



Bayesian island biogeography in a continental setting: the Rand Flora case

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Bayesian island biogeography in a continental setting: the Rand

Flora case

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We here explore the use of a Bayesian approach to island biogeography for disentangling the evolutionary origins of a continental-scale floristic pattern, the enigmatic "Rand Flora". The existence of disjunct distributions across many plant lineages between Macaronesia-northwest Africa, Horn of Africa-southern Arabia, and east-south Africa has long intrigued botanists, but only now can we start analysing it within a statistical framework.

Phylogenetic and distributional data from 13 plant lineages exhibiting this disjunct distribution were analyzed to estimate area carrying capacities and historical rates of biotic exchange between areas. The results indicate that there has been little exchange between southern Africa and the northern African region, and that this exchange occurred via east Africa. Northwest Africa-Macaronesia shows the smallest carrying capacity but highest dispersal rate with other regions, suggesting that its flora was built up by immigration of lineages, probably from the Mediterranean region and western Asia. In contrast, southern

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3 **Africa shows the highest carrying capacity and lowest dispersal rate, suggesting**
4 **a flora formed by *in situ* diversification.**
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8 **We discuss further improvements of the method for addressing more complex**
9 **hypotheses, such as asymmetric dispersal between regions or repeated cyclical**
10 **events.**
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20 **Keywords:** Rand Flora, disjunct pattern, Bayesian analysis, Africa, island
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24 25 26 27 1. INTRODUCTION

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29 One of the best known examples of continental floristic disjunctions is the so-called
30 “Rand Flora” pattern: an *Afro-Mediterranean phytogeographic pattern* that
31 evolutionarily relates floras of disjunct regions such as Macaronesia (the Azores,
32 Madeira, Canary and Cape Verde archipelagos), northwest Africa, southern Arabia
33 and western Asia, with the floras of east and south Africa (Le Brun, 1971; Bramwell,
34 1985). The most-cited example of this enigmatic floristic pattern is the Canary Islands
35 “dragon tree” (*Dracaena draco*) that presumably has its closest relatives in northeast
36 Africa, the Socotra islands and southern Arabia, but many other plant groups have
37 also been suggested as having a similar distribution pattern (Bramwell, 1985; Andrus
38 *et al.*, 2004).
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53 Two main hypotheses about the evolutionary origin for the Rand Flora pattern
54 have been suggested: 1) the "vicariance hypothesis": extant species are the remnants
55 of an ancient widespread African flora that went partly extinct as a result of
56 increasing aridification from the Miocene onwards, leaving relict biotas in climatic
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refuges at the east and west continental margins of Africa (Axelrod & Raven, 1978; Quezel, 1979; Bramwell, 1978; Andrus *et al.*, 2004; Thiv *et al.*, 2009), or 2) the "dispersal hypothesis": the species' present disjunct distributions are the result of more recent long-distance dispersal events between geographically isolated areas, followed by *in situ* diversification (figure 1). For the dispersal hypothesis, two main directional routes have been proposed: a) southwards, either from the Mediterranean region or from west-Asia via the Arabian Plate (e.g., Levyns, 1964), or b) northwards from the southern African region via eastern Africa (e.g., Galley *et al.*, 2007).

So far, biogeographic studies on the Rand Flora have been mainly descriptive, focusing on reconstructing biogeographic patterns in one or several groups (Bramwell, 1985; Andrus *et al.*, 2004). However, in the last years many new phylogenetic studies of plant taxa exhibiting this disjunction have been published, allowing us for the first time to conduct a meta-analysis to test general hypotheses within a statistical framework. At the same time, the development in the last years of new model-based methods of biogeographic inference (Ree & Sanmartín, 2009) have made it possible to reconstruct the spatio-temporal evolution of individual lineages and regional biotas with increasing detail. One such method is the Bayesian approach to island biogeography (BIB) proposed by Sanmartín *et al.* (2008). It uses a Bayesian statistical approach that integrates phylogenetic and biogeographic uncertainty to estimate carrying capacities (equilibrium frequencies of species diversity) and rates of dispersal/biotic migration between geographically isolated areas (i.e., "islands"), using DNA sequence data and species distributions. An advantage of the method is that estimates of biogeographic parameters are integrated over the phylogeny of each group (phylogenetic relationships and divergence times), so the method can be used across multiple taxonomic groups differing in their age, evolutionary rate, and/or

