Modeling of endemic plant species of Madagascar under climate change

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Introduction

Environmental niche modeling, or species distribution modeling, involves the analysis of environmental variables associated with the known distribution of a taxon to predict the total potential suitable habitat of the taxon. Human-induced increasing levels of carbon dioxide and other greenhouse gases in the atmosphere since the onset of the industrial era are now generally acknowledged as the direct causal agent for increases in global mean temperature and concomitant changes in precipitation and circulation patterns both in the atmosphere and the ocean. As carbon dioxide levels continue to rise, coupled atmospheric and oceanic general circulation models can be utilized to construct future climate variables to correspond to different levels of carbon dioxide, and therefore at different future time periods. Thus, current known and potential distribution areas of species as defined by a set of environmental variables can be projected on to and modeled according to future climate surfaces. Depending on the modeled distribution of the suitable environmental niche, the future distribution area may remain relatively constant and in place, or significantly expand or contract, and/or shift markedly away from the current area. To examine the potential changes in distribution areas of the plants of Madagascar, a subset of 74 endemic species was modeled under six climate change model/scenarios at three future time periods (2020, 2050, and 2080).

Methods

Species Selection

Species strictly endemic to Madagascar known from at least seven unique localities were chosen to represent all vegetation types, bioclimatic zones, and geographic areas (Appendix 1).

Eastern Humid Littoral Forest: *Asteropeia micraster, Asteropeia multiflora, Rhopalocarpus coriaceus, Rhopalocarpus thouarsianus, Schizolaena elongata, Schizolaena laurina, Schizolaena rosea*

Low Elevation Humid Forest: *Asteropeia matrambody, Brexia maroniae, Dialyceras coriaceum, Dialyceras parvifolium, Humbertia madagascariensis, Rhodolaena altivola, Rhopalocarpus binervius, Rhopalocarpus crassinervius, Rhopalocarpus excelsus,* *Rhopalocarpus longipetiolatus, Schizolaena cauliflora, Schizolaena exinvolucrata, Schizolaena gereaui, Tsebona macrantha*

Low to Mid Elevation Humid to Subhumid Forest: *Brexia alaticarpa, Dilobeia thouarsii, Physena madagascariensis, Rhodolaena coriacea, Rhodolaena humblotii, Rhopalocarpus macrorhamnifolius, Schizolaena hystrix, Schizolaena pectinata*

Mid Elevation Subhumid Forest: *Asteropeia mcphersonii, Asteropeia rhopaloides, Brexia montana, Rhodolaena acutifolia, Rhodolaena bakeriana, Tabernaemontana sessiliflora*

Southeastern Humid to Subhumid to Dry Forest to Central Plateau Subhumid Forest: *Brexia humbertii*

Central High Plateau Subhumid to Montane Tapia Woodland: *Asteropeia densiflora, Asteropeia labatii, Schizolaena microphylla*

Northwestern Subhumid to Dry Forest: *Schizolaena parviflora, Schizolaena viscosa*

Northwestern Dry Forest and Low to Mid Humid Forest: *Asteropeia amblyocarpa, Rhopalocarpus alternifolius, Rhopalocarpus louvelii*

Western Dry Forest: *Adansonia grandidieri, Perriera madagascariensis, Tsoala tubiflora*

Northwestern/Far Northern Dry Forest: *Adansonia madagascariensis*

Far Northern Dry Forest: *Boswellia madagascariensis, Diegodendron humbertii, Rhopalocarpus suarezensis, Rhopalocarpus triplinervius, Rhopalocarpus undulatus*

Far Northern Dry to Subhumid Forest: *Adansonia perrieri*

Subarid Dry Forest to Western Dry Forest to Subhumid Plateau Forest: *Rhopalocarpus similis*

Southwestern Subarid Forest-Thicket: *Alluaudia ascendens, Alluaudia comosa, Alluaudia dumosa, Alluaudia humbertii, Alluaudia procera, Alluaudiopsis fiherenensis, Alluaudiopsis marnieriana, Brenierea insignis, Decarya madagascariensis, Delonix decaryi, Didierea madagascariensis, Didierea trollii, Gonioma malagasy, Moringa drouhardii*

Southwestern Subarid Forest-Thicket and Western Dry Forest: *Adansonia rubrostipa, Adansonia za, Physena sessiliflora, Rhopalocarpus lucidus*

