CORRESPONDENCE

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Early recognition by Ball and Hooker in 1878 of plant back-colonization (boomerang) events from Macaronesia to Africa

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Within island biogeography, it has traditionally been believed that whereas mainland to island colonization is key to stocking oceanic islands with species, reverse colonization events from islands to continental mainlands are so uncommon as to be without wider significance (Whittaker & Fernández-Palacios 2007). However, the completion in recent decades of sound phylogenies incorporating almost entire sets of insular and continental related taxa has revealed a surprising frequency of instances of continental populations or species that are intermingled within insular clades, or which are derived from insular ancestors (Figure 1).

Accepting these phylogenies as working hypotheses of the true evolutionary relationships allows the inference of reverse colonization events, which are also sometimes referred to as retro-colonization, back-colonization, or boomerang events (Caujapé-Castells 2004, 2011, Heaney 2007, Bellemain & Ricklefs 2008, Laenen et al. 2011). While it has also been hypothesized that islands have provided stepping stones for cross-ocean colonization of continental mainlands (as reviewed e.g., in Whittaker et al. 2017), the terms 'back-colonization' and 'boomerang events' specifically imply that species that have diversified in islands from continental ancestors disperse back to the original continent (e.g., Mort et al. 2002, Carine et al. 2004, Laenen et al. 2011).

While the available evidence tends to support progression-rule patterns of colonization from older to younger land-masses as being far more common, evidence of back colonization within archipelagos and between archipelagos and continents has gradually accumulated. Today we know about many boomerangs from Macaronesia to Africa and Europe, but also elsewhere, that have happened across multiple taxa (Mort et al. 2002, Bellemain & Ricklefs 2008, Caujapé-Castells 2011).

But when did the idea of island-to-continent retro-colonization first emerge? By chance, inquiring in old texts we have found that the idea was already in use in the late 19th century for explaining the same unexpected pattern of the presence of a few species with Macaronesian characteristics in Moroccan territory. The British botanist and phytogeographer Joseph Dalton Hooker [born Halesworth 1817, died Sunningdale 1911] together with the Irish botanist John Ball [Dublin 1818 – London 1889] published in 1878 a book entitled *Journal of a tour in Marocco* [*sic*] *and the Great Atlas*. On p. 405 in appendix E of this book, written by Hooker, and entitled *On the Canarian Flora compared with that of Maroccan,* Hooker wrote:

> Amongst the exceptional cases to continental proximity being accompanied by close botanical relationship is the Flora of the Canarian Archipelago, which differs so greatly from that of the northern part of its neighbouring continent, namely from that of Marocco, that it demands notice in any work treating of the vegetation of the latter country.
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> This diversity between the Maroccan and the Canarian Flora has been pointed out in John Ball's (1878) 'Introductory observations to the *Spicilegium Florae Maroccanae*,' where it appears that whilst Marocco, out of 1,627 species of flowering plants, contains 165 endemic plants, it has only 15 that are confined to it and to the Canaries or to it and Madeira. And Ball goes on to remark (p. 301), in respect of these few species in common to both Floras: '**I think it is safe to say that the facts rather tend to show the accidental diffusion of a few Macaronesian species on the adjacent coast of Africa,** than to indicate the direct connection between the continent and those islands within a geological period at all recent.' [our emphasis in bold].

Consulting Ball's work, cited in the above extract, it is evident that of the 15 species, all but one of them are Canarian species that are also found in the coastal region of South Morocco, the other being common to Madeira and West Morocco (Table 1).

Hooker went on to set out possible explanations for the common elements, including (i) extensionism (vicariance by the loss of a land-bridge connection), which he largely dismissed due to the depth of the