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3 dispersal capabilities. So far, it has only been used in an island context (i.e., areas
4 separated by oceanic barriers), but Sanmartín *et al.* (2008) argued that the method
5 could also be useful for scenarios in which areas are isolated by ecological barriers,
6 such as high-mountain biotas separated by lowlands.
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12 Here we explore the usefulness of the BIB method for disentangling the origin
13 of a complex continental floristic pattern such as the Rand Flora, where subtropical
14 floras in the margins of Africa are now separated by tropical lowlands (west-east
15 Africa) or by arid and semi-arid terrains such as the Saharan desert. We combine
16 phylogenetic molecular data of multiple taxonomic groups exhibiting this disjunction
17 into a large meta-analysis for inferring the rate of dispersal/historical migration
18 between these now-isolated floras.
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32 2. MATERIAL AND METHODS

33 DNA sequence data from well-sampled molecular phylogenies including a broad representation of
34 species within each lineage and area of distribution (either previously published or from our own
35 ongoing research), were gathered for 13 groups exhibiting the disjunct Rand Flora distribution:
36 *Aeonium* (Crassulaceae), *Adenocarpus* (Fabaceae), *Androcymbium* [*Colchicum*] (Colchicaceae),
37 *Convolvulus* (Convolvulaceae), *Monsonia* (Geraniaceae), *Moraea* (Iridaceae), *Sideroxylon*
38 (Sapotaceae), *Ceropegieae* (Apocynaceae), *Geranium* (subg. *Robertium*) (Geraniaceae) *Solanum* (subg.
39 *Leptostemonum* p.p.) (Solanaceae), two subgroups of the large genera *Euphorbia* (subg. *Rhizanthium*
40 and subg. *Esula* p.p.) (Euphorbiaceae), as well as the family Campanulaceae. See Electronic
41 Supplementary Material (ESM) for details on distributions, phylogenetic studies, and references.
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51 Carrying capacities of the study areas and dispersal/migration rates between areas were
52 estimated using the Bayesian island biogeography method of Sanmartín *et al.* (2008) implemented in
53 MrBayes 4.0 (Ronquist *et al.* 2008, beta version). As input for the analysis, we used a matrix of aligned
54 sequences for each separate plant group, together with distributions for all included species (see ESM).
55 Five distributional areas were defined: 1: Macaronesia-northwest Africa, 2: eastern Africa and southern
56 Arabia, 3: southern Africa, and the "outside" areas: 4: Mediterranean region and 5: western Asia (see
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3 figure 1 and ESM for area definitions). We set up an individual General Time Reversible (GTR)
4 molecular model for each group and a common GTR biogeographic model for the entire dataset, so
5 that phylogeny and molecular parameters were estimated (independently) per group while
6 biogeographic parameters were estimated across all groups. Differences in age, molecular evolutionary
7 rate, and dispersal rate among groups were accounted for by using group-specific molecular and
8 dispersal rate scalars. For further details and specific settings, see ESM.
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17 3. RESULTS

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20 Posterior probabilities of parameters were surprisingly narrow (table 1, figure ESM-
21 3), indicating good behaviour of the model despite the low number of potential
22 dispersal events. Among regions the lowest carrying capacity was estimated for the
23 northwest Africa-Macaronesian region, whereas southern Africa showed the highest
24 carrying capacity. The opposite pattern was found for dispersal rates, which were
25 lowest for south Africa and highest for the northwest Africa-Macaronesian region,
26 both with east Africa-southern Arabia and the Mediterranean (table 1, figure 2). The
27 results showed very little or no exchange between southern Africa and northwest
28 Africa-Macaronesia. If any, this biotic exchange took place via the eastern African
29 region, the only region that exhibits significant exchange with southern Africa (table
30 1, figure 2).
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50 4. DISCUSSION

51 The high dispersal rate observed between northwest Africa-Macaronesia and
52 the eastern Africa-southern Arabia (table 1, figure 2) gives some support to the
53 vicariance hypothesis (figure 1a), which postulates the fragmentation of a continuous,
54 subtropical flora in northern Africa that was divided by climatic events into eastern
55 and western refuges (Axelrod & Raven, 1978). However, rather than one vicariant
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3 event across multiple groups, this rate is likely to reflect repeated events of dispersal
4 and vicariance between east and west Africa following the alternation of cycles of
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6 arid and humid periods in the Saharan Desert since the Late Miocene/Pliocene (Thiv
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10 *et al.* 2009).