Southeastern Subhumid to Subarid Transition Forest: *Brexia australis*

In addition, species were selected to maximize higher taxon endemism at the family and genus level. All species in the endemic families Asteropeiaceae (8 spp. of *Asteropeia*) and Physenaceae (2 species of *Physena*) were included, as well as 16 species in the endemic family Sarcolaenaceae in the genera *Rhodolaena* (5 spp.) and *Schizolaena* (11 spp.), and 13 species in the endemic family Sphaerosepalaceae in the genera *Dialyceras* (2 spp.) and *Rhopalocarpus* (11 spp.). All 11 species in the 4 endemic genera of Malagasy Didiereaceae (*Alluaudia*, *Alluaudiopsis*, *Decarya*, and *Didierea*) were included. Other endemic genera included: *Brenierea* (Fabaceae), *Diegodendron* (Bixaceae), *Humbertia* (Convolvulaceae), *Perriera* (Simaroubaceae), *Tsebona* (Sapotaceae), and *Tsoala* (Solanaceae).

A second set of Montane species that occur above 2,000 m has been selected for modeling by Tantely Raminosoa during the Pre-Workshop (Appendix 2).

Data Preparation

All points constitute primary occurrence data vouchered by herbarium specimens. Coordinates vary in precision from contemporary GPS-derived to historical *post facto* georeferenced to ca. +/- one minute of latitude/longitude. All points were then assigned to climate and forest layers. Points from prior to 1975 were assigned to the 1950 climate layer; points from 1975 to the present were assigned to the 2000 climate layer. Points were assigned to four different forest cover layers: prior to 1950 to a 1950 layer; from 1950-1969 to the 1950 layer; from 1970-1989 to the 1970 layer; from 1990-1999 to the 1990 layer; and from 2000 to the present to the 2000 layer. Duplicate spatial points within each time period of climate and forest cover were then removed, thus retaining temporal duplicates.

Variable Layers

Variable layers included climate, percent forest cover, and geological substrate. Climate layers for 1950, 2000, 2020, 2050, and 2080 were prepared by Robert Hijmans, and include the following variables:

1) RealMat = Mean annual temperature (°C)

2) RealMar = Mean annual rainfall (sum of mean monthly rainfall) (mm)

3) MinTemp = The minimum temperature of the coldest month (°C)

4) MaxTemp = Maximum temperature of the hottest month (°C)

5) MinPrec = Minimum precipitation of the driest month (mm)

6) MaxPrec = Maximum precipitation of the wettest month (mm)

7) Etptotal = evaportanspiration total for 12 months added together (mm)

8) Wbyear = Water balance for the year (mm) (wbyear = realmar – etptotal)

9) Wbpos = Number of months with a positive water balance (integer value between 1 and 12)

Separate future climate layers for 2020, 2050, and 2080 were prepared under three different Coupled Atmospheric-Oceanic General Circulation Models: (1) CCCM (Canadian Center for Climate Change Modelling); (2) CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia); and (3) HadCM3 (Hadley Centre, United Kingdom), and for two different IPCC (Intergovernmental Panel on Climate Change) response scenarios (A and B).

Points were assigned values for Percent Forest Cover layers prepared by Conservation International for 1950, 1970, 1990 or 2000, depending on collection date as stated above.

Points were also assigned integer values for Geological Substrate according to the Simplified Geology map of Du Puy & Moat, 1996.

Modeling: Constraints and post-modeling treatments of results

Models were produced using Maxent (Phillips, 2006). Models were run based solely on Climate (C), Climate and Forest Cover (CF), and Climate, Forest Cover and Geology (CFG). Random background cells for modeling were selected from either 1950, 2000, or a mixture of 1950 and 2000 (MixBackground). A plant mask based on all known plant collecting localities in Madagascar was used to correct for collection bias (Debias). Models were constrained by elimination of any clamped area within the area of prediction, i.e., cells with variable values outside the range of known values (NoAdapt). Models were thresholded according to species specific threshold values based on the 10 percentile training presence. Models are also currently being pruned to eliminate overprediction based on the Extent of Occurrence plus a continuous thresholded buffer.

