applied Science Leiden, Zernikedreef 11, 2333 CK Leiden, The Netherlands

7Barbara.Gravendeel@naturalis.nl

8Rutger.Vos@naturalis.nl

Submission includes the following: letter of submission, one Word text file and another Word file including five Figures, five Tables, two Appendix Figures and one Appendix Table.

Ecological niche models (ENMs) are increasingly used as tools to study the role of ecology in evolution, however the majority of these investigations so far have focused on animal-based systems. Here, we use ENMs to analyze ecological niche variability and its dynamics in speciation in the enigmatic tropical pitcher plant genus *Nepenthes* in order to quantify future climate effects from a phylogenetic perspective. In this study, geo-referenced live plant and herbarium records were used to model distributions and reconstruct ecological niches for selected *Nepenthes*species. Our results show that highland species have less divergent niches given their available habitat compared to lowland species, suggesting that highland species may have speciated allopatrically, in contrast with lowland species, which speciated in sympatry. We conclude that over the past million years, the environmental niches of highland and lowland *Nepenthes* species evolved differently due to historical climate and geographical changes. Furthermore, highland species will experience a greater habitat reduction due to future climate shifts compared to lowland species. Given these results, we conclude that especially highland species will likely face a severe decrease in habitat area with little capacity to adjust to the impacts of current global warming trends.

**Key words – Climate change, Ecological niche modeling, Niche evolution, *Nepenthes***

**Introduction**

The foundation of study for many ecologists, evolutionary biologists and conservationists is to understand the mechanisms and processes that result in species diversity. Many processes driving the formation of new species have been identified. Among these are stochastic processes that only require the absence of homogenizing gene flow, and adaptive processes in response to disruptive natural selection. These two distinct drivers of diversity, traditionally termed allopatric and sympatric speciation, highlight the central role of ecology in divergence. The former results from geographic isolation where physical barriers constrain interbreeding of populations, and the latter classically occurs due to ecological distinctions between populations that are uninhibited by geographic constraint (Couvreur et al. 2011). These two types of speciation, from an ecological perspective, imply contrasting niche evolutions within a phylogeny (i.e. the gradient between the parameters needed for population viability differ between the two types of speciation). For geographically isolated speciation, one would expect lower rates of change, or conservatism of niches (Wiens 2004), than those without geographic isolation, which would inherently produce higher rates of niche divergence (Pearman et al. 2008). Debate whether niches in general evolve quickly or remain conservative over long time-scales persists (Holt 2009; Peterson 2011; Yesson and Culham 2006a), but through these investigations, family and genus-scale ecological niche models have been identified as useful tools in signaling the role of ecology in speciation (Kozak and Wiens 2006, Graham et al. 2004).

A species’ niche and its geographic distribution is shaped by abiotic factors, biotic interactions and dispersal ability, as outlined by the BAM framework of Soberón and Peterson (2005, 2007). Recent efforts have focused intently on the environmental parameters of the species’ niche (Broennimann et al. 2012, Colwell and Rangel 2009, Holt 2009; Yesson & Culham 2006a, Evans et al. 2009), largely due to advances in computer algorithms and increasing access to locality data. These algorithms use locality data and environmental predictors (especially climatic data) to produce ecological niche models (ENMs) (Araujo and Peterson 2012). ENMs predict geographic distributions of species based on abiotic correlates of the realized niche (Peterson 2003, Kozak et al. 2008), shed light on species delimitation (Raxworthy et al. 2007) and predict likely effects of habitat alteration (Carroll et al. 2010). All of these contribute to effective and responsible conservation management practices (Araujo et al. 2011). Coinciding with growing concern over global climate change, this surge has led to numerous studies of evolutionary response to climate shifts in history (Zimmerman et al. 2010) and what effect a changing climate will have on future organism distributions and survival (Lawler et al. 2009; Saupe et al. 2011; Swenson 2008; Thomsan 2004). Here we report on the application of ecological niche modeling to shed light on the divergence and diversification in climatic preference in the carnivorous plant genus *Nepenthes*.