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12 The high dispersal rate between northern Africa and the eastern region stands in
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14 contrast with the low dispersal rate between this region and southern Africa (table 1,
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16 figure 2). This can be interpreted as either a historical low rate of biotic exchange
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18 between southern and northern Africa, or, alternatively, that this exchange is too old
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20 to leave a signal in our phylogenetic data, that is, the south-north disjunctions may be
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22 older than the northwest-eastern disjunctions and therefore more likely to have been
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24 obscured or wiped-out by later extinction events. Indeed, there is some support for
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26 this hypothesis. The fossil record suggests that forests covering the whole of
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28 tropical/central Africa appeared in the Oligocene-Miocene, and geological data gives
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30 the same time frame for mountain formation and the establishment of drier areas in
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32 northern Africa. In contrast, direct contact between the African continent and Eurasia
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34 was not established until the Miocene, when the Arabian Plate collided with the
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36 Eurasian Plate 16 Ma ago. If southern Africa was a part of a continuous Rand Flora,
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38 the region is likely to have been separated by climatological barriers from the
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40 northern areas earlier than the start of major biotic exchange between northern Africa
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42 and Eurasia.
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50 Interestingly, northwest Africa plus Macaronesia show the smallest carrying
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52 capacity but present the highest dispersal rate (table 2), suggesting that the flora of
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54 this region was built up by immigration of new lineages. Migration from the
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56 Mediterranean region was probably the dominant route (figure 2), but dispersal from
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3 west Asia via the Arabian Plate and across the Saharan desert is another possible
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5 route supported by our data.
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8 Conversely, the high carrying capacity of southern Africa (table 1) gives some
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10 support to the hypothesis that the highly diverse South African Cape flora has
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12 diverged *in situ*, facilitated by the relative climatological stability of the area from the
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14 Miocene onwards (Linder, 2005). Similarly, the low dispersal rate with all other
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16 regions but eastern Africa agrees well with the idea that, following the formation of
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18 the eastern African mountains in the Pliocene, some south African lineages migrated
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20 to the north (via the Grand Rift and the Drakensberg mountains) and gave rise to the
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22 highly endemic eastern African mountain flora (Linder, 2005; Galley *et al.* 2007).
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26 The results from this analysis should be considered preliminary for several
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28 reasons: the dataset only represents a sample of groups showing this disjunction (see
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30 Andrus *et al.* 2004); all phylogenies are not complete and some of the relevant
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32 disjunct taxa are missing (e.g., *Monsonia*, see ESM); finally, there is a potential
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34 underestimation of groups with southern African distributions (e.g., *Euphorbia*).
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36 Despite these drawbacks, our results suggest that the Bayesian island model may be
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38 useful in a continental setting, where the number of inferred dispersal/migration
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40 events between areas is low.
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45 Although originally designed to study dispersal patterns in islands, the BIB
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47 method may also be used to detect possible vicariance events, by incorporating
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49 estimates of absolute divergence times. Vicariance predicts biogeographical and
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51 temporal congruence in disjunct distribution patterns across different plant groups,
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53 and that the disjunct distribution is at least as old as the geological barrier that caused
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55 it. By plotting the rate of dispersal over time, the appearance of a vicariance event can
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57 be detected: a decrease in dispersal frequency between two areas would suggest the
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3 formation of a new geographic barrier between them. BIB can even be used to
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5 estimate the timing of the paleogeographic barrier from the dated phylogenies, by
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7 comparing a one-rate model, in which the rate of biotic exchange is constant before
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9 and after the barrier, with a two-rate model in which there are two parameters, the rate
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11 of exchange before and after the barrier.
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15 Future work should focus on testing asymmetric dispersal patterns, e.g.,
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17 northward vs. southward migration between southern Africa and northern-eastern
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19 Africa, as well as on incorporating absolute times to the inference, either directly as
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21 molecular divergence time estimates or, indirectly through the use of fossil and
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23 paleogeographical information (Ree & Sanmartin, 2009).
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FIGURE CAPTIONS

Figure 1. The main hypotheses to explain the origin of the "Rand Flora" pattern (left) and plant groups that have been argued to exemplify these hypotheses (right). 1) Vicariance - Climatological changes lead to vicariance of a once continuous Paleogene flora. 2a) Dispersal southwards - The pattern is a consequence of immigrants from Asia and the Mediterranean spreading to south Africa via eastern Africa. 2b) Dispersal northwards - The elements of the flora dispersed from south Africa to Horn of Africa region, and from there to the west and north.

