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## The importance of windows of opportunity for long-distance dispersal to or from oceanic islands: examples from the Macaronesian archipelagos

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The current species composition of entire oceanic islands or specific insular ecosystems is the result of a complex scenario where several historical and ecological processes, including long-distance dispersal (LDD), subsequent colonization, speciation (within or among islands) and extinction may have played an important role.

Recently, one of us (Carine, 2005) coined the concept of colonization window, referred to the colonization opportunities in some islands or archipelagos that emerged for vagile continental taxa when either specific geological events (such as volcanic eruptions that destroy entire communities and ecosystems, creating open space) or ecological events (e.g., the availability of vacant resources in the insular ecosystems due to species impoverishment or disharmony), create the conditions for those species to establish.

In a parallel approach, here we vindicate the concept of window of opportunity for a long-distance dispersal (LDD) event, that could be defined as the time interval throughout which the different factors controlling LDD become simultaneously functional or available, in reference to the opportunities that appeared for vagile taxa to arrive to destinations usually locked to them due to the prevailing wind or marine current regimes. Usually, the occurrence of LDD windows of opportunity is analysed in retrospect; for instance, when palaeo-biogeographers try to reconstruct the past events that may have enabled a present bizarre (fossil or extant) species distribution.

Among the items that have to be checked for hypothesizing the existence of such window(s) we should consider:

- A) The existence in the proper historical moment of continental ecosystems where the focal taxa thrived and may have later persisted *in situ* or not. This may have been, for instance, the case for the Iberian and North African Tethyan Palaeotropical Geoflora with respect to Macaronesia; its elements are not extant today, but they were present in the continental margins until the Pleistocene climate deterioration (Postigo-Mijarra *et al.*, 2010).
- B) The existence in the proper historical moment of islands available to be reached and subsequently

colonized, which may as well have later persisted or vanished under the sea, as was the case for several Palaeo-Macaronesian islands, that are today seamounts (Fernández-Palacios *et al.*, 2011).

- C) The historical occurrence of the proper dispersal facilitator agents, either physical (for instance, palaeo-sea-currents, palaeo-wind regimes, important rivers) or biological (birds, bats, etc.), which may be still active/extant today or not.
- D) The availability of stepping-stones facilitating dispersal; for instance, through the emergence of non-subsided flat-topped seamounts (guyots) due to eustatic sea-level transgressions.
- E) The existence of peak periods, i.e. the availability of discrete windows in time where the simultaneous occurrence of an array of downstream or leeward high islands enabled the transference (through island hopping) of species restricted to mountain and summit ecosystems in the decaying island before erosion and subsidence processes remove those ecosystems and their associated biota. For instance, Stillman (1999) and Acosta *et al.* (2003) argue that Fuerteventura may have reached 3,500 m of height in the past. Therefore, it is feasible that some of the species that, at present, only occur at high elevations in Tenerife originated in Palaeo-Fuerteventura and colonized Tenerife before losing their habitats in the former island.

Until very recently, it was considered that islands were evolutionary dead-ends of lineages, like no-way-out streets for taxa able to colonize them in proper moments, but unable to leave them, thus awaiting extinction (for instance, due to the taxon cycle). Nevertheless, increasing phylogenetic and phylogeographical evidence accumulated in the last years (from e.g., Bellemain & Ricklefs, 2008; Laenen *et al.*, 2010), challenges the traditional perspective of islands as dead-ends, and points to the putative role of oceanic islands as refugia for continental taxa, especially during Plio-Pleistocene Glaciations, when the climatic conditions were much milder on the islands (due to the buffer effect of the oceans and to the opportunity for altitudinal migration) than on the continent.

Thus, windows of opportunity for long-distance dispersal can be hypothesized as well for explaining these bizarre (at least under today's prevailing conditions) retro-colonization or back-colonization events from the islands to the mainland, i.e. the colonization of ecologically similar and available mainland ecosystems by insular (usually neoendemic) species, originally derived from mainland ancestors, when abrupt tectonic (for instance the closure of Gibraltar or Panamá straits) or climate changes (e.g., Plio-Pleistocene glaciations) have transformed in specific moments of the past history the marine-currents and wind-regimes nowadays prevailing in the zone.

In this context, recently published coupled-model simulations for the Last Glacial Maximum (LGM) evidence a substantial equatorward shift in the Westerlies position, 7° for a 3 K degree cooling and 11° for a 6 K degree cooling, in the Northern Hemisphere (Williams & Bryan, 2006) (Fig. 1). In the same line, Rognon & Coudé-Gausen (1996) asserted more than a decade ago that several geomorphological features of Canarian

and Maghrebian natural landscapes point towards the dominance of the Westerlies wind regime across the Madeiran-Canarian latitudes (25-30° N) during the glacial periods in the Pleistocene. A shift of the Azores high southwards occurs due to the pressure exerted by the North Polar Front.