Carnivorous plants have inherently proven their ability to adapt to changing environments. Under conditions of poor soil-nutrient availability they have evolved prey-capturing mechanisms to supplement their nutrition on six times independent occassions across the angiosperm phylogeny (Ellison and Gotelli 2009). The tropical pitcher plant genus *Nepenthes* has developed modified tendril tips filled with liquid known as pitfall traps. These traps aid in the attraction, retention, digestion and acquisition of nutrient sources. Their diet consists primarily of insects, although other surprising sources such as leaf litter and feces have been found in their nutrient uptake (Clarke et al. 2009; Moran 1996; Moran et al. 2003). Among the 130 recognized *Nepenthes* species there is much variation in geographic distribution patterns. These range from lowland to highland, from narrowly endemic to widely distributed, and from coastal marshes to mountain peaks (McPherson 2009). Species diversity is concentrated in the Malay Archipelago (Raes and van Welzen, 2009a), with the majority occurring in Borneo, Sumatra, the Philippines, the Malay Peninsula, and smaller numbers identified in Thailand, Cambodia, Vietnam, Laos, Sulawesi, New-Guinea, Australia, Sri Lanka, India and Madagascar (Meimberg and Heubl, 2006, Jebb and Cheek 2001).

Throughout its distribution, the genus generates valuable tourism income and has horticultural interest owed primarily to its carnivory and impressive insect trapping pitchers (Clarke 1997; Ellison 2003). In addition to monetary motivations for conservation, preservation of *Nepenthes* populations may also ensure stability of other taxa. Pitcher plantshave been argued to be foundation species by Jennings and Rhor (2011) as they may provide habitat for entire communities that completely rely on pitcher plants for their existence. *Nepenthes* provide habitat to roosting bats (Grafe et al. 2011), frogs and snails along with their eggs (Das and Haas 2010 and personal observation) and other aquatic invertebrates (Clarke and Kitching 1993; Mogi and Yong 1996; Sota et al. 1998). Additionally, there are some interesting mutualistic relationships in which *Nepenthes* species provide food sources to animals. *Camponotus schmitzi* ants (Bonhomme et al. 2011) associated with *N. bicalcarata*, and *Synema obscuripes* spiders living in *N. madagascariensis* (Rembold et al. 2012), feed off prey attracted to the pitchers. Small mammals have also been found to eat the nectar produced in the lid of *N. lowii and N. rajah* (Clarke et al. 2009; Greenwood et al. 2011). The loss of these tropical carnivorous plants, therefore, could result in associated biodiversity losses.

Predicting estimations of current and future *Nepenthes* distributions can therefore be valuable for conservation strategy development and resource planning so that present and potential future habitats persist. Characteristics within the genus, such as reproductive constraints and high endemism, suggest that their environmental niche may be conserved - meaning that they must continue to inhabit areas to which they became adapted during evolutionary history (Wiens 2004). All *Nepenthes* are dioecious, which minimizes colonization abilities because according to Baker’s law (1953), both male and female seeds need to arrive in the same space to create new populations. Perhaps resultant of this feature, a considerable number of *Nepenthes* species are narrow endemics (Mao and Kharbuli 2002; Nongrum et al. 2012; Robinson et al. 2008) suggesting that at least some species have constrained habitat requirements or are strongly limited in seed dispersal.

Two-thirds of the 84 *Nepenthes* species documented on the IUCN Red List of Threatened Species (2012) are categorized as vulnerable, endangered or critically endangered, with primary threats including habitat loss and wild collection (Jennings and Rohr 2011). The limited distribution of a number of *Nepenthes* species further predisposes them to be at higher risk of extinction (Yesson and Culham 2006b). These risks, conservation motivations, and the varied distribution patterns of the genus, make *Nepenthes* an attractive study organism for ENM. Because of variation in geographic constraints between highland and lowland species, and as evidenced by other mountain endemics (Kozak and Wiens 2006), we hypothesize that our models will indicate differing levels of niche conservatism, with highland species being more conserved. The primary goal of this study was to determine the role of niche divergence during the diversification of *Nepenthes.* To do so, we investigated how niche divergence has evolved on the phylogeny for six closely related species of *Nepenthes.* We also predict how a future climate scenario may affect distribution and habitat availability of these species based on the level of conservatism or divergence.