Figure 2. a) Scheme of the Bayesian island biogeography method used in this study. For details see text and ESM. **b)** Relative dispersal rates between areas (purple arrows) and area carrying capacities (green circles) obtained from an analysis of 13 plant groups. Dispersal rates lower than $1.0E^{-6}$ are not shown. See ESM for details.

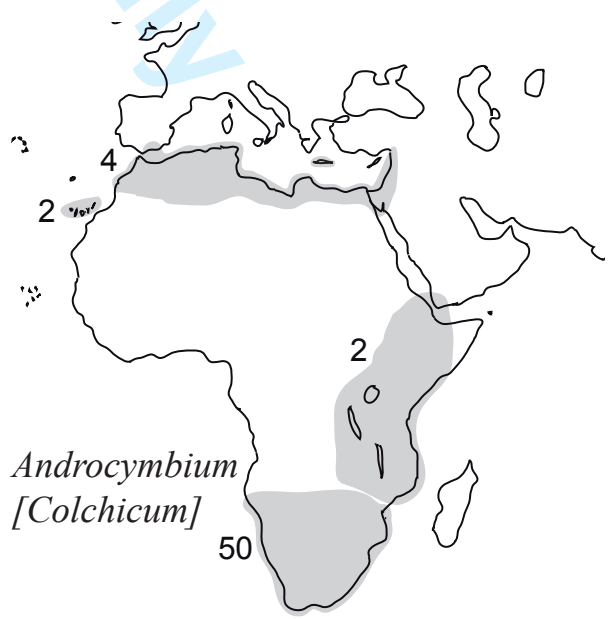
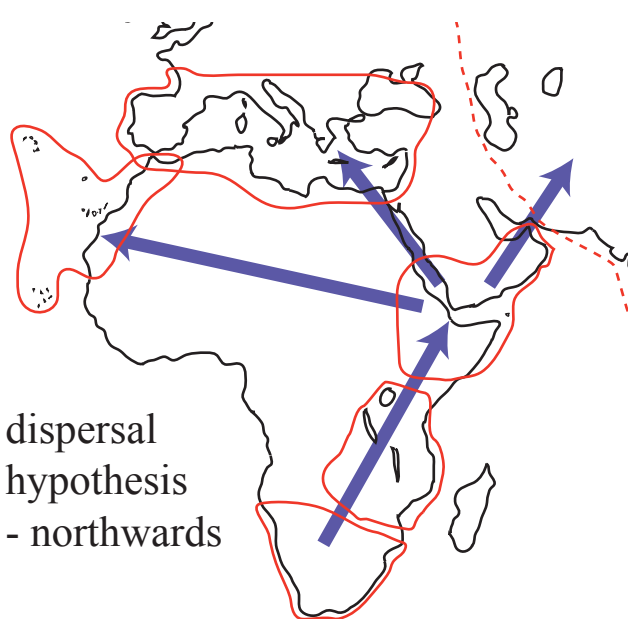
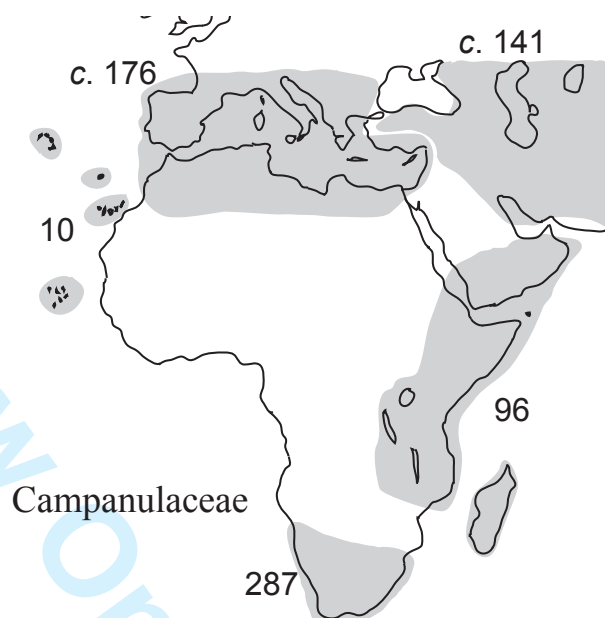
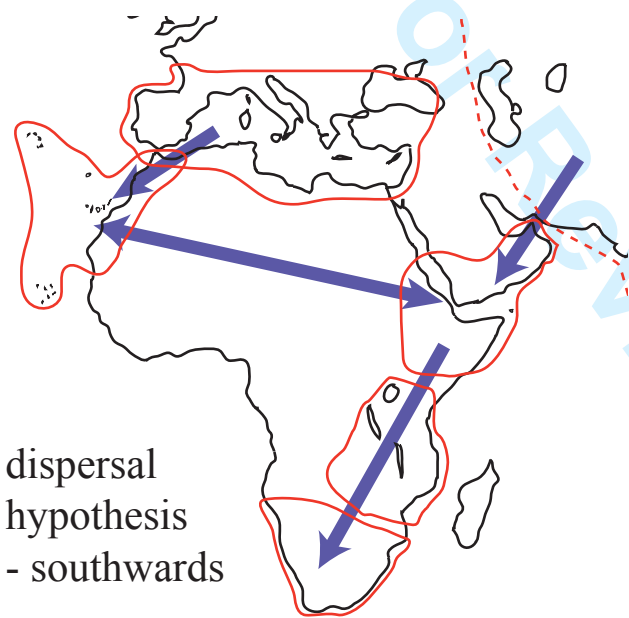
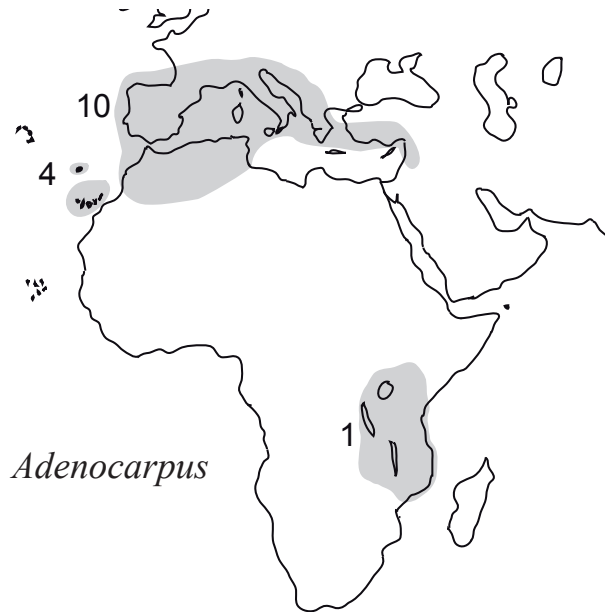