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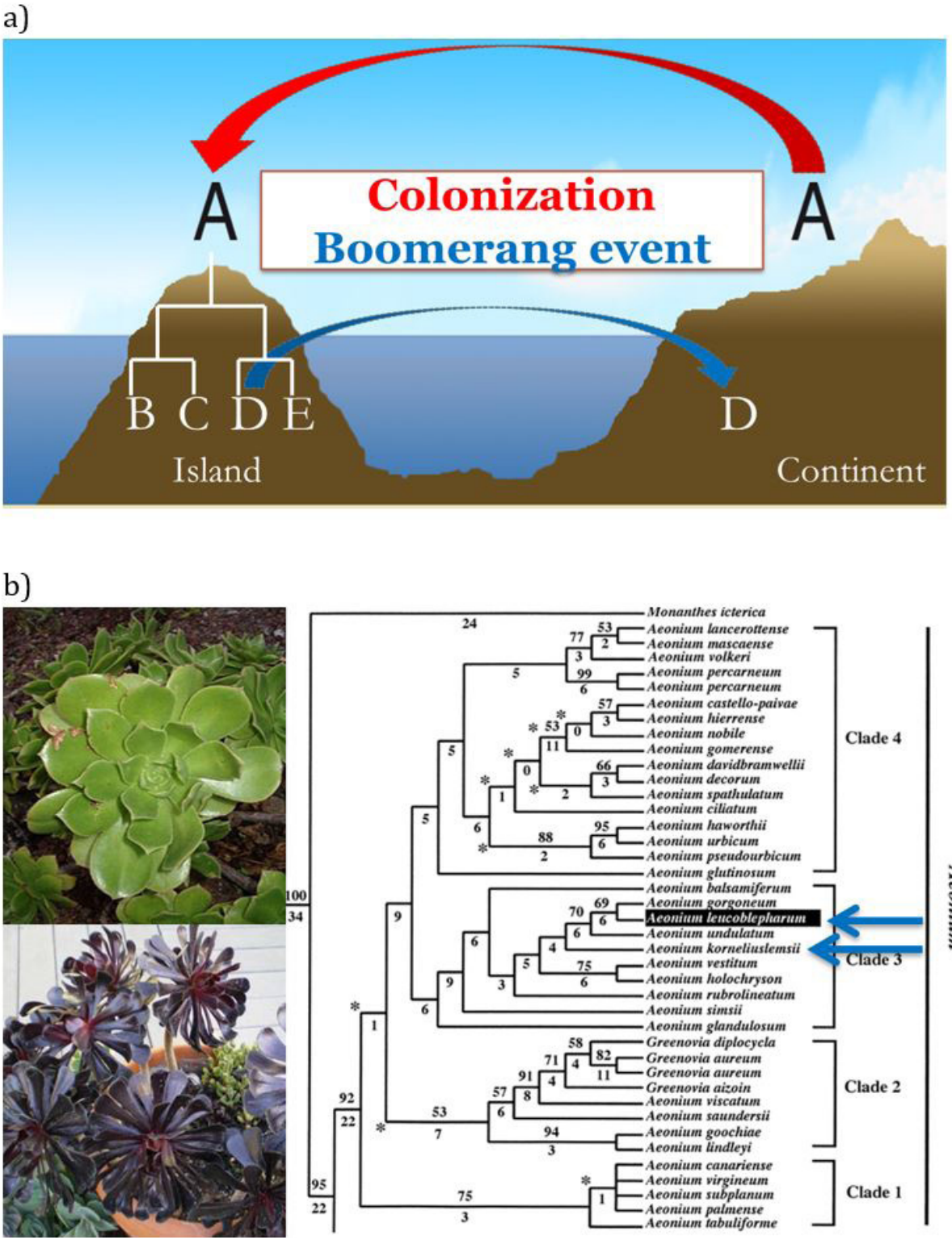

Figure 1. Boomerang events. a) Schematic representation of a retro-colonization or boomerang event. A continental ancestor (A) colonizes the island (colonization, depicted with a red arrow), where with sufficient time and isolation, it radiates, giving rise to four insular neoendemic species: B, C, D and E. One of them (D) jumps back to the continent from which the clade's ancestor originated (boomerang event, depicted with a blue arrow). b) *Aeonium* phylogeny based on a cpDNA/ITS data set, which includes two African boomerangs within a Macaronesian clade: *Aeonium leucoblepharum* (above) and *A. korneliuslemsii* (below), identified with blue arrows. Part (b) was excerpted from Mort *et al*. (2002) (with kind permission of *Systematic Botany*), photos of *A. leucoblepharum* (above) and *A. korneliuslemsii* (below) from https://plantasdemitierra.blogspot.com/2007/12/aeonium-leucoblepharum.html and https://es.gardenmanage.com/statuses/1000153167.html, respectively.

Table 1: Species listed by Hooker (1878, p416) as putative back-colonizations from Macaronesia to Morocco.

Hooker's (1878) name	Present name	Origin	Observations
Helianthemum canariense	Same	Canaries	
Polycarpia (sic) nivea	*Polycarpaea nivea*	Canaries	The generic name was misspelled by Hooker
Zygophyllum fontanesii	*Tetraena fontanesii*	Canaries	
Cytisus albidus	*Chamaecytisus albidus*	Canaries	The species present in the Canaries is not *Ch. albidus,* but *Ch. proliferus*
Ononis angustissima	Same	Canaries	Today it is considered a Canarian endemic
Astydamia canariensis	*A. latifolia*	Canaries	
Bowlesia oppositifolia	*Drusa glandulosa*	Canaries	
Odontospermum odorum	*Astericus graveolens* subsp. *odorus*	Canaries	
Lithospermum macrospermum	*Mairetis microsperma*	Canaries	
Linaria sagittata	*Kickxia sagittata*	Canaries	
Chenolea canariensis	*Chenoleoides tomentosa*	Canaries	
Salix canariensis	Same	Canaries and Madeira	Hooker considered this rather uncertain, and we consider today that the species is absent from Morocco
Romulea grandiscapa	*R. columnae*	Canaries	
Asparagus scoparius	Same	Canaries	
Astragalus solandri	Same	Madeira	

ocean floor between the Canaries and west Africa, and (ii) the role of fishermen from the islands visiting points on the opposite coast. Of greater interest in the present context is the following extract, which in his cautious way, he presented as one of the possibilities: "We may believe in the trans-oceanic migration of some African species to the nearer islands, along with the transport of some Canarian species (those enumerated in p. 416, and others which may be hereafter found) to the neighbouring continent." (p. 418).