**Methods**

*Study system and accessions*

We selected species belonging to two clades in the most recently reconstructed molecular phylogeny of *Nepenthes* from Meimberg and Heubl (2006). Low resolution in the *Nepenthes* phylogeny and recent prompts to include ecological information in collection material (Clarke and Moran 2011), motivated our use of niche models to increase the understanding of relationships and drivers of evolution within this genus. Insufficient occurrence records for many species, due to either narrow endemism or low collection records, however, limit a wide-scale analysis of the genus. We chose to use 10 species for which we had sufficient data records and which could be closely associated with another species in order to form pairs (Figure 1). For the two clades encompassing these pairs, one clade is chiefly comprised of lowland species and the other is chiefly comprised of highland species (Table 1). These two clades are from here forward referred to as the lowland and highland clade, respectively.

Locality data of 12 species comprising the 6 selected pairs were used for analysis of diversification (Table 1). The bulk of the locality data was derived from the specimen databases of Naturalis Biodiversity Center, the Global Biodiversity Information Facility, the Smithsonian Institution and the New York Botanical Garden. Verified and closely examined herbarium records were either geo-tagged in the field, or had named localities that were geo-referenced using online gazetteers. We removed replicate species records per 5 arc-minute spatial raster cell (Table 1).

*Ecological Niche Modeling*

Ecological Niche Models (ENMs) identify the relationship between species presence records and the (a)biotic conditions occurring at those sites (Peterson 2011). When this relationship is projected in geographic space it allows us to predict habitat suitability for the given species in areas where no collection data is available. Similarly, when projected in time, it allows predicting habitat suitability under past or future climatic conditions.

*Climate and Soil data*

Soil data was derived from the International Soil Reference and Information Centre (ISRIC) (Batjes 2012). Climate data was sourced from WorldClim  (<http://www.worldclim.org/>*)* and Climate Change Agriculture and Food Security (<http://www.ccafs-climate.org/data/>*)* for the present and future time periods, respectively. A spatial resolution of ESRI-grids of 5 arc-minutes was used. The future climate period of 2070-2099, hereafter referred to as the 2080s, for climate scenario A2a HadCM3 was chosen, which involves high population growth, slow economic development due to less world cooperation, and some local and regional concern for environmental improvements (IPCC 2007). Considering recent economic, political and CO2 emissions, this simulated data is a plausible condition for the future (Moss et al. 2010).

In order to select which climate and soil variables were strongest indicators for distribution, we first made a buffered area of one degree around each presence locality following Nakazato et al*.* (2010) so as not to overestimate species range. This was done independently for each of the five pairs, so that a buffered area around both clade-species presence localities was created (Warren et al. 2010). We then extracted climate, soil and altitude data for each grid cell present in each buffered area for each pair. Of the 19 soil variables, 4 of them were eliminated immediately due to large gaps in grid data (Table 2). Selection of our environmental variables for each clade-pair was based on highest vector loading using Principal Component Analysis (PCA), which gave us the variables that had the highest variation in the buffered area. Variables that were correlated (|Spearman rho| > 0.7) to these highest predicting variables were excluded. We used Pearson’s correlation for altitude and bioclimatic variables (|r|>0.7) (Nakazato et al. 2010). All statistical analyses were performed in R (R Development Core Team 2008) and SPSS 21.0 (IBM corp. 2012).