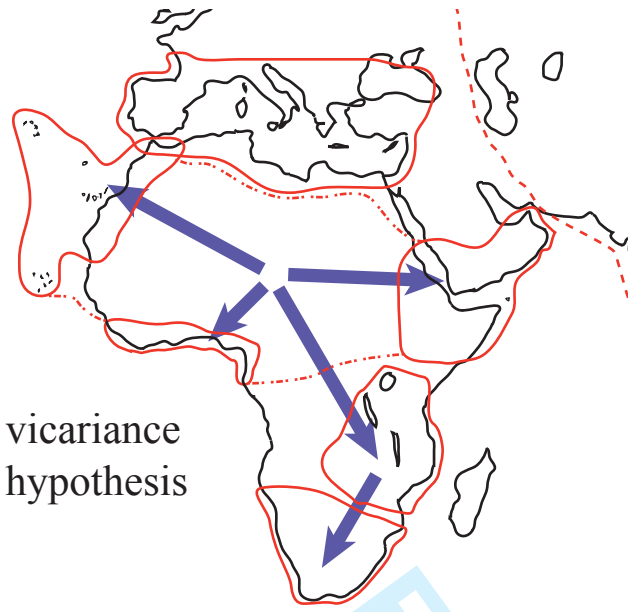
TABLE CAPTIONS

Table 1. Bayesian estimates (mean, standard deviation, and 95% credibility interval of the posterior probability distribution) of the parameters of the biogeographic model described in figure 2a. Abbreviations: π , island carrying capacity; r , relative dispersal rate; NW, Macaronesia-northwest Africa; SAF, southern Africa; EAF, eastern Africa; MED, Mediterranean region; WAS, western Asia. PSRF: Potential scale reduction factor: a value close to one indicates a good sampling from the posterior probability of the parameter.