Results

For the purposes of preliminary analysis, results from a single thresholded model (CFG_NoAdapt_MixBackground_Debias) have been investigated. Geology contributed to the models of 62 of the 74 species, although the contribution was negligible (< 1%) in 14 of those species. With regard to the predicted change in distribution area between 1950 and 2000, the areas of 29 species are predicted to have expanded, whereas the areas of 45 species are predicted to have contracted. Then, using the 2000 distribution areas as a baseline, predicted distribution areas for 2080 under each of the 6 model/scenarios can be summarized as exhibiting expansion (up) or contraction (down) as follows:

All 6 model/scenarios up: 13 (*Adansonia grandidieri, Adansonia madagascariensis, Alluaudia comosa, Alluaudia humbertii, Alluaudia procera, Alluaudiopsis fiherenensis,* *Didierea madagascariensis, Moringa drouhardii, Perriera madagascariensis, Physena sessiliflora, Rhopalocarpus lucidus, Schizolaena viscosa, Tsebona macrantha*)

5 up/1 no change: 1 (*Gonioma malagasy*)

5 up/1 down: 7 (*Adansonia za, Alluaudia ascendens, Alluaudiopsis marnieriana, Brexia humbertii, Decarya madagascariensis, Rhopalocarpus crassinervius, Schizolaena rosea*)

4 up/2 down: 4 (*Boswellia madagascariensis, Delonix decaryi, Rhopalocarpus excelsus, Rhopalocarpus similis*)

3 up/3 down: 7 (*Adansonia rubrostipa, Alluaudia dumosa, Dialyceras coriaceum, Dialyceras parvifolium, Didierea trollii, Rhopalocarpus binervius, Schizolaena pectinata*)

2 up/4 down: 5 (*Asteropeia labatii, Rhodolaena acutifolia, Rhodolaena altivola, Schizolaena exinvolucrata, Schizolaena laurina*)

1 up/5 down: 4 (*Asteropeia amblyocarpa, Humbertia madagascariensis, Rhopalocarpus triplinervius, Tsoala tubiflora*)

All 6 down: 33 (*Adansonia perrieri, Asteropeia densiflora, Asteropeia matrambody, Asteropeia mcphersonii, Asteropeia micraster, Asteropeia multiflora, Asteropeia rhopaloides, Brenierea insignis, Brexia alaticarpa, Brexia australis, Brexia marioniae, Brexia montana, Diegodendron humbertii, Dilobeia thouarsii, Physena madagascariensis, Rhodolaena bakeriana, Rhodolaena coriacea, Rhodolaena humblotii, Rhopalocarpus alternifloius, Rhopalocarpus coriaceus, Rhopalocarpus longipetiolatus, Rhopalocarpus louvelii, Rhopalocarpus macrorhamnifolius, Rhopalocarpus suarezensis, Rhopalocarpus thoaursianus, Rhopalocarpus undulatus, Schizolaena cauliflora, Schizolaena elongata, Schizolaena gereaui, Schizolaena hystrix, Schizolaena microphylla, Schizolaena parviflora, Tabernaemontana sessiliflora*)

"**Worst Case Scenarios**", in which at least one model/scenario predicted zero (= 100% reduction) (or essentially zero, i.e., >99.9% reduction) suitable habitat by 2080, are predicted for 14 species: *Asteropeia densiflora, Asteropeia labatii, Asteropeia mcphersonii, Asteropeia micraster, Brexia alaticarpa, Brexia australis, Humbertia madagascariensis, Rhodolaena coriacea, Rhopalocarpus coriaceus, Rhopalocarpus, longipetiolatus, Rhopalocarpus suarezensis, Rhopalocarpus thouarsianus, Schizolaena microphylla, Schizolaena elongata*.

Discussion

Models and scenarios for future climate in Madagascar predict significant changes by 2080 in the distributions of nearly all of the 74 species examined. Reduction in the area of distribution according to a majority of models/scenarios is predicted for 42 species, whereas the distribution areas of 25 species are predicted to expand; contraction versus expansion is equivocal for 7 species. However, expansion versus contraction is by no means the only response. Many species, both those exhibiting expansion and contraction, also manifest significant shifts in their predicted distribution areas in comparison to their known (historical and contemporary primary occurrence points) and predicted current (= 2000) distributions. Significant shifts in distribution areas will thus require migration/dispersal in order to track suitable habitat during the next 80 years.

A number of robust patterns of congruent response among sympatric species emerge with respect to vegetation types, bioclimatic zones, and geographic areas. Among the 25 species for which expansion is predicted from 2000 to 2080, all but 5 species occur in Western and/or Southwestern Dry to Subarid Forest and Thicket (the exceptions are: Low Elevation Humid Forest species *Rhopalocarpus crassinervius, Rhopalocarpus excelsus,* and *Tsebona macrantha*; Humid Littoral Forest species *Schizolaena rosea*; and *Brexia humbertii*, a species with broad ecological tolerance in the SE to Central High Plateau in Dry to Subhumid Forest). However, despite the predicted overall expansion of distribution area for these W and SW Dry and Subarid species, the predicted distribution areas generally shift significantly to the E for Western species, i.e., inland and away from the coastal area, or to the S and E for Southern and Southwestern species, i.e., toward the southern coastal area and eastward toward Fort Dauphin and away from the central Southern area, such that most or all current localities are predicted to be unsuitable by 2080.