*Modeling*

We used Maxent version 3.3.3k (Phillips et al. 2006, Elith et al. 2011) with default settings to model the projections of the present and future distributions for each pair given the chosen variables. Maxent uses presence-only data to predict approximate species distribution based on a probability distribution of maximum entropy, an approach that has been shown to outperform other modeling algorithms (Elith et al*.* 2011, Aguirre-gutiérrez et al. 2013) especially when the sample size is small (Wisz et al. 2008). The models were trained in the buffered area of each pair and subsequently projected onto the phytogeographical subareas (van Welzen et al. 2005) in which the species in each pair has already been recorded. The regions were delimited based on floral and biogeographical analysis and include Borneo, Java, the Lesser Sunda Islands, the Moluccas, Papua New Guinea, the Philippines, the Malay Peninsula, Sulawesi and Sumatra. One clade pair (*N. ampullaria/N. mirabilis*) also extended into Cambodia, Laos, Thailand and Australia, units that were therefore included in the modeling and projections for this pair. Application of these unit areas was done in order to minimize over-estimating distribution to islands with suitable abiotic conditions but no recorded species presence, as the sea is a likely dispersal barrier (Holt et al. 2005, Schupp et al. 2002). All records were used for model training and models were subsequently tested against a null-distribution.

In this study we considered both geographic distribution and ecological niche. These are linked, but restricted by their own factors, so for visual presentations we re-modeled the distribution of each species as outlined above, but used a buffered area of each species independently projected onto the unit area only in which it individually occurs (despite its sister species’ occurrence areas). This was done to make map projections onto the species-specific unit areas, accounting for dispersal barriers. With these models, we predict the geographic overlap between each sister pair in Figure 2, using the 10-percentile training presence threshold in Maxent. This presents the 90% of the presence records falling into the distribution area. The remaining 10% were considered those with an atypical environment and were excluded from the distribution, which is a conservative approach making optimal use of the spatial distribution information provided by the collection and survey records (Liu et al. 2005).

We tested whether niche models differed more from a suitable null model (Raes and ter Steege, 2009) than would be expected by chance alone. The Area Under the Curve (AUC) (Fielding and Bell 1997) generated by Maxent was made from the n number of presence only points and compared to a null model generated in R (R Development Core Team 2008), which draws n randomly 99 times for each species. These random points were drawn from the buffered area in the same way as the Maxent-produced AUC values. The AUC value for each niche model was compared with the upper-side of a 95% confidence interval. All species’ AUC values rejected the null model (*p* < 0.05), indicating reliable model performance.

*Tests of Ecological Divergence*

To measure geographic overlap between species in a pair, we used the range overlap tool of ENMTools version 1.3 (Warren et al. 2008). In addition, we derived niche overlap measurements between species using ENMTools, which employs the statistical measures Schoener’s *D* (1968) and the similarity metric Hellinger’s *I*. We tested this against the null hypothesis created in the niche identity test. This procedure tests if the ENMs generated for each species are more different than expected if they were drawn from the same underlying distribution (Warren et al. 2008). We also evaluated if the clade-species were more or less similar to each other given the soil and climatic conditions available to them using the background test. To make a standardized background area for this test, which functions as the available environmental area to each species, we used a buffer of one degree around each locality for each species independently to pull points for our null (Nakazato et al. 2010). This background area was then compared to the occurrence points of its clade species and vice versa for each pair. The two-tailed test null results were again compared to niche overlap to indicate level of divergence in environmental niche.

We extracted the environmental variables of collection localities as indicated in Table 3 for each species and used them to test whether the climate/soil variables differed between the clade-pairs in two ways (Nakazato et al. 2010). First with analysis of variance (ANOVAs) on each of the abiotic variables to test for species effects and second with multivariate analysis of variance (MANOVA; Wilk’s λ) with all variables together to test if environmental conditions were different between each pair. Finally, we visualized niche overlap of abiotic predictor variables in environmental space using PCA following Couvreur et al. (2011). These analyses were performed in SPSS 21.0 (IBM corp. 2012) and similar to Couvreur et al. (2011) did not meet the criteria for parametric analysis (normal distribution of the data and homogeneity of the variance) and so the non-parametric Mann-Whitney U test was used to compare the principal components (PC1, PC2, PC3).