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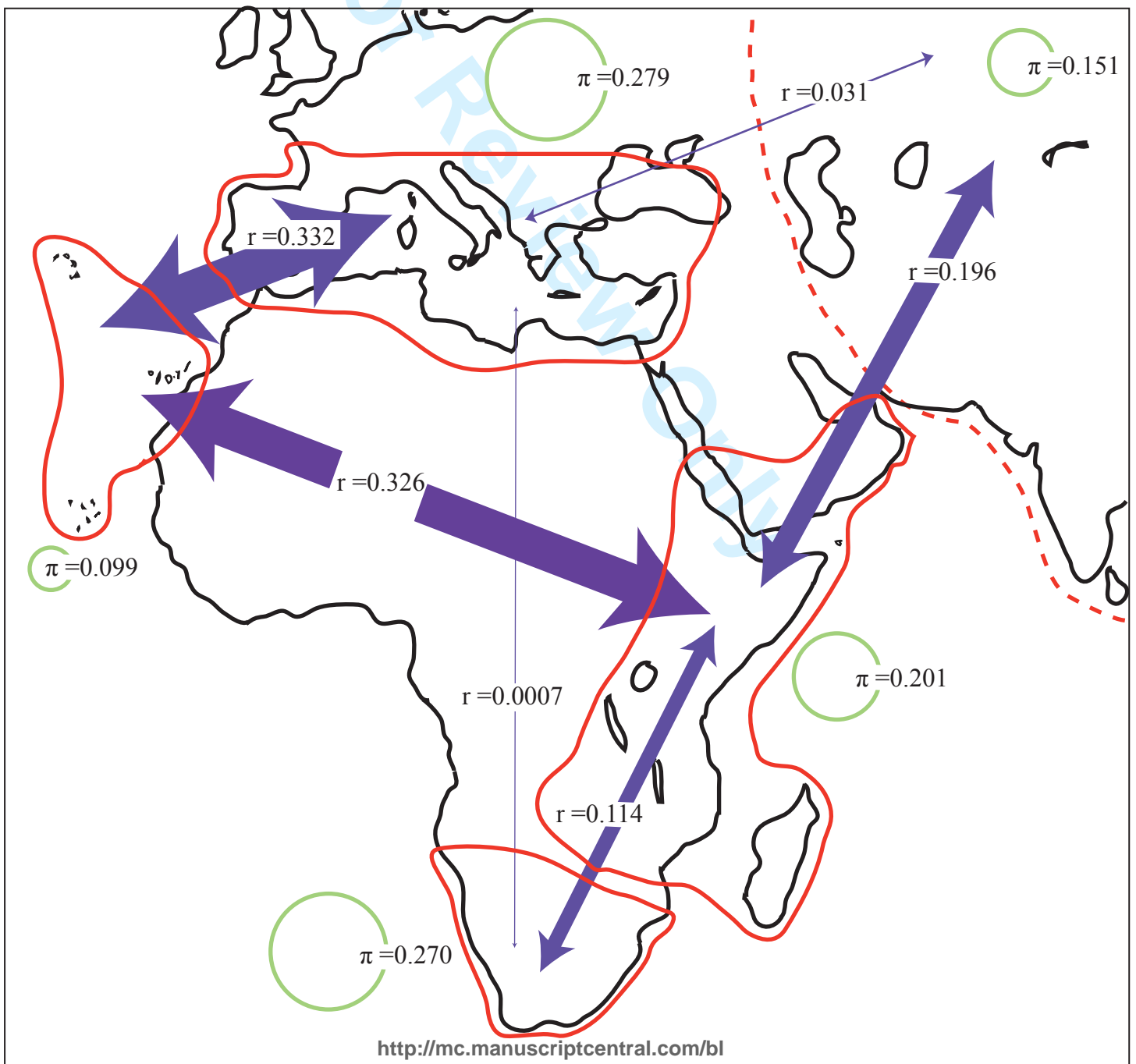
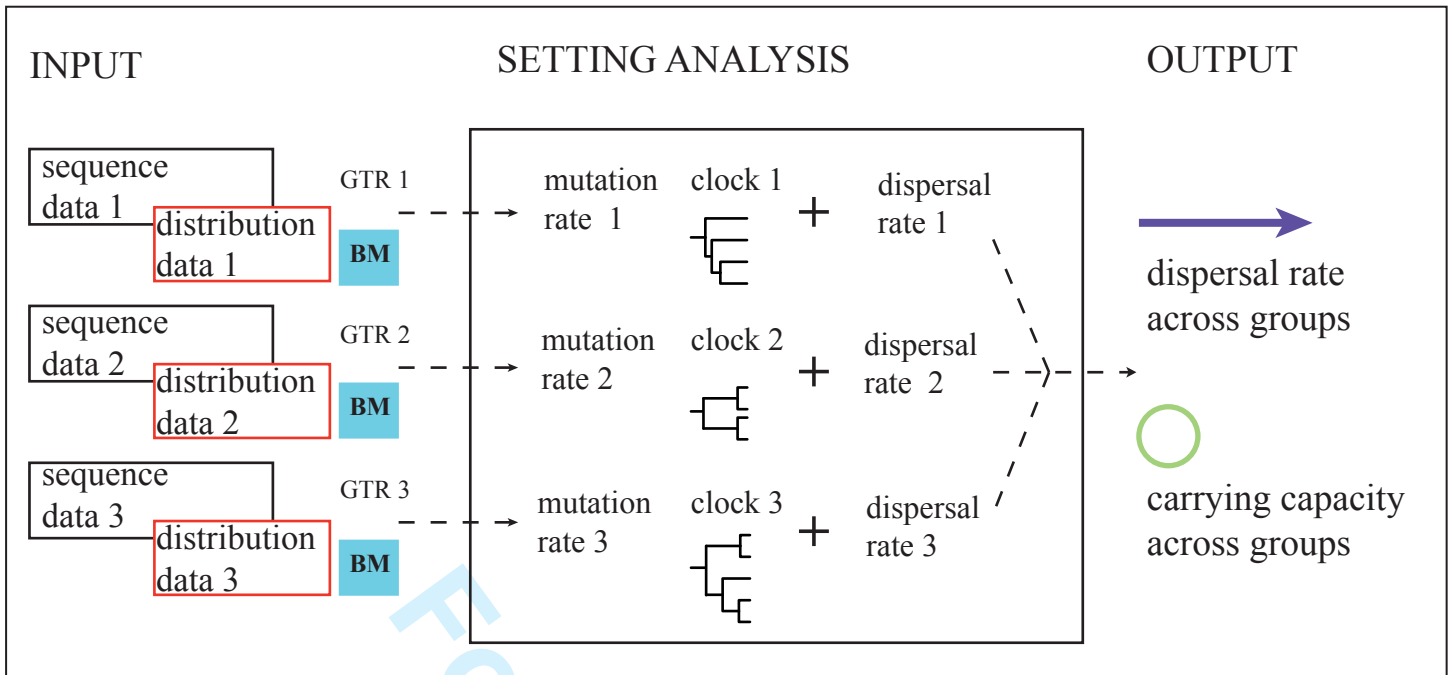