Among the 42 species exhibiting reduction in predicted range size from 2000 to 2080, similar coherent geographic patterns emerge, including relative stability despite the predicted contraction. With the one exception noted above (*Schizolaena rosea*), all Humid Littoral Forest species exhibit dramatic reduction in distribution area, with 4 species (*Asteropeia micraster, Rhopalocarpus coriaceus, Rhopalocarpus thouarsianus, Schizolaena elongata*) among the “Worst Case Scenarios” with 100% loss predicted by at least one of model/scenarios. Such predicted distribution reduction for littoral species constitutes an additional burden beyond the expected rise in sea level that may well effect all remaining littoral forest, and thus place the ca. 380 species endemic to littoral forest at significant risk of extinction (Consiglio et al., 2006). Another habitat exhibiting dramatic range reduction is the Central High Plateau Subhumid to Montane Tapia Woodland (Ibity and Itremo), for which all three examined species (*Asteropeia densiflora, Asteropeia labatii, Schizolaena microphylla*) are also among the “Worst Case Scenarios”. A third area exhibiting both dramatic declines and range shifts is the Far Northern Dry Forest, where all species with the exception of *Boswellia madagascariensis* are predicted to contract significantly, including one “Worst Case Scenario” species, *Rhopalocarpus suarezensis*. In general, ranges shift significantly southwards, as well as to some extent climb up the lower slopes of Mt. D’Ambre, such that virtually all current localities in the region of Antsiranana become unsuitable by 2080. Thus, although *Boswellia madagascariensis* exhibits overall range expansion, that expansion is mostly or entirely outside of its current distribution. Such a shift southwards of dry bioclimate explains the expansion and stable continuous strong prediction for more southerly *Schizolaena viscosa*, whose current distribution extends into the Dry to Subhumid low elevations of the Sambirano region.

With the few exceptions noted above, virtually all Humid to Subhumid Forest species are predicted to experience range size contraction by 2080, with 5 additional species among the "Worst Case Scenarios" (*Asteropeia mcphersonii, Brexia alaticarpa, Humbertia madagascariensis, Rhodolaena coriacea, Rhopalocarpus longipetiolatus*). However, despite predicted contraction, a number of species remain relatively stable with respect to continuous prediction of their current localities through 2080. In particular, the Bay of Antongil region and especially the Masoala Peninsula remains continuously and strongly predicted for such species as *Brexia maroniae, Dialyceras coriaceum, Dialyceras parvifolium, Rhodolaena humblotii, Rhopalocarpus binervius, Rhopalocarpus excelsus, Rhopalocarpus macrorhamnifolius, Schizolaena cauliflora, Schizolaena exinvolucrata, Schizolaena hystrix,* and *Tsebona macrantha*. In contrast, however, *Rhopalocarpus longipetiolatus*, with a current distribution nearly exclusively coastal, is among potential "Worst Case Scenarios" exhibiting 100% reduction. Other Low Elevation Humid Forest species among the "Worst Case Scenarios" include *Brexia alaticarpa* and *Rhodolaena coriacea,* both with a central distribution, and *Humbertia madagascariensis*, with a southern distribution. Subhumid Mid Elevation species are also predicted to suffer significant range size reduction, including "Worst Case Scenario" species *Asteropeia mcphersonii*. Other Subhumid Mid Elevation species with relatively large predicted range sizes in 2000 also exhibit significant potential reduction by 2080, which would trigger threatened status: *Brexia montana*, from 40,707 km^2 to 2,440 km^2 (-94% under the worst case scenario); *Rhodolaena bakeriana,* from 56,529 km^2 to 3,547 km^2 (-94% under the worst case scenario).

Finally, with regard to possible phylogenetic signal, it is interesting to note that all 8 species of the endemic family Asteropeiaceae are predicted to experience significant range size reduction by 2080, including 4 species (*Asteropeia densiflora, Asteropeia labatii, Asteropeia mcphersonii, Asteropeia micraster*) among the "Worst Case Scenarios" with potential zero suitable habitat, and a fifth (*Asteropeia multiflora*) with a potential reduction of between 81% (to 8,000 km^2) and 99.4% (to 240 km^2).