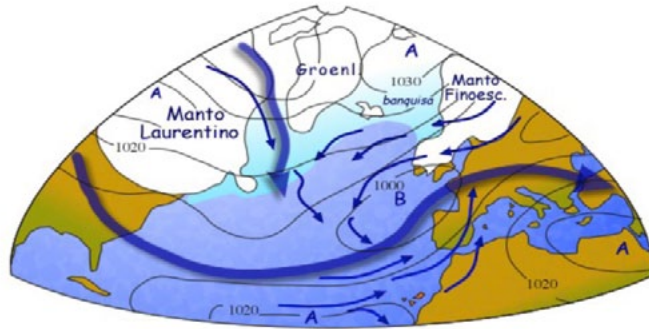


Figure 1. Hypothesized southwards shift of the Northern Hemisphere Westerlies during the LGM, affecting the Canarian latitude (Source: Uriarte, 2003).

These pieces of evidence include the existence of dune fields (*ergs*) in several Canary Islands (especially Esquinzo and Lajares dune fields in Fuerteventura) and Maghrebian areas (especially Agadir dune fields) that could not be formed under the influence of the present wind regime –the dune fields exhibit a triangle shape with the basis on the coast and the vertex pointing to the interior– (Fig. 2). The great amount of organogenic sands that have been deposited forming the dune fields that can only have been originated from deposits, today unavailable, located under the sea level, but available in the past due to the sea level transgression during the glaciations.

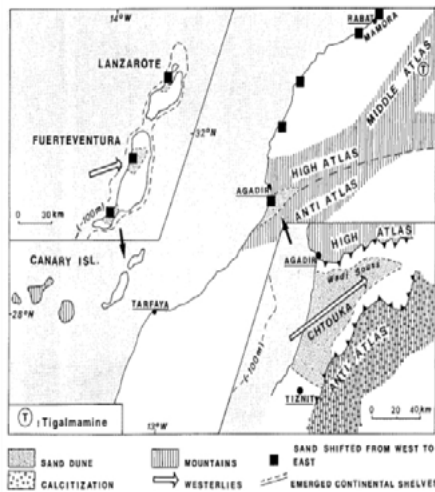


Figure 2. Recent ergs (dune fields) in the Eastern Canaries and Morocco formed due to the Westerlies activity during the LGM (Source: Rognon & Coudé-Gaussen, 1996).

Among other major climatic features (for instance, lower temperatures and precipitations), the Plio-Pleistocene glacialiation climatic context on the Madeira–Canaries region implied: the existence of archipelagos larger (almost twice as large as today), higher (ca. 120 m higher) and less isolated from the African continent (just 60 km away) than during interglacial periods. Concomittantly, the reiterative emergence of an important array of seamounts feasibly facilitated the dispersal processes among archipelagos (Fig. 3; for instance Selvagens and Dacia for the Madeiran-Canarian connection, but also between the archipelagos and the Iberian and North African mainland (Conception, Seine, Ampere, Coral Patch, Ormonde, etc.) (Fernández-Palacios *et al.*, 2011) (Fig. 3).



Figure 3. Reconstruction of Palaeo-Macaronesia ca. 18 Ky BP (Source: Fernández-Palacios *et al.*, 2011).

Today, it is considered that these climatic conditions have prevailed several times, perhaps as much as twenty, during the Late Pliocene and Pleistocene (Lisiecki & Raymo, 2007) coinciding with the different glacial maxima. Westerlies may have enhanced the retro-colonization from Macaronesian lineages to the African mainland. We also know that several Macaronesian lineages have representatives in the African and European continents (Table 1), and a number of recent molecular phylogenetic studies place Macaronesian taxa as basal to continental congeners (Table 1, Fig. 4). Retro-colonization events involving insular taxa have been termed *boomerangs* elsewhere (Caujapé-Castells, 2004, 2011).

**Table 1.** Some putative boomerangs suggested by molecular evidence for the Macaronesian flora (extracted from Caujapé-Castells 2011) and fauna. (A = Azores, CV = Cape Verde, E = Europe, EA = E-Asia, I = Iberia, Mac = Macaronesia, Ma = Madeira, Me = Mediterranean, Mu = Multiple, NEA = NE-Africa, NWA = NW-Africa, NW = New World, SA = S-Africa).