**Results**

*Environmental niche variation in Nepenthes*

Potential distribution ENMs of *Nepenthes* clade-pairs generated from Maxent are presented in Figure 2. Individual species maps without thresholded values can be found in the Appendix in Figures 1 and 2. In general, highland species (Figure 2; left) have a much more narrow distribution compared to lowland species (Figure 2; right). This relates to the fact that the total surface of highland area is much smaller than lowland area, as indicated by the gray-shaded highland regions (>1000m) in Figure 2. Visually, the geographic overlap between each species-pair for highland species when thresholded is also less. Geographic overlap of highland species ranges between 0 and 25% and lowland spanning from 23-31% of total covered area of both species in each pair (Table 3).

The highland clade pair, *N. maxima/N. stenophylla* had the lowest predicted geographic distribution (Table 3) and niche overlap of all of the sister-pairs in this study (Table 3). The other highland sister-pair, *N. fusca/N. veitchii,* had a geographic overlap more similar to those within the lowland clade (Table 3) and also had the highest niche overlap score, with a 76% overlap for Schoener’s *D* and 92% for the Hellinger’s *I*. Niche identity tests showed significant differentiation in niche space for all clade-pairs when compared to the null expectation, which indicates that there is niche divergence between these pairs, possibly resultant of allopatric species being exposed to differing environmental conditions. To account for available habitat, we performed the background test, which generally confirmed niche divergence for all species of the lowland clade and refuted niche divergence in the highland clade (Table 3). Within the highland clade, *N. fusca/N. veitchii* and *N. maxima/N. stenophylla,* showed that they are more similar than expected by chance when reciprocally comparing occurrences of one species with the environmental background of known localities of the other.

Three clade-pairs showed significant differences amongst each other (*p*<.05) for MANOVA on all environmental variables tested simultaneously (Appendix Table 1). Two clade-pairs, *N.fusca/N.veitchii* and *N.bicalcarata/N.gracilis*, showed no significant difference in environmental conditions when presence occurrences were compared. Predictably, these two sister-pairs did not show much variance with the ANOVA of individual variables either (Appendix Table 1). The two sister-pairs with the highest environmental differentiation indicated in the MANOVA also had the highest number of environmental variables with significant difference between species in the ANOVAs (Appendix Table 1).

When a PCA was performed for each species pair for the buffered zone made around each presence locality, the first three components explained between 58% and 78% of the environmental variation between each clade-pair (Figure 3). The loadings for each component varied amongst the different species pairs, but in general each component was largely dominated either by soil, temperature or precipitation. Soil was the most dominant component for all clade pairs, with the carbon/nitrogen ration being a leading variable for most pairs.

*Current versus future distributions*

All highland species had an overall loss in suitable habitat with the future model prediction, losing an average of 62% of their total area by the turn of the century (Table 4). This loss is evident in the visual representations of Figure 4. In contrast, seven of the eight lowland species showed an overall gain in suitable habitat in the future, ranging in a gain from 6-56% of the current area (Table 4). The widest ranging species, *N. mirabilis,* was the only lowland species to have an overall future loss in suitable habitat of 43% (Table 4, Figure 5). The lowland clade species also has a higher proportion of areas available with shared abiotic supportive habitats in the present and future than those in the highland clade (Table 4, Figures 4 & 5). Ninety-four percent of the current suitable habitat of *N. gracilis* will also be suitable in the future scenario, while only 11% of the current *N. stenophylla* habitat will be suitable in the future.

**Discussion**

This is, to our knowledge, the first study to use ecological niche modeling to investigate niche evolution in tropical carnivorous plants. Our ENMs predicted potential distribution of *Nepenthes* species with significant confidence (p<0.05), indicating that *Nepenthes* species occur in predictable abiotic environmental conditions. This environment has contributed and still plays an important role in determining geographic distributions within the genus. Furthermore, our results confirm that mountain endemics maintain a more narrow distribution than lowland species within the genus, which is to be expected because the surface area of mountains is smaller than lowland surface areas. The four *Nepenthes* highland species studied are present in the mountainous regions of Malaysia and Papua New Guinea whereas the lowland species are more expansive across all of Southeast Asia. The lowland species are also more likely to occur in the same geographic space, which is confirmed by personal observations and by McPherson (2009), as they often co-occur in dense clusters. PCA analyses for lowland species confirm this with large overlap in ecological space (Figure 3). The predicted distribution ranges are as expected, although actual distributions are not likely to occupy all of the area predicted by the model due to human development, geographic or dispersal barriers.

The distribution range for *Nepenthes* had a tumultuous and eventful geological history, including many changes in sea level and climate within the Pleistocene epoch (Hall 1998). Our results show that highland sister-species show less ecological and geographic (Table 3) overlap than lowland species. Highland species pairs, then, might be expected to have more conservative niches and therefore overlap more in their climatic and soil suitability. Consistent with this, the background test shows evidence that the highland clade-pairs have conservative niches (Table 3), i.e. are significantly more similar to each other than can be expected given the environmental conditions available to them. These findings support our hypothesis that highland species may have undergone allopatric speciation as evidenced in other mountain endemics (Kozak and Wiens 2006). Both the niche identity test and PCA for highland species show that there is divergence in niches, however, these tests are not representative of the conditions involved with allopatric species. The background test is a more appropriate test of divergence for the highland sister-pairs because it takes into account the environment available to each species. Furthermore, the identity test has been identified in other studies as being too strict in that it rejects similarity of two species only if they tolerate the exact same set of environmental variables and have these same variables available to them (Couvreur et al. 2011, Jakob et al. 2010), which is unlikely to be the case in allopatric speciation. It has been argued that using current locality records might not account for actual ranges when speciation occurred (Losos and Glor 2003), however, major range changes in *Nepenthes* are unlikely due to dispersal constraints.

The lack of resolution in the published molecular phylogeny (Meimberg and Heubl, 2006) indicates that there may have been a rapid evolution within the genus. *Nepenthes* species have persisted through major shifts in climate through the last 33 to 56 million years. First records of *Nepenthes* are from Eocene pollen fossils of the Northern Tethys humid evergreen forest from France to southeast Europe and the Caucasus (Krutzsch 1989). This finding expanded earlier hypotheses of Gondwanan origin (Danser 1928) and others that postulated that the center of current diversity is likely the origin of diversity (Raven and Axelrod 1974). Krutzsch’s (1987) focus on the pollen fossil led him to view SE Asia as a secondary center of diversity colonized during the Middle Tertiary before the mountain and drought barriers of Iran and Afghanistan formed. More recent phylogenetic work by Meimberg and Hubl (2001) found strong biogeographic correlations within the genus and inferred that SE Asia was colonized via the Indian subcontinent. Continued molecular work (Meimburg and Hubl 2006) shows geographic clustering and favors the hypothesis that highland species evolved from lowland species. As climates became warmer and dryer in this region, the conserved niches caused the now highland species to be restricted to their current mountainous regions similarly as documented for salamanders by Kozak and Wiens (2006). To extend this, our data show that highland and lowland species may have undergone polar forms of speciation, with allopatric speciation of the highland clade and sympatric speciation of the lowland clade. Arguably, the highland pair *N. fusca/N. veitchii* may indeed be a recent speciation from the recent formation of the Crocker range mountainous regions on Borneo (Beaman 2005). This is also evidenced in their high niche overlap as confirmed by MANOVA and PCA. The other highland clade-pairs must have diverged in a much earlier time when sea levels were lower resulting in the temporary absence of a water barrier - as they now only occur on islands separate from each other. Geographic isolation of these species requires little need of niche divergence.

Niches that are more conserved (Williams et al. 2009) and in narrower habitat ranges (Bush et al. 2004) will likely suffer greater consequences of environmental changes such as shifts or reductions of accessible habitat. Climate models estimate the Earth to warm at a rate of about 0.2 ºC/decade for the next two decades (Soloman et al. 2007) and many organisms have already been documented to respond with range shifts as a result of climate change (Peterson et al. 2002 & 2008, Saupe et al. 2011). Responses of species will be to follow their preferred habitat, to adapt or to go extinct. Habitat tracking for *Nepenthes* is inherently difficult due to the reproductive constraints of being dioecious. Lowland species are predicted to respond slightly more adequately due to fewer geographic barrier limitations compared to mountainous highland species. However, one notable constraint for lowland species is that they may need to migrate over long distances due to shallow environmental gradients nearby. According to our results, lowland species niches are more diverged and, therefore, also likely to be more adaptable to the changing environment. In addition to this, lowland species hybridize more readily because of proximity to other lowland species populations. In our experience, lowland species also have higher numbers of individuals within a population compared to highland species. Reproductive capacity, and therefore ability to track habitat is greater for lowland populations than, for example, the sole highland individual of *N. rajah* located on the summit of Mt. Kinabalu (personal observation). Lowland species have the additional option to expand to higher altitudinal gradients to adjust to changing environments, as seen with other vascular plants (Gottfried et al. 1999, Klanderud and Birks 2003). In extension, if lowland species begin to upslope this may further increase competitive pressure on highland species (Bush et al. 2004).

Our results show that the highland clade will lose a greater amount of preferred predicted habitat in the next 80 years compared to the lowland clade (Table 4, Figures 4 & 5).All highland species will face an overall loss of suitable habitat under the tested future climate scenario (Table 4) and will have a much smaller area of original habitat remaining compared to the lowland species. It is estimated that some climates, along with many combinations of these climates with other contributing environmental facets, may disappear completely in the forthcoming climate change (Williams et al. 2007), which appears to be especially the case for the highland species in our study. Thermal specializations in tropical species (Janzen 1967, Huey and Webster 1976) suggest further inabilities for highland *Nepenthes* to adjust to a changing environment as species exposed to low variation in temperature have been shown to have a reduction in thermal tolerance (Addo-Bediako et al. 2000, Ghalambor et al. 2006). The small overlap areas remaining (Table 4, Figures 4 & 5) are likely to be the only areas supporting highland species’ populations in the future. Assisting in migration to newly established areas of preferred habitat remains controversial (Thomas 2011), therefore, preservation of these overlap areas is critical for the conservation of these highland species along with preservation of genetic diversity through live collections and seed saving.

In addition to the abiotic environment, success of *Nepenthes* populations also depends on many biotic interactions. Habitat shifts would also need to account for interactions concerned with diet (Clarke et al. 2009, Greenwood et al. 2011, Merbach et al. 2001 & 2002, Moran et al. 2001), the symbiotic specializations that are very pronounced in some species (Bonhomme et al. 2011, Rembold et al. 2012), and the necessary pollinators. Chen et al. (2009) found that in the last 40 years, Lepidoptera have retreated up the mountain on Mt. Kinabalu. Mobility and life history traits of animals and insects may contribute to their arriving in their preferred habitat at an earlier stage, leaving gaps in the range shifts for both these organisms and for *Nepenthes*.

Dispersal is also likely to play a significant role in the future stability of populations of *Nepenthes.* Therefore, it is in our interest to investigate seed dispersal and its effects on meta-population dynamics. In addition to this, we plan to investigate how character traits correspond to the environmental preferences seen in our models. Also meriting further work is the geographic and niche range of males versus females - as other dioecious plants have been shown to have differing altitudinal and climatic preferences (Field et al. 2013). For these and other investigations within the genus, it would be highly beneficial to incorporate the increasing number of newly discovered *Nepenthes* species in molecular sampling to create a more complete phylogeny and to experiment with additional markers providing higher resolution among closely related species. This would also make timing of allopatric and sympatric speciation possible.

**Conclusion**

Over the past million years, different species of *Nepenthes* became adapted to different environmental niches with environmental conditions contributing to the evolution of *Nepenthes* species. We found that the highland clade has higher levels of niche conservatism, likely the result of allopatric speciation. Our predictions for future distributions show that ongoing climate shifts will have deleterious effects, which will be especially apparent for the highland species due to a disappearance in preferred habitat. Lowland species are much more likely to adapt to a changing climate.

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