This is to our knowledge the very first explicit account of an island-to-continent retro-colonization or back-colonization event, although this is not to rule out the possibility of an earlier mention that has yet to be rediscovered.

Demonstration of persuasive evidence for Macaronesian to North African retro-colonization had to wait for more than a century, until the development of molecular tools enabled the construction of sound phylogenies that could confirm it. It was 124 years later when Mort et al. (2002) first described, for the Macaronesian genus *Aeonium* (Crassulaceae), derived from a *Sedum*-like ancestor, which colonized the Canaries ca. 15 Ma (Kim et al. 2008), the existence of two boomerangs in North Africa (*A. korneliuslemsii* in Morocco and *A. leucoblepharum* in Yemen, Ethiopia, Somalia, Kenia and Uganda; Figure 1). These findings in fact led to the loss of the status of *Aeonium* as an endemic Macaronesian genus!

We are now aware of many more Macaronesian genera that appear to have generated boomerangs. These occur both in plants, such as *Androcymbium, Andryala, Bupleurum, Chamaecytisus, Convolvulus, Dactylis, Euphorbia, Hedera, Limonium, Lotus, Matthiola, Olea, Phoenic, Plantago, Pulicaria, Reichardia, Reseda, Spartocytisus, Teline, Tinguarra* and *Tolpis*, among others (Caujapé-Castells 2011), and in animals, such as in the passerine genera *Regulus, Erythacus* and *Fringilla* (Fernández-Palacios et al. 2013) and the weevil genus *Laparocerus* (Machado et al. 2017). Very likely, the future will provide us with a much larger species list involving additional taxonomic groups to those listed here.

References

Ball, J. (1878) Introductory observations to the Spicilegium Florae Maroccanae. Journal of the Linnean Society, 16, 377–772.

Bellemain, E. & Ricklefs, R. (2008) Are islands the end of the colonization road? Trends in Ecology and Evolution, 23, 461-468.

Carine M.A., Russell S.J., Santos-Guerra A., Francisco-Ortega, J. (2004). Relationships of the Macaronesian and Mediterranean floras:

Molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). American Journal of Botany, 91, 1070–1085.

Caujapé-Castells, J. (2004) Boomerangs of biodiversity? The interchange of biodiversity between mainland North Africa and the Canary Islands as inferred from CPDNA RFLPS in genus *Androcymbium*. Botánica Macaronésica, 25, 53–69.

Caujapé-Castells, J. (2011) Jesters, red queens, boomerangs and surfers: a molecular outlook on the diversity of the Canarian endemic flora. In: The Biology of Island Floras (ed. by D. Bramwell and J. Caujapé-Castells), pp. 284–324. Cambridge University Press, Cambridge.

Fernández-Palacios, J.M., Carine, M. & Caujapé-Castells, J. (2013) The importance of windows of opportunity for long-distance dispersal to or from oceanic islands: examples from the Macaronesian archipelagos. In: *Proceedings of the Amurga International conferences in Island Biodiversity* (ed. by J. Caujapé-Castells, G. Nieto Feliner and J.M. Fernández-Palacios). Pp. 16-23. Fundación Amurga, Las Palmas de Gran Canaria.

Heaney, L.R. (2007) Is a new paradigm emerging for oceanic island biogeography? Journal of Biogeography, 34, 753–757.

Hooker, J.D. (1878) On the Canarian Flora compared with that of Maroccan. In: Journal of a Tour in Marocco and the Great Atlas (J. D. Hooker and J. Ball). MacMillan, London. 553 pp.

Kim S.-C., McGowen M.R., Lubinsky P., Barber, J.C., Mort, M.E. & Santos-Guerra, A. (2008) Timing and tempo of early and successive adaptive radiations in Macaronesia. PLoS ONE, 3, e2139.

Laenen, B., Désamoré, A., Devos, N., Shaw, A.J., González- Mancebo, J.M., Carine, M.A. & Vanderpoorten, A. (2011) Macaronesia: a source of hidden genetic diversity for postglacial recolonization of western Europe in the leafy liverwort *Radula lindenbergiana.* Journal of Biogeography, 38, 631–639.

Machado, A., Rodríguez-Expósito, E., López, M. & Hernández, M. (2017) Phylogenetic analysis of the genus *Laparocerus*, with comments on colonisation and diversification in Macaronesia (Coleoptera, Curculionidae, Entiminae). Zookeys, 651, 1-77.

Mort, M.E., Soltis, D.E., Soltis, P.S. Francisco-Ortega, J. & Santos-Guerra, A. (2002) Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from nuclear and chloroplast sequence data. Systematic Botany, 27, 271-288

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: taking the long view of nature's laboratories. Science, 357, eaam8326.

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