TAXON	FAMILY	ORIGIN	TARGET	REFERENCE
<b>PLANTS</b>				
<i>Aeonium balsamiferum</i> <sup>E,S</sup>	Crassulaceae	Mac <sup>1</sup>	NEA ( <i>A. leucoblepharum</i> )	Mort et al. 2002
<i>Andryala pinnatifida</i> <sup>S</sup>	Asteraceae	Ma	Me ( <i>A. ragusina</i> , <i>A. integrifolia</i> )	Fehrer et al. 2007
<i>Arbutus canariensis</i> <sup>E,S</sup>	Arbutoideae	NW	Me ( <i>A. andrachne</i> , <i>A. unedo</i> )	Hileman et al. 2001
<i>Convolvulus</i> <sup>S</sup>	Convolvulaceae	Mac	I ( <i>C. fernandezii</i> )	Carine et al. 2004
<i>Helichrysum gossypinum</i> <sup>S,P</sup>	Asteraceae	Ma <sup>1</sup>	Me (ancestor of several spp.)	Galbany-Casals et al. 2009
<i>Ilex perado</i> <sup>F</sup>	Aquifoliaceae	Mu	EA ( <i>I. leucoclada</i> , <i>I. latifolia</i> , <i>I. rugosa</i> )	Manen et al. 2002
<i>Kleinia nerifolia</i> <sup>S</sup>	Asteraceae	EA	NWA ( <i>K. anteuphorbium</i> )	Pelser et al. 2007
<i>Lotus campylocladus</i> <sup>S</sup>	Fabaceae	NWA	NWA ( <i>L. assakensis</i> )	Allan et al. 2004
<i>Matthiola bolleana</i> <sup>S</sup>	Brassicaceae	NWA	NWA ( <i>M. bolleana</i> , <i>M. longipetala</i> ssp. <i>viridis</i> )	Jaén-Molina et al. 2009
<i>Sideroxylon mirmulano</i> <sup>E</sup>	Sapotaceae	EA	CV ( <i>S. marginatum</i> ), SA ( <i>S. inerme</i> )	Smedmark et al. 2006
<i>Teline stenopetala</i> (ssp. <i>micropauci</i> ) <sup>S</sup>	Fabaceae	NWA	NWA ( <i>T. monspessulana</i> )	Percy & Cronk 2002
<i>Tinguarra montana</i> <sup>E</sup>	Apiaceae	NWA	NWA ( <i>T. sicula</i> )	Downie et al. 2000
<i>Tolpis azorica</i> <sup>S</sup>	Asteraceae	A <sup>1</sup>	NWA ( <i>T. virgata</i> , <i>T. barbata</i> )	Moore et al. 2002
<b>BIRDS</b>				
<i>Regulus regulus</i> ssp. <i>ellen-thareae</i>	Regulidae	E	E ( <i>R. regulus</i> ssp. <i>regulus</i> )	Päckert et al. 2006
<i>Erythacus rubecula</i>	Muscicapidae	E	E ( <i>E. rubecula</i> )	Dietzen et al. 2003
<i>Fringilla teydea</i>	Fringillidae	E	NWA, E ( <i>F. coelebs</i> )	Marshall & Baker 1998

<sup>E</sup> Possible major influence of extinction. <sup>P</sup> Phylogenetic tree poorly resolved (i.e., low support for the derived position of the mainland taxa, or polytomic topology combining mainland and island populations). <sup>S</sup> Sampling deficiencies, especially in mainland areas near the Canaries (i.e., the 'Macaronesian enclave' and its surroundings). <sup>1</sup>Canarian taxa with putative origin in Macaronesia have been included in this list on the grounds on their ultimate origin via a continental ancestor.

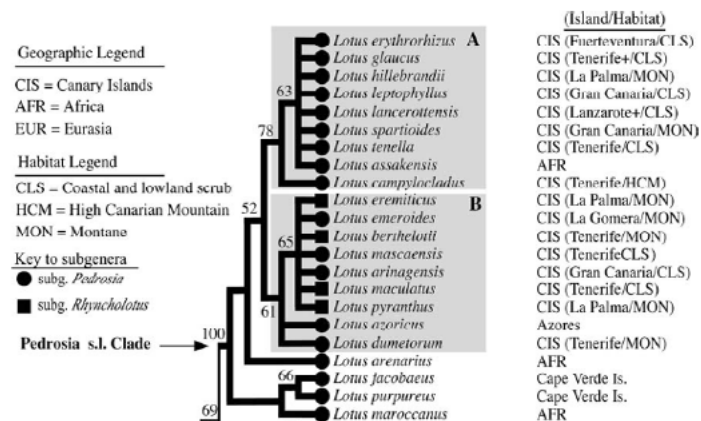


Figure 4. Cladogram showing Lotus subgenus Pedrosia + L. subg. Rhyncholotus (= Pedrosia s.l. Clade), where *L. assakensis* is a possible example of a boomerang (Source: Allan et al., 2004).

If transient in nature, such a dispersal window will be followed by a period where the dispersal route is impossible or highly improbable, because the transportation means it ceased to exist. Of course, the existence of a certain dispersal window does not preclude a colonization event in exactly the opposite direction, but it makes it much unlikely. Thus, biodiversity boomerangs can't be older than the window onset, and several colonization events may be recognized within a specific taxon.

Dispersal windows may also disrupt the "normal" dispersal patterns within archipelagos. It has been postulated that in the Canaries the more common dispersal route within the archipelago is the so-called progression rule (Whittaker & Fernández-Palacios, 2007), which implies a general propagule movement from the older, eastward Canaries to the younger, westward islands. Under Westerlies conditions the normal dispersal routes may have been substituted by other usually bizarre routes, for instance: from the western to the eastern islands within the Canaries, from Azores to Madeira or the Canaries or from Macaronesia to Iberia (Carine et al., 2004).

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