Table 1.

Biogeographic parameter	Mean	Standard deviation	Lower	Upper	Median	PSRF
π_{NW}	0.099	0.030	0.053	0.168	0.096	1.010
π_{SAF}	0.270	0.083	0.130	0.452	0.263	1.002
π_{EAF}	0.201	0.043	0.126	0.293	0.198	1.020
π_{MED}	0.279	0.083	0.137	0.462	0.272	1.002
π_{WAS}	0.151	0.057	0.066	0.288	0.141	1.006
$r_{\text{NW} \leftrightarrow \text{EAF}}$	0.326	0.093	0.154	0.517	0.322	1.000
$r_{\text{NW} \leftrightarrow \text{MED}}$	0.331	0.121	0.122	0.591	0.322	1.008
$r_{\text{SAF} \leftrightarrow \text{EAF}}$	0.114	0.052	0.041	0.238	0.105	1.007
$r_{\text{SAF} \leftrightarrow \text{MED}}$	0.001	0.005	<1.0E-6	0.007	<1.0E-6	1.023
$r_{\text{EAF} \leftrightarrow \text{WAS}}$	0.196	0.089	0.061	0.408	0.184	1.004
$r_{\text{MED} \leftrightarrow \text{WAS}}$	0.031	0.051	<1.0E-6	0.168	<1.0E-6